Sustainability and Biodiversity Assessment on Forest Utilization Options

Research Institute for Humanity and Nature
Project 2-2

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Preface

This is the final report for the Research Institute for Humanity and Nature (RIHN) project entitled “Sustainability and Biodiversity Assessment on Forest Utilization Options”. The project was led by Prof. Tohru Nakashizuka (now affiliated with Tohoku University) from 2002 to 2006, and by Dr. Masahiro Ichikawa from 2006 to 2008.

The RIHN was established in 2001 in order to tackle to environmental problems on a global scale. The RIHN, understanding that global environmental problems originate from problems of human culture, is conducting research on the relationship between human and nature, forming projects consisting of researchers from a variety of academic fields. Our project has focused on the degradation and loss of forests and biodiversity, which have been progressing rapidly in recent decades.

We approached that subject in our project by establishing 4 study sites in Japan and Malaysia. For each site, we studied how forest use had changed in terms of human activities, what kinds of impact the changes had brought to forest ecosystems, biodiversity and ecological services, and what kinds of social and cultural institutions for the sustainable use of forests and biodiversity exist. The studies were conducted through collaborative research by biologists, ecologists, and researchers with backgrounds in social studies.

The findings of our project provide answers to research topics including questions concerning how ecological services of biodiversity should be evaluated and how options for the future of forests can be projected. In addition to their value to the academic community, the findings will be useful in practical areas, including being of use to people working in policy, regional planning, and forest management to tackle the loss and degradation of forests.

Acknowledgements

This project has benefited from the cooperation of many researchers and research institutions. We could not have accomplished the project without their devoted cooperation. In particular, many thanks go to the Center for Ecological Research, Kyoto University, a RIHN 'partner organization for fluid association', in which our project was proposed and established. I would also like to express my deepest gratitude to the following institutes.

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Sarawak Planning Unit (SPU)
Yakushima Forest Environment Conservation Centre, Forestry Agency of Japan

ICHIKAWA, Masahiro
Project Leader
Research Institute for Humanity and Nature (RIHN)

Chapter 1

INTRODUCTION

Chapter 1 Introduction

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1. Research Objectives

The biodiversity of forest ecosystems is closely related to their ecological soundness, which refers to the ability of the ecosystem to provide us with various kinds of ecosystem services. The rapid decrease in the area occupied by forest ecosystems and the deterioration in their quality have been caused by social, economic, and ecological factors that vary among regions, and these factors are insufficiently well understood. The mechanisms responsible for biodiversity loss as a result of forest utilization are thus still unknown. Developing sustainable forest management systems thus requires an understanding of these mechanisms, which have become a priority for research.

As a practical way to increase the awareness of citizens of the importance of environmental sustainability, and particularly that of forests, quality labeling initiatives such as FSC (Forest Stewardship Council) are currently the subject of ongoing trials. Several movements to establish criteria and indices for “sustainability”, such as the Montreal and Helsinki processes, have been started as a result of international collaborations. Maintaining high biodiversity is one of the most important criteria, though it sometimes requires considerable study to establish appropriate indices.

In some parts of the Earth, traditional forest utilization systems have been considered to be sustainable, but these traditional systems are at risk of collapse due to the rapid recent changes in human lifestyles without waiting long enough for a scientific evaluation of the sustainability of these changes, particularly from the viewpoint of biodiversity. It is also urgent to find sustainable models for many regions that currently lack sustainable systems.

In the project described in this report, we are trying to evaluate the sustainability of various aspects of forest utilization in tropical and temperate regions in Asia, with a particular emphasis on biodiversity. The ecosystem services that are at risk of being lost as a result of decreasing biodiversity should be identified by this research. In addition, we are evaluating the socioeconomic and cultural aspects of each forest utilization system, including both traditional and modern management systems, in the study region. The driving forces and incentives behind recent changes in forest utilization systems are also being studied. Finally, we are trying to present new and comprehensive ways to assess these forest utilization systems.

To accomplish these goals, we have developed the following four research questions that will be answered for four selected temperate and tropical forest areas in Asia:

1. What are the historical changes that have occurred in forest utilization, and the social and economic backgrounds for these changes?
2. What are the impacts of forest utilization on biodiversity and ecosystem function?
3. What changes in ecosystem services have been caused by forest biodiversity changes?

4. Is it possible to develop an integrated evaluation system for evaluating the degrees of sustainable utilization of forest ecosystems and of biodiversity?

The following chapters describe our results in studying these questions. In Chapter 2, we discuss the changes in forest utilization in recent decades (the past 50 to 100 years) and the driving forces behind these changes. The effects of such changes on biodiversity and ecosystem function will be discussed in Chapter 3, and the effects on ecosystem services will be discussed in Chapter 4. Chapter 5 will discuss our analyses of existing systems of forest and biodiversity utilization. Finally, Chapter 6 will present an integrated assessment system for the degree of sustainable use of forest ecosystems and of biodiversity.

2. General Design of the Research

Research sites and target forest systems

Considering the biodiversity information that has already been obtained and forest utilization in the past and at present, we selected four sites with different forest types for our studies. These sites represent a range of types of forest utilization, including natural forests with the least extent of human impacts, man-made forests (plantations) developed for timber production, forests subject to so-called sustainable traditional forest use, and forests managed using modern forest utilization techniques. The four forests selected for our study are:

1. The Lambir Hills National Park, a tropical lowland rain forest (including forest reserves, forests used for ecotourism, forests used for commercial logging, forests managed by traditional and recent shifting cultivation, and oil palm plantations)
2. The Kinabaru Ntional Park and the Deramakot Forest, which are tropical montane and lowland forests, respectively (including forest reserves, forests used for ecotourism, forests used for commercial logging, man-made forests, forest areas used for vegetable cultivation, and environmentally certified forests included in the Deramakot Forest).
3. The Yaku Island warm-temperate rain forest (including forest reserves, forest used for ecotourism, commons forest, and forest plantation)
4. The Abukuma Mountains temperate deciduous forest (including forest reserves, the satoyama system of traditional forest management, forests managed with natural regeneration practices, forest plantation, and pasture land)

Research subjects

The following subjects were studied in parallel at the four sites to permit a comparison and integration of the results:

1. Historical changes in forest utilization and their social and economic backgrounds

- Historical changes in forest utilization: Forest utilization and its changes during the past 50 to 100 years were studied using land-use maps, aerial photographs, and satellite images. This data will be entered into a geographical information system (GIS) to permit comparative analyses among the sites.
- Social and economic backgrounds: The incentives that motivated people or organizations to cause the observed changes in forest utilization were analyzed by means of sociological and economic analyses.

2. Evaluating the impacts of forest utilization on biodiversity

- Screening of target organisms: The target organisms were selected through screening tests based on their suitability as index species for detecting the impacts of forest utilization.
- Biodiversity assessment for the forest types: Using the screened organisms, the variations in flora and fauna among forest types were investigated quantitatively. Organisms were classified into functional groups such as trees and forest floor plants.
- The mechanisms responsible for biodiversity loss: The mechanisms through which forest changes lead to biodiversity losses were studied, in particular, we focused on the change of interactions between organisms.
- Biodiversity and ecosystem functions: The ecosystem functions, and particularly those that are closely related to the ecosystem's self-maintenance systems, should be carefully studied. This study includes intensive studies of gene flow using DNA markers.

3. Evaluation of ecosystem services provided by biodiversity

- Biodiversity and ecosystem services: The impacts of biodiversity loss on human life were studied. This analysis focused on the services provided by biodiversity, and particularly on the provision of non-timber forest products, regulatory services such as pollination and pest control, and cultural services such as educations and/or ecotourism.

4. Conditions necessary for sustainable forest management

- Biodiversity and sustainability of local communities: Institutions and economic incentives that serve to enable sustainable resource use and preserve local cultures were examined so as to develop effective methods and criteria for evaluating the sustainability of local communities.
- National or regional institutions that promote sustainable use of forest ecosystems and biodiversity were studied to identify their operating mechanisms and any problems that prevent these mechanisms from working properly.
- Policy and economics: Several political systems and economic models that have been applied to assess the sustainable use of forest ecosystems and biodiversity were analyzed and evaluated.

To effectively integrate the results, we created a matrix that combined the research sites with the research subjects. The biodiversity researchers focused more specifically on individual sites, whereas the sociologists and economists tried to work across sites.

Chapter 2

CHANGES IN FOREST USE AND ITS FACTORS

Chapter 2 Introduction

Masahiro Ichikawa
Research Institute for Humanity and Nature

This chapter examines the influences of human activities on forest utilization at the four study sites. The study period covered 50 to 100 years, depending on the availability of reliable information at each site. This project examined the sustainable use of forests and biodiversity, with the objectives of clarifying the land-use changes at each site, identifying the drivers responsible for these land-use changes, and elucidating the characteristics of these drivers. The study methods included analysis of old maps, aerial photographs, and satellite images to understand the land-use changes. A review of published literature and interviews of relevant persons were also performed to learn more about the drivers responsible for the observed land-use changes.

For Sarawak Malaysia, Ichikawa examines the drivers responsible for the land-use changes using land-use maps from the 1960s to the 1990s. For Sabah, Kitayama et al. analyze the characteristics of land-use changes in the Kinabaru Mountain area and in the Deramakot lowland using satellite images from the 1970s to 2002. Three papers discuss Japan's Yaku Island. In the first, Otani et al. deal with forest-use changes in the western part of the island and in part of the World Heritage Site in the study area. Since this is a main area for their ecological study, this paper provides basic data on the impacts of human activities on the forests of the area. In the second, Sprague et al. perform a GIS analysis of land-use changes along the rim of the island, where human activity has been most intense. In the third, Hirai discusses the role of forests, the benefits they generate, and changes in forest values during six periods from the 17th century until the present. In addition, Miyamoto et al. created maps of land-use changes at Abukuma from 1908 to 1997 using old maps and aerial photographs, and analyzed the background factors responsible for the changes. Finally, Takada et al. describe the possibility of transitions in the land-use changes for the four sites using matrices, and examine methods for the projection of land use under different scenarios.

By comparing the land-use changes at each site, such as the relationship between Japan and Malaysia resulting from the timber trade, land-use changes in each region can be better understood. The results of these analyses of land-use changes provide basic information for the projection of land-use changes under different scenarios and permit the creation of maps of biodiversity, ecological functions, and ecological services in the final chapters.

Land Use Changes during the 1960s–1990s around the Lambir Hills National Park, Sarawak, and Backgrounds to the Changes

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2) Toyota Foundation

Introduction

In order to examine influences of human-activity impacts on forest biodiversity, this paper clarifies the land use changes during these 40 years and the social and economic backgrounds behind the changes. It also examines the differences between land use changes according to the actors of the land use. The main actors in the study area are: the Iban, a native people of Sarawak, and enterprises and government. The study area is around the Lambir Hills National Park, Sarawak (Figure1) and the area is around 27,000 ha. The area was almost all covered by primary forests around 100 years ago. The question is, how have the forests been converted to today's land uses, which are swidden agricultural fields, secondary forests, mono-crop plantations, and small areas of primary forest?

Methods

The methods of the study are: 1) to read land use from aerial photographs taken in 1963, 1977 and 1997 by colonial and state government and draw land use maps for each year, 2) to calculate the transition of each land use and transition possibility, and 3) to conduct document surveys and interviews on the background to the land use changes with local villagers and governments staff who know about those changes.

Results

Land-use maps:

Figure 2 shows the land-use changes from 1963 to 1997 as a result of reading aerial photographs. The actors who have caused the land-use changes are mainly divided into two. One is the Iban, a native people of Borneo who have lived in the area for a long time and who use forests products and the forests themselves for their subsistence economy. The other is government and corporate actors who have used forests to gain economic benefits on a bigger scale. In figure 2, those areas are shown as "Iban territory" and "state land," respectively.

Matrix and its graphing:

The area of land-use transition and transition possibility from 1963 to 1977, and from 1977 to 1997 are calculated (Table 1) and the result is graphed out (Figure 3). As the next step, the transitions for each area, the Iban territory and state land, are calculated and also graphed out (Figure 4 and 5). Historical trend of the changes in the 2 areas is shown in the figure 6 and 7. From those figures, some trends and characteristics of the land use can be extracted: 1) conversion from primary forest to other land use in the Iban territory started earlier (around 1900) than that in the state land (1960s). The conversion in the Iban territory was mainly for subsistence agriculture, for example for hill and swamp paddy fields. These fields are relatively small (more or less 1 ha) and dispersed, dotted around the Iban territory. 2. The land use in the state land started for commercial logging and large-scale rubber plantation development from the 1960s.

Backgrounds of the land use changes (figure 7): The main land use changes in the Iban territory and the social and economic backgrounds to such changes are: Settlement of the Iban in the study area around 1900, supported by government policies; swidden agriculture in hills and swamps until the 1960s to maintain subsistence economy; expanding area of rubber groves in the 1950s and 1960s after an increase of rubber price in the international market; expanding swamp paddy fields in the 1960s and 1970s as a result of increase in rice demand from logging camps appearing when commercial logging was prosperous, and; value of forest products and fruits as commodities increased in the 1980s and 1990s following the urbanization of Miri city.

The main land-use changes in the state land and those social and economic backgrounds are: rubber plantation development and its failure in the 1960s in the period when rubber price fluctuated in the international market; commercial logging in large areas from the 1960s following increasing demand in the international market; the establishment of the National Park in 1974 when international movements of nature conservation appeared, and; oil palm plantation development after the 1980s when the price increased in the international market.

Conclusion

The land-use changes around the Lambir Hills National Park would be evaluated as below from the viewpoint of biodiversity conservation. In both the Iban territory and state land, a common trend of land use changes is conversion of primary forest into other land uses for economic improvement and development. However, in more detailed observation, the way the changes occur differ between the two types of land. In the Iban territory, the primary forests were mainly converted to small agricultural fields, and those have always been left for fallow and the land returned to secondary forests. The Iban's lands are seen as a mosaic pattern consisting of small patches of agricultural fields in the large secondary forests. In contrast, in the state land, commercial logging started in the 1960s and large areas became logged forests. After the 1980s, oil palm plantation development in large scale started around the study area. In conclusion, in state land, large scale developments have been brought about in a relatively short period, which seriously affects biodiversity conservation, while the land use of the Iban territory is characterized as relatively slow change in small scale in individual patches of agricultural fields. However, if the national park had not been established, the primary forest in it would have been logged by enterprises and also by the Iban. The roles of both the native's land use and government policies are important for biodiversity conservation.

Reference

Ichikawa, M. (2007) Degradation and loss of forest land and land use changes in Sarawak, East Malaysia: a study of native land use by the Iban. *Ecological Research* 22. 403-413.

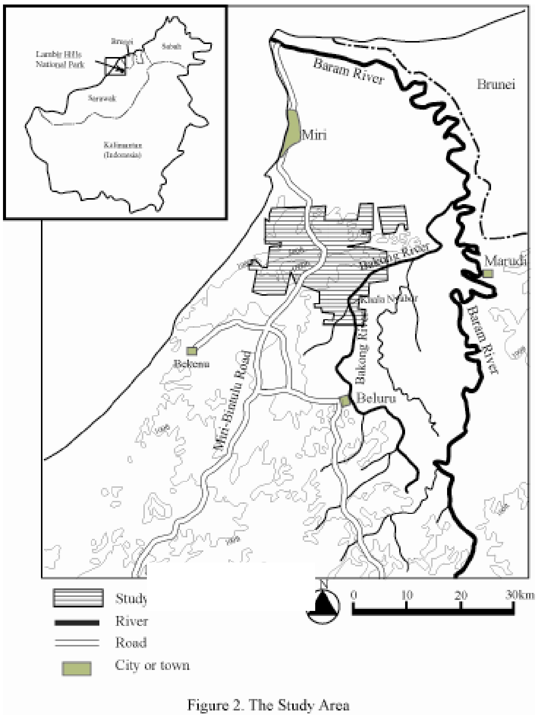
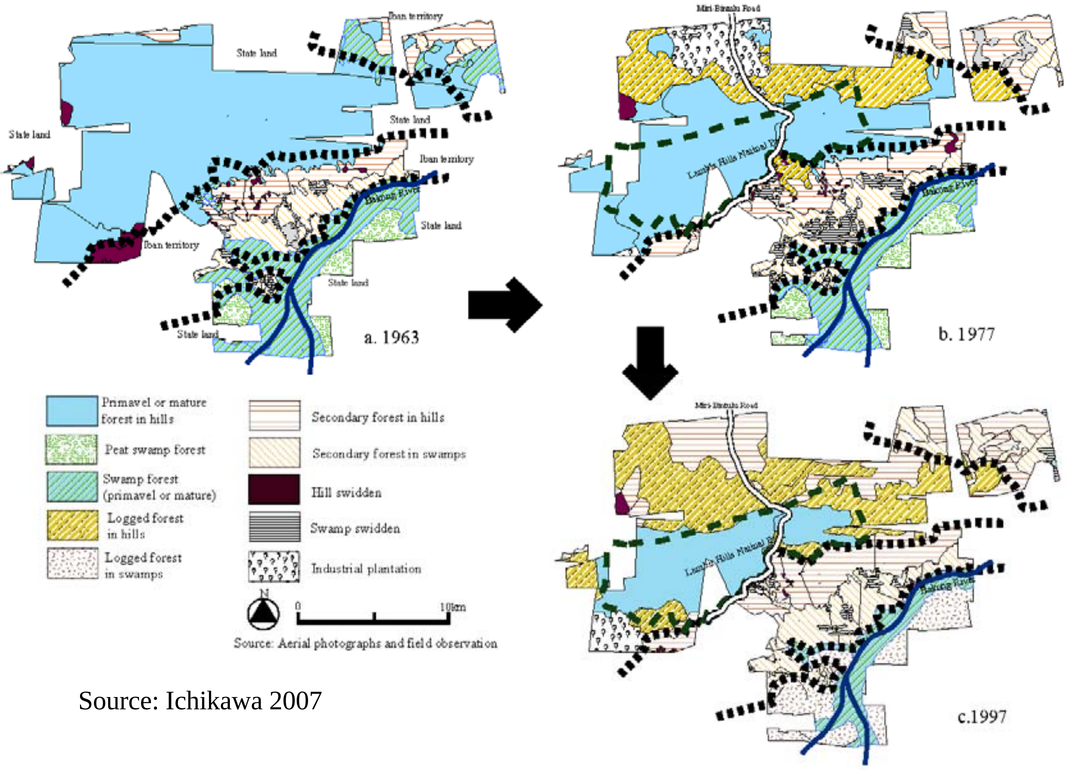


Figure 1 The study area



Source: Ichikawa 2007

Figure 2 Land use maps in each year

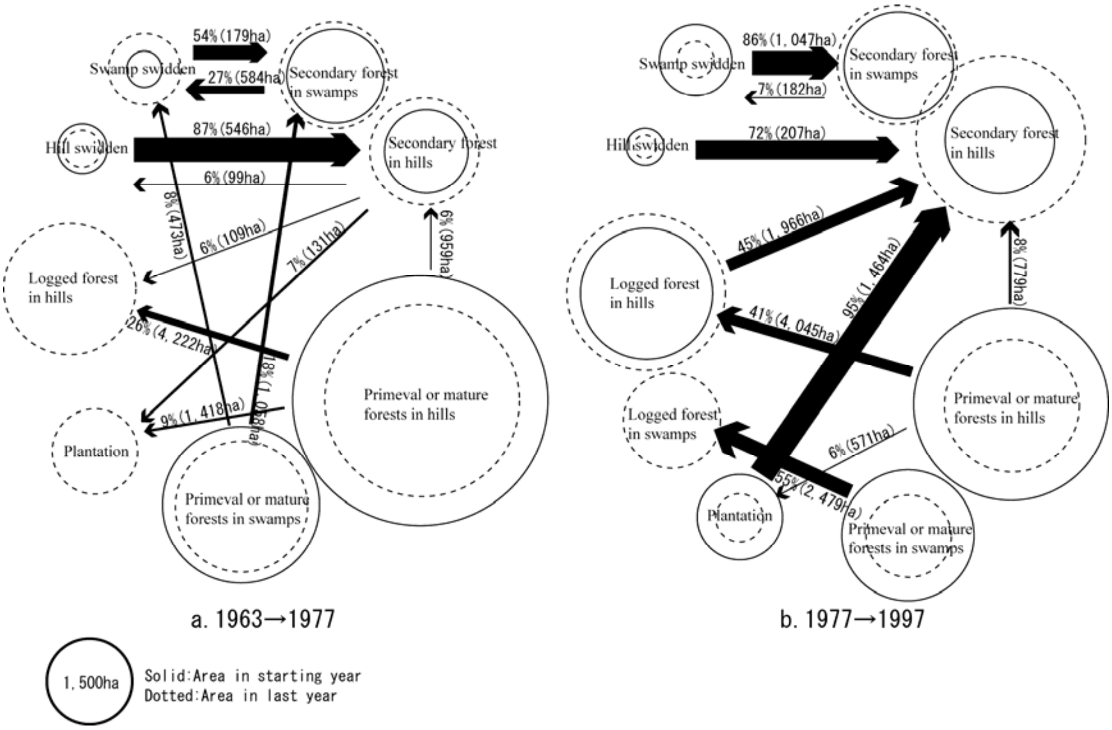
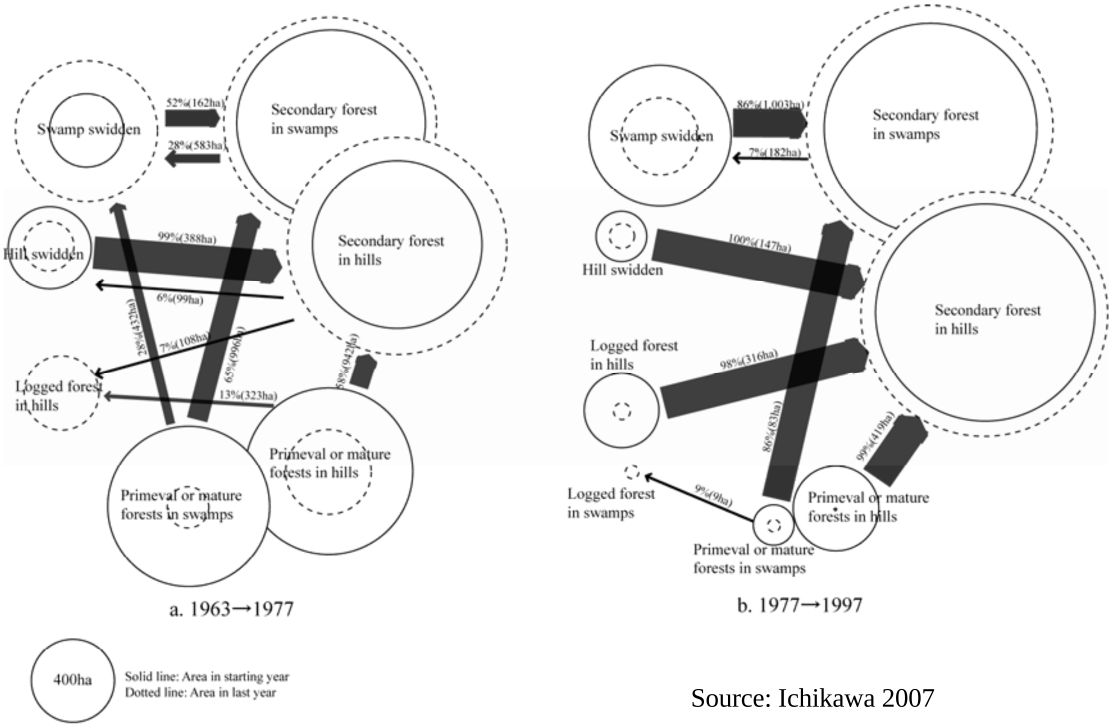
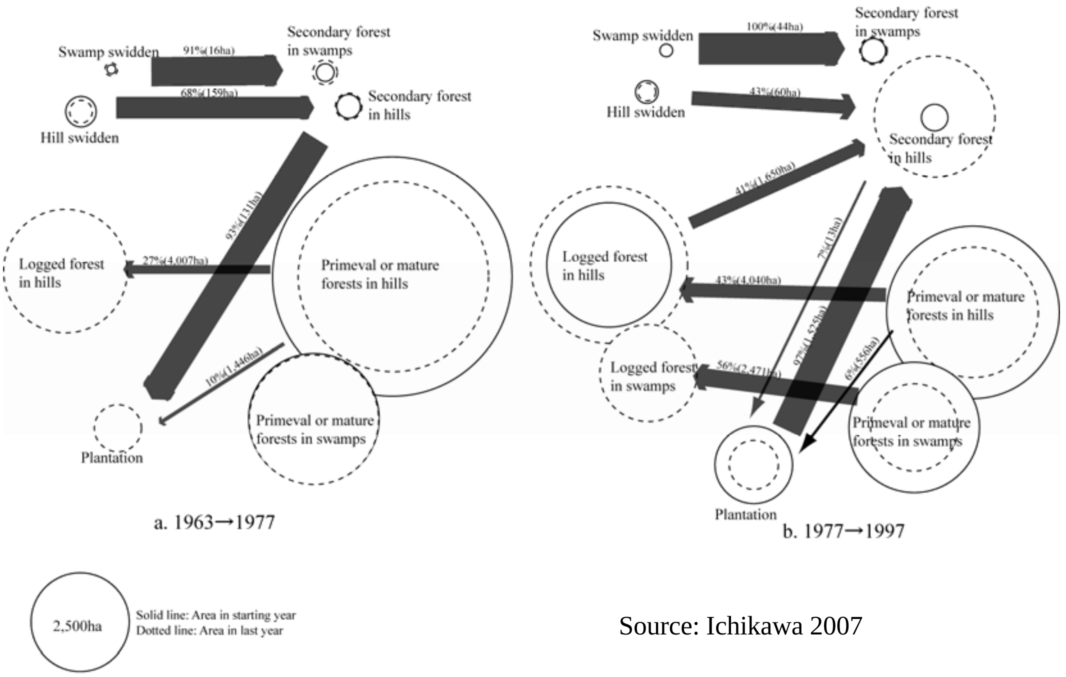


Figure 3 Land use changes in whole study area, 1963 to 1977, and 1977 to 1997



Source: Ichikawa 2007

Figure 4 Land use changes in the Iban territory, 1963 to 1977, and 1977 to 1997



Source: Ichikawa 2007

Figure 5 Land use changes in the state land, 1963 to 1977, and 1977 to 1997

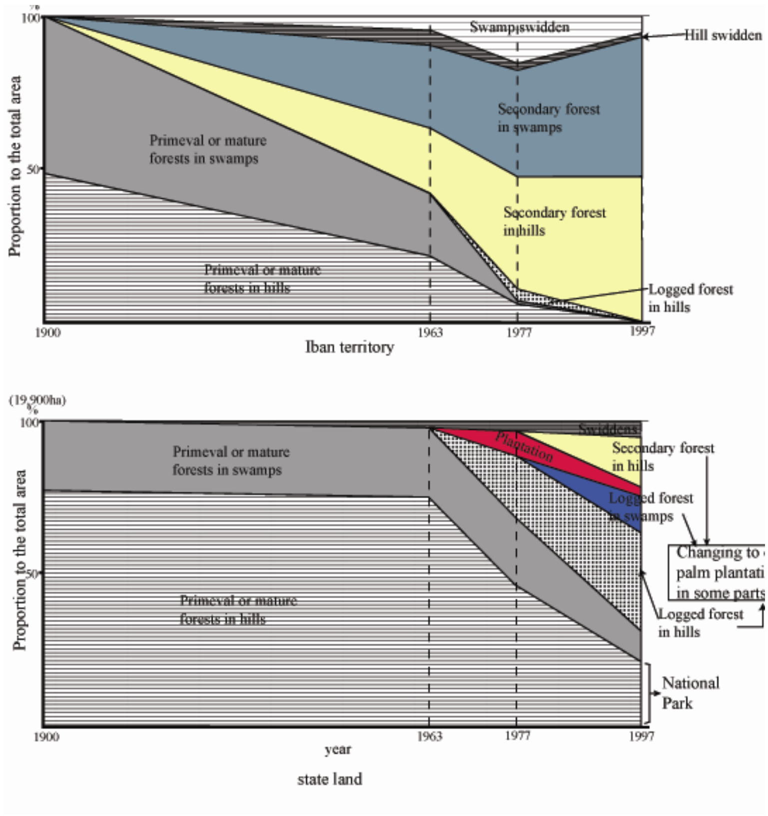


Figure 6 Characteristics of land use changes in the Iban territory and the state land
Source: Ichikawa 2007

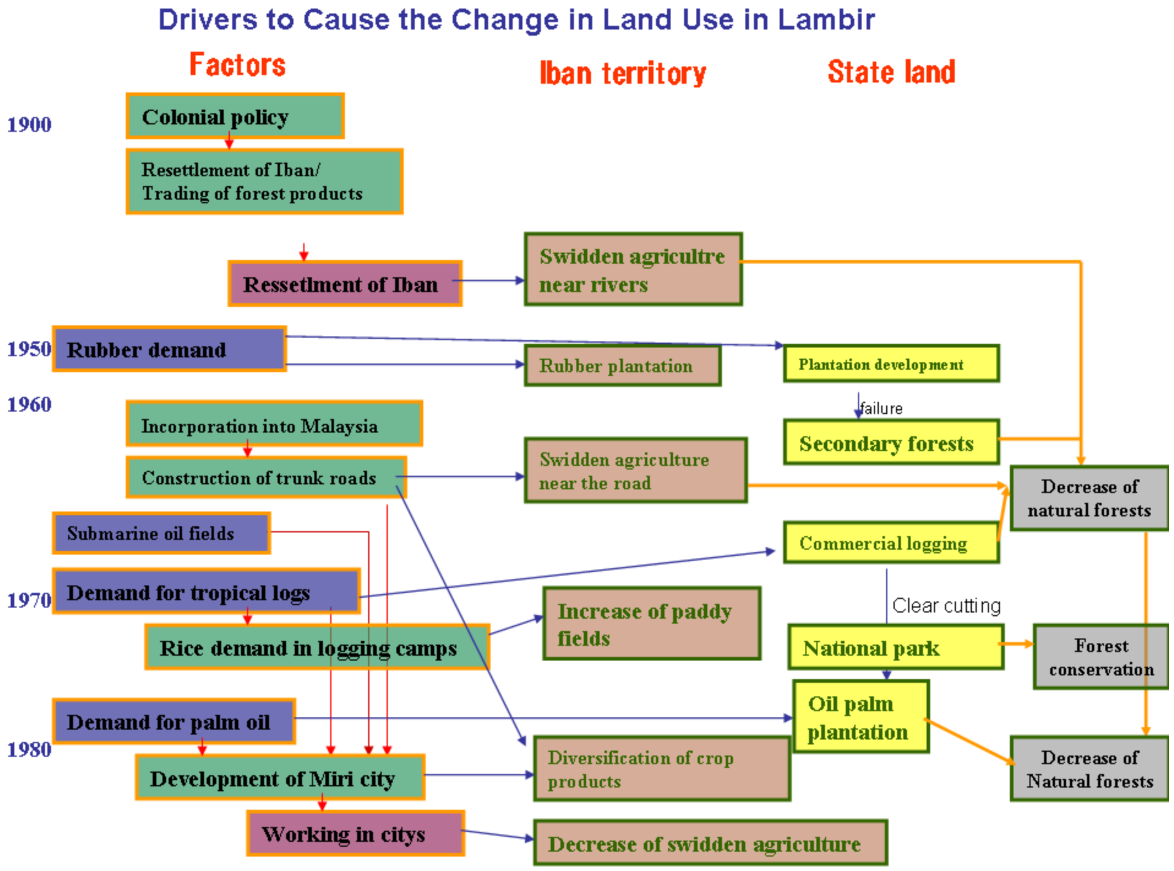


Figure 7 Background of land use changes

Modern Land-use Changes in the Upland and the Lowland Terrains of Sabah, Malaysia, and their Causal Interpretation

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Introduction

The conversion of tropical rain forests has been wide-spread and rapid in Southeast Asia (Sodhi and Brook 2006). Presently, this region demonstrates the highest rate of the loss of tropical rain forests (Laurance 1999). Approximately, 1.5 million ha of tropical forests were converted annually from the major four islands of Indonesia (Sumatra, Borneo, Sulawesi and Irian Jaya) (Sodhi and Brook 2006). For the entire world, Laurance (1999) estimated that 15.4 million ha was destroyed annually between 1980 and 1990 based on the FAO data on forest cover; the same author also suggested that additionally 5.6 million ha was degraded. These numbers are based on broad categories of land cover types over large areas. Achard et al. (2002) argued that the rate of forest loss in the world tropics was much lower (5.8 million ha per year), using satellite data, than previously believed.

This kind of controversy may arise from several factors. We suggest that one of such factors is related to the resolution of analysis in terms of time and space. The rate of progressive, secondary succession such as the one in old fields or in selectively logged forests can be quite fast in the tropics. If one analyzes the land-use changes in which vegetation recovery is involved, over an extended period longer than the recovery process, the analysis will result in an underestimate of forest conversion. In addition, land conversion can often take place in a smaller spatial extent than 1ha (100 x 100m) on the ground, in which case the conversion cannot be adequately detected by a large-scale analysis that commonly uses a larger mesh size than several km. Mismatch of spatial resolution may under- or over-estimate the area of forest conversion.

The spatial scale of land-use changes is intimately related to their drivers. Land use for subsistence farming may be small in scale, while the land use caused by large-scale socio-economic drivers at regional to international levels can be quite extensive. The changes of any given landscape in Southeast Asian tropical rain forests are actually driven by several different drivers. Contemporary landscapes must demonstrate a complex pattern of small-scale land cover types intermixed with large-scale land cover types. Therefore, we analyzed the spatio-temporal patterns of land use in contemporary Sabah, Malaysia, with the use of Landsat data (resolution of 30x30 m), so that we can analyze the land-use patterns of subsistence farming as well as of large-scale developments.

Although the drivers of land use are the same, the type of land cover and the consequences (e.g. spatial patterns) can be quite different if physical environments are different. For instance, for the same driver (i.e.

the demand for cash and cash crop), farmers will choose the crop that yields the best return for an investment in each environmental setting. The sate of Sabah is mountainous and environmental setting is contrasting between upland and lowland. Therefore, we hypothesize that the same driver will result in different types of land cover and consequences in the upland versus the lowland. We compare the land-use type and patterns between the two climate zones.

Materials & Methods

Land-use and modern history of the study areas

The state of Sabah is located in the northernmost part of Borneo and presents mountainous upland to undulating low-lying terrains. The mountainous topography culminates on Mount Kinabalu and a typical undulating low-lying terrain is found in the Deramakot area.

Kinabalu: The summit of Mount Kinabalu (4,095m, 6N 116E) and its surrounding area was first gazetted as the Kinabalu National Park in 1964. Originally, the purpose of gazetting the area was to preserve the mountain as a permanent war memorial. Later, park boundaries were modified and it was re- gazetted as Kinabalu Park with a total area of 73,500 ha in 1984. In 2000, the entire park was designated as a World Natural Heritage site because the continuum of pristine vegetation from the lowland to the summit together with its high biological diversity was recognized as a common human heritage. The vegetation consists of mixed dipterocarp lowland tropical rain forests up to 1200 m, montane tropical rain forests up to 2700 m, subalpine forests up to 3400 m and alpine vegetation up to the summit. Park Headquarters are located at 1560 m asl and serve as the base for mountain climbers and tourists. Mean annual air temperature at the Park Headquarters is 18.3℃ with mean annual rainfall of 2380mm between 1996 and 1997 (Kitayama et al. 1999).

The majority of the area within the park is pristine with only 6.56% of the total area being substituted by man as of 1986 (Kitayama 1991). No permanent farming and little encroachment within the park are recognized as of 2007. However, the surrounding areas are heavily used by man. Particularly, the southeastern upland plateau (Mesilau Plateau) in the elevation range of 800 to 1600 m are now used for intensive agriculture (mostly temperate-vegetable growing), large-scale dairy farming, golf course, and etc. The southern to western slopes are mostly used for subsistence agriculture and shifting cultivation. Logging activities were once rigorous in the eastern and the northern areas, but now subsided. Noteworthy is the cupper mining which began in 1970 and was recently shut down. A total area of 2,555 ha was removed as the mining area from the national park in 1970 and it produced 15,000 tons of ore daily at its full operation.

The land conversion by modern agriculture around Mount Kinabalu began probably as early as 1958 when a jeep track connected the Park Headquarters with the capital city of Kota Kinabalu. By 1960, there were 8 ha of land under vegetable cultivation. The jeep track was not enough to support a fuller production of temperate vegetables and production rate did not increase drastically. In 1971, a total area of 162 ha was under “cabbage ladang” which means temperate vegetables cultivated in shifting cultivation system. The agricultural production drastically changed after 1982 when a sealed highway connected Mount Kinabalu with Kota Kinabalu. Fig. 1 depicts the change in the number of visitors to Kinabalu Park. The number drastically increased after the highway was completed. Better transportation changed attitude of farmers from “cabbage ladang” to permanent terrace farming, and triggered systematic land conversions.

Deramakot: Deramakot Forest Reserve (5N 117E) is part of Sabah’s 2,674,570-ha Class II Commercial Forest Reserves, which are meant to conserve forest for commercial timber production. Deramakot Forest Reserve consists of one forestry management unit of 55,149 ha and is situated at the upper Kinabatangan River. The climate is humid equatorial with a mean annual temperature of about 26℃ with a mean annual rainfall of approximately 3,500 mm. The elevation ranges from 100 to 300m and the entire area represents a lowland undulating terrain. The entire area is covered with mixed dipterocarp lowland tropical rain forests.

Commercial logging started in Deramakot in 1956 (Huth and Ditzer 2001). The initially adopted logging method was the Malayan Uniform System (MUS), which allowed harvesting all commercial timber trees over 45 cm in diameter at breast height (DBH). In 1971, the Sabah Uniform System (SUM) was newly introduced following the timber boom in the late 1960s. This method employed heavy machinery for harvesting, skidding and transportation without appropriate consideration for forest stand and site condition (Kleine and Heuvedlop 1993). The area was licensed for logging from 1955 to 1989. The minimum diameter for harvesting was 60 cm and the felling cycle was 60 years. The majority of the Deramakot area was probably affected mildly to heavily by this logging system. Variable cutting intensities of past management practices resulted in an extremely heterogeneous condition of the residual forests (Lagan et al. 2007). Only 20 % of the area was considered well stocked with harvesting trees and more than 30% was covered by very poor forest with virtually no mature growing stock left. The demise of timber resources in Deramakot might have followed the same track of economic downfall of Sabah (Fig. 2). The state annual revenue from forestry and forest-related industries peaked in 1988 with an approximate amount of 1,100 million ringgits, but sharply dropped since then. This triggered the reform of Sabah’s old forestry system into a new sustainable forestry system (Ong and Sinajin 2003).

For the period 1989–2000, the Sabah Forestry Department, in collaboration with the German Technical Agency implemented the Malaysian-German Sustainable Forest Management Project, and Deramakot Forest Reserve was chosen in 1989 as the project site. The project was made up of four phases (Lagan et al. in press): 1) a strong research emphasis with a component for management planning (1989–1992), 2) management planning, training and consolidation (1992–1994), 3) institution building, human resource and development, consolidation/ implementation and extension (1995–1998), and 4) consolidation, planning and human resource development (1999–2000). Deramakot Forest Reserve was certified as “well managed” by an international certification body, the Forest Stewardship Council (FSC), in 1997. It is the first natural forest reserve in Southeast Asia managed in accordance with sustainable forestry principles.

Deramakot Forest Reserve is now divided into 134 compartments, a smallest operational unit where annual timber production takes place. Sabah Forestry Department harvests timber at a rate of two compartments per year, with an intention of 67 years of recovery time before the next harvest takes place.

For the details of the guidelines currently adopted in the Deramakot Forest Reserve, see Sabah Forestry Department (2000).

Adjacent to the western border of Deramakot Forest Reserve lies Tangkulap Forest Reserve where until recently conventional intensive logging was continuously applied by a private sector. Therefore, compared with Deramakot training area, Tangkulap Forest Reserve represents more dynamic timber harvest and the rapid reduction in forested area. There are no statistical data available for the amount or the rate of past timber harvest in the Tangkulap area.

To the north of Deramakot and Tangkulap is located a vast area of oil palm fields. The development of oil palm plantation involve~~s~~ large-scale mechanical removal of above-ground vegetation and the establishment of the monoculture of single oil palm. However, land conversion in this area in recent years has been less dynamic, as fruits only are collected if once developed, although the development of oil palm fields still occurs in marginal areas. Replanting of juvenile oil palm trees also takes place in the senescent fields.

Methods

The following nine data of Landsat imagery of Multi-Spectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper plus (ETM$^+$) were acquired in time series for classifying land cover and use types from the archives of Tropical Rain Forest Information Center (TRFIC) (http://www.bsrsi.msu.edu/trfic/index.html) and from Earth Resource Observing System (EROS) data gateway of USGS (http://edc.usgs.gov/products/satellite.html):

Kinabalu	January 12th, 1973, Landsat MSS; June 29th, 1985, Landsat MSS;
	June 14th, 1991, Landsat TM; Oct 22nd, 1999, Landsat ETM$^+$;
	May 19th, 2002, Landsat ETM$^+$
Deramakot	August 25th, 1985, Landsat MSS; May 22nd , 1991, Landsat TM
	Sept. 9th, 1999, Landsat ETM$^+$; May 28th, 2002, Landsat ETM$^+$

Radiometric and geometric correction were applied to these Landsat data before analyzing them in time series to eliminate some errors commonly produced during data acquisition (see Darmawan 2004 for the details). Land cover and use types were categorized based on supervised classification with maximum likelihood method. In the first stage, unsupervised classification was applied to each date of Landsat data with the fuzzy C mean and K mean method for selecting training area. By evaluating dendrogram and co-occurrence, about 50 classes of land cover types were analyzed and regrouped into a fewer number of classes. Land cover type was assigned to each of the classes based on ground truth and spectral patterns. Subsequently, the tasseled cap transformation was used to develop the temporal pattern of land cover and use types in each of the two areas (see Darmawan 2004 for the details).

We attempted to link the land-use change with the change of the taxonomic diversity of canopy trees based on the relationships between above-ground biomass and the taxonomic diversity of canopy trees. As the satellite data of the Kinabalu area are often noisy due to haze and clouds, we used the data of Deramakot only. Because there is an inherent problem that normalized indexes using spectral reflectance saturate at higher biomass (Nakazono et al. submitted), we employed the biomass values that were estimated with a special algorithm by Nakazono et al. (submitted) and Kitayama et al. (2006). First, we regressed the number of canopy-tree taxa per 0.2 ha at species, genus and family level with actually measured biomass values using the census data of Seino et al. (2006) (N=10). The number of families yielded the highest correlation coefficient ($r^2=0.552$; $P=0.014$). Therefore, we used the number of families per 0.2ha as dependent variable. We extrapolated this regression model to the entire Deramakot area using the biomass values estimated by Nakazono et al. (submitted) and Kitayama et al. (2006) for 1985 and 2002. We arbitrary assigned the value 1 to oil palm plantations. Subsequently, we calculated frequency distribution of canopy diversity classes.

Results

Land use types changed drastically in both areas through time (Figs. 3 and 4). In the Kinabalu area, the most drastic change was the rapid increase of agricultural and bare lands between 1973 and 1991. In 1991, patches of agricultural and bare lands occurred in the southeast and southwest slopes. In 1973, the most wide-spread cover type in the Kinabalu area was secondary forests, which decreased in area later (Fig. 5). After 1991, shrub land and rangeland increased drastically. The area of “pristine forests” temporary increased in 1991, probably due to the re-growth of secondary forests.

In the Deramakot area, land-use changes were also dynamic and rapid (Fig. 4). Most obvious change was the steady increase of oil palm plantations. The development of oil palm plantations is massive but not patchy unlike the agricultural development in the Kinabalu area. Oil palm plantation expanded in area steadily after 1985 (Fig. 6). On the other hand, the area of pristine forests decreased successively from 1985 to 2002 (Figs. 4 and 6). The reduction of pristine forests from 1991 to 2002 occurred as the disappearance of the remnant forests which were interspersed among selectively logged production forests. Some areas that were recognized as bare or sparse vegetation interspersed in the logged-over forests in 1991 recovered to secondary forests, probably reflecting the protection from severe logging. A new land cover category “other agriculture” appeared in 2002; however, we could not confirm the actual land use of this category on the ground.

The frequency distribution of species richness (indexed by the number of families per 0.2ha) changed considerably from 1985 to 2002 because the above-ground biomass of the vegetation changed between the two years (Fig. 7). The mode of the richness occurred at 27-28 families per 0.2 ha in 1985. It became 23-24 families per 0.2 ha in 2002. The frequency of the mono-culture with reduced canopy diversity increased in 2002.

Discussions

Both areas (Kinabalu and Deramakot) demonstrated rapid and dynamic changes in land use. However, land-use type and spatial pattern (patchiness and extension) differed much between the areas.

On Kinabalu, small patches of agricultural lands occurred in the southeast and southwest slopes and surrounded the park boundaries in 1991. Most of these patches corresponded with the intensive agriculture employing terracing and with sporadic shifting cultivations. This contrasts with the occurrence of sparse shrubby vegetation in 1973, the time when traditional shifting cultivation was more widespread. Although our time resolution is coarse (i.e. 1973, 1991 and 2002 only in time series), the increase of intensive agriculture fields is likely to correspond with the development of the sealed highway that connects the Kinabalu area with Kota Kinabalu in 1982. The development of the highway improved the transportation ability of harvested temperate vegetables to the coastal town and contributed to the cash yield of local farmers. This might have triggered the expansion of intensive-agricultural land to the interior.

Although intensive, farmers frequently lay land fallow in their terrace system. During fallow time, pioneer trees such as *Trema orientalis* form a shrub land in three years (Ohtsuka 1999). Such fallow system and fast secondary succession in this area form a dynamic land-cover system of retrogressive and progressive successions. Cool upland climate is a prerequisite for the formation of such a system because temperate vegetable is grown only in this upland area. Secondly, small-scale tenant farming is still the major faming method here and hence the patchy land-uses occur throughout the area.

The existence of the protected area (Kinabalu Park) must have indirectly influenced the land use of the surrounding non-protected area. As the passage of the highway was completed and the number of climbers rapidly increased, more local people were engaged as the park staff or in the tourism industry, bringing capital to the local village for further development. Thus, the mountainous topography, cool climate and the passage of the highway provided the basis for both protection and development forming a dynamic land-use system in the Kinabalu area. In contrast to the Indonesian state of Kalimantan, where the area of protected areas declined by more than 56% (Curran et al. 2004), we did not find any trace of encroachment into the park.

In the lowland Deramakot area, selective logging and the development of large-scale oil-palm plantations are the driving force of the land-use changes. The original vegetation of the entire area of Deramakot must have been mixed dipterocarp lowland tropical rain forests. The pristine forests that have consistently retained high stocks from 1985 to 2002 are recognized in the west mountainous area and the southwest area as of 2002 by dark green color in Fig. 4. More than one half area of this region had been heavily affected by selective logging by 1985 as indicated by light green color in Fig. 4. By 1991, many stands of the selectively logged forests had obviously recovered in stock by 1991 as patches of dark green color occurred. Therefore, the Deramakot area again represents a dynamic landscape with selective logging and fast secondary successions.

The area of oil palm plantations increased rapidly between 1985 and 1991; the timing of the rapid expansion appears to correspond with either or both the downfall of logging industry or/and the increased commodity price of palm oil products. Between 1991 and 2002, the area of oil palm plantations was extended into the south towards Deramakot Forest Reserve. It is an interesting subject as to how the capital for the oil palm development has been collected, but it is beyond the scope of our paper. Because the Class II Commercial Forest Reserves (Deramakot is one of them) are the designated areas by law with boundaries, the oil palm plantations will not proceed to the south anymore.

The frequency diagram of the family numbers of canopy trees demonstrated impoverished diversity in 2002. Although our assumption is based on a simple regression between above-ground biomass and family number, the depicted pattern reflects a generally impoverished trend of diversity due to harvest and land conversions. The expansion of oil palm plantations will further lead to the increase of monoculture stands. Our estimate depicts a crude spatiotemporal pattern only and it is not known what are the biological consequences of reduced diversity.

Overall, our analysis demonstrated dynamic land-use changes in two tropical rain forest areas. Both areas simultaneously demonstrated progressive and retrogressive successions in a range of patch scales. The simultaneous occurrence of progressive and retrogressive changes was detected because we employed satellite data of relatively-high resolution (30x30 m) in a time series. This type of dynamism would not have been elucidated if we employ coarse-scale data (e.g. 1x1 km) that are conventionally used for processes at global scales.

Acknowledgements

We are grateful to Prof. Tohru Nakasizuka and Dr. Masahiro Ichikawa, who as the head of the RIHN project supported our activities in all aspects. We are also grateful to Datuk Sam Mannan, Director of Sabah Forest Department, Drs. Lee Ying Fah, Robert Ong and Arthur Chung of Forest Research Centre, Sabah, for their encouragements and assistance in every aspect.

References

Achard F, Eva HD, Stibig HJ et al. (2002) Determination of deforestation rates of the world’s humid tropical forests. Science 297: 999-1002

Darmawan M (2004) Study on forest degradation dynamics of Borneo tropical rain forest based on historical land cover change analysis using remote sensing. Doctoral Thesis, Department of Global Agricultural Sciences, The University of Tokyo

Huth A, Ditzer T (2001) Long-term impacts of logging in a tropical rain forest –a simulation study. Forest Ecol Manage 142: 33-51

Kitayama K (1991) Vegetation of Mount Kinabalu Park, Sabah, Malaysia. Map of physiognomically classified vegetation Scale 1: 100,000. Project Paper, Protected Areas and Biodiversity, Environment and Policy Institute, East West Center, Honolulu, USA

Kitayama K, Lakim M, Wahab MZ (1999) Climate profile of Mount Kinabalu during late 1995-early 1998 with special reference to the 1998 drought. Sabah Parks Nature Journal 2: 85-100

Kitayama K, Nakazono E, Seino T, Matsubayasi H, Gobilik J, Ong R (20026) Landscape-level evaluation of carbon and biodiversity in the tropical rain Forests of Deramakot Forest Reserve, Sabah, Malaysia. In: Lee YF, Chung AY, Kitayama K (eds) The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation in Tropical Rain Forests, DIWPA, Kyoto

Kleine M, Heuveldop J (1993) A management planning concept for sustainable yield of tropical forests in Sabah, Malaysia. Forest Ecol Manage 61: 277-297

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Ecol Res 22: 414-421

Laurance WF (1999) Reflections on the tropical deforestation crisis. Biological Conservation 91: 109-117

Ohtsuka T (1999) Early stages of secondary succession on abandoned cropland in north-east Borneo Island. Ecol Res 14: 281-290

Ong RC, Sinajin J (2003) The status and management of protection forests in Sabah. A paper presented at the Conference of Forestry and Forest Products Research 2003: “Forestry for Society”, 6-8 October, 2003, Kuala Lumpur

Sabah Forestry Department (2000) RIL operation guide book specifically for crawler tractor use, second edition, Sabah, Malaysia.

Sabah Forestry Department (2002) Annual Report 2002. Sabah Forestry Department, Sabah, Malaysia

Sodhi NS, Brook B (2006) Southeast Asian biodiversity in crisis. Cambridge Tropical Biology Series. Cambridge University Press, Cambridge, UK

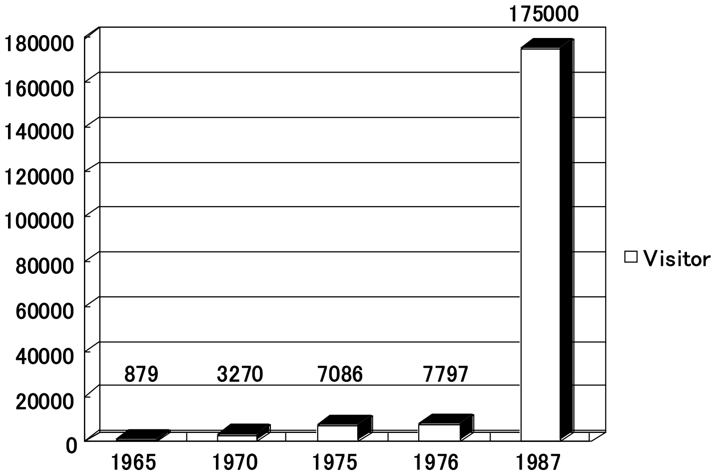

Fig. 1 The number of visitors to Kinabalu Park through time.
Data based on the unpublished statistical data of the Sabah Parks.

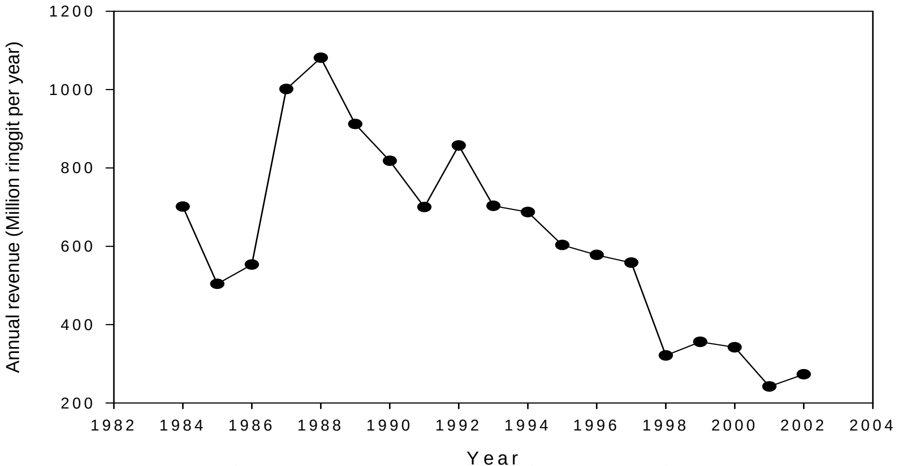

Fig. 2 The change of annual state revenue from forestry and forest-related industries in Sabah
Data after Sabah Forestry Department (2002).

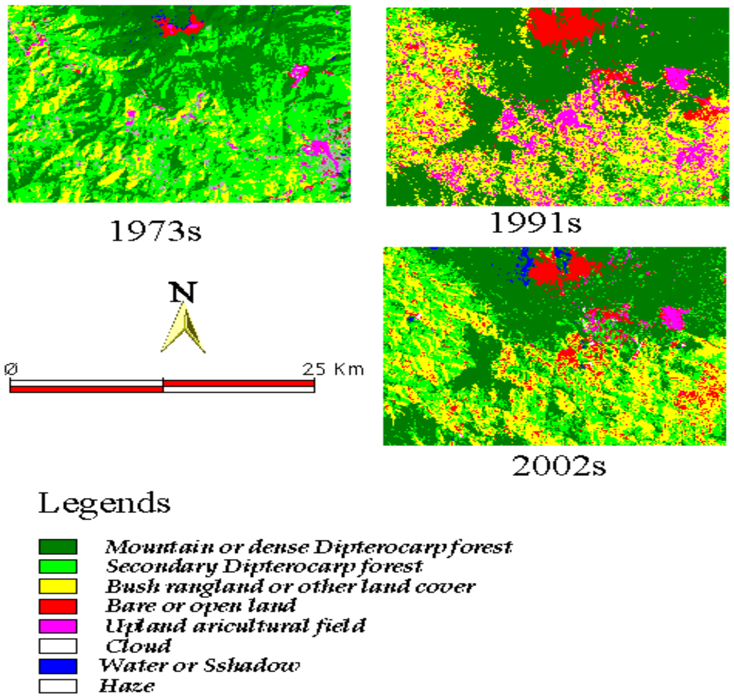

Fig. 3 Land cover changes in the Kinabalu area from 1973 to 2002.

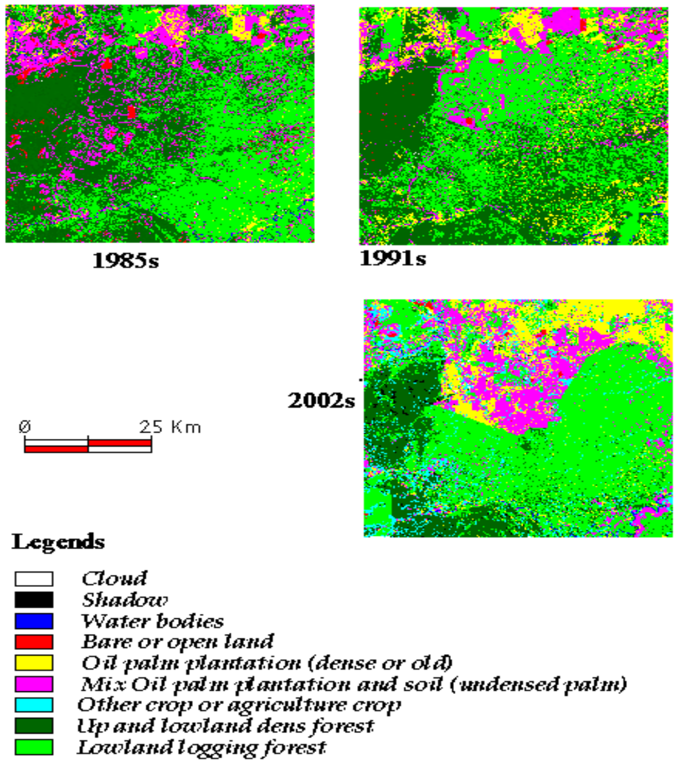

Fig. 4 Land cover change in the Deramakot area from 1985 to 2002.

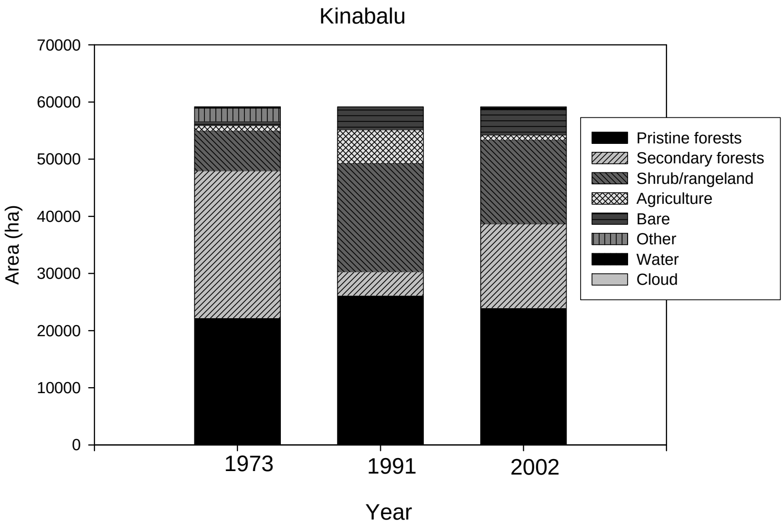

Fig. 5 The change in the relative area of land cover categories in the Kinabalu area from 1973 to 2002.

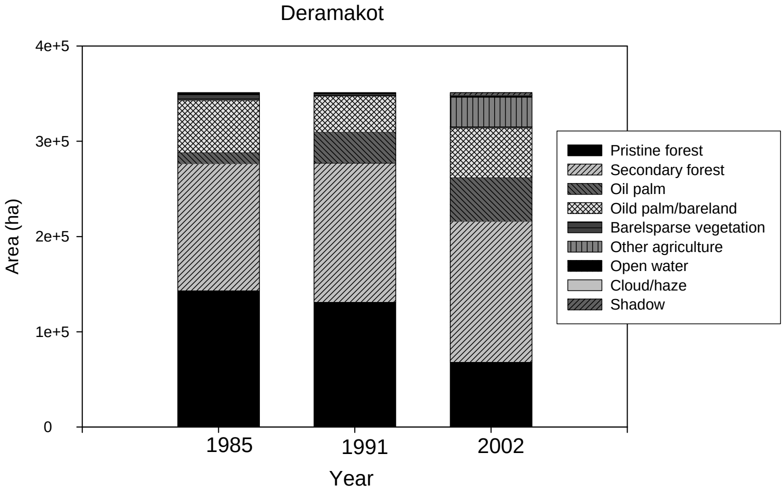

Fig. 6 The change in the relative area of land cover categories in the Deramakot area from 1985 to 2002.

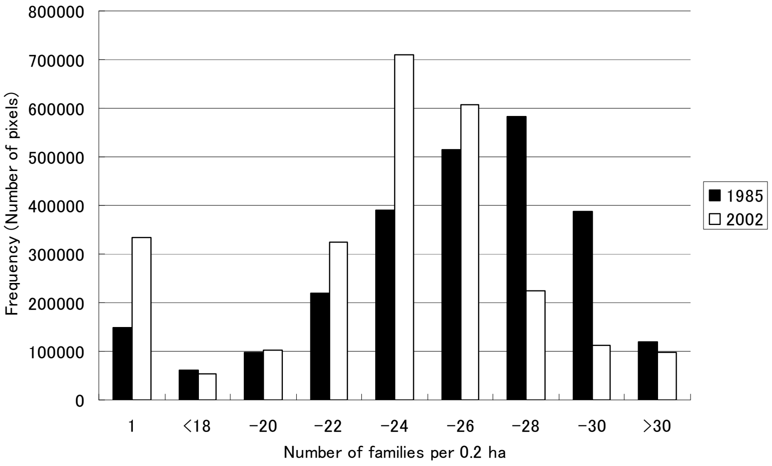

Fig. 7 The frequency distribution of the number of the families of canopy trees per 0.2 ha in year 1985 and 2002. Frequency indicates the number of pixels that fallen to each of diversity classes (the number of canopy trees per 0.2 ha).

History of Forest Utilization in the World Natural Heritage Area of Western Yakushima Island

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Introduction

The western lowland of Yakushima Island, the World Natural Heritage area, is covered by broad-leaved evergreen forest subjected human disturbance, such as cultivation, wood charcoal production, and camphor distillation. However, details of the forest utilization remain unclear, because most of this area was owned privately prior to 2005 with no available records for land use. Comprehension of the human impact in the past, as well as biological and ecological studies, is required for understanding the current condition of the forest and to develop an effective conservation scheme. We conducted field research and literature surveys, including interviews with local people, in order to review the history of forest utilization in the western lowland area of Yakushima Island.

Materials & Methods

The study area was located in the Han-yama and Kawahara sites in the western lowland of Yakushima Island (ranging from 0 to 300 m in altitude, and covering approximately 1 × 4 km; Fig.1). There are no settlements within the study area except a single road traversing it. Approximately, a 200-m contour line was considered a boundary for the land management: government-owned forest at the upper side, and Kagoshima prefecture-owned forest at the lower side. The latter was privately owned prior to 2005.

We referred to some documents, old maps, and aerial photographs taken in 1947 and 1969. The aerial photographs were subjected to orthometric correction using ERDAS Imagine ver.8.7, and logged sites in the photographs were surveyed with ArcGIS ver.9.

From March to August 2006, we located abandoned artificial structures, such as charcoal kilns and farm fields with stone masonry using a GPS receiver (MobileMapper Pro, Thales Navigation Inc.). Size and characteristic features of charcoal kilns were also recorded.

In order to date the period of human activities such as charcoal production and camphor distillation, we extracted tree-ring cores using an increment borer, and determined tree ages by counting tree rings under a stereoscopic microscope. For the charcoal production, we determined the tree ages of *Melia azedarach* var. *subtripinnata* standing adjacent to abandoned charcoal kilns to estimate the year of abandonment of the kilns. For the camphor distillation, we determined the ages of *Cinnamomum camphora* trees, the raw material of camphor.

Results

In the Han-yama and Kawahara sites, a total of 37 abandoned charcoal kilns were found (Fig.2). Most of the kilns were located in concaved sites and had an oval or clam shell-shaped bottom. The horizontal and vertical inner widths ranged from 3.1 to 5.1m and 2.4 to 4.1m, respectively. Many artificially squared plots with stone masonry surrounds were recorded, mainly on gentle slopes in Han-yama and Kawahara (Fig. 2).

In total, seven *M. azedarach* var. *subtripinnata* trees were estimated at ages ranging from 44 to 86 years old, suggesting the approximate abandonment years of 1920 to 1962 for seven of the charcoal kilns (Fig. 2). The ages of 12 camphor trees in three sites of Kawahara (Fig. 2) averaged 70 years, ranging from 58 to 86 years, indicating the establishment year of around 1936 for the camphor trees in Kawahara.

From the aerial photographs taken in 1947, logged areas totaling 50.3 ha were identified, and 32.2 ha of them appeared to have been clear-felled in the period near to 1947 (Fig. 3). Areas of 44.8 ha were seen from the aerial photographs of 1969 to experience logging between 1947 and 1969 (Fig. 3). These photographs also showed bare ground (1.5 ha) due to waste soil associated with road construction in 1967. The location of houses and farm fields recorded by GPS usually fell into the clear-cut areas identified from the photographs of 1947.

Discussion

Here, we describe the history of forest utilization in the study area, taking events in chronological order. The Kamiyaku-town Local History Editing Committee (1984) stated that the area stretching from Nagata to Segire (Fig. 1) had been managed by Nagata village since early times. There is, however, no description of a village in the western part of the island on an old map drawn in 1882 (unknown publisher 1882) or a 1/200,000 geographical map drawn in 1889 (Land Survey Division 1892). Nishiwada (1894) listed the names of villages in Yakushima Island; however, the three villages, Han-yama, Kawahara, and Segire, were not included. On the other hand, we were able to find descriptions of Han-yama, Kawahara, and Segire, with symbols of accommodation units, on geographical maps drawn in 1921 (Land Survey Division 1923). Furthermore, the operation plan for the national forest (Kagoshima Regional Forest Office 1922) contained a description “Segire, farmers, three families.” The tree-ring analysis suggested that two charcoal kilns in the northern Kawahara area were abandoned in 1920 and 1921 at the latest (Fig. 2), suggesting human activities before this time. Yaku-town Local History Editing Committee (1993) said that Mr. Y. Kitazono from Kurio village (Fig. 1) had produced camphor at Kawahara in 1914–1915. According to the Monopoly Bureau (1942), at least several people were needed to work for the raw procurement and kiln management, and to stay over near to a camphor factory. For the reasons mentioned above, people appear to have first colonized these sites around 1900 to undertake cultivation, wood charcoal production, and camphor distillation.

From the tree-ring analysis of 12 camphor trees in the Kawahara site, these trees seemed to have been established around 1936, suggesting logging for camphor trees until this point of time. As mentioned earlier, we were only able to obtain information for camphor production in Kawahara for 1914-1915, and there is a time discrepancy of approximately 20 years between the documentary information and the tree ages. Yaku-town Local History Editing Committee (1993, 1995, 2003) said that camphor production had been an active form of industry in Yakushima Island in the 1920s and 1930s, and that camphor factories in Nakama village (Fig. 1) had obtained raw materials from various sites, including Ohko near to Segire. Camphor trees in Kawahara may have been felled around the 1920s and 1930s for factories in remote areas, such as Nagata and Kurio.

Dr. J. Miyamoto, a folklorist who visited Yakushima Island in 1940, described the situation as follows, “Kawahara village is deserted now, and Han-yama village is almost abandoned with a few farmers (Miyamoto 1974).” We could not find any information on the status of Segire village at that time. In the period around 1940, it seems that few activities were conducted in connection with charcoal production and camphor distillation in the study area.

We obtained information from local people about logging at Kawahara for military purposes in the early 1940s, during World War 2. The information gleaned was as follows: Mr. D. Hidaka from Nagata worked as a punch marker for logs; a Korean group of 50–60 or even 70–80 loggers lodged in Kawahara; and Mr. Kim, a 75-years-old Korean, received a letter in 1942 from his father who was working at Kawahara (Nishinihon news-paper, 2006.08.06). Logging at Kawahara in the early 1940s must be a fact, although there is no available documentation telling of this activity. Logging for military purposes in the early 1940s presumably caused the large-scale deforested areas in the Kawahara site found in the aerial photographs of 1947 (Fig. 3).

In the late 1940s, people lived in Han-yama for sweet-potato cultivation and charcoal production (Ankei & Ankei 2000). At that time, the “Satsuma method,” promoted by Kagoshima prefecture, was employed widely in Yakushima Island (Uchida 1952, Kamiyaku-town Local History Editing Committee 1984, Yaku-town Local History Editing Committee 1993, 2003). Some abandoned charcoal kilns found in the study area had distinguishable features that accorded with the Satsuma method kiln, such as the clam shell bottom shape and one exhaust port on the back side. Using a Satsuma method kiln could produce approximately 1,750kg of charcoal (70 strew bags) twice a month (Yaku-town Local History Editing Committee 2003). Yield percentage was reported at approximately 20% for this method (Kagoshima Foresters Association 1925, Uchida 1952), so that 8 to 9 t of raw wood was needed for one charcoal burning. According to the above-ground biomass data recorded at the research plot located in the upper side of Han-yama (Forestry and Forest Products Research Institute, http://fddb.ffpri-108.affrc.go.jp/index.html), the forest contained approximately 103 t/ha biomass of tree species for good charcoal such as *Pinus thunbergii*, *P. densiflora*, *Quercus phillyraeoides*, *Q. salicina*, *Castanopsis sieboldii*, *Lithocarpus edulis*, *Rhaphiolepis indica* var. *umbellate*, *Rhus javanica* var. *roxburghii*, *R. succedanea*, and *Distylium racemosum*. Assuming the continuous running of a charcoal kiln, a 4-ha of raw material would seem to have been depleted over 2 years. Some charcoal kilns were located as close as approximately 100m apart from each other in the study area (Fig. 2), because of which charcoal makers may have built a new kiln every few years.

Meisei Timber, a civil corporation, purchased the private land in the western lowland of Yakushima Island from Shinwa Timber in 1951. According to someone who worked as a field overseer, Meisei Timber conducted intensive logging for wood pulp mainly in the Segire site, and cut down trees of the two species *Cryptomeria japonica* and *P. armandii* var. *amamiana* in Kawahara. Matsuda (1997) suggested that the forest in the Han-yama area also experienced logging by Meisei Timber in around 1955. Logged areas shown in the aerial photographs of 1969 (Fig. 3) are additional indications of the accuracy of information about pulp logging. From the scattered distribution of abandoned charcoal kilns in the gaps of logged areas shown in aerial photos, it was deduced that almost the entire area of the Han-yama and Kawahara sites experienced logging of varying intensity for charcoal and wood pulp between the 1940s and the end of the 1950s. The logging operations of Meisei Timber continued in the Segire site until around 1965 (Ohyama 2006).

In 1958, only Mr. & Ms. Tanaka lived in Han-yama, and they stayed there until around 1965 for potato cultivation and mushroom growing, as well as fuel wood gathering. However, someone was conducting charcoal production and rosin collection in Han-yama between 1960 and 1964 (Ankei & Ankei 2000). The evidence of resin collection was backed by fallen trees with V-shaped scars in Han-yama and Kawahara. There are no records of dwellers in the western lowland of Yakushima Island after 1965, except for around the Nagata lighthouse. Other than for the road construction in 1967, the Han-yama and Kawahara sites have been free from organized logging since around 1960.

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References

All listed documents are written in Japanese.

Ankei Y. & Ankei T. (2000) Life in Han-yama colony – interview with Mr. F. in Nagata, Kamiyaku-town. Seimeino-shima 52: 71-80.

Kagoshima Foresters Association (1925) Wood charcoal production. Kagoshima Foresters Association, Kagoshima.

Kagoshima Regional Forest Office (1922) Operation plans for the north, east, and south blocks of Yakushima. (Details unknown)

Kamiyaku-town Local History Editing Committee (1984) Local history of Kamiyaku-town. Kamiyaku-town Education Board, Kamiyaku-town.

Land Survey Division (1892) 1:200,000 geographical map “Yakushima.” Land Survey Division, surveyed in 1889.

Land Survey Division (1923) 1:50,000 geographical map “South-western Yakushima,” and “North-western Yakushima.” Land Survey Division, surveyed in 1921.

Matsuda T. (1997) Mysterious stories in Yakushima, the World Natural Heritage. Shusaku-sha Publishing, Tokyo.

Miyamoto J. (1974) Yakushima folklore. The inclusive edition of Johichi Miyamoto 16, Mirai-sha, Tokyo.

Monopoly Bureau eds. (1942) Lectures for camphor production. Monopoly Bureau.

Nishiwada K. (1894) Report for adventure trips to Tanegashima and Yakushima. (publisher unknown).

Ohyama Y. (2006) Transition of the western area of Yakushima. (In Ohsawa M., Tagawa H., and Yamagiwa J. eds., Yakushima the World Heritage – Nature and ecosystem of subtropical), Asakura Shoten, Tokyo.

Uchida K. (1952) Wood charcoal and processed charcoal. Asakura Shoten, Tokyo.

Yaku-town Local History Editing Committee (1993) Local history of Yaku-town 1 – Rural community 1. Yaku-town Education Board. Yaku-town.

Yaku-town Local History Editing Committee (1995) Local history of Yaku-town 2 – Rural community 2. Yaku-town Education Board. Yaku-town.

Yaku-town Local History Editing Committee (2003) Local history of Yaku-town 3 – Rural community 3. Yaku-town Education Board. Yaku-town.

Details unknown (1882) Old map of Yakushima, owned by the Kagoshima prefecture library.

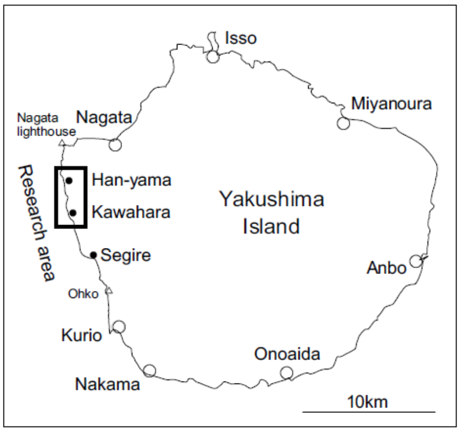

Fig. 1. Location of study site in the western lowland of Yakushima Island.
Black circle, abandoned villages; white circle, major towns; triangle, places related to text.

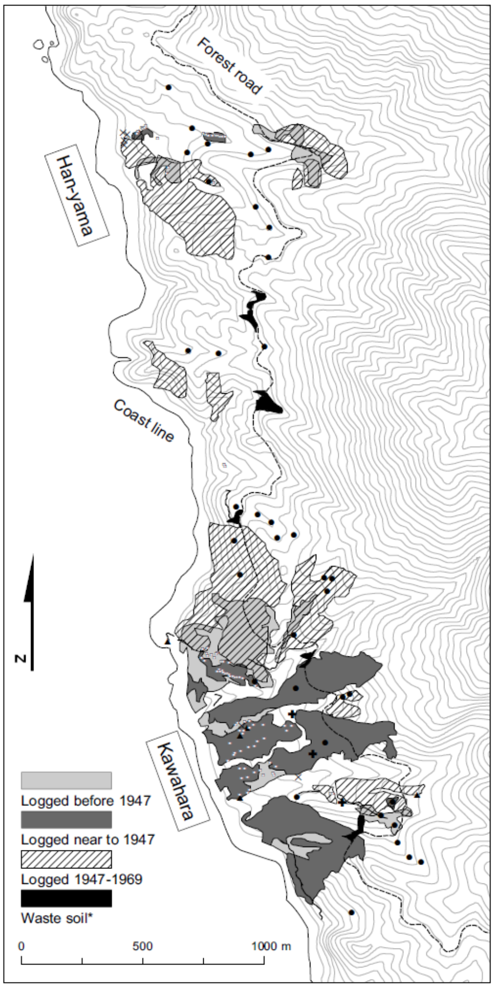

Fig. 2. Location map of abandoned artificial structures such as charcoal kilns, houses, farm fields, and trails with stone masonry. Numbers on some stone kilns indicate the year of abandonment, estimated by tree-ring analysis for *Melia azedarach* var. *subtripinnata* standing adjacent to a kiln.
* Camphor trees, *Cinnamomum camphora* trees extracted tree-ring cores (12 trees at 3 sites).
** Pine stumps, fallen trees and stumps with V-shaped scars to collect resin.
The forest road was constructed in 1967. Contour interval is 20 m.

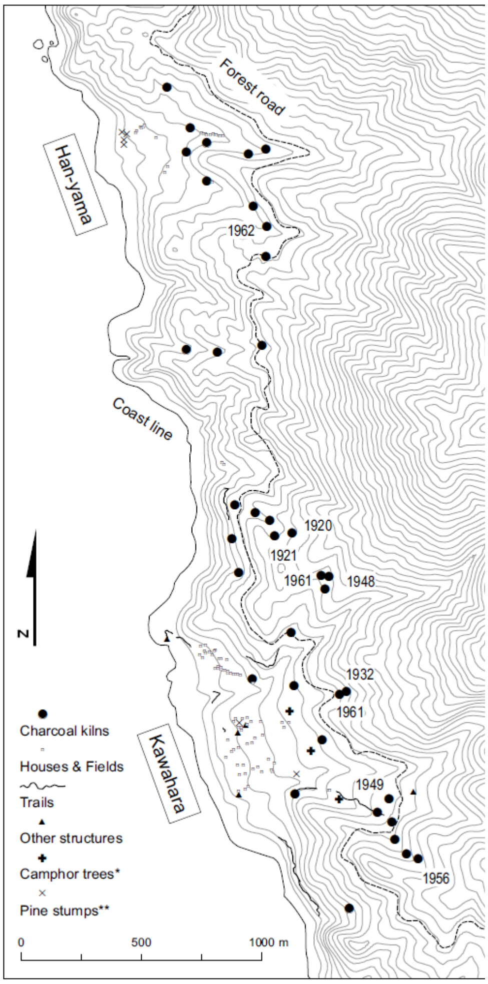

Fig. 3. Logged areas derived from aerial photos taken in 1947 and 1969.
Waste soil, bare ground due to waste soil associated with road construction in 1967.
See legends of Fig. 2 for the other symbols.

Historical GIS of Yakushima Island and the Extent of Human Subsistence Activities

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Introduction

Maps often provide important information about land use. Arranged in a time-series, maps can show land use change. However, cartographers have produced a wide variety of maps. For any particular study site, historical geographers need to examine available maps to determine what type of information can be obtained from the maps. For a research project applying a Geographic Information System (GIS), determining exactly how maps depict land use will point towards a strategy for data entry and analysis.

The most commonly used maps in Japan are the topographic maps produced by the Geographical Survey Institute (GSI) of the Ministry of Land, Infrastructure and Transport, and its predecessor institutions. These maps cover the entire land area of Japan. A historical geography project in Japan often starts by obtaining the map history for the topographic maps of a study site. While some parts of Japan may have been surveyed repeatedly by various Japanese government institutions, the earliest topographic map of the GSI will often be the first maps surveyed by modern methods, and the earliest extensive and complete record of land use, for many parts of Japan. A historical GIS project to study environmental changes in Japan must start first with an examination of the topographic maps to determine what they can tell researchers about land use changes on this island.

The objective of this project is to construct a historical GIS database for Yakushima Island in southern Japan. The first step of this project was to examine exactly how Yakushima is depicted in the topographic maps issued by the GSI, and, second, use the topographic maps to carry out time-series analysis to identify major patterns of land use change associated with the livelihoods of the inhabitants.

The goal of this analysis is to identify the spatial extent of the daily subsistence activities carried out by the inhabitants of Yakushima. Human activity has undoubtedly affected the vegetation and land cover of Yakushima. The island has been inhabited since the neolithic Jomon period. In early modern times, the people of Yakushima lived by a combination of farming, fishery, and forestry. However, Yakushima is a mountainous island and human habitation is largely restricted to the coastal plains. While this fact is obvious, the extent to which human subsistence activities extended up the mountain-side is a critical research issue. Research on land use history is linked to a judgment about whether human activity in modern times is expanding or shrinking. In the case of Yakushima, modern farms, especially orchards, have expanded uphill into forested mountains in the post-WWII period. Thus, historical geographical research is necessary to determine whether human activity is expanding into new, previously unused areas.

This study focused, in particular, on a type of land use depicted in topographic maps called “are-chi,” which can be translated as roughland or wasteland. In Japanese topographic maps, wasteland denotes unforested grasslands or bushland (Japan International Map Association, 1990). In a heavily forested landscape as in Yakushima, wasteland implies the presence of human activity that cleared forest. First, the

GIS analysis mapped the estimated extent of wasteland, as well as farmland, as indicators of human activity on Yakushima. Second, time-series analysis identified the location of new land uses in relation to older land uses to determine whether the new land uses were expanding into previously unused areas.

Methods

Yakushima is covered by four map sheets at 1/50,000 scale and seven map sheets at 1/25,000 scale. This project used maps from three time periods for GIS analysis, as folllows: (1) 1/50,000 scale maps issued in 1921 in the Japanese polyhedral projection, the oldest topographic maps of Yakushima, (2) 1/50,000 scale maps issued in 1972-73, the earliest in the universal transverse mercator (UTM) projection, based on 1/25,000 maps drawn from 1969 aerial photographs and 1970 ground survey, and (3) 1/25,000 scale maps in the UTM projection issued in 1992 based on 1990 aerial photographs and 1991 ground survey. The maps were georeferenced to the same UTM projection (Tokyo datum, Zone 52) using corner latitude-longitude coordinates printed on the maps, and joined together into single maps for each period.

Land uses demarcated by lines were entered into the GIS as polygons. Land uses marked by free labels were first entered as points from which the GIS generated Theissen polygons, followed by merging all adjacent polygons with the same land use.

The data on altitude was based on the 50 meter-interval topographic data issued by the GSI. The analysis was confined to the area from the coast line up to an altitude of 500 meters above sea level since this project focused on the rural landscape, and large-scale forestry in the higher altitude mountains is beyond the scope of this particular analysis.

Land use change was analyzed, first with a comparison of land uses among the maps of the three time periods, and, second, with an overlay analysis of the three maps at two intervals between maps 1 and 2, and maps 1 and 3.

Results

Mapping history

The mapping history of Yakushima island shows that the first topographic maps of Yakushima were surveyed in 1921 at 1/50,000 scale. The mapping history for one of the 1/50,000 maps is shown in Table 1. These maps were probably the very first time Yakushima was mapped completely by modern cartographic methods. Examination of the maps issued in 1946, 1954, and 1962 found that cartographers had made almost no changes whatsoever compared to the 1921 map. The first map series drawn in UTM in 1972-73 was the first to be completely redrawn, and the map from this year at 1/50,000 scale is used for the present analysis. Subsequently, the GSI updated the maps periodically at both 1/25,000 and 1/50,000 scales. The 1/25,000 map issued 1992 is used as the third map in the present analysis.

Table 1. Mapping history of one of the four 1/50,000 topographic maps of Yakushima titled Northeast Yakushima.

Map number	History			Issue date
153-6- 1	1921	Taisho 10	Surveyed	30 Aug 1921
153-6- 2	1921	Taisho 10	Surveyed	30 Nov 1946
153-6- 3		Missing		
153-6- 4	1953	Showa 28	Updated	30 Apr 1962
153-6- 5	1972	Showa 47	Edited	28 Dec 1973
153-6- 6	1953	Showa 28	Updated	30 Nov 1954
153-6- 7	1978	Showa 53	Modified	30 Nov 1978
153-6- 8	1989	Heisei 1	Additions	1 Sep 1990
153-6- 9AB	1993	Heisei 5	Modified	1 Jul 1994

Land use depicted on Japanese topographic maps

An important characteristic of the GSI topographic maps is that some land uses are demarcated with linear boundaries while others are free labels. The land uses with line boundaries in the maps of Yakushima are rice paddy, dry field, orchard, villages, and some urban areas. These land uses entered the GIS as polygons. The free labels depict broad leaf forest, coniferous forest, wasteland, and some free-standing buildings. These labels are scattered throughout the maps outside of the land uses depicted as polygons. The labels can be used in GIS analysis as points, or they can be used to generate polygons estimating the areas of the two forest types and wasteland. Polygon boundaries were generated from Thiessen polygons based on label points of forests and wasteland as described above. No free-standing buildings were depicted in the 1921 map, and the free-standing buildings in the later maps were ignored for this analysis. Since the labels for forests or wasteland were often clustered, the Thiessen-based polygons depict zones of forest or wasteland. The under-500 m area of Yakushima comprises 45% of the island. All rice paddies, fields, orchards and villages existed in the under-500 m area in all three maps. Figures 1 and 2 show land use within the under-500 m area as depicted in the three topographic maps. The 1921 map depicts the same villages that exist today, although the village settlements appear to be confined to smaller areas. Only a single road is drawn into the 1921 map linking the villages. The map shows large fields and rice paddies around some of the larger villages, and small fields scattered along the coast. Otherwise, the 1921 map is devoid of detail compared to later maps. Wasteland labels, however, are found in many parts of the under-500 m area of the island in the 1921 map. The polygons generated from the wasteland labels cover large areas. Orchards did not exist at all in 1921 map. In the maps of 1972-73 and 1992, orchards are a prominent land use. Many orchards are located along the foothills of the mountains (Figure 2). The highest orchard reach an altitude of about 285 m.

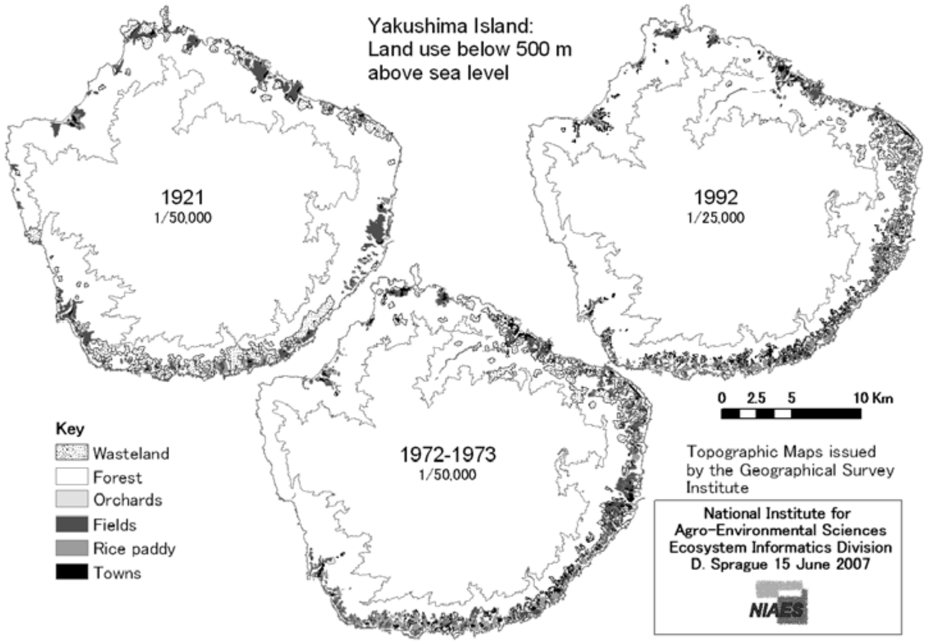

Figure 1. Land use below 500 m above sea level on Yakushima Island reconstructed from topographic maps of three periods.

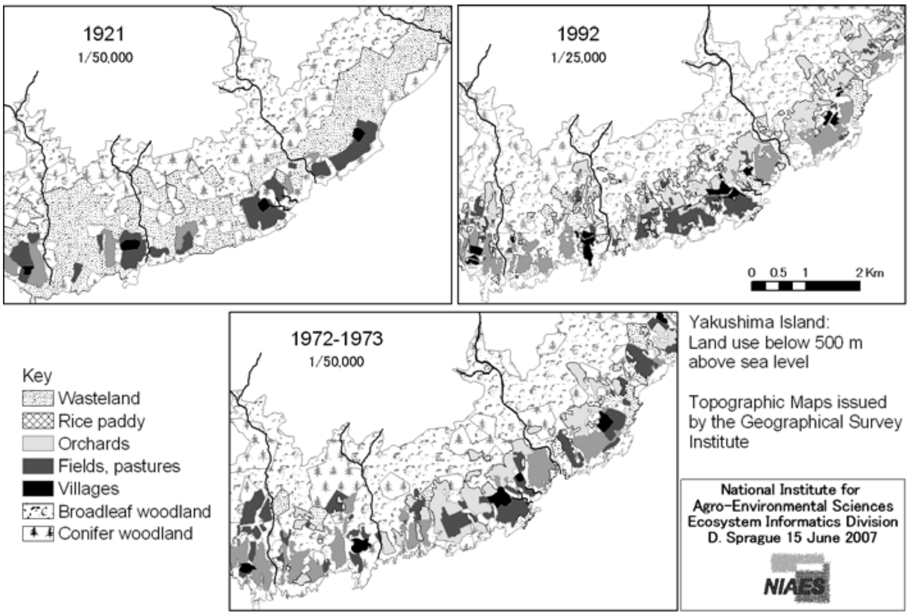

Figure 2. Detail of land use below 500 m above sea level on the southwest side of Yakushima Island reconstructed from topographic maps of three periods.

The proportions of land use depicted in the maps changed among the three periods (Figure 3). Wasteland area was highest in the 1921 map and subsequently declined. Nevertheless, wasteland continued to be the largest land use type, excluding forests, in the area under-500 m in all three periods. Rice paddy and field areas were highest in the 1972-73 map and declined in the 1992 map. Orchards, which did not exist in the 1921 map, appeared from the 1972-73 map, and increased in area in the 1992 map. Villages and urban areas increased steadily from the earliest to the latest map, although urban area is slightly underestimated in the later periods since the free-standing buildings are ignored in this analysis.

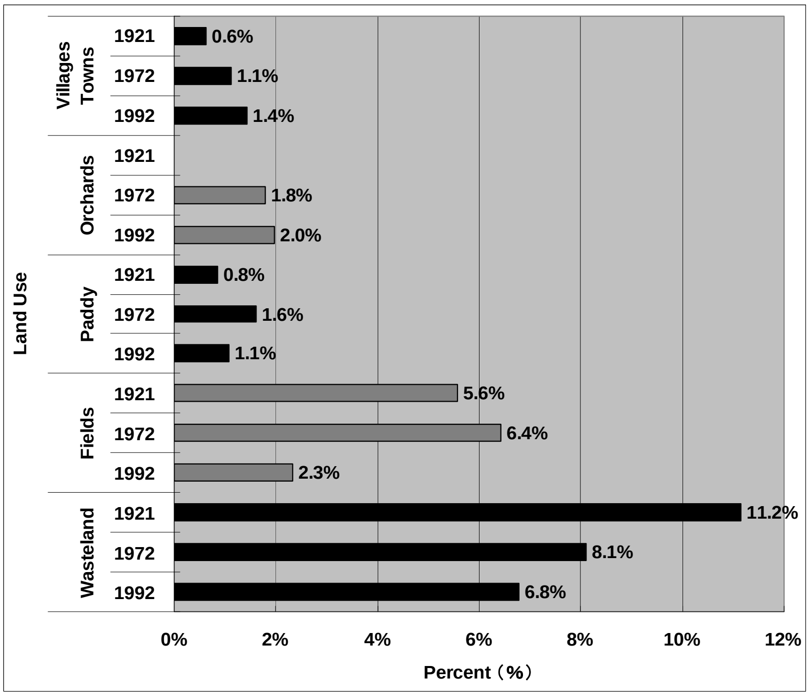

Figure 3. Land use change below 500 m above sea level in Yakushima Island as reconstructed from topographic maps of three periods

Altitude distribution of wasteland

The 1921 map contained 430 wasteland label points. The wasteland point farthest inland was located 2,015 m from the coast. The altitude distribution of the wasteland points showed that a large proportion were distributed at fairly low altitudes, with 90% located under about 200 m. However, the highest wasteland point was located at 459.6 m above sea level (Figure 4).

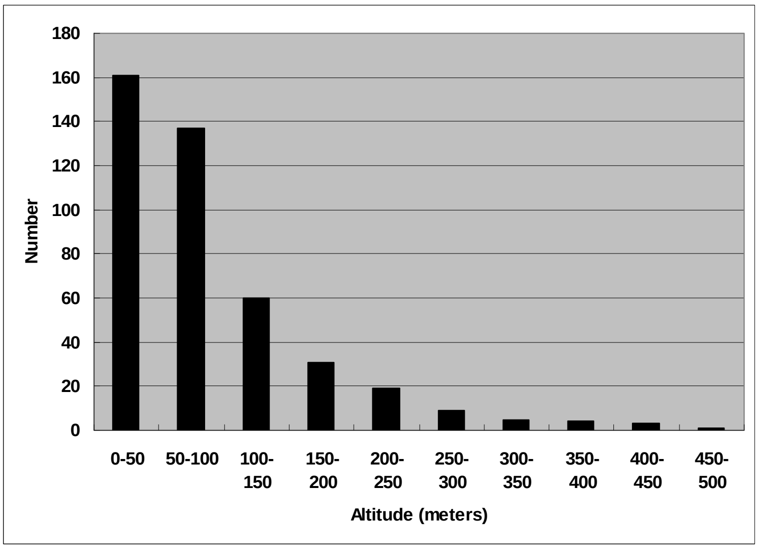

Figure 4. Altitudinal distribution of wasteland labels on 1921 topographic map of Yakushima Island.

Source land uses of orchards

The central research question of this project is whether modern land uses, especially orchards, can be considered an expansion of intensive human activity over a larger area compared to historical land uses. The expansion hypothesis would be supported if land uses in later maps tended to be located in what had been forests in earlier maps. A land use change hypothesis is supported if some type of land use besides forestry had been taking place in a particular location in both earlier and later maps.

The maps reveal that the orchards were cleared in the same area and altitude generally as wastelands (Figures 1 and 2). The overlay analysis provides a more precise, quantitative measure of the overlap between orchards and past wastelands (Table 2). Wasteland in the 1921 map was the source land use for 42% of orchards in the 1972-73 map, and 36.8% in the 1992 map. Other past land uses in 1921 made way for orchards in later periods. In the 1972-73 map, 6.8% of orchards existed in former fields or rice paddy, and in the 1992 map, 19.2% of the orchards existed in former fields or rice paddy. It is important to point out, however, that about 50% of orchards in 1972, and 43% of orchards in 1992, were located in areas depicted as some type of forest in 1921.

Table 2. Source land use in the 1921 topographic map of orchards in the maps of 1972-73 and 1992 after overlay analysis.

	Land use in:	
Source land use:	1972	1992
1921	Orchard	Orchard
1 Wasteland	42.8%	36.8%
2 Broadleaf	21.3%	14.4%
3 Conifer	29.1%	28.5%
4 Fields	6.1%	15.7%
5 Wet paddy	0.0%	0.0%
6 Dry paddy	0.7%	3.5%
7 Villages	0.0%	1.1%
Total	100.0%	100.0%

Discussion

No geographical study on Yakushima, or in any other part of Japan, would be complete without an examination of topographic maps, and they provide the initial data for further detailed research. Wasteland accounted for a large proportion of land in the under-500 m area of the island, implying that some sort of human activity had prevented these areas from succeeding naturally to forest. Although fields and rice paddies were confined to a smaller area in the 1921 map compared to later maps, the large wastelands suggest that human subsistence activity had extended more broadly throughout the lower altitude regions of Yakushima compared to the extent of permanent fields or villages. Wasteland could extend quite far uphill, up to nearly 500 m above sea level.

Wasteland depicted on topographic maps may have been produced by a variety of human activities. Wasteland may have been grasslands that farmers maintained by repeated cutting or firing. Under traditional Japanese agriculture, farmers obtained natural resources locally to support their livelihoods, such as green fertilizer, fodder, firewood, or charcoal. On Yakushima, the town histories refer to the practice of swidden agriculture around villages, the importance of charcoal production, and some pasturing of horses (Yaku Township, 1994).

Orchard expansion can give a present-day observer the impression that human activity in general had been expanding. Orchards are a modern form of agriculture. The first orange plants were introduced to the island in 1924 (Yaku Township, 1994). Orchards are absent from the 1921 map but appear from the 1972-73 map. Orchard area has expanded, and often expanded upwards to become the fields located at the highest altitudes among all forms of agriculture. Orchard expansion in some places was accompanied by the expansion of road networks uphill. Mature forests surround many orchards today (Sprague, 2007).

However, the GIS overlay analysis found that a large proportion of the orchards had been built in former wasteland or former fields. The 1921 topographic map shows large areas of wasteland. The altitudinal distribution of orchards generally matches that of wasteland. The highest orchards in the 1992 map reached 285 m. Although 90% of the wasteland labels were located less than 200 m, wasteland labels were located as high as 460 m above sea level. These data lend support to the hypothesis that the orchards were expanded into altitudes that had historically been under the influence of the subsistence activities of the residents of Yakushima.

Some orchards were built in areas that had been labeled as forest in the 1921 map. The topographic maps do not provide sufficient details about forests to judge whether these forests were primary or secondary forests. However, it is reasonable to assume that many of these forests were secondary forests or tree plantations. These forests were within the same altitudinal zone as orchards and wasteland, and the residents of Yakushima were known to have harvested forest resources, such as charcoal or firewood. In addition, natural conifer at low altitudes is unusual in Yakushima, although this island is famous for natural, old-growth cedar forests at higher altitudes (Miyawaki, 1986). The low altitude conifers may have been pines, which were very common in rural Japan under traditional agriculture. Thus, the orchard expansion in forest perhaps can be considered a type of land use change rather than the expansion of human influence into previously pristine natural environments.

References

Japan International Map Association (1990) Handbook of Topographic Map Cartography. Japan Map Center, Tokyo. (In Japanese)

Miyawaki, T (1986). Vegetation of Japan: Vol. 1 Yakushima. Shibundo, Tokyo. (In Japanese)

Sprague DS (2007) Identifying wildlife crop damage area on Yakushima Island. In: Akiyama T, Ishitsuka N, Ogawa S, Okamoto K, Saito G, Uchida S (eds) Handbook of Agricultural Remote Sensing. Japan Agricultural Systems Society, pp. II80-83. (In Japanese)

Yaku Township (1994) Yaku Township Local History Volume 1. Yaku Township History Editorial Committee, Yaku Township. (In Japanese)

Changes in Human Benefits and Values from Forest Services in Yakushima Island

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Introduction

Since the pre-modern period, the forest area in Yakushima Island, Japan, has experienced extensive human influence. Some of this influence has led to crucial changes in the forest environment in this area, and some reflects conflicts among stakeholders of the forest. These impacts fundamentally emerged because the range of forest services offered various types of benefits and values to the people. This paper aims to analyze the details and composition of and the changes in human benefits and values from the forest services in Yakushima Island in order to clarify how the relationship between the people and the forest has changed from the seventeenth century.

Basic Framework: Forest Services, Benefits, and Values

Table 1 classifies and details the existing forest services, benefits, and values provided by the forest in Yakushima Island. According to the results of analyses in field studies and the field of forest science (Clawson 1975, Hageneder 2005), I assume four basic forest services available to humans: provision of space for alternative uses, provision of materials for products, protection of the natural environment, and favorable effects on people’s spiritual aspects. Further, I assume nine specific services that can clearly shed light on the human conflicts pertaining to this forest. Then, I also assume specific human benefits, based on nine fundamental human values regarding nature classified by S. Kellert (Kellert 1996, 1997) and my own research experience in the field.

This classification of and relationship among the forest services and their human benefits and values form the basic framework of the analysis presented in this paper, using which it can be clarified how humans, based on the benefits and values, formed the social structure surrounding the forest in each period and how they worked on and changed the forest environment in the island.

Six figures (Figure1-6) seen in the next chapter actually show overall compositions of these human values and benefits from the forest services in specific periods from the seventeenth century. In these figures, identified recipients who have same combinations of the benefits are represented as ellipses. Colors of the ellipses show attributes of the recipients. Black means the recipients living in the outside of the island, gray includes both living in the inside and outside, and white means almost all of them are living in the island. The benefits from the forest services recognized and enjoyed by them are represented as rectangles. Colors of the rectangles correspond to the colors that identify the nine specific forest services in the Table1. For example, a dark red rectangle of “material wealth” corresponds to the “material wealth” benefits from the forest service of “provision of commercial products.”

Historical Change in the Composition of Human Benefits and Values from Forests

The Pre-modern Period （Seventeenth to the Early Nineteenth Century）

＜Figure 1＞

From the beginning of the Edo Period, the pre-modern period in Japan, feudal rulers such as Tokugawa Shogunate and the Satsuma Domain focused on the forest service of provision of materials for commercial products in the island. Based on the benefit of “material wealth,” they expected to obtain large-diameter timbers for large constructions from the dense forest in the island. Satsuma Domain also regarded the forest, especially the ancient cedar trees (*Cryptomeria japonica*) known as *yakusugi* and aged over 1,000 years old, as a means of strengthening their finances. As a feudal obligation, they decided to charge sliced *yakusugi* timber known as *hiragi* toward the villagers. *Hiragi* and other forest products from the island were mainly sold in the western parts of Japan by domain-designated merchants from Kagoshima (the capital of the Satsuma Domain and Kagoshima Prefecture today) or Osaka. It can be concluded that this period is characterized by the process in which feudal organizations gradually conferred utilitarian values to the forest in the island; these organizations shared the benefit of material wealth from the forest service of provision of commercial products.

On the other hand, these feudal rulers also partly implemented afforestation in order to keep away wind and sand in coastal areas. This implies that they attempted to secure the benefits of local villagers on the forest service of “protecting lands, water, and daily life” in this period. Moreover, the fact that they designated hunting areas for the loads of the domain in the forest shows that the rulers also recognized the benefit of “spiritual elevation” on the forest service of offering human recreation at that time.

The villagers in the island mainly enjoyed the benefits of the forest service whereby they were provided space for living and farming, and provided products for daily use by the forest. They also relied on and felt an affinity toward the dense forest and old trees covering the island. The spiritual benefits enjoyed by the villagers are confirmed by the fact that one of the public events involved visiting mountains to pay homage to the god and spirit residing in the forests and mountains. Of course, they simultaneously enjoyed the benefit of accumulating commercial goods and material wealth while they engaged in *hiragi* production and illegal timber trading.

In general, the recipients of the benefits and values were limited under the Shogunate system under which access to the outside world was restricted in this period. Therefore, the composition of the benefits and values from the forest services in Yakushima Island was relatively simple and did not reflect serious conflicts among the recipients, or drastic changes in the forest environment.

From the Meiji Restoration to the Administrative Lawsuit （1868–1920）

＜Figure 2＞

In the Meiji period when Japan initiated industrialization and modern nation-state building, the composition of the benefits and values from the forest became increasingly complex.

Soon after the Meiji Restoration, the new administration decided to abolish class distinctions in the old regime, including the warrior class, and promote industrial development in order to increase state power.

Because of these policies, the former warrior class of the Satsuma Domain had to find a new means of earning a living, and the local government supported their immigration to Yakushima Island and allowed them to engage in forest production and exploitation in order to make them contribute to regional development. However, when both the number of immigrants and the amount of timber harvested by them increased in the island, the local villagers felt that the benefits they were receiving from forest services, such as obtaining products for daily use or accumulating commercial goods, were under threat. As a result, conflicts concerning forest usage occurred between the villagers and immigrants on the forest border.

The other factor that changed the composition of benefits and values in this period was the nationalization of the forest under the prevalence of the modern property rights system. After several investigations conducted in the late nineteenth century, more than 90% of the forest area in the island was designated as state owned. This nationalization reflected the commercial benefit of material wealth of the Meiji administration. The connection between the Ministry of Agricultural and Commercial Affairs and local forestry offices represented this stance, and the administration intended to exclusively maintain and produce high-quality timber in order to satisfy the demand for nation-state building.

Facing the tightening of bans and regulations in the nationalized forest area, the villagers again felt that their benefits and values were being restricted. They not only repeatedly sent petitions to the local government and forestry offices in order to regain their right to the forest surrounding their villages but also engaged in illegal lumbering to express passive resistance.

This latent conflict between the administration and villagers surfaced in the administrative lawsuit from 1904 to 1920 in which villagers claimed to regain the state-owned forest. However, during these 16 years of the trial, the claim of the complainant was not based on the benefits and values of the villagers alone. Large capitalist organizations, such as newly formed conglomerates producing timbers, actively supported villagers as a proxy for the plaintiff. In return for the support, the villagers signed a contract stating that if they won the lawsuit, these organizations could get more than around half of the commercial revenue from the disputed forest. It was clear that these external capitalist organizations wanted to enjoy the commercial benefit of material wealth from the forest in this island and therefore supported the villagers during the trial. At the last stage, different strategies toward the lawsuit and paybacks offered by multiple external organization led to internal rifts among the villagers.

This process shows that in the context of industrialization, the diffusion of modern market economy, and property rights, the recipients who focused on the benefits and values of the forest in Yakushima Island were divided. Based mainly on the commercial benefit of material wealth, the human relationship concerning the forest became more complex with many conflicts. On June 7, 1920, the administrative lawsuit concluded with the dismissal of the villagers' claim. This result legitimatized continued forest management by the state for most of the forest area in the island from then on.

The Start of Full-scale Operation by State Entities during the War Period （1921–1945）

＜Figure 3＞

The harsh result of the lawsuit put the villagers in very difficult situation since they had been deprived of means by which to accumulate goods from the forest and had accumulated substantial debt during the 16 years of the lawsuit. In 1921, the local office of the national forestry administration, in response to this situation, decided to allocate 7,000 ha of the forest area in the coastal mountains as “commitment forest” (*itaku-lin*). In this zone, the villagers were allowed to purchase forest products for commercial trade and daily use. At the beginning of the war period in the 1930s, this commitment forest gradually became the area in which materials for military demands were produced, such as charcoal for fuel, camphor for gunpowder, and birdlime for medical products. Through the regional and local government and the national forestry administration, the central government mobilized the villagers to large-scale operation to produce these goods in this zone. In particular, the charcoal formed in dense broadleaf forests in this zone was highly valued in this period.

In the other forest areas of the island, full-scale operation conducted by the national forest administration started immediately after the lawsuit ended. This operation, based on purchasing the commercial products of the forest, involved the cutting and use of large-diameter timber, such as those from ancient cedars. The operation was partly restricted to the zone in which the administration had decided to preserve forest vegetation for water purification and land protection, which meant that at least the benefit from the forest service involving protection of the natural environment was publicly recognized.

Another restriction of the operation based on commercial benefits rose from the increase in the benefits characterized by the scientific and aesthetic values of the forest. In 1921, two areas comprising 4,413 ha of state-owned forests were designated as “forest preserved for scientific purposes” and were also designated as a national monument managed by the Ministry of Home Affairs. These designations reflected the growing calls for preservation from famous biologists, ecologists, and forest scientists who had visited the island forest for research. They insisted on the importance of the extremely beautiful physiognomy and biodiversity of the forest in terms of future development of sciences and human wisdom, and many government officials and foresters also supported this argument. Based on the framework of this paper, this claim can be regarded as a combination of the “knowledge expansion” benefit of the “preservation of biodiversity” forest service, and “spiritual elevation” benefit of the “beautiful and communal landscape” forest service, both of which are strongly characterized by scientific and aesthetic values. As a reflection of these benefits and values, the national forestry administration had to begin, at least to some extent, preserving a part of the forest in Yakushima Island around the same time as starting full-scale operation.

The Period of Economic Growth after the War（*1946–1960s*）

＜Figure 4＞

For more than 20 years after the Second World War, Japan experienced postwar reconstruction and economic growth, and the commercial benefit of material wealth based on utilitarian value was still a core factor for the characterization of the composition of the benefits and values from the forest in the island. However, changes in the stakeholders and produced materials concerning this benefit distinguished the composition in this period from those in the previous periods.

The first phenomenon that was observed after the war was an increase in the number of immigrants to the island, including those who came back from the front and former colonies, and these immigrants exploited the forests around the coastal areas to earn a living. This implied that at the end of the war, the benefits from the forest service of provision of space for alternative uses were highlighted again. Due to this movement, the area covered by the state-owned forest decreased around 660 ha in this period (Local Offices of National Forestry Administration, 1951).

In this period, a second movement arose in the former commitment forest that was renamed "shared-use forest" (*kyoyo-lin*). As the war ended and an energy revolution from biomass fuels to gas and oil occurred in local societies in Japan, the benefits for the government and villagers who produced materials for commercial and daily use from the commitment forest in the previous periods were suddenly eliminated. From 1945 to the 1950s, cooperatives that comprised villagers and led the production in the commitment forest in the war period were dissolved. Therefore, the stakeholders, especially the villagers, were forced to find new ways to enjoy the benefits offered by the zoned forests near residential areas.

An increase in the demand for timber and pulp during the Korean War and economic reconstruction yielded a solution to this situation. In 1963, encouraged by the government of Kagoshima Prefecture, major paper enterprises and local timber and paper companies jointly established the Yakushima Forest Development Cooperation. This cooperation and the companies involved signed contracts with the national forestry administration, and they hired residents and undertook the task of cutting broadleaf forests in this zone and producing pulp. The Public Corporation for Forest Development handled regeneration and management of the cleared area; this other new entity was run by the prefecture government, the town councils (two former villages grew into two towns at the end of the 1950s), and local communities (natural villages) that formed the cooperatives for the shared-use forest.

Reflecting this increase in the demand for timber, logging in other state-owned forest areas also increased in this period. The local office of the national forestry administration allowed immigration of many workers specialized in logging. They lived in the dense forest in the center of the island and engaged in logging of large-diameter timbers. Further, from the 1960s, some people living in the capital of Kagoshima Prefecture started the business of processing ancient cedars from the island for crafting products. They were distributed the cedars for crafts by the local office and enjoyed commercial benefits such as material wealth, knowledge expansion, and worker identity.

Based on the above movements, this period can be characterized by the replacement of the old style of forest usage by the new stakeholders who also enjoyed the commercial benefits of the forest, and gave new valuations. Reflecting this replacement, the people and organizations associated with the forest clearly changed. However, the recipients of the benefits and values from outside the island, such as the governments and companies, remained the key players in the drastic changes in the forest environment.

In this period, one of the human actions in the forest that clearly deviated from the commercial benefits was observed, as well as the previous period, in the benefits and actions supported by the scientific and aesthetic values on the forest. As a reflection of the benefits they received, i.e., expanding scientific knowledge on biodiversity and the spiritual elevation afforded by the beautiful forest landscapes in the island, scientists and conservationists lobbied for the Ministry of the Health and Welfare of the central government to designate the core forest area in the island as a national park. In March 1964, some forests in the central part of the island were designated as conservation areas of a national park. This designation also enhanced the potential human benefits from the forest services in the island, whereby people could enjoy the beautiful forest landscape and recreation and receive healthcare. Many tourists and trekkers subsequently visited the island to enjoy these benefits.

Another action against the distribution of the commercial values of the forest was based on a sense of danger regarding the clearing of the forest for timber and pulp production. In the late stage of this period, this sense gradually transformed into a voice that demanded the cessation of reckless clearing. Besides the scientists and conservationists from outside the island, some of the local residents also played a major role in this movement, and this reflected their sentiments toward the ancient cedar trees or the local identity felt toward the communal forest. In the next period, these residents behaving as conservationists played the main roles in consecutive campaigns for protecting the forests against the national forestry administration and companies promoting the operation who desired commercial benefits. However, the benefits and values they received from the forest were related to their life on the island; therefore, latent hostility toward foreign entities such as tourists and environmentalists who actually supported the campaigns also gradually surfaced since the population and garbage in the forest increased because of the tourists in this period.

Increasing Conservation Campaigns and the Decline of Commercial Forestry （1972–1993）

＜Figure 5＞

In Yakushima Island, the period from the 1970s to the 1980s was characterized by two movements: forest conservation campaigns extending from the conservational action from the previous period and the downfall of commercial forestry in Japan due to a sharp increase in amount of timber imported under the global market economy.

In this period, people acting toward protecting the forest from clearing due to the associated commercial benefit had already formed one faction among the island residents. The leaders of this faction were “boomerang people” who had once lived and worked outside the island and then decided to return to their native villages. Their claim in the consecutive campaigns for forest conservation was based on the protection of three specific benefits from the forest: gaining security of life in the context of increasingly frequent landslides due to forest clearing, spiritual elevation, and shared awareness of the beautiful and communal forest landscape under the slogan of “protecting the beautiful forest in our home island.” The environment agency, biologists, ecologists, and environmental groups from outside the island, according to their own benefits and values, supported these campaigns. Their joint effort led to the designation of several protected forest areas, such as a Wilderness Area at Hanayama, and the expansion of special protection areas in the national park.

On the other side, the stakeholders of the forest interested in its commercial usage, such as the local office of the national forestry administration; timber and pulp companies; and residents engaged in forest production, including forestry workers and the managers of the processing business for crafting products, jointly tried to protect their commercial benefits from the forest in the beginning of the 1970s. At that time, the Kamiyaku and Yaku Town Councils became the battle stage for the two sides. However, global changes such as a decreasing demand for domestic wood production given the increase in the amount of timber imported and the switch-over in energy source and building materials from wood, and a worldwide increase in environmental awareness clearly supported the conservationists’ side. As a result, the councils authorized a series of resolutions that ordained a ban on cutting the ancient cedar trees or the forests in important areas, aiming to protect the land, precious species, and landscapes; this reflected the three main benefits from the forest that the resident conservationists regarded as local “common sense.” These resolutions contributed to spreading awareness of these benefits to all the residents.

In response to these campaigns and the decline in the commercial benefits from timber and pulp production, the national forestry administration gradually shifted their main purpose of forest management from materials production to land protection. Through this process, the focus of the conflict related to the commercial benefits of the forest changed from forest clearing to the production of old stumps of the ancient cedar trees for craft production. In this period, many people living outside the island operated the craft industry involving wood from the ancient cedars. From the 1980s onward, they continued to negotiate with the local office of the national forestry administration, conservationists, and craft industries within the island over the amount of old stumps available to them.

Overall, due to previous human actions on the forest and the global changes, a new type of human conflict concerning the forest surfaced for the first time on Yakushima Island. Both sides of the stakeholders concerning clearing the forest held clearly different benefits from the different categories of the forest services. This was not as previous conflicts only over the commercial benefits and services.

After the Designation of a World Natural Heritage （from 1993）

＜Figure 6＞

In the 1990s, the change in the benefits and values accelerated from that in the previous period. Forest operations based on commercial benefits were no longer sustainable. The benefits and values received by the villagers realigned according to this change. They seemed to internalize the benefits from the forest that the resident conservationists held in the past. Therefore, prominent conflicts that divided the residents cannot be identified in this period.

In December 1993, 10,263 ha of the forest area in Yakushima Island was designated as a World Natural Heritage based on a request by the Ministry of Environment and scientists who enjoyed the benefits and values regarding scientifically or ecologically precious biodiversity from the forest, and the tourism industry that expected to receive the benefit of material wealth through the development of ecotourism on the island. Due to this designation, Yakushima Island attracted worldwide attention, and the number of tourists increased dramatically. This led to the development of the tourism industry, which included not only large tourism enterprises from outside the island but also island residents who managed guesthouses, produced handicrafts as souvenirs, or worked as forest guides. Further, the number of people referred to as “new immigrants” also increased; these people came from outside the island and wished to live in the rich forest environment. Today, they account for around 10 percent of the population.

However, these people’s attention and social changes in the island due to the designation gradually highlighted a potential conflict between the foreigners and island residents with regard to differences in the benefits and values received. The new beneficiaries of the development of tourism in the 1990s, such as the tourism enterprises or the forest guides of the new immigrants, enjoyed the benefit of “material wealth” from the forest services of provision of “beautiful landscape” or “healthcare and recreation.” Further, the tourists and new immigrants enjoyed the benefits of “spiritual elevation” and “peace of mind” by visiting and living in the forest, sightseeing, or participating in recreational programs. However, the benefits and values enjoyed and internalized by the island residents in the previous periods differed from those of the tourists and new immigrants. Those residents’ benefits are, even equally from the forest service of giving favorable effects on human spirit, including the benefit of “shared awareness” of the communal forest landscape, “reliance” or “affinity” toward the forest and trees, “security of life” by protecting the forest, or accumulating knowledge and culture through contact with the diverse species in the forest, and all of these developed because they had lived for a long time in the villages on the island.

The abovementioned difference in the benefits and values from the forest led the island residents to feel that their benefits were ignored and interfered since the designation of a World Natural Heritage. Except for some recipients of the “new” benefits, several villagers were frustrated because in some cases, the recreational benefits were enjoyed entirely by the tourists or tourism enterprises and because the increased population hampered their original benefits due to changes in the shared forest because of an increase in the amount of garbage, deterioration around forest trails, and expansion of resort buildings.

The environmental administration, environmental groups, and scientists who had their own combinations of the benefits and values and supported the increase in the benefits for the residents with regard to forest protection in the previous period now appeared to be in a difficult position between the new recipients and residents.

Concluding Remarks

Based on the historical changes in the composition of the benefits and values from the forest services, the following concluding remarks can be derived.

First, it is concluded that the relationship between the people and the forest in Yakushima Island from the pre-modern period to recent times is very special in that almost all types of forest services, benefits, and values were recognized by various people and organizations. In this regard, the human conflicts and relationships concerning the forest created many variations within each period. The type of conflicts mainly over the commercial benefits in the pre-modern to war periods no longer existed in the 1970s when the conservationist side expressed its desire to protect the forest with their benefits and values. Further, this side was also divided, especially since the forest was designated a World Natural Heritage in 1993, and thus, it enjoyed the different benefits and values from the forest services.

Second, it can be confirmed that during the change in the relationship, the benefits and values received by the entities from outside the island, such as the modern state administration, large capitalist firms and companies from the Meiji period to the 1970s, scientists, and tourists, had strong impacts on the relationship while reflecting the global changes in each period, and these entities actually spearheaded the actual changes in the forest environment. The considerable attention and impact of these foreigners often created situations in which the residents of the island felt that their benefits and values from the forest were under threat.

However, the third conclusion is that these island born residents who accepted external impacts were not stable stakeholders who received only one combination of benefits and values. Besides the members changing over time because of the various types of immigrants, they also changed their standpoints and internal structure, while they accepted the impacts and revised the combinations of benefits and values from the forest. The shift to commercial benefits from the Meiji period and the internalization of the benefits for forest protection through the conservation campaigns in the 1970s are good examples of this.

An understanding of this complex and dynamic change in the composition of human benefits and values from forest services can clarify the human relationships and actions surrounding the forest in Yakushima Island and will offer good examples and implications in an effort to consider a sustainable relationship between the people and forests worldwide.

References

English

Clawson, M. (1975), *Forests for Whom and for What?*, The Johns Hopkins university Press.
Hageneder, F. (2005), *The Meaning of Trees: Botany, History, Healing, Lore*, Chronicle Books.
Kellert, Stephen R. (1996), *The Value of Life*, Island Press.
Kellert, Stephen R. (1997), *Kinship to Mastery: Biophilia in Human Evolution and Development,* Island Press.

Japanese

Minaminihon Shinbun (Newspaper), 1898-2006
The Asahi Shinbun (Newspaper),1898-2006
Editing Committee of Local History of Kamiyaku Town (1984), *Local History of Kamiyaku Town*.
Editing Committee of Local History of Yaku Town (1993), *Local History of Yaku Town*, Vol. 1, The School Board of Yaku Town.
Editing Committee of Local History of Yaku Town (1993), *Local History of Yaku Town*, Vol. 2, The School Board of Yaku Town.
Editing Committee of Local History of Yaku Town (2003), *Local History of Yaku Town*, Vol. 3, The School Board of Yaku Town.
Local Offices of National Forestry Administration, (1923, 1941, 1951, 1967, 1972, 1982, 1987, 1988, 1993, 1996, 1999, 2001), *National Forest Management Plan*.

Table1: Forest Services and Human Benefits and Values

Forest Services, Benefits, and Values			
Forest Services		Human Benefits	
Basic Services	Specific Services	Benefits	Merits of Benefits
Provision of Space for Alternative Uses	Provision of Space for Alternative Uses	Having Spaces for Life	People can exploit and divert forests in order to have spaces for building houses, clearing farmlands, or constructing factories.
		Having Material Wealth	From the diversions, people become able to accumulate goods through having products and selling it in the market. This is a typical way for people to accumulate goods and have material wealth in the modern world.
		Having Feeling of Accomplishment	Through the diversions of forests, people can have feeling of accomplishment and satisfaction, since they could change natural environment as they liked.
Provision of Materials for Products	Provision of Commercial Products	Having Material Wealth	Through the production and market trade of forest products, people can accumulate goods evaluated by the market.
		Expanding Knowledge	Through the commercial production, people can develop their knowledge about economic efficiency of using forest materials and species. This expantion of knowledge will not only help accumulating goods, but also bring intellectual satisfaction of some people.
		Having Worker Identity through Productions	Through the production and process of specific forest products, people can form identity as the workers and proud themselves on it. This feeling tends to be synonymous with their meaning of life.
	Provision of Products for Daily Use	Having Products for Daily Use	Through the securement of fuel, lumber, or food by hunting-gathering in forest, people can maintain and enjoy their affluent daily life.
		Expanding Knowledge	Through the process of the production, people can develop their knowledge about the reasonability of using forest materials and species. This expantion of knowledge will not only help having products, but also bring intellectual satisfaction of the people.
Protection of the Natural Environment	Preservation of Bio-Diversity	Having Material Wealth	In addition to "material wealth" in the other categories, this forest service can facilitate the enjoyment of this benefit in its own way. The best example of this is to increase agricultural or forest production by regulating ecosystem process in forest.
		Expanding Cultural Knowledge	Through the relationship with diverse species and ecosystems in forest, people can get local knowledge about their use, develop communication capability by featuring them, and increase ability for self-protection.
		Expanding Scientific Knowledge	To understand the mechanism, functions, or characteristics of diverse forest species and ecosystems, correlated with the whole mechanism of the earth and life, satisfies people's intellectual curiosity, and develops people's rational, scientific way of thinking.
	Protection of Lands, Water, and Daily Life	Gaining Security of Life	The functions of forest, such as water purification, protection of soil runoff and disruption, air purification, protection of wind, sand or tide, and mitigation of local crimate change prevent natural disasters. And people can reduce threats to their life.
		Indirectly Having Material Wealth	Through preserving and securing water, and protecting lands and soils, this forest service can support various types of human productive activities in which people purchase goods accumulation.
		Expanding Knowledge	To understand those functions can develop people's knowledge about the importance of forest on the secrity of their life or goods accumulation. This expantion of knowledge will help enjoying those benefits, and bring intellectual satisfaction of the people.
	Absorbance of Carbon Dioxide	Gaining Security of Life	Through prevention of the global warming, people can reduce potential risks from it, and gain the security of their life.
		Expanding Scientific Knowledge	According to the development of scientific knowledge about the mechanism and effects of forest as a carbon sink, people can get intellectual satisfaction.
Giving Favorable Effects on Human Spirit	Provision of Beautiful or Communal Landscape	Having Spiritual Elevation	Beautiful forest landscapes stimulate and satisfy human aesthetic sense, creative ability, or the spirit of self-sufficiency.
		Having Material Wealth	People can accumulate goods evaluated by the market through engaging in service-sector jobs based on beautiful, communal forest landscapes, such as tourist business, or fine arts dealers.
		Having Shared Awareness from Communal Landscape	To share communal forest landscape, people can form some sort of local identity or sense of unity. This supports to keep up someone's mental stability.
	Provision of Human Health Care and Recreation	Having Peace of Mind	Forest can creat the space and mood that reduce people's stress, depressive feeling, or tiredness, and make them relaxed.
		Having Spiritual Elevation	Mountain climbing, fishing, hunting, hiking in forest environment can stimulate and satisfy people's spirit of inquiry, adventure, and curiosity.
		Having Material Wealth	People can accumulate goods evaluated by the market through engaging in service-sector jobs on the recreations in forest, such as tourist business, forest guides, and instructors.
	Cultivation of Human Spiritual Cultures	Having Feelings of Reliance	People living in forests usually respect and have faith in dense forests or large, ancient trees surrounding them. This feeling becomes their cultural backborn, and increase their comfort in daily life.
		Having Feelings of Affinity	Wildlife, including forest species, can give people an avenue for developing the emotional capacities for attachment, bonding, intimacy, and companionship. This sense of affiliation reduces isolation or loneliness of them.

		Human Actions on Forest				Valuations
Human Values	Recipients	Human Actions on Forest		Characteristics of Human Actions on Forest		Economic Valuation
Values on Nature	Main Recipients of Benefits and Values	Human Actions on Forest	Objects of Human Actions in Forest	Imagined Term of Enjoyment of Benefits	Main Impacts on Forest Environment	
(S. Kellert)						
Utilitarian, Dominionistic, Negativistic	Residents, Farmers, Industrial Enterprises, Governments	Clearing, Diversion	Zone, Whole Area	Short Term	Decrease	Probable
Utilitarian	Farmers, Industrial Enterprises, Governments	Clearing, Diversion	Zone	Short Term	Decrease	Done
Dominionistic, Negativistic, Aesthetic	Settlers, Farmers, Scientists, Industrial Enterprises, Governments	Clearing, Diversion	Zone	Short or Middle Term	Decrease	Questionable
Utilitarian	Forest Farmers, Enterprises and Workers, Intermediate Agents, Consumers	Cutting, Regeneration, Plantation	Species, Zone	Short or Middle Term	Decrease, Constancy, Simplification	Done
Scientific, Utilitarian, Dominionistic, Aesthetic	Forest Scientists, Forestry Engineers, Forest Farmers, Enterprises and Workers	Cutting, Regeneration, Plantation	Species, Zone	Short or Middle Term	Decrease, Constancy, Simplification	Questionable
Utilitarian, Moralistic, Aesthetic, Dominionistic	Forestry Engineers, Forestry Enterprises and Workers, Processors	Cutting, Regeneration, Plantation	Species, Zone	Short or Middle Term	Decrease, Constancy, Simplification	Questionable
Utilitarian	Gatherers, Consumers	Cutting, Gathering, Regeneration	Species, Zone	Middle or Long Term	Constancy, Decrease, Second-Growth Forest	Probable
Scientific, Moralistic, Naturalistic, Utilitarian, Dominionistic, Aesthetic	Gatherers, Forest Scientists, Sociologists, Anthropologists	Cutting, Gathering, Regeneration	Species, Zone	Middle or Long Term	Constancy, Decrease, Second-Growth Forest	Questionable
Utilitarian, Moralistic(?)	Producers, Consumers, Engineers, Governments	Preservation, Afforestation, Gathering	Species, Zone	Long Term	Constancy, Increase, Diversification	Probable
Symbolic, Scientific, Naturalistic, Negativistic, Utilitarian	People in Local Societies, Producers, Engineers, Forklorists, Anthropologists	Preservation, Afforestation, Gathering	Species, Zone, Whole Area	Long Term	Constancy, Increase, Diversification	Questionable
Scientific, Aesthetic, Naturalistic, Dominionistic, Moralistic	Biologists, Ecologists, Earth Scientists	Preservation, Afforestation, Gathering	Genes, Species, Zone, Whole Area, Global Environment	Long Term	Constancy, Increase, Diversification	Questionable
Negativistic, Dominionistic, Moralistic, Utilitarian, Aesthetic	Residents, Governments	Preservation, Afforestation	Zone	Long Term	Constancy, Increase	Probable
Utilitarian	Farmers, Enterprises	Preservation, Afforestation	Zone	Long Term	Constancy, Increase	Probable
Scientific, Naturalistic, Moralistic, Utilitarian	Forest Scientists, Agriculturalists, Engineers, Farmers	Preservation, Afforestation	Zone	Long Term	Constancy, Increase	Questionable
Utilitarian, Moralistic	Everyone, Residents on Coast Areas, Governments, Environmental NGOs	Afforestation, Preservation	Whole Area, Global Environment	Long Term	Increase, Constancy	Questionable
Scientific, Naturalistic, Moralistic, Utilitarian, Negativistic	Scientists	Afforestation, Preservation	Whole Area, Global Environment	Long Term	Increase, Constancy	Questionable
Aesthetic, Naturalistic, Dominionistic	Everyone, Tourists, People in Local Societies	Preservation, Visting, Afforestation	Zone, Whole Area	Short, Middle, or Long Term	Constancy, Increase	Questionable
Utilitarian	Tourist Enterprises, Governments	Preservation, Visiting, Afforestation	Zone, Whole Area	Short, Middle, or Long Term	Constancy, Increase	Done
Moralistic, Aesthetic, Utilitarian	People in Local Societies, Governments	Preservation, Afforestation	Zone, Whole Area	Middle or Long Term	Constancy, Increase	Questionable
Naturalistic, Symbolic	Everyone, Tourists	Visiting, Preservation, Afforestation	Zone	Short, Middle, or Long Term	Constancy, Increase, Degradation	Questionable
Dominionistic, Naturalistic, Aesthetic, Negativistic	Nature Lovers, Outdoorsmen, Tourists	Visiting, Preservation, Afforestation	Zone	Short, Middle, or Long Term	Constancy, Increase, Degradation	Questionable
Utilitarian	Tourist Enterprises, Nature Guides, Instructors of Forest Recreations	Visiting, Preservation, Afforestation	Zone	Short, Middle, or Long Term	Constancy, Increase, Degradation	Done
Moralistic, Negativistic, Aesthetic, Naturalistic, Scientific, Utilitarian	Believers in Animism or Buddism…, Religious Leaders, Governments	Preservation	Species, Zone, Whole Area	Long Term	Constancy	Questionable
Humanistic, Aesthetic, Dominionistic, Naturalistic	People in Local Societies, Benefactors of Forestry, Nature Lovers	Preservation	Species, Zone, Whole Area	Long Term	Constancy	Questionable

Figure 1: The Pre-modern Period (17th to the early 19th Century)

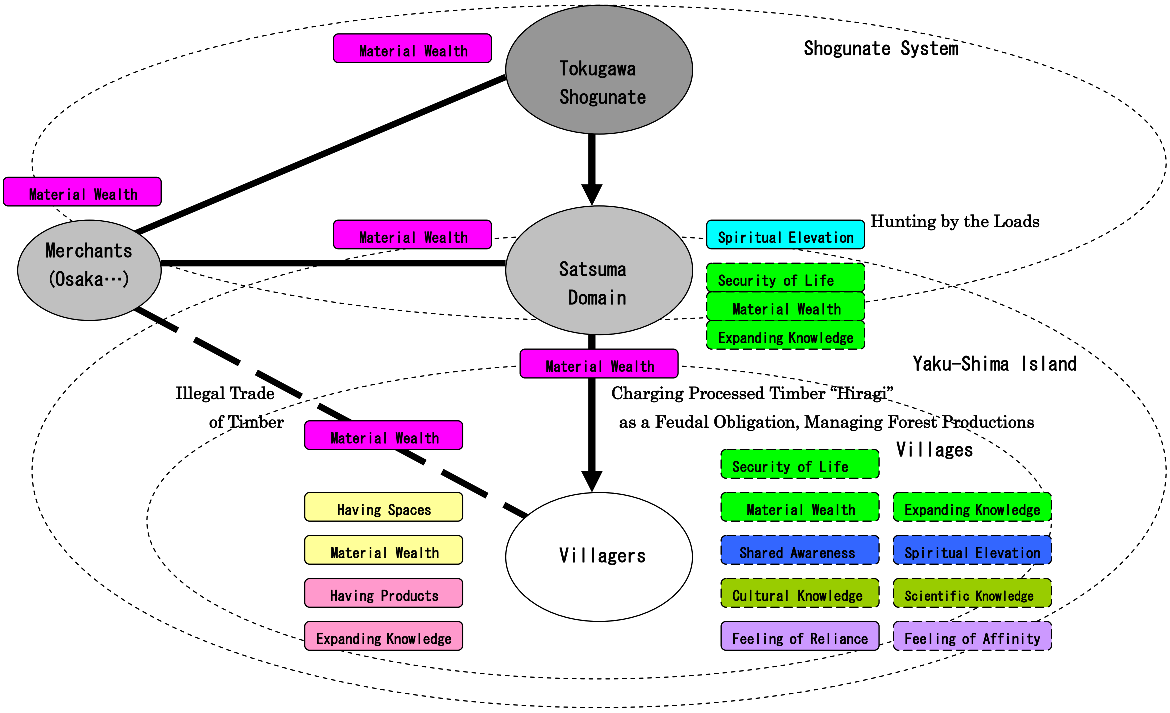


Figure 2: From the Meiji Restoration to the Administrative Lawsuit (1868 to 1920)

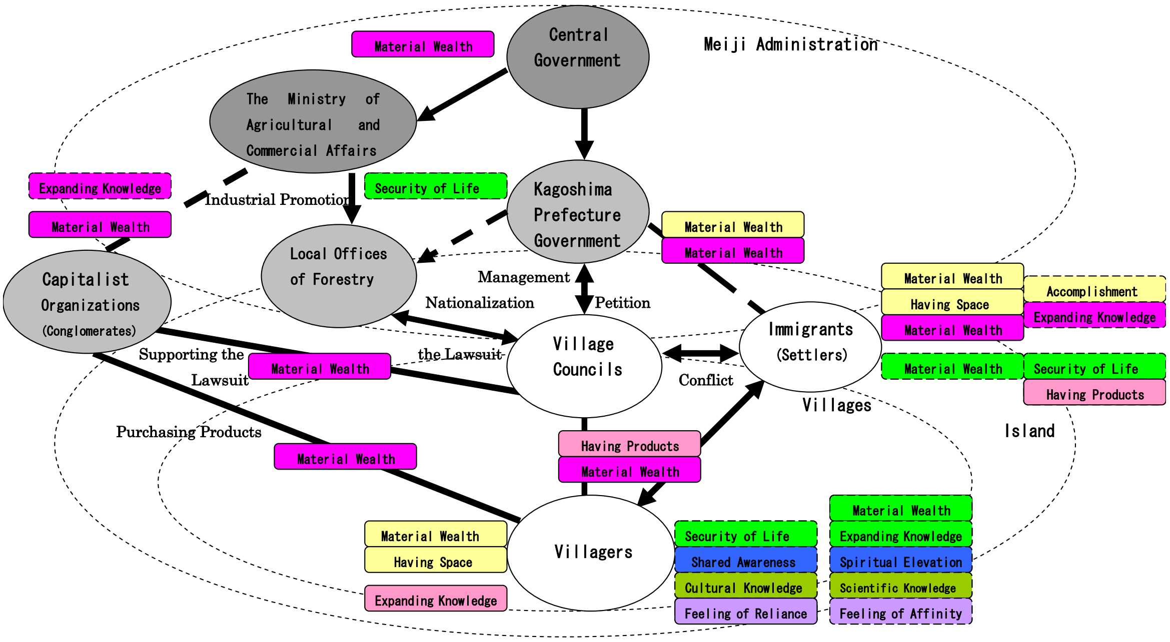


Figure 3: Under Full-Scale Operation during the War Period (1921 to 1945)

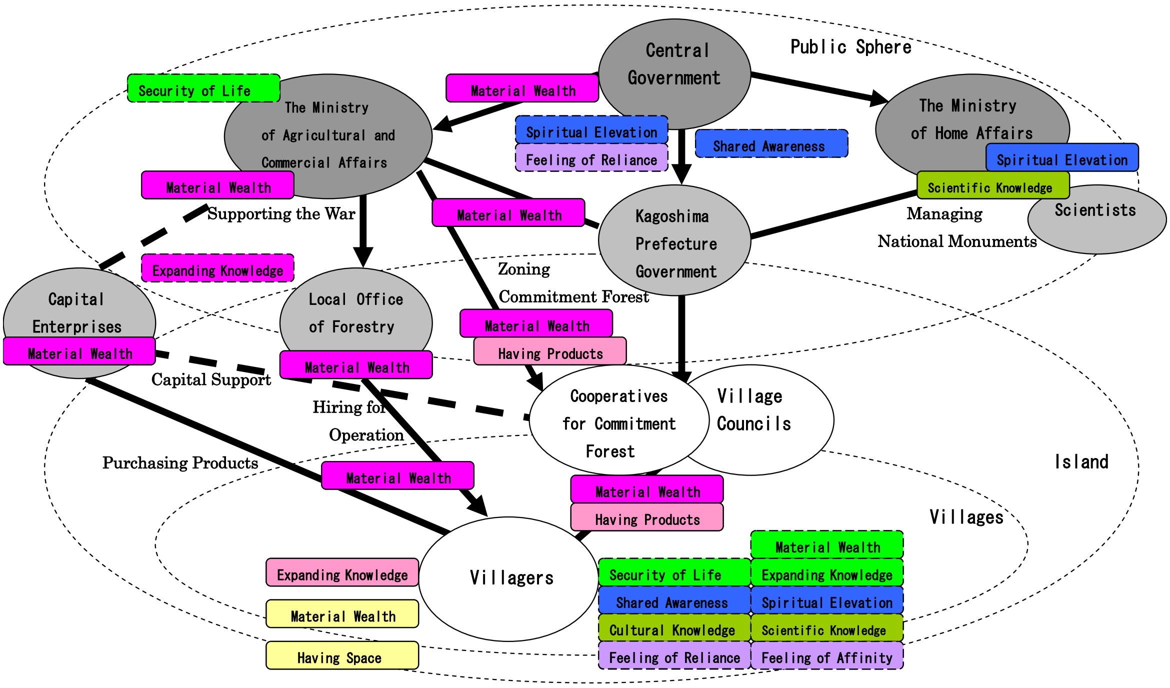


Figure 4: The Period of the Economic Growth after the War (1946 to 1960s)

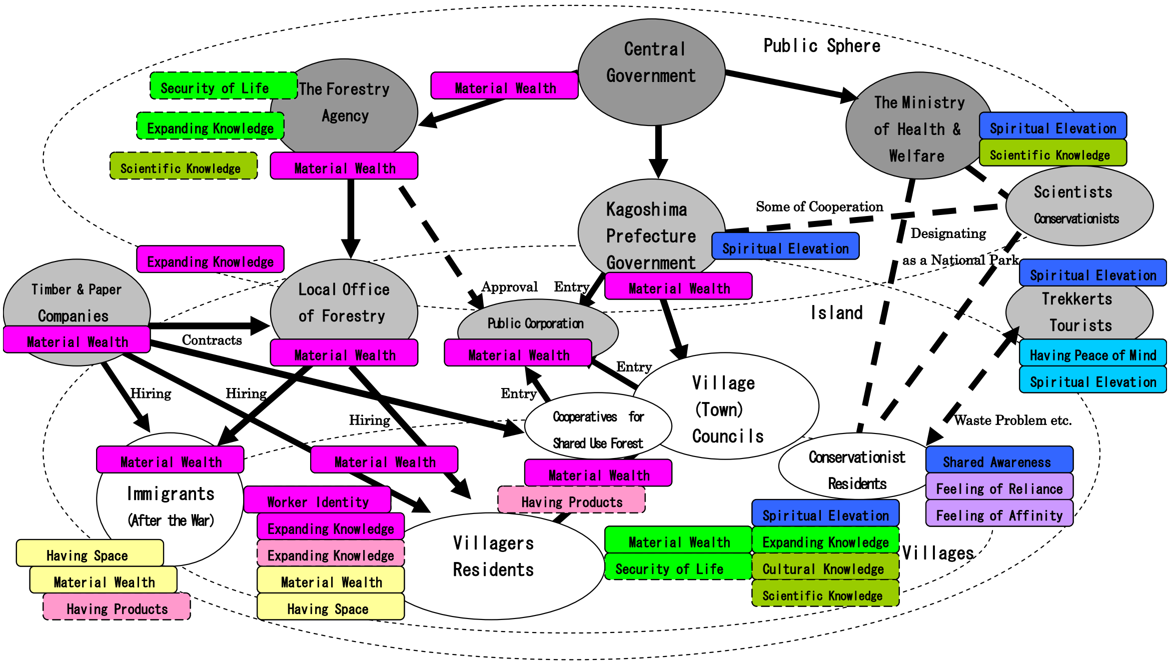


Figure 5: Conservation Campaigns and the Decline of Commercial Forestry (1972 to 1993)

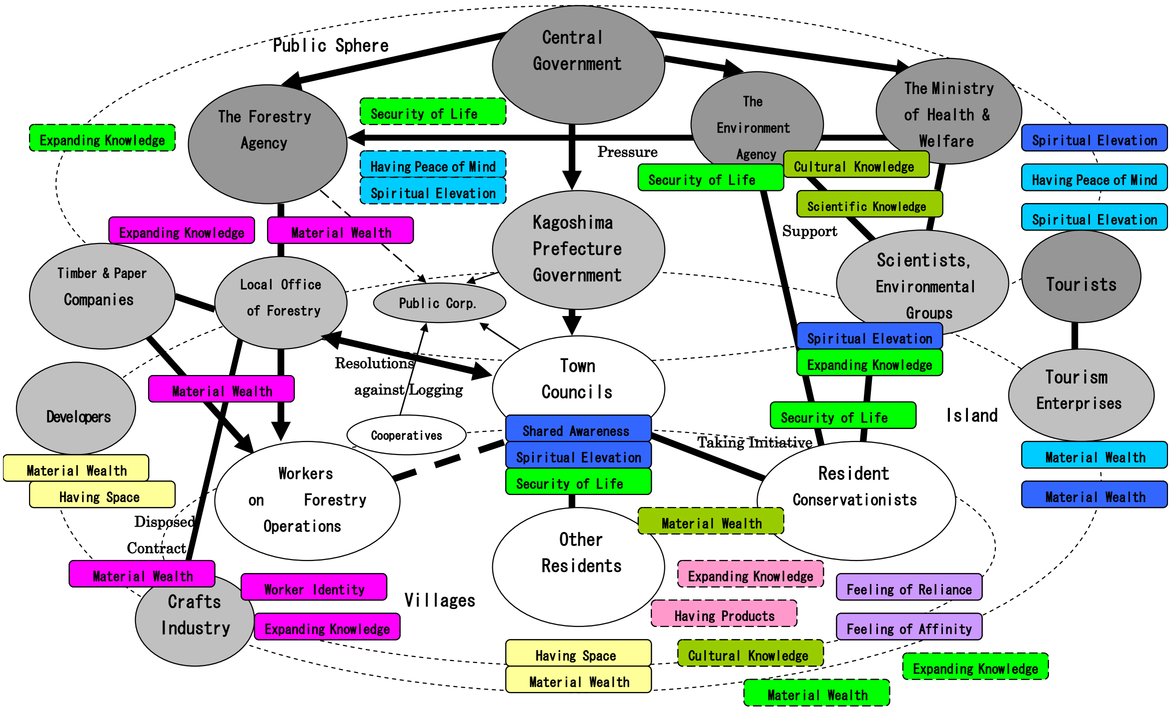
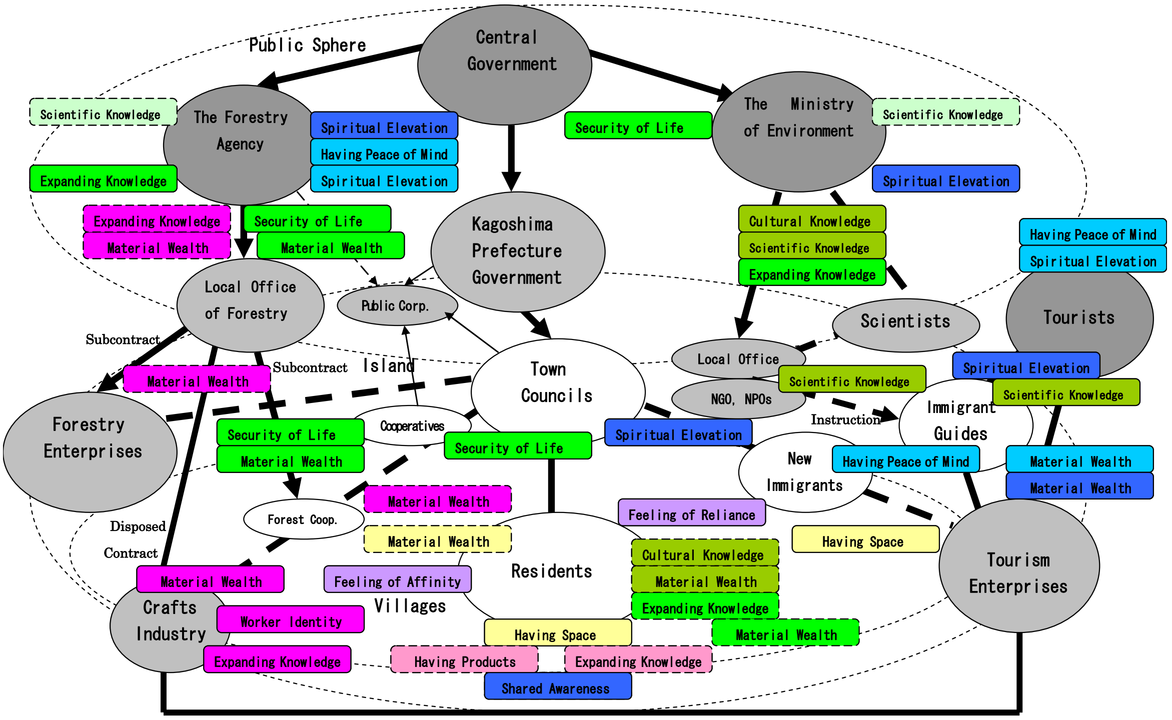


Figure 6: After the Designation of a World Natural Heritage (From 1993)



The Influence of Forest Resource Use on Forest Landscapes in the Abukuma Mountainous Area in the Past 90 Years

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Introduction

Understanding historical backgrounds can provide valuable insight into current ecosystems and biodiversity (Foster1992). Recent studies have further demonstrated that past land use and landscape changes significantly affect biodiversity (Courins and Eriksson 2002; Gachet et al. 2007).

Many studies have been conducted in Ogawa Forest Reserve, a remnant old-growth Fagus crenata forest in the southern part of the Abukuma mountains in Japan (Nakashizuka and Matsumoto 2002). It has been reported that the forest has been much affected by large-scale disturbances due to past land use (Suzuki 2002), but there is still a lack of detailed information concerning land use and landscape history in this region. Integration of comprehensive information on land use with the landscape history of the area surrounding the remnant old-growth forest could provide practical and useful information for planning the optimum conservation and management of this forested area as well as provide deep insights into the current biodiversity there.

The purposes of this study are 1) to clarify the socioeconomic forces which brought about changes in forest landscape around Ogawa Forest Reserve in the southern Abukuma mountains, utilizing literature surveys and interviews with local residents, and 2) to reconstruct past forest landscapes and quantify the landscape changes that have occurred from the beginning of the 20th century to the present, using old topographic maps and aerial photographs.

Methods

Study site

The study area covers about 10,000 ha of the Abukuma mountainous area in the Ibaraki and Fukushima prefectures of central Japan (Fig.1). The mean annual temperature is approximately 10.7°C and the mean annual precipitation is 1,910 mm (Mizoguchi et al., 2002). Hilly areas ranging from 600–700 m a. s. l. dominate a large part of the study area, and these have allowed horse production to prosper in the past. The forests have been subjected to substantial influence from human activity such as horse grazing, clearcutting for charcoal and fuelwood, and burning to maintain grasslands (Suzuki 2002). Most of the forest is now secondary forest or coniferous plantations, and only a few areas of old-growth forest remain. Ogawa Forest Reserve (OFR) was established in the national forest area in 1969 to preserve one of such rare old-growth, temperate, deciduous forests composed of *Fagus crenata*, *F. japonica Quercus mongolica* var. *crispula* and *Carpinus spp*. Forest covered approximately 8,800ha of the study area, and 77% of that is national forest. The area of private forest is minor, and most of the lands owned by private landowners are small in size.

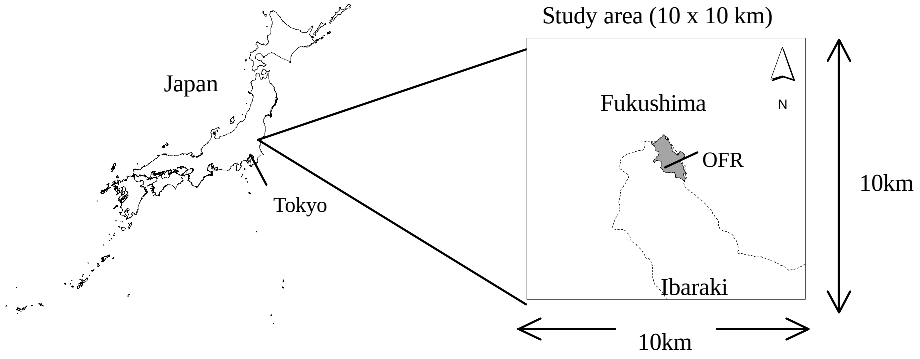

Fig.1 Location of study area. The study area covers about 10,000ha of the southern Abukuma mountainous area. It incorporates the 100 ha Ogawa Forest Reserve(OFR).

Interview and literature survey about forest resource use

We conducted interviews with local residents to clarify the socioeconomic forces which caused changes in land use. In the interviews, we inquired about the changes in forest types and forest resource uses, and also about their causes. Since we focused particularly on the changes around OFR, we conducted interviews with local residents of the Sadanami and Ogawa areas of Kitaibaraki city, Ibaraki prefecture where OFR is located. Interviews were conducted with elderly people in the village, such as the village headman, people who had worked at the local forestry office, and people who knew the history of village well. Since it was difficult to interview a large number of people and to obtain precise information on detailed conditions dating as far back as 90 years ago from interviews alone, we also referenced literature about local history and national forest management plans.

Reconstruction of past land uses

We identified the major turning points of the forest resource use from the interviews, and prepared multiple land use maps corresponding to them to understand landscape transitions. Data on past forest landscapes was obtained from old topographic maps at a scale of 1:50,000 published by the Geographical Survey Institute in 1908. In addition, we used aerial photographs at four time points: (1) the earliest available black and white aerial photographs, at a scale of 1:40,000, taken by the U.S. military in 1947; (2) black and white aerial photographs at a scale of 1:16,000 taken by Japan’s Forest Agency in 1962; (3) color aerial photographs at scale of 1:10,000 taken by Japan’s Geographical Survey Institute in 1975; and (4) the most recent black and white aerial photographs, available at scale of 1:16,000, taken by Japan’s Forest Agency in 1997. The land use patterns were classified into four categories: grasslands, deciduous broad-leaved forests (deciduous forests), coniferous plantations, and other land uses. Grasslands include pastures, meadows, and cutover lands. Deciduous forests are dominated by Quercus serrata, Q. crispula, Castanea crenata, Carpinus laxiflora, and Carpinus tschonoskii. Coniferous plantations include Cryptomeria japonica and Chamaecyparis obtusa. Other land uses include agricultural fields, villages, and public facilities. All land use maps were prepared as vector maps using GIS software TNTmips Ver. 6.8 (MicroImages Inc.). The areas of each land use were calculated to determine the quantitative changes of the land use.

Results

Changes in forest resource uses

Based on the literature survey and the interviews, the pattern of forest resource uses was divided into three periods: (1) the period from pre-war to the post-war reconstruction period, characterized by multi-use of timber and non-timber forest products such as producing fuelwood and charcoal, pasturing and mowing, and collecting fertilizer for agricultural fields, (2) the economic growth period, characterized by the start of a decrease in most uses of forest resources and by the promotion of conifer planting, and (3) the stable growth period, characterized by the decline of forest resource use (Fig.2).

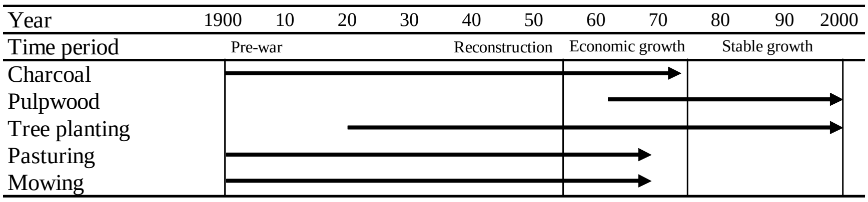

Fig.2 Changes in forest resource uses

Pre-war to reconstruction period (1900s to the first half of the 1950s)

The major industries of this period were charcoal production and horse production. Charcoal production was a side job for most farmers. Generally, they produced charcoal only in the farmers' off-season, although some of them produced it throughout the year. Charcoal producers built rough lodges in the forest and moved there in the winter season for charcoal production (Hanawa-machi 1986). In this region, private forest accounted for only 23% of the forest area and most of the private forests were small. Therefore, the role of the national forest was important for forest resource uses. The local forestry office established custodial forest for the purpose of mowing for agriculture or for charcoal production, and made it available to the neighboring villages (Tokyo Regional Forest Office 1925). Horse production was one of the main industries. At that time, villagers accessed both national and private forests freely to use them as pasture and mowing sites. However, after the demarcation between the national and the private forest ownership, it became difficult for the villagers to use national forest freely for pasture and mowing (Hanawa-machi 1986).

Economic growth period (the latter half of the 1950s to the first half of the 1970s)

After the war, the traditional wood consumption patterns changed. Demand for pulpwood and construction timber increased with the growth of the Japanese economy, whereas fuelwood and charcoal production gradually decreased due to the energy revolution. Government promoted expansive afforestation with conifer plantations, which led to deciduous forests being cut down and converted to conifer production. Villagers were engaged in labor for site preparation, tree planting, and brushing in the national forest (Forest Agency 1964). Villagers used to collect grass, fallen leaves and twigs in common lands and forests. As tree planting in the grasslands gradually accelerated, the amount of available grass decreased. Up to the first half of the 1960s, horse production was converted to cattle production and utilization of grassland as pasture and mowing sites continued to decrease (Society of Sociology of Law of Ibaraki University 1956).

Stable growth period (after the first half of the 1970s)

During this period, the area of tree planting kept on decreasing. Forest resource uses in villages were continuously decreasing due to the decline of plantation activity in the national forest, and due to depopulation and aging of villagers.

Changes in land uses

Pre-war to reconstruction period (1900s to the first half of the 1950s)

Before this period (in 1908), the area was dominated by deciduous forest (70.5%) and grassland (27.3%), while there was no significant coniferous plantation in the study area (Fig.3, Table 1). Because the main industries were charcoal production and horse production, grasslands were utilized frequently as pasture and mowing, and the majority of grasslands were located close to the village (Fig.3).

Grassland decreased to 20.2% in 1947, and the majority of the decrease was replaced by deciduous forest and coniferous plantation during this period (Fig.3). Coniferous plantation emerged as a landscape element and accounted for 18.1% of the total area (Table 1).

Table 1 Changes in proportion of land use from 1908 to 1997

	1908	1947	1962	1975	1997
Coniferous plantation	0	18.1	28.1	46.2	48.4
Broad-leaved forest	70.5	64.0	58.6	35.9	32.9
Grassland	27.3	7.1	1.9	6.3	3.7
Others	2.3	10.8	11.4	11.5	15.1

Economic growth period (the latter half of the 1950s to the first half of the 1970s)

During this period, grassland decreased to 1.9% by 1962 before increasing again to 6.3% in 1975 (Table 1). In this same period, deciduous forest decreased from 58.6% in 1962 to 35.9% in 1975 (Table1). In contrast, coniferous plantation increased gradually, and it occupied approximately half of the study area (46.2%) in 1975 (Table 1). Coniferous plantation replaced deciduous forest, and became the most abundant landscape element in the study area.

Stable growth period (after the first half of the 1970s)

The areas of deciduous forest and coniferous plantation remained largely stable relative to the areas in 1975 (Table 1). However, many small narrow patches of deciduous forest appeared in the coniferous plantations (Fig.3).

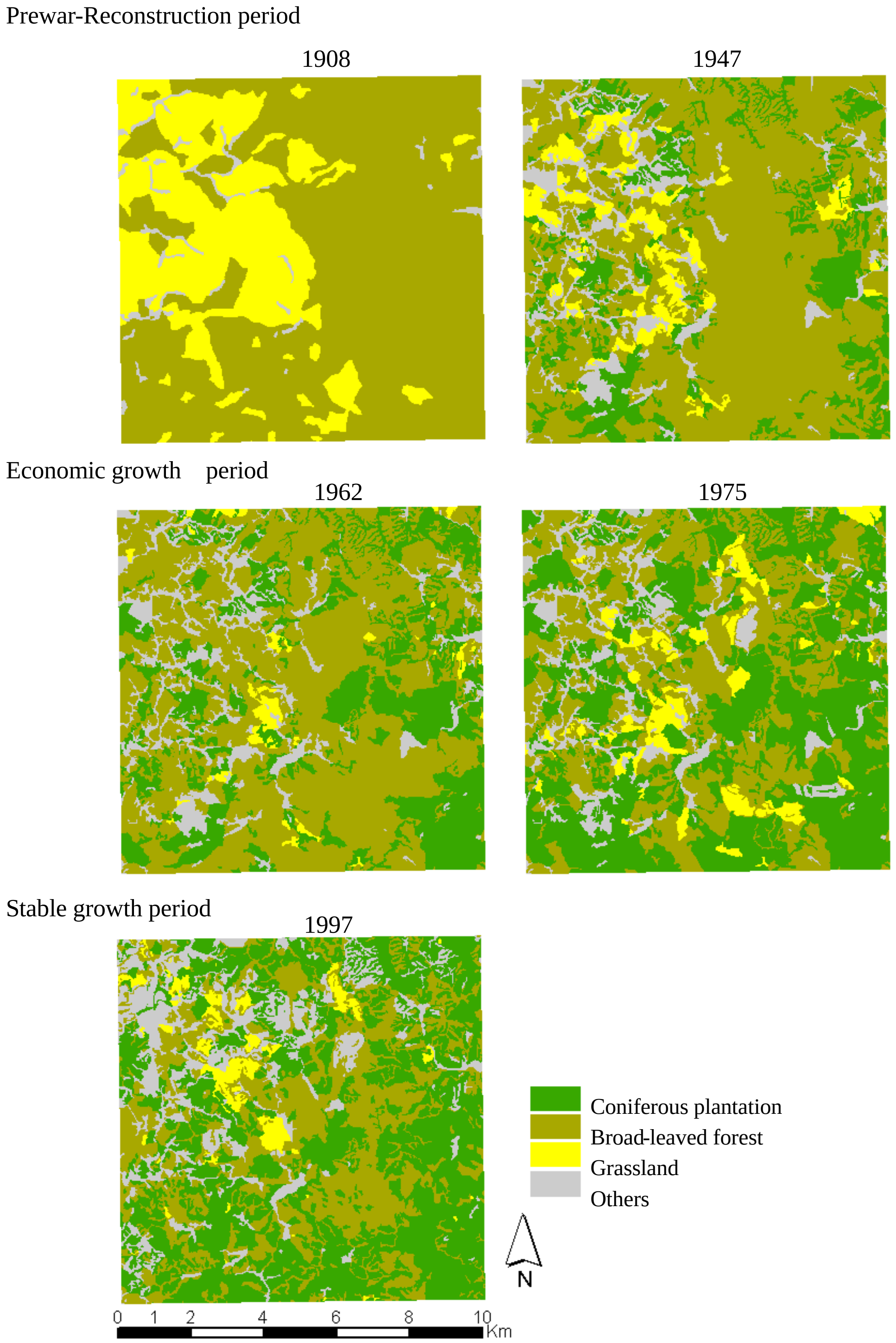

Fig.3 Land use change from 1908 to 1997

Discussion

The pattern of forest resource use changed drastically over the 20th Century, with the history of resource use being divisible into three periods (Fig.2) that paralleled the stage of economic growth. The landscape also changed along with these changes in forest resource uses. Before the war a lot of grasslands remained in the study area. However, most of the grasslands were replaced by deciduous forests or coniferous plantations. These changes seem to be caused by the prohibition of burning in national forests in 1929, the cessation of management of mowing sites due to labor shortages during the war, and the planting of conifer trees in grasslands (Tokyo Regional Forest Office 1947). In the economic growth period, the Forest Agency promoted expansive afforestation to supply the increasing demand for wood and to meet changes in fuel demand. The changes in the landscape of the study area clearly reflected these changes. Furthermore, the decrease of grassland in 1962 may have been caused by the introduction of chemical fertilizer instead of grass mowing, the growth in demand for beef, and the decline in the use of horses due to improvements in agricultural machinery and changes in the industrial structure. As a result of these driving forces, the use of grasslands as mowing sites and pasture declined drastically. In 1975, the area of grasslands increased a little (Table 1). In those days, the grasslands were abandoned, although parts of them remained, being improved from semi-natural grasslands to artificial grasslands for cattle, and new artificial grasslands were established. These grasslands and cut-over lands were included in the grasslands category of 1975, and the usage and the content of grasslands were completely different from the previous period. In the stable period, the total area of secondary forest patches remained almost stable from 1975 to 1997 (Fig.4), but many small, narrow secondary forest patches emerged in coniferous plantations (Fig.3). While logging proceeded in secondary forests, some plantation areas were abandoned due to labor shortages and an aging farming population, and those areas were replaced by secondary forests. Narrow patches must also have been kept as buffer strips to protect cut-over land and preserve scenic beauty under the “New forest management in the national forest” in 1973.

In the study area, many deciduous forests and grasslands had been kept for long periods of time because deciduous forest was an important resource for producing charcoal (coppiced every 20-30 years), and grassland was needed as mowing sites and pastures. However, the deciduous forests and the grasslands became fragmented or disappeared with the changes in forest resource uses. As a result, the landscape has drastically changed. Such modification and the loss of landscape elements mean the modification and loss of natural habitat for wildlife. In coppice forest of the Kanto district, clear relationships have been found between fragmentation of woodlands and the decrease of rare species and forest floor plants (Iida and Nakashizuka 1995). Loss of biota and biodiversity is feared as a result of stopping the cyclic use of forest resources in rural areas (Okubo et al. 2000; Kamihogi 2002). Maintaining or reconstructing suitable forest environments may be effective methods for preserving flora and fauna maintained in relation to traditional land use. However, this would require an enormous expenditure of effort and time. Therefore, as suggested by Inoue (2003), consideration should be given to effective methods to create an alternative environment through variations on current forest operation, such as rotated logging operation, which provides alternative habitats for wildlife as a substitute for those provided by traditional forest operation (coppicing) and grass mowing.

In this study, we were able to show the close relationships between the changes in society and human activities and forest landscape. Quantification of the land use and landscape history may contribute to the development of biodiversity research in fields such as biodiversity change at the regional scale, the contribution of landscape structure to regional biodiversity, the influence of fragmentation on biodiversity, and the prediction of future biodiversity in association with change of land use.

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References

Coursins SAO, Eriksson O (2002) The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. Landscape Ecol 17: 517-529

Forest Agency (1964) Ringyo roudou no syugyou keitai ni kansuru jittai tyosa-Fukushima ken Iwaki gun Tabito mura oyobi Kawamae mura- (Investigation of actual condition concerning forest labor-Tabito village and Kawamae village, Iwaki county, Fukusima prefecture) (in Japanese)

Foster DR (1992) Land-use history (19730-1990) and vegetation dynamics in central New England, USA. J Ecol 80: 753-772

Gachet S, Leduc A, Bergeron Y, Nguyen TX, Tremblay F (2007) Understory vegetation of boreal tree plantations: Difference in relation to previous land use and natural forest. Forest Ecol Manag 242: 49-57

Hanawa-machi (ed) (1986) Hanawa machi shi (History of Hanawa Town), Hanwa-town, Fukushima (in Japanese)

Iida S, Nakashizuka T (1995) Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan. Forest Ecol Manag 73: 197-210

Kamihogi A, Yamazaki A, Satou H (2002) A study of the factors in the natural and social environments which have an impact on the habiatas of Gastrosteus microcephalus. J Jpn Inst Landsc Architect 65: 533-538 (in Japanese with English summary)

Mizoguchi Y, Morisawa T, Ohtani Y (2002) Climate in Ogawa Forest Reserve. In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community—Ogawa Forest Reserve of Japan. Ecological Studies vol. 158, Springer, pp. 11–18

Nakashizuka T and Matsumoto Y (2002) Diversity and interaction in a temperate forest community-Ogawa Forest Reserve of Japan. Ecological Studies vol. 158, Springer.

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomol Sci 6: 151-163

Okubo S, Fukamachi K, Kuramoato N (2000) Toward Conservation of Rural Landscapes. J Jpn Inst Landsc Architect 63: 177-207 (in Japanese)

Society of Sociology of Law of Ibaraki University (1956) Iriaiken no kenkyu dainisyu (Study of common forest right, the second collection), Society of Sociology of Law of Ibaraki University, Mito

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community-Ogawa Forest Reserve of Japan. Ecological Studies vol. 158, Springer, pp. 27-41

Taga Livestock Industry Cooperation (1982) Taga koma shi (History of horse breeding in Taga Country),Kyodohensyusitsu, Mito (in Japanese)

Tokyo Regional Forest Office (1925) Second forest management plan for Takahagi District National Forests (in Japanese)

Tokyo Regional Forest Office (1947) Sixth forest management plan for Takahagi District National Forests (in Japanese)

Comparison of Transition Matrices of Land-use Dynamics in Two Research Sites

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Introduction

Several international research projects on the intensity of land use change have been started since the late 1980's, e.g. the Land Use and Cover Change program (Messerli, 1997) of International Geosphere-Biosphere Project (1988). These studies indicated the necessity of intensive studies on land-use changes, their speed and their driving forces. Developments all over the country cause the loss of a significant amount of agriculture land and natural forest. Local land-use and land-cover change can influence environmental and ecological changes. Two research sites we selected, Lambir National Park (Malaysia) and Deramakot Forest Reserve (Malaysia), have also been affected by the influence over 50 years, and the historical, social and ecological reasons would be very different depending on the locality and periods. To identify those reasons, quantitative research is necessary on the speed and the driving forces of their changes. As the first step to examine them, we here tried employing a mathematical model approach using transition matrix models.

Transition matrix model is a useful tool to analyze the characteristics of the land-use change and to forecast future dynamics and is easily constructed from area-based transition tables among land-use classifications. Popular GIS software, e.g. ARCGIS and RAMASGIS, supports a command to calculate the area-based transition tables from satellite images and aerial photographs. Therefore, many authors employed transition matrix models in these fifteen years (Ehlers et al., 1990; Meyer 1991; Hathout, 2002; Ademola, 2004).

We, in the present paper, quantified area-based transition tables and transition matrices of land-use in two research sites in order to grasp historical change of transition probabilities among census periods. To evaluate the historical change of transition probabilities properly, they should be compared under the same census interval. Unfortunately, satellite images or photographs of the research site in question are not always prepared every year or by a constant time interval in the specific research site. It's necessary to adjust the difference of census intervals of transition matrices mathematically. Therefore, we developed a formula of obtaining the yearly (annual) transition matrix to compare them among census periods. Using the formula, two yearly matrices in the research sites were obtained and the ten-year matrices were also calculated.

Methods

(i) Area-based transition tables and transition matrices of land use

We can quantify the type, amount and location of land use change in satellite images and aerial photographs, and some GIS computer programs provide a procedure to classify the land use and land cover, and to calculate the transition in the areas of the classifications of land use. We have three aerial photographs (of 1963, 1977 and 1997; Table 1a and 1b) in a part of Lambir National Park, Malaysia (about 275 square kilo-meters) and only two satellite images (of 1985 and 2002; Table 1c) in a part of Deramakot Forest Reserve, Malaysia (about 3500 square kilo-meters). Therefore, we calculated the area-based transition tables from those satellite images and aerial photographs of two research sites, and obtained 3 area-based transition tables in all (Table 1).

Probability-based transition tables, i.e. transition matrices, were also obtained from Table 1 (Table 2) because they are very convenient in comparing among research sites with different sizes and in calculating the dynamical projection of classifications of land use as:

$$\mathbf{x}_{t+c} = \mathbf{A}\mathbf{x}_t \ , \qquad (1)$$

where $\mathbf{x}_t$, $\mathbf{A}$ and c represent the area vector at a census each of whose elements is the area of each classification, a transition matrix in question and the census interval, respectively. "$t+c$" in equation (1) generally means the next census. Unfortunately, the census intervals in Table 2 ranged from 14 to 20 years because of the lack of satellite images or aerial photographs. It implies that these obtained matrices cannot be compared directly because the transition probability during 14 years would be actually different from that during 20 years even if they are the same.

(ii) Formula of yearly transition matrix

The discrepancy of census periods in transition matrices does not allow us to evaluate two of them directly. Therefore, the normalization of census periods is necessary, that is, to obtain yearly transition matrix in every census period, which means the c-th power root of an original transition matrix, where c is census interval of the matrix. We developed a theorem on the c-th power root of a matrix and obtained the formula and the number of the solutions:

<u>Theorem</u> If a n by n matrix has n distinct eigenvalues and all of them are not equal to zero, the c-th power root of the matrix is:

$$\mathbf{A}^{\frac{1}{c}} = \begin{pmatrix} \mathbf{u_1} & \cdots & \mathbf{u}_n \end{pmatrix} \begin{pmatrix} (\lambda_1)^{1/c} & & 0 \\ & \ddots & \\ 0 & & (\lambda_n)^{1/c} \end{pmatrix} \begin{pmatrix} \mathbf{u_1} & \cdots & \mathbf{u}_n \end{pmatrix}^{-1} \ , \qquad (2)$$

where $\mathbf{A}$, λ_i and $\mathbf{u}_i$ are a transition matrix with census interval of c years, the i-th eigenvalue of matrix $\mathbf{A}$ and its corresponding eigenvector, respectively.

Table 1 Area-based transition tables among land use classifications.

The numerics in cells represents the area of transition from a classification to another (ha).

(a) From 1963 to 77 in Lambir National Park. The total area is about 275 square kilo-meters

	1963				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	230.2	683.3	588.1	0	0
Secondary Forest	724.9	3,027.4	2,016.9	0	0
Natural Forest	1.7	4.2	14,226.0	0	0
Selectively logged forest	0.0	108.6	4,222.4	0	0
Plantation	0.0	130.6	1,446.0	0	0
Total	956.8	3,954.1	22,499.4	0.0	0.0

(b) From 1977 to 97 in Lambir National Park. The total area is about 275 square kilo-meters

	1977				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	245.2	211.3	2.2	5.8	0.0
Secondary Forest	1,253.5	5,517.8	888.9	1,965.7	1,524.8
Natural Forest	0.0	6.7	6,364.5	0.0	0.0
Selectively logged forest	0.3	11.6	6,524.2	2,356.8	0.0
Plantation	0.0	13.4	556.3	0.0	51.8
Total	1,499.0	5,760.8	14,336.1	4,328.3	1,576.6

(c) From 1985 to 2002 in Deramakot Forest Reserve.

The total area is about 3500 square kilo-meters.

	1985				
	Cropland	Secondary Forest	Natural Forest	Selectively logged forest	Water
Cropland	41370.6	2259.3	49166.2	35269.8	777.5
Secondary Forest	563.2	45.8	549.7	146.5	3.3
Natural Forest	6189.9	1855.0	40801.9	19146.1	86.1
Selectively logged forest	17560.2	1558.2	50514.1	77961.3	162.4
Water	422.3	136.4	30.0	103.1	886.0
Total	66106.3	5854.7	141061.8	132626.8	1915.3

Table 2 Transition matrices among land use classifications.

The numerics in cells represents the transition prpbability from a classification to another.

(a) From 1963 to 77 in Lambir National Park.

	1963				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	0.241	0.173	0.026	0	0
Secondary Forest	0.758	0.766	0.090	0	0
Natural Forest	0.002	0.001	0.632	0	0
Selectively logged forest	0.000	0.027	0.188	0	0
Plantation	0.000	0.033	0.064	0	0

(b) From 1977 to 97 in Lambir National Park.

	1977				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	0.164	0.037	0.000	0.001	0.000
Secondary Forest	0.836	0.958	0.062	0.454	0.967
Natural Forest	0.000	0.001	0.444	0.000	0.000
Selectively logged forest	0.000	0.002	0.455	0.545	0.000
Plantation	0.000	0.002	0.039	0.000	0.033

(c) Deramakot Forest Reserve in Malaysia.

	1985				
	Cropland	Secondary Forest	Natural Forest	Selectively logged forest	Water
Cropland	0.626	0.386	0.349	0.266	0.406
Secondary Forest	0.009	0.008	0.004	0.001	0.002
Natural Forest	0.094	0.317	0.289	0.144	0.045
Selectively logged forest	0.266	0.266	0.358	0.588	0.085
Water	0.006	0.023	0.000	0.001	0.463

Collorary If a n by n matrix has n distinct eigenvalues and all of them are not equal to zero, the number of the c-th power root of the matrix is c^n .

<The proof is abbreviated>

$(\lambda_i)^{1/c}$ means the c-th power root of the scalar λ_i. Since λ_i could be a complex number, we may set

$\lambda_i = re^{i\theta} = r(\cos\theta + i\sin\theta)$ ($r > 0$ and $0 \le \theta < 2\pi$), using polar coordinates. Therefore, $(\lambda_i)^{1/c} = r^{1/c}(\cos\frac{\theta + 2\pi k}{c} + i\sin\frac{\theta + 2\pi k}{c})$ for $k = 0, 1, \ldots c-1$ and generally has c solutions including complex numbers, which is why the number of the solutions are c^n.

We also developed computer programs of Mathematica (Wolfrum Research, Inc.) and C++ to calculate equation (2) and to obtain all of c^n solutions at the same time. It is opened on the website, http://hosho.ees.hokudai.ac.jp/~takada/eindex.html. The program by C++ is about 800 times faster than that by Mathematica.

Result

(i) Quantification of land use change

The quantification of land use change for the analyzed classifications are given in Table 1 and 2. The former is an area-based table and the latter is a probability-based table, i.e. transition matrix. "Natural forest" was the largest class in Lambir and Deramakot of Malaysia (Table 1a, 1b and 1c). The speed of land use change cannot be compared using the area-based tables because their total areas are different among two research sites, and cannot be compared using the probability-based tables because their census periods varied largely. We refer to the comparison of the speeds in land use change later, when we obtain the yearly transition matrices and ten-year transition matrices.

(ii) Yearly transition matrix and several problems

Yearly matrix has plural solutions and, for example, the yearly matrix in Lambir Park during 1977 and 1997, has 20^5 (= 3,200,000) solutions, elements of which could include negative and complex numbers, as explained in Method. The elements of a correct yearly matrix should range from 0 to 1 because those elements are probabilities. Therefore, we should omit solutions with negative or complex numbers after the calculation. The computer program is actually made to omit matrices with large negative real parts or imaginary parts, taking into account of rounding errors in numerical calculation.

At the second stage (1977-97) in Lambir National Park, we unfortunately obtained no positive solution. A solution among 20^5 solutions includes only one negative element whose absolute value is very small (Table 3b), and all of the other solutions include elements smaller than minus 0.5 and/or complex numbers. We think the former is the appropriate solution and its negative elements might be brought from rounding errors in numerical calculation or the failure of image analysis in land use classification. In Deramakot (Table 3c), we similarly have single appropriate solution among about a million solutions. In Lambir National Park (Table 3a), we couldn't obtain the yearly transition matrix at the first stage, using equation (2), because the transition matrix during 1963-77 in Table 2a has two zero eigenvalues

Most of diagonal elements of yearly transition matrices are larger than 90% and the land-use changes in all the research sites is very slow by yearly rate. We calculated the ten-year matrices (10-th power matrices of yearly ones) in all the sites to understand the speed of land-use change intuitively (Table 4).

Table 3 Yearly transition matrices. .

(a) From 1963 to 77 in Lambir National Park. We couldn’t obtain the matrix at the first stage

	1963				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland					
Secondary Forest					
Natural Forest			NONE		
Selectively logged forest					
Plantation					

(b) From 1977 to 97 in Lambir National Park. Though the matrix includes negatibe element, it is only appropriate solution among 20^5 solutions.

	1977				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	0.906	0.004	0.002	−0.002	−0.020
Secondary Forest	0.095	0.995	−0.019	0.032	0.180
Natural Forest	0.000	0.000	0.960	0.000	0.000
Selectively logged forest	0.000	0.000	0.045	0.970	0.000
Plantation	−0.001	0.000	0.011	0.000	0.840

(c) Deramakot Forest Reserve in Malaysia. Though the matrix includes negatibe element, it is only appropriate solution among 17^5 solutions.

	1985				
	Cropland	Secondary Forest	Natural Forest	Selectively logged forest	Water
Cropland	0.965	0.052	0.041	0.022	0.043
Secondary Forest	0.004	0.712	0.001	−0.001	−0.002
Natural Forest	0.006	0.251	0.915	0.021	0.004
Selectively logged forest	0.025	−0.026	0.045	0.958	−0.001
Water	0.001	0.012	0.000	0.000	0.955

Table 4 Ten–year transition matrices in three research sites.

(a) From 1963 nto 77 in Lambir National Park. We couldn't obtain the matrix at the first stage,

	1963				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	NONE				
Secondary Forest					
Natural Forest					
Selectively logged forest					
Plantation					

(b) From 1977 nto 97 in Lambir National Park. The elements in matrices are sometimes negative.

	1977				
	Cropland	Secondary Forest	Natural forest	Selectively logged forest	Plantation
Cropland	0.383	0.027	0.005	−0.005	−0.042
Secondary Forest	0.620	0.969	−0.042	0.268	0.868
Natural Forest	0.000	0.001	0.666	0.000	−0.001
Selectively logged forest	0.000	0.001	0.324	0.738	−0.001
Plantation	−0.002	0.002	0.046	−0.001	0.176

(c) Deramakot Forest Reserve in Malaysia. The elements in matrices are sometimes negative.

	1985				
	Cropland	Secondary Forest	Natural Forest	Selectively logged forest	Water
Cropland	0.635	0.029	−0.001	0.000	0.005
Secondary Forest	−0.001	0.037	0.003	−0.001	0.010
Natural Forest	0.027	0.482	0.445	0.120	0.064
Selectively logged forest	0.033	0.141	0.284	0.698	0.189
Water	0.306	0.311	0.269	0.182	0.733

Discussion

In examining the land use change in terms of satellite images or aerial photographs, we often don't have enough number of photographs and cannot construct transition matrices with constant census intervals. We here developed a way to calculate the yearly transition matrix from a transition matrix with long census period. This way would be useful when we want to compare among transition matrices with different census intervals, as shown in Table 3 and 4. While we applied the formula for yearly transition matrix to three transition matrices in two research sites (Table 2), we are confronted with two difficulties. One is that no positive matrix is obtained in all the cases. From our experience, small negative elements in yearly transition matrices are likely to occur when many zero or small elements are included in the original matrix. For example, in Deramakot, there are 9 elements under 0.01 among 5x5 elements (Table 2c). Since the transition among classification is usually slow in forest ecosystems, there might be many small elements in the original matrix. Then, we would obtain a yearly transition matrix with negative elements close to zero, and those negative elements could be assumed to be approximately zero. It would be derived from rounding errors in numerical calculation.

In the yearly transition matrix of Lambir National Park, there were large negative values in Table 3e, i.e. the transition probability from “plantation” to “cropland” and that from “natural forest” to “secondary forest”. It’s difficult to think those negative values are derived from rounding errors in numerical calculation. One of the possibilities is that GIS software made a mistake in the classification of land use and improbable transition was picked up from photographs. It is also probable that the drastic change of land use occurred during the census period and it is not adequate to calculate the average transition rate (yearly transition matrix). We have not identified the causes yet.

The other difficulty is that we couldn’t obtain the yearly transition matrix at the first stage in Lambir National Park (Table 3a), Mathematically speaking, the reason is why two of the eigenvalues of the original transition matrix are zero and equation (2) could not be applied to the matrix. It also means that ”selectively logged forest” and “Plantation” of the land use classification newly appeared in 1977. The appearance of new land-use classification could occur occasionally where human activity is strong. Therefore, a question remains unsolved, how to obtain yearly transition matrix where there are zero eigenvalues of the original matrix.

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References

Braimoh AK and Vlek PLG (2004) Land-Cover Dynamics in an Urban Area of Ghana. Earth Interactions, 8: 1-15.

Ehlers M, Jadkowski, M.A, Howard, RR and Brostuen, DE (1990) Application of SPOT data for regional growth analysis and local planning. Photogrammetric engineering and remote sensing. 56: 175–180.

Hathout S (2002) The use of GIS for monitoring and predicting urban growth in East and West St Paul, Winnipeg, Manitoba, Canada. Journal of environmental management. 66: 229–238.

Messerli B (1997) Geography in a rapidly changing world. International Geographic Bulletin 47: 65–75.

Meyer WB and Turner II BL (1991) Changes in Land Use and Land Cover: A Global Perspective. Cambridge University Press, Cambridge.

Chapter 3

EFFECTS OF CHANGES IN FOREST USE ON BIODIVERSITY

Chapter 3 Introduction

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In Chapter 2, the changes in forest utilization during the past 50 to 100 years were revealed for each study site. Based on this understanding, we will discuss the effects of forest utilization on the biological community at each study site in section 3.1 and the effects of human activities on ecosystem functions in section 3.2.

In section 3.1, we discuss the effects of forest utilization on communities or populations of living organisms at each study site. At Lambir, species diversity and the species composition of plants (Momose *et al.*), insects (*i.e.* butterflies (Itioka *et al.*), beetles (Kishimoto-Yamada *et al.*), ants (Matsumoto *et al.*)), mammals (*i.e.* bats (Fukuda *et al.*), small mammals (Nakagawa *et al.*)), and macrofungi (Yamashita *et al.*) were compared among several forest types (*i.e.* rubber plantation, secondary forest after swidden agriculture, isolated natural forest, and primary forest). In every biological community except for the beetle community, species diversity was highest in the primary forest and generally decreased with increasing disturbance of the forest. At Sabah, species diversity and the species composition of plants (Aiba *et al.*), insects (*i.e.* flies (Akutsu *et al.*)), soil animals (Ito *et al.*) and mammals (Onoguchi & Matsubayashi) were compared between forest managed under reduced-impact logging, forest managed under conventional logging, and primary forest. Species diversity of plants and mammals was higher in forest managed under reduced-impact logging than in forest managed under conventional logging methods. On Yaku Island, the species diversity and biomass of plants (Aiba *et al.*, Tsujino *et al.*) and insects (*e.g.*, beetles, horseflies, wasps (Yamauchi *et al.*)) and the density of the Japanese macaque (Hanya *et al.*), were surveyed in primary forest, plantations of Japanese cedar, and secondary forest. Species diversity of plants and insects was lower in the plantation forest than in the primary forest. At Abukuma, the community structure of the forest-floor vegetation (Tanaka *et al.*, Nagaike *et al.*) and of arthropods (*e.g.*, butterflies, moths, wasps, beetles, springtails, mites (Makino *et al.*)) was surveyed in several different forest types (*e.g.*, plantations of Japanese cedar and secondary and old growth broadleaved deciduous forest) for a range of forest ages. Species diversity of the forest-floor vegetation was higher in young stands than in intermediate-aged and old stands in both the secondary forest and the plantation forest. Species composition differed among the forest types. Arthropods could be divided into three groups based on the response of their species diversity to the age of the forest: in one group, species diversity decreased with increasing forest age (*e.g.*, butterflies, longhorn beetles); in the second group, species diversity increased with increasing forest age (*e.g.*, mycophagous mites); and in the third group, species diversity did not change with increasing forest age (*e.g.*, moths, ground beetles).

In section 3.2, we discuss the effects of human activities on ecosystem functions. Here, we define ecosystem functions as the functions that are necessary for the growth or sustenance of the ecosystem, such as pollination, the food chain, and matter and energy flows. Recently, the area of forest has decreased rapidly, accompanied by fragmentation of large stands into smaller stands, as was seen in Chapter 2. We hypothesized that fragmentation of forests would reduce the size of plant populations, leading to reductions in visitation by pollinators, reductions in the number of individuals capable of reproduction, and inbreeding depression. In section 3.2.1., we discuss the results of some basic studies of plant ecology at Lambir (Aiba &

Nakashizuka, Kenzo *et al*., Ichie *et al*.) and Yaku island (Tanabe *et al*.). In section 3.2.2., we introduce studies on plant reproductive ecology (Momose *et al*.) and plant–pollinator interactions (Kumano & Yamaoka, Ushimaru *et al*.), and then we discuss the effects of forest fragmentation caused by human activities on plant community. Studies of one tree species at Lambir (Takeuchi *et al*.) and two tree species at Abukuma (Matsuki & Isagi, Tateno *et al*., Kikuchi *et al*., Shibata *et al*.) revealed that forest fragmentation does not always have a negative influence on tree reproduction.

In section 3.2.3., we discuss the results of studies of changes in seed-dispersal systems in response to changing human utilization of the forest. At Lambir, the pattern of fruit utilization by bird communities is described (Kamoi *et al*.). At Sabah, the loss of large mammal seed-dispersers after conventional logging appeared to have detrimental effects on the regeneration of two *Durio* species (Nakashima & Matsubayashi). On Yaku Island, the restoration of a *Ficus* species population after logging conducted 60 years ago is not yet complete (Otani & Sei-ichi). The behavior of the Japanese macaque determines the spatial distribution of the tree *Myrica rubra* (Terakawa *et al*.), and seeds of *M. rubra* was attacked by lepidopteran insects before dispersal (Fujita *et al*.). At Abukuma, forest fragmentation positively affected the growth of seedlings of plant species that are dispersed by birds (Naoe *et al*.).

The second and third sections of this chapter show that the effects of human activities on plant regeneration are highly variable. The effects on species interactions might affect plant–seed disperser systems, plant–pollinator systems, or some other combination of these systems described in section 3.2.4. (Tanaka *et al*., Handa *et al*., Tzuchiya & Itioka, Okubo & Itioka). At Lambir, swidden cultivation reduced the species diversity of ants and plants, which means that simplification of the species composition also simplified the interspecific interactions, and the effects were still detectable at least 20 years after the initial disturbance (Tanaka *et al*.).

Some studies of the effects of human activities on interspecific interactions have pointed out that human activities sometimes affects these interactions and that the response of the system differs depending on a range of factors. Such changes in community structure might affect matter and energy flows through the forest ecosystem. In section 3.2.5., we focus on matter flows, especially through the decomposition system (Wagai *et al*.). At Sabah, the decomposition rate of leaf litter was highest in the forest managed under conventional logging (Hasegawa *et al*.).

In this report, we will present an assessment method for evaluating the level of sustainable forest use. The results permit an assessment of the ecological situation at the study sites. The results clearly demonstrate the different responses of species diversity of various organisms and of ecological functions to human activities, and suggest that understanding the traits of individual organisms is needed before evaluation can occur.

Effect of Forest Use on Microhabitat Environment and Vegetation Structure in Sarawak, Malaysia

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Introduction

Tropical rain forests in Southeast Asia have been exposed to drastic and rapid deforestation because of an increasing human population and a rapidly developing economy. The annual deforestation rate in this region is 1.9%, whereas the average global rate is only 0.2 to 0.3% (Matthews 2001). Elucidation of the effects of forest use on plant biodiversity and on the microhabitat environment is an urgent subject for species conservation and proper forest management. Many studies have been performed on the effects of forest fragmentation on changes in tree species composition or abundance (e.g., Laurance et al. 2000). These studies have revealed that the structure of a forest remnant might be affected by its area, its distance from primary forest, and the elapsed time since fragmentation began (Laurance et al. 2002).

In Southeast Asia, forests are used for various purposes, including traditional ones. Slash-and-burn agriculture remains a widespread method of cultivation; local people (the Iban) abandon a field and shift to a new site after harvesting. As a result, secondary forests (fallows) at various developmental stages form a mosaic of landscape. Because rubber trees have been planted in abandoned fallows, particularly since the 1950s to produce crude rubber as a cash crop in Sarawak, Malaysia, rubber plantations operated by small holders are another widespread vegetation type (Ichikawa 2003). To understand the effect of forest use on a region's vegetation structure, research must be conducted on the diverse vegetation types that form the forest mosaic. The alternation of vegetation structures may also be accompanied by changes in the microhabitat environment, such as canopy openness and soil-water content (Beaudet and Messier 2002). However, the effect of forest use on the microhabitat environment of various vegetation types remains unknown.

The objective of the present study was thus to compare the microhabitat environment and vegetation structure in fragmented primeval forests, abandoned fallows at three developmental stages, and rubber plantations, with those of primary forests so as to determine the effects of human forest use on the ecological traits of the vegetation in Sarawak, Malaysia. For fragmented primeval forests, the effects of the area, distance from a primary forest, and elapsed time since the fragmentation on vegetation structure were also examined.

Materials and methods

Study site and vegetation structure

A field survey was conducted in August 2003 in and around Lambir Hills National Park (LHNP), Sarawak, Malaysia (4°2’N, 113°5’E). The study site contained 32 plots (each 10×100 m) in six forest types: primary forests (four plots); fragmented primeval forests (nine plots); abandoned fallows at three developmental stages (i.e., new, 1 year after abandonment, four plots; young, 5 to 6 years after abandonment, four plots; and old, > 20 years after abandonment, six plots); and rubber plantations (five plots).

All trees in each plot ≥10 cm diameter at breast height (DBH, 1.3 m above ground) were tagged, mapped, measured DBH to the nearest mm, and identified to the species level. Voucher specimens were stored in the Herbarium of the Forest Research Center, Sarawak. Digitized satellite image was also used to identify the location of each plot, measure the shortest straight distance from the edge of each fragmented primeval forest plot to the primary forest of the park, and calculate the area of the fragmented primeval forest plots (Fig. 1). Since the exact date of fragmentation for each fragmented primeval forest was unknown, to estimate the date of fragmentation, we used the area of surrounding primary-forest-like vegetation within 200 m of each study plot calculated using a digitized aerial photograph of the region taken in 1977. The surrounding vegetation was classified into seven types: secondary forest (rubber plantation and fallow), open land (roads and grassland), wetland (wet rice fields and ponds), oil palm plantation, fragmented primeval forest, logged forest, and primary forest. The primary-forest-like vegetation included fragmented primeval, logged, and primary forest.

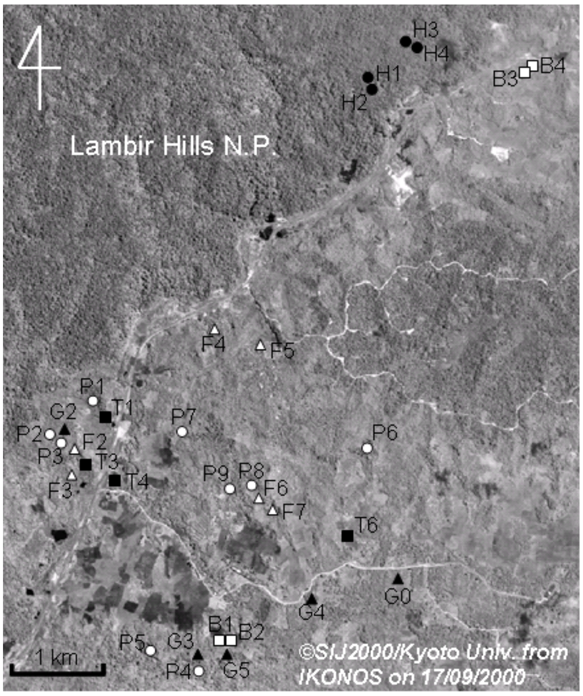

Fig. 1 Location of the study plots in and around Lambir Hills National Park, Sarawak, Malaysia. Symbols indicate the vegetation types: solid circle, primary forest; open circle, fragmented primeval forest; solid square, young fallow; open square, new fallow; solid triangle, rubber plantation; open triangle, old fallow. See Table 1 for plot codes.

Microhabitat environment

To characterize the light conditions at the forest floor, we measured the percent canopy openness using a digital camera with a fisheye lens (CoolPix 910, Nikon). Ten images were taken from the ground in each plot at 10-m intervals and analyzed using the CanopOn2 software (CanopOn 2003).

The soil-water potential was quantified using the method of Deka et al. (1995) in each study plot. Soil samples were taken on 20 February 2005, after a relatively dry spell during which no rain fell for six consecutive days. We sampled 10 soil cores to a 10-cm depth (3-cm in diameter) at 10-m intervals after removing the surface litter. Each soil sample was sealed in a plastic box for 8 days with filter paper (No. 42, Whatman) placed in the middle of the soil. On 1 March 2005, the filter paper was then weighed to within 1 mg after quickly removing the soil with a small paintbrush, and the soil-water potential was calculated (Deka et al. 1995).

Data analysis

We calculated the Shannon-Wiener *H’* parameter as a species diversity index using basal area data for each plot. Analysis of variance (ANOVA) was used to compare the effects of forest use on vegetation structure and microhabitat environment among the vegetation types, after log (absolute values) or arcsine (percentage values) transformation. For plots of fragmented primeval forest, we evaluated the relationships between vegetation structure traits (density, number of species, basal area, and H’) and the area, distance to primary forest, or area of surrounding primary-forest-like vegetation within 200 m of each study plot using a Pearson’s correlation coefficient. All statistical analyses were performed using the JMP 6.0 software (SAS Institute 2005).

Results

Vegetation structure and microhabitat environment

Since no trees ≧10 cm in DBH were found in the new fallow plots, we excluded this category from the ANOVA for vegetation structure. All variables that described vegetation structure and microhabitat environment differed significantly among vegetation types (Table 1). Primary forest and fragmented primeval forest had similar vegetation structures and dominant trees (Dipterocarpaceae), and they showed high tree density, number of species, basal area, and *H’*. Young fallow and rubber plantation plots had significantly low number of species and *H’*, though the density and basal area in young fallow were similar to those of old fallow, which had intermediate vegetation structure traits. The dominant trees were *Vitex pinnata* (Verbenaceae) in young fallow plots, *Artocarpus elasticus* (Moraceae) in old fallow plots, and *Hevea brasiliensis* (Euphorbiaceae, rubber tree) in rubber plantation plots (Table 1). In new fallow plots, grasses (Cyperaceae) grew thickly, mixed with small *Macaranga* and *Artocarpus* trees. Canopy openness and soil-water potential were highest in new fallow and fragmented primeval forest, respectively.

Table 1 Vegetation structure and microhabitat environment of six vegetatoin types studied in and around Lambir Hills National Park. Average variables of each vegetation type were shown.

Vegetation type (plot code)	*N*	Density (/0.1ha)	Species no (/0.1ha)	BA (m^2/ha)	H'	Canopy openness (%)	Water potential	Dominant tree[a]
Primary forest (H)	4	58	44.0	43.1	3.2	7.3	1.5	Dipterocarp trees
Fragmented primeval forest (P)	9	70	47.0	40.1	3.0	7.9	2.4	Dipterocarp trees
New fallow (B)	4	-	-	-	-	20.5	1.9	-
Young fallow (T)	4	40	15.5	7.9	2.0	9.8	1.9	*Vitex pinnata*
Old fallow (F)	6	53	32.7	20.9	2.8	8.2	1.9	*Artocarpus elasticus*
Rubber plantation (G)	5	60	19.2	20.6	1.8	10.8	1.9	*Hevea brasiliensis*

[a] Based on basal area.

Fragmented primeval forest

No significant correlations between forest area and vegetation structure were found for fragmented primeval forest. Tree density and species richness were significantly and negatively correlated with the distance to primary forest (Fig. 2). In contrast, we found significant and positive correlations between the area of the surrounding primary-forest-like vegetation within 200 m of each plot and tree density, species richness, and basal area.

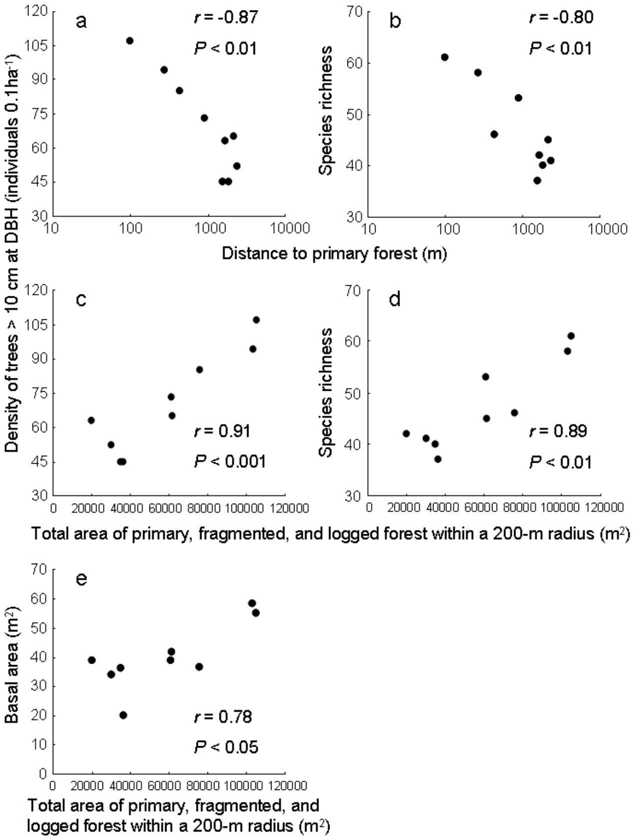

Fig. 2 Correlations between distance to primary forest from each fragmented primeval forest plot and (a) tree density (individuals $0.1ha^{-1}$) and (b) species richness (species numbers $0.1ha^{-1}$), and between area of surrounding primary-forest-like vegetation within 200 m of each fragmented primeval forest plot and (c) tree density, (d) species richness, and (e) basal area (m^2 ha^{-1}).

Discussion

Characteristics of the vegetation structure and microhabitat environment differed obviously among the vegetation types. Primary forest and fragmented primeval forest had larger and denser trees, with higher species richness and a darker forest floor (i.e., reduced canopy openness). However, the soil-water potential was highest in fragmented primeval forest. This might be because these forests are located mainly on ridges. Old fallow had the third-highest species richness, though the trees were smaller than those of primary forest or fragmented primeval forest and the dominant trees were also different. The differences in density and basal area between the young fallow and rubber plantation plots may have been caused by the planting of rubber trees. The vegetation structure and canopy openness in new fallow were distinctive, our results indicate that trees were able to recover from the disturbance and begin growing again relatively quickly, within several years after slash-and-burn agriculture. The alternation of the vegetation structure and microhabitat environment might affect not only the regeneration success of plants and forest dynamics (Bruna 1999; Cascante et al. 2002; Takeuchi et al. unpublished data) but also the biodiversity of fauna and the interactions between plants and animals (Medellín and Equihua 1998; Ferraz et al. 2003; also see several papers in this report).

Although species-area relationships have been widely used both to predict the effects of habitat loss on extinction rates and to guide conservation design (e.g., Wilson 1989), we observed no effects of the area of remnant forest on vegetation structure. Tree density, species richness, and basal area were instead affected by the characteristics of the surrounding vegetation, and particularly by the distance to primary forest and the area of surrounding primary-forest-like vegetation. This indicates that a small-scale mosaics composed of a range of forest types may be important because it enables trees to regenerate or immigrate to neighboring remnants by means of seed dispersal, thereby mitigating otherwise drastic habitat alterations. Gascon et al. (1999) also suggested the importance of a matrix of modified habitats surrounding forest fragments in terms of its effects on the dynamics or composition of vertebrate communities in tropical forest remnants. To practice proper land-use management, it will thus be necessary to consider the distribution of various vegetation types at the landscape level.

Acknowledgments

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References

Beaudet M, Messier C (2002) Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. Agric For Meteorol 110:217-228

Bruna EM (1999) Seed germination in rainforest fragments. Nature 402:139

CanopOn (2003) User's manual for CanopOn 2. Available from http://takenaka-akio.cool.ne.jp/etc/canopon2/

Cascante A, Quesada M, Lobo JJ, Fuchs EA (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree Samanea saman. Conserv Biol 16:137-147

Deka RN, Wairiu M, Mullins PWC, Mullins E, Veenendaal EM, Towsend J (1995) Use and accuracy of the filter-paper technique for measurement of soil matric potential. Eur J Soil Sci 46:233-238

Ferraz G, Russell GJ, Stouffer PC, Bierregaard RO Jr, Pimm SL, Lovejoy TE (2003) Rates of species loss from Amazonian forest fragments. Proc. Natl Acad Sci USA 100:14069-14073

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Conserv 91:223-229

Ichikawa M (2003) One hundred years of land-use changes: political, social, and economic influences on an Iban village in Bakong river basin, Sarawak, East Malaysia. In: Tuck-Po L, de Jong W, Ken-ichi A (eds) The political ecology of tropical forests in Southeast Asia: historical perspectives. Kyoto University Press and Trans Pacific Press, pp 177-199

Laurance WF, Delamônica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature 404:836

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Dedham RK, Stouffer PC, Gascon C, Bierregaard RO,

Laurance SG, Sampaio, E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol 16:605-618

Matthews E (2001) Understanding the FRA 2000. In: Forest Briefing 1, World Resources Institute, Washington, DC

Medellín RA, Equihua M (1998) Mammal species richness and habitat use in rainforest and abandoned agriculture fields in Chiapas, Mexico. J Appl Ecol 35:13-23

SAS Institute (2005) JMP user's guide. SAS Institute, Cary, NC, USA

Wilson EO (1989) Threats to biodiversity. Sci Am 261:108-116

Effects of Deforestation on Butterfly Diversity in and around Lambir Hills National Park, Sarawak, Malaysia

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Introduction

Tropical rainforests have been greatly disturbed by various kinds of human activities. In the lowlands of Sarawak, Malaysia, shifting cultivation based on slash-and-burn agriculture has been widely and conventionally adopted (Ichikawa 2003, 2004). The shifting cultivation accompanies deforestation of primary or secondary forests and is thus likely to influence the biodiversity of these forests. Moreover, this practice usually generates patches of remnant primary (undisturbed) forests and increasingly leads to isolation of these remnant areas (i.e., to forest fragmentation). This isolation is itself thought to reduce biodiversity in remnant forests (Laurence and Bierregaard 1997). To conserve the extremely rich biodiversity of the lowland dipterocarp forests of Sarawak, and to support the required policy development, the effects of human activities (e.g., shifting cultivation) on biodiversity must be qualitatively and quantitatively assessed.

From this perspective, various kinds of arthropods, which are considered to be the richest taxon in terms of species diversity, have been studied (e.g. Vasconcelos 1999, Willott 1999, Willott et al. 2000, Davis et al. 2001, Watt et al. 2002). Among these species, butterflies are a good indicator of biodiversity because they are mostly oligophagous herbivores. They are thus likely to reflect the status and species composition of the vegetation and the characteristics of microhabitats because they are easy to monitor by means of relatively brief, low-labor field surveys based on the observation of flying adults and because it is relatively easy to identify the different species.

In this study, we investigated the butterfly community in a lowland dipterocarp forest in Sarawak and in patchily distributed secondary forests around this primary forest. In particular, we determined the absence and presence of butterfly species in forest stands of different ages based on the elapsed time since slash-and-burn agriculture had been abandoned and in primary forest. By comparing the patterns of absence and presence among forest types, we attempted to determine the effects of the deforestation that accompanies shifting agriculture on the diversity of butterfly species.

Methods

All of our research was conducted in and around the Lambir Hills National Park (LHNP), Sarawak, Malaysia (4°2'–4°11'N, 113°50'–114°3'E; 150 to 200 m a. s. l.). The area of LHNP is ca. 70 km^2 (Yumoto and Nakashizuka 2005), and the climate is humid-tropical, with only a weak seasonal change in rainfall (Kato et al. 1995). Most of LHNP is covered by lowland mixed dipterocarp forest. Details of the vegetational features were described by Kato et al. (1995). The park is surrounded by secondary forest of different stand ages (i.e., different elapsed times after the last slash-and-burn cultivation) and by cultivated fields, rice paddies, extensively managed rubber plantations, and intensively managed oil palm plantations.

In the secondary forest around LHNP, we chose four stand types for our survey: sapling secondary forest stands (abbreviated as SSF) that were 1 year old at the initial time of the survey, young secondary forest stands (YSF) and extensively managed rubber plantations (ERP) that were 7 to 15 years old, and old secondary forest stands (OSF) that were more than 30 years old. In ERP, rubber trees were planted and extensively cultivated, but some of the dominant tree species observed in YSF were also present and grew to a size similar to that of their conspecifics in YSF. In addition, we studied two types of remnant primary forest that were isolated from the primary forest in the national park: distant remnant forest stands (DRF) and nearby forest stands (NRF). The former were more than 1.0 km from the reserved area and the latter were located within 500 m of the border of the reserved area.

For each of the stand types except OSF, we chose three representative study stands; for OSF, we chose six study stands. In each of the 21 forest stands, we established a 100-m line transect at the approximate center of the stand. We also randomly chose two open areas (forest gaps or bordering areas) 20 m in diameter in each forest stand. In addition to the six types of forest stands, we randomly set up three line transects, separated by more than 800 m, in the reserved primary forest of LHNP; we called this type of forest "primary forest" (PF). For each of the line transects in PF, we chose two open areas similar to those in the other six types of forest stand. Nakagawa et al. (2006) provided more details on stand characteristics such as tree species composition, total basal area of trees, and physical environmental conditions. Our study plots were generally similar to those in Nakagawa's study.

We conducted surveys to determine the absence and presence of butterfly species along the line transects and in the two open areas in each study stand. To perform our census in each study stand, we walked along the line transect for ca. 10 min and stayed in each of the open areas for ca. 10 min. During this time, we attempted to capture all butterflies that we encountered. More than half of the butterflies observed were caught using nets and then all caught were identified to the species level. We were also able to visually identify most butterflies that escaped our nets to the species level. We were unable to identify fewer than about 5% of the butterflies, and we omitted these individuals from the census data. All the species were recorded and some butterflies were mounted as voucher specimens, especially for individuals of species that are difficult to identify. The census at each site, which lasted for 30 to 45 min. in total, including handling time, took place in a period under clear skies between 0930 and 1300. The absence and presence data for each species and forest type was obtained twice during this period. We obtained four data matrices (presence or absence of a given species in each type of forest): in August 2003, September 2003, January 2005, and June 2005.

Based on these four matrices, we calculated the number of species observed in each stand. We then compared this number among forest types in order to determine the effects of deforestation on the butterfly species diversity.

Results and Discussion

We identified a total of 159 butterfly species throughout the study period. The number of species observed at least once for each type of forest stand is shown in Fig. 1. The mean number of species was highest in the primary forest stands (PF) and second highest in the nearby remnant forest stands (NRF), followed by the distant remnant forest stands (DRF), the old secondary forest stands (OSF), and the young secondary forest stands (NSF). It was lowest in the sapling secondary forest stand (SSF) and second lowest in the extensively managed rubber plantations (ERP), suggesting that both stand types have substantial negative effects on the butterfly diversity. Approximately 90% of all species recorded throughout the study period were observed in PF. These results suggest that deforestation due to slash-and-burn agriculture drastically decreased the butterfly species diversity in and around the affected area and that it is likely to take a long time (at least several decades based on the results for OSF) for butterfly species diversity to recover. In addition, forest fragmentation (NRF and DRF stands) also remarkably decreased the butterfly species diversity (to roughly half the levels in PF).

The results of our study clearly demonstrate that the disappearance of or large reductions in the area of primary forest clearly threatens to seriously damage the butterfly species diversity in lowland dipterocarp forests of the Southeast Asian tropics. It is likely that similar adverse consequences will occur for other species, but further research will be required to quantify these losses.

References

Davis AJ, Holloway JD, Huijbregts H, Krikken J, Kirk-Spriggs AH, Sutton SL (2001) Dung beetle as indicators of change in the forests of northern Borneo. J Appl Ecol 38:593-616

Ichikawa M (2003) Sarawaku shu Iban Sonraku no Setai nimirareru Seigyo Sentaku (Choice of livelihood activities by Iban household members in Sarawak, East Malaysia). Tropics 12:201-219 (in Japanese with English summary)

Ichikawa M (2004) Relationships among secondary forests and resource use and agriculture, as practiced by the Iban of Sarawak, East Malaysia. Tropics 13:269-286

Inoue T, Yumoto T, Hamid AA, Lee HS, Ogino K (1995) Construction of a canopy observation system in a tropical rainforest of Sarawak. Selbyana 16:24-35

Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T (1995) Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. Res Popul Ecol 37:59-79

Laurance WF, Bierregaard RO Jr (eds) (1997) Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. The University of Chicago Press, Chicago.

Nakagawa M, Miguchi H, Nakashizuka T (2006) The effects of various forest uses on small mammal communities in Sarawak, Malaysia. For Ecol Manage 231:55-62

Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity and Conservation, 8:409-420

Watt AD, Stork NE, Bolton B (2002) The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. J Appl Ecol 39:18-30

Willott SJ (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. Phil Trans R Soc Lond B, 354:1783-1790

Willott SJ, Lim DC, Compton SG, Sutton SL (2000) Effects of selective logging on the butterflies of a Bornean rainforest. Conservation Biology. 14:1055-1065

Yumoto T, Nakashizuka T (2005) The canopy biology program in Sarawak: scope, methods, and merit. In: Roubik DW, Sakai S, Hamid AA (eds) Pollination ecology and the rain forest Sarawak studies. Springer, New York, pp 13-21

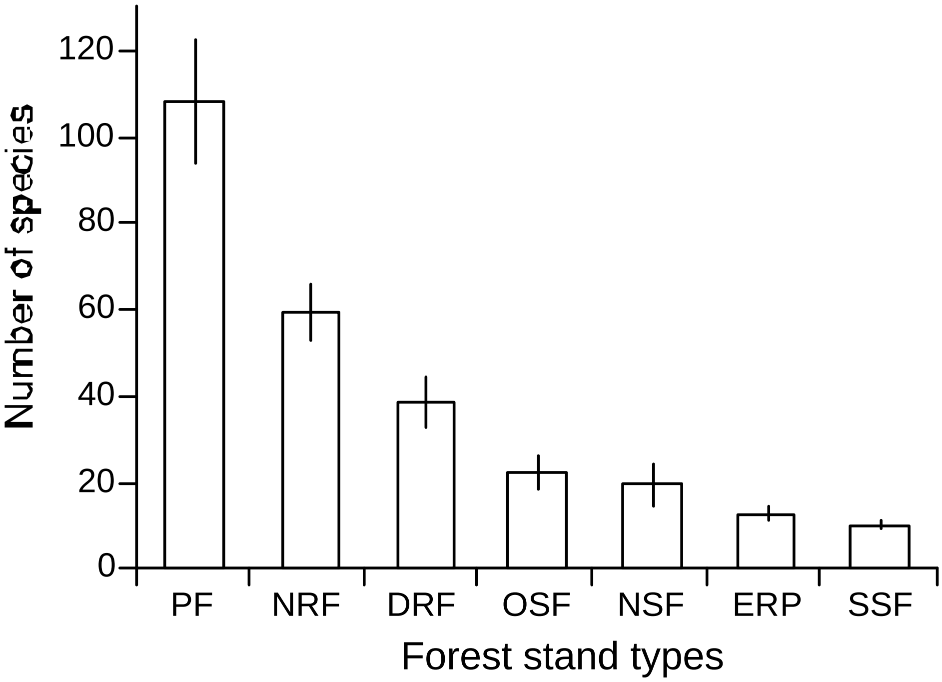

Figure 1. Number of species observed at least once for each forest stand types. Bars and vertical lines indicate the means and standard deviations, respectively. See text for abbreviations of the forest stand types.

Effects of Forest Changes after the Abandonment of Slash-and-Burn Cultivation on the Beetle Diversity in Sarawak, Malaysia

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Introduction

Human impacts on the biodiversity of tropical forests are a widespread concern. To date, several studies have estimated these impacts by using various kinds of insect as indicators (e.g., Lawton et al. 1998; Liow et al. 2001). Such insect indicators have revealed a loss of species in secondary forests and cultivated fields compared to the original species diversity in tropical primary forests (e.g., Chey et al. 1997; Vasconcelos et al. 2000; Davis et al. 2001).

Slash-and-burn agriculture is an important and problematic human impact on forests, leading to significant changes. Around the primary forest of Sarawak, Malaysia, various kinds of forests have developed that represent different developmental stages after the abandonment of slash-and-burn cultivation. Microhabitat structures such as canopy openness, tree species richness, and tree density differ among these forests (Nakagawa et al. 2006). Have these forest changes affected on the insect diversity? Unfortunately, the effects of the different ages of the regenerated forests that resulted from the abandonment of slash-and-burn cultivation on insect diversity are poorly understood.

Since beetles exhibit extreme diversity in form and function, we chose the diversity of this taxon as a useful indicator of the effects of forest changes on biodiversity. In this study, we estimated the species richness, abundance, and composition of beetle assemblages in primary forests and in forests at different stages of regeneration after the abandonment of slash-and-burn cultivation.

Methods

Study Site

The study was conducted from August to September 2003 in and around Lambir Hills National Park, Sarawak, Malaysia (4º20'N, 113º50'E, 150 to 200 m a.s.l.). We established 12 study plots (100x20 m) in each of six forest types representing different stand ages: primary forest (plots H2 and H5), fragmented primeval forest (P2, P7), new fallow (1 year after abandonment; B1, B4), young fallow (5 to 6 years after abandonment; T1, T4), old fallow (>20 years after abandonment; F4, F5), and rubber plantation (G0, G9). Details of the study plots are provided by Nakagawa et al. (2006).

Insect Collections

The beetles were collected in the 12 study plots using a net with a 150-cm stretch at its longest extent. At each plot, we selected 100 thickets and swung a net 10 times in each thicket so that the sweeping covered ca. 196.25 m^2 foliage in total at each plot. The collected beetles were sorted to the family and morphospecies level on the basis of external characteristics.

Diversity and Similarity indices

Simpson's index of diversity (Lande 1996) was adopted to understand what degrees of the beetle diversity were at the 12 study plots. We also calculated Morishita's similarity index (C_λ) (Morishita 1959) to assess the similarity of the chrysomelid fauna between pairs of plots in all combinations of the 12 study plots.

Results and Discussion

Beetle family composition, species richness, and abundance

Of the 166 coleopteran families listed by Lawrence and Newton (1995), 54 families were recorded in the 12 study plots. In terms of the number of species, Chrysomelidae was the most abundant family (ca. 23% of the total) caught throughout the study period, followed by Curculionidae (9%) and Anthicidae (7%). In terms of the number of individuals, Chrysomelidae was the most abundant (32%), followed by Anthicidae (16%) and Coccinellidae (7%). In Sabah, Malaysia, the most abundant coleopteran families were Staphylinidae and Pselaphidae (Chung et al. 2000). The differences in family composition may have resulted from the sampling methods; Chung et al. used three different methods to collect beetles, including ground-dwelling beetles. The most abundant families in the present study were the plant-associated beetles (Chrysomelidae and Curculionidae) and potential predators of herbivorous insects (Anthicidae and Coccinellidae).

The total number of individuals captured during our study was 1937, representing at least 556 species. The number of species was lowest in the primary forest and new fallow plots, but the abundances (number of individuals) shown in the new fallow plots were high (Table 1). The diversity indices were lower in the new fallow plots than in the other plots; in all plots except the new fallow plots, the diversity indices tended to be high (> 0.95; Table 1). A previous analysis at our study site using various microhabitat structure variables (Nakagawa et al. 2006) distinguished three groups of forest types: (A) primary forest plots, (B) new fallow plots, and (C) other plots. Since the plots for groups A and C were characterized by relatively high basal area, tree density, and tree species richness, the resulting microhabitat structures may enhance the beetle diversity in these plots. The primary forest plots were relatively shady, with a thick canopy layer, and we never included any of the gaps that occasionally appeared in primary forests in our study. Thus, we may

Table 1 The number of species, abundances (number of individuals), and Simpson's index of diversity (SID) of beetles in the 12 study plots

Forest type Plot	No. of species	No. of individuals	SID
Primary forest			
H2	23	28	0.980
H5	35	51	0.980
Fragmented primeval forest			
P2	51	85	0.980
P7	96	208	0.946
New fallow			
B1	38	172	0.710
B4	37	114	0.930
Young fallow			
T1	100	218	0.990
T4	70	129	0.975
Old fallow			
F4	61	183	0.950
F5	84	236	0.950
Rubber plantation			
G0	98	213	0.960
G9	100	262	0.960

have underestimated the species richness on the primary forest floor, because shady floor and brighter gaps are often mixed on the primary forest floor.

Species richness and abundance (number of individuals) data revealed that Chrysomelidae dominated most of the study plots (Table 2). Carabidae, most of which are carnivores, were abundant in one primary forest plot, but their numbers were low in other plots.

Table 2 List of top two abundant families in regard of species number and abundances in the 12 study plots

Top two abundant families in regard of species richness						
	H2	H5	P2	P7	B1	B4
1	Curculionidae (36%)	Chrysomelidae (23%)	Chrysomelidae (24%)	Chrysomelidae (19%)	Chrysomelidae (32%)	Chrysomelidae (34%)
2	Elateridae (14%) Chrysomelidae (14%)	Carabidae (11%)	Anthicidae (20%)	Anthicidae (18%)	Anthicidae (13%)	Coccinellidae (10%) Elateridae (10%)
	T1	T4	F4	F5	G0	G9
1	Chrysomelidae (28%)	Chrysomelidae (27%)	Chrysomelidae (38%)	Chrysomelidae (30%)	Chrysomelidae (14%)	Chrysomelidae (22%)
2	Anthicidae (7%) Curculionidae (7%)	Coccinellidae (11%)	Anthicidae (11%)	Anthicidae (10%)	Anthriidae (10%) Curculionidae (10%)	Coccinellidae (11%)
Top two abundant families in regard of abundances						
	H2	H5	P2	P7	B1	B4
1	Curculionidae (38%)	Carabidae (22%)	Chrysomelidae (25%)	Anthicidae (23%)	Anthicidae (59%)	Chrysomelidae (49%)
2	Chrysomelidae (10%) Coccinellidae (10%) Elateridae (10%)	Chrysomelidae (20%)	Anthicidae (22%)	Ptinidae (20%)	Chrysomelidae (27%)	Anthicidae (12%)
	T1	T4	F4	F5	G0	G9
1	Chrysomelidae (23%)	Chrysomelidae (40%)	Chrysomelidae (42%)	Chrysomelidae (50%)	Chrysomelidae (30%)	Chrysomelidae (30%)
2	Anthicidae (16%)	Phalacridae (9%)	Cantharidae (16%)	Cantharidae (9%)	Anthicidae (12%)	Cantharidae (15%)

Numbers in the parentheses represent the propotion of the family to total species or individuals captured in each plot

Distribution of species-abundance in the 12 study plots

The species rank-abundance curves showed that the primary forest plots and one of the fragmented primeval forest plots had relatively shallow curves compared to those of the other plots (Fig. 1). This suggests that the evenness of the species abundance in the former plots is high. A single species of Anthicidae dominated (more than half of all individuals) in one new fallow plot (B1; Fig. 1). Such dominant species may be rare in primary forests and forests that retain most of the characteristics of primary forests.

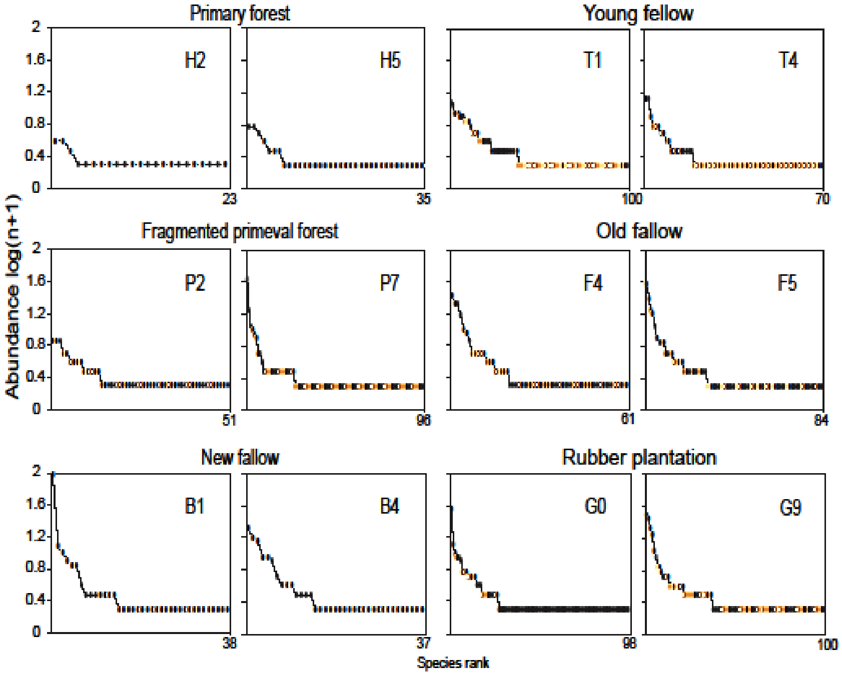

Fig. 1 Species rank-abundance curves for the beetles at the 12 study plots

Chrysomelid fauna in the 12 study plots

For the paired combinations of the same forest type, we found high similarity indices for the chrysomelid fauna in primary forest, new fallow, and old fallow, but the similarity indices were low between the two plots belonging to the fragmented primeval forest, young fallow, and rubber plantation (Table 3). The highest similarity index (0.990) was between H5 and G9 (Table 3), suggesting that the chrysomelid faunas in these plots strongly resemble each other; however, the microhabitat structures of these two plots were not particularly similar (Nakagawa et al. 2006). The chrysomelid species found in the new fallow plots rarely appeared in other plots and never appeared in primary forest and fragmented primeval forest (Fig. 2). Only two species caught in some plots (P7, T1, F4, G0, G9) were found in the primary forest plots (Fig. 2), suggesting that few species that inhabit deforested areas can invade primary forests.

Table 3 Similarity of chrysomelid fauna (C_λ) of the 12 study plots

	H2	H5	P2	P7	B1	B4	T1	T4	F4	F5	G0	G9
H2	-	-	-	-	-	-	-	-	-	-	-	-
H5	**0.950**	-	-	-	-	-	-	-	-	-	-	-
P2	0.000	0.000	-	-	-	-	-	-	-	-	-	-
P7	0.000	**0.690**	0.000	-	-	-	-	-	-	-	-	-
B1	0.000	0.000	0.000	0.000	-	-	-	-	-	-	-	-
B4	0.000	0.000	**0.070**	0.000	**0.680**	-	-	-	-	-	-	-
T1	0.000	**0.250**	**0.170**	**0.150**	**0.130**	**0.110**	-	-	-	-	-	-
T4	0.000	0.000	0.000	**0.010**	**0.390**	**0.410**	**0.170**	-	-	-	-	-
F4	0.000	**0.160**	**0.630**	**0.280**	**0.006**	**0.060**	**0.210**	**0.050**	-	-	-	-
F5	0.000	**0.380**	**0.730**	**0.340**	**0.008**	**0.070**	**0.220**	**0.010**	**0.700**	-	-	-
G0	0.000	**0.030**	0.000	**0.030**	0.000	**0.008**	**0.130**	**0.070**	**0.130**	**0.020**	-	-
G9	0.000	**0.990**	**0.020**	**0.420**	**0.070**	**0.060**	**0.230**	**0.060**	**0.290**	**0.330**	**0.080**	-

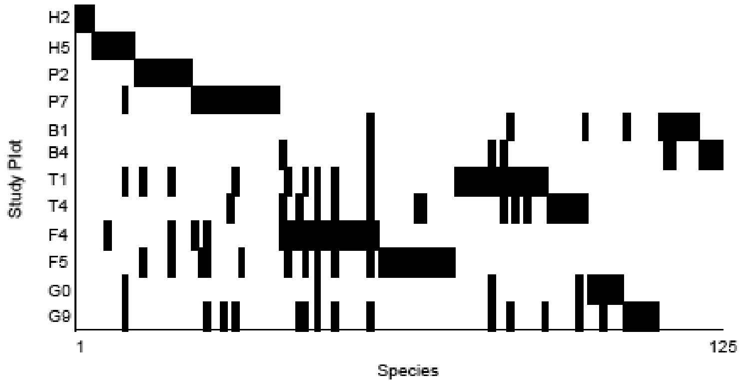

Fig. 2 Species overlap of chrysomelid assemblages among the 12 study plots

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References

Chey VK, Holloway JD, Speight MR (1997) Diversity of moths in forest plantations and natural forests in Sabah. Bull Entomol Res 87:371–385

Chung AYC, Eggleton P, Speight MR, Hammond PM, Chey VK (2000) The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. Bull Entomol Res 90:475–496

Davis A J, Holloway JD, Huijbregts H, Krikken J, Kirk-Spriggs AH, Sutton SL (2001) Dung beetles as indicators of change in the forests of northern Borneo. J Anim Ecol 38:593–616

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76:5–13

Lawrence JF, Newton AF Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera papers celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa, pp 779–1006

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Liow LH, Sodhi N, Elmqvist T (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. J Appl Ecol 38: 80–192

Morishita M (1959) Measuring of interspecific association and similarity between communities. Mem Fac Sci Kyushu Univ Ser E (Biol) 3:65–80

Nakagawa M, Miguchi H, Nakashizuka T (2006) The effects of various forest uses on small mammal communities in Sarawak, Malaysia. For Ecol Manage 231:55–62

Vasconcelos HL, Vilhena JMS, Caliri GJA (2000) Responses of ants to selective logging of a central Amazonian forest. J Appl Ecol 37:508–514

Effects of Traditional Forest Uses on the Number of Colonies of Army Ants

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Introduction

The rapid and widespread loss of biological diversity is a matter of considerable concern. Destruction of tropical rain forests, one of the most diverse terrestrial ecosystems, is one of the major factors responsible for the high rates of species extinction in recent years (Myers 1988). Globally, tropical rain forests are disappearing at a rate of 12 million ha per year (Cyranoski 2007). Furthermore, less than 5% of the total land area of tropical rainforests is protected as reserves or national parks (Western 1989). Thus, the development of methods of using tropical rain forests that can prevent biodiversity loss is urgently needed.

In Southeast Asia, swidden (slash-and-burn) agriculture has been widely used by local residents and is frequently regarded as one of the primary causes of forest degradation and loss (Freeman 1955; Lanly 1982). Others, however, have stated that traditional methods of swidden agriculture are sustainable and maintain the ecosystem because of long fallow periods as well as the complex mosaic pattern of agricultural fields, abandoned fields in various stages of forest regrowth, and primary forest (Salafsky 1993; Aumeerudy and Sanonnens 1994; Coomes et al. 2000). To better understand whether traditional swidden agriculture is sustainable in terms of conservation of biodiversity, we need to examine whether biodiversity in secondary forests recovers to initial levels following cultivation and, if so, how long it takes.

In the present study, we compared encounter rates between primary forests and secondary forests with various fallow periods for the top predator found among litter arthropods, the army ant (*Aenictus* and *Leptogenys* species). The top predator was chosen as an indicator for biodiversity loss caused by disturbance because it is vulnerable to disturbance and degradation (Noss et al. 1996) and also because it frequently plays an important role in structuring communities (Polis et al. 2000; Schmitz et al. 2000; Schmitz and Suttle 2001).

Material and Methods

Study site

The study was conducted in and around Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E; 150 to 200 m a.s.l.). Details of the park were described in Inoue et al. (1995). Local residents near the park have practiced swidden agriculture to cultivate rice and vegetables for about 100 years (Ichikawa 2002). To examine the effect of traditional swidden agriculture on biodiversity, we established two plots within the park, 11 plots in secondary forests at various developmental stages, and six plots in isolated primary forests near the park. Secondary forests were categorized into three groups depending on time since the abandonment of cultivation: new fallow (NF), <2 years after abandonment (*N*=3); young secondary forest (NSF), 5 years after abandonment (*N*=3); and old secondary forest (OSF), >20 years after abandonment

(*N*=5).

Field census

We visually located army ant colonies from August to September 2003 and from January to February in 2005. Above-ground ant foraging activity is readily detected by observers because the ants move in coordinated columns on the forest floor, tree trunks, or vines. Three 1-h searches were conducted at each plot during each census period. Censuses were performed between 0800 and 1700 hours on days with good weather. Results from the three 1-h searches were combined for analysis for each census period. Prior to analysis, the numbers of ant colonies were log-transformed (y = log [x + 0.5]) to stabilize the variances (Yamamura 1999).

Results

A total of nine *Aenictus* species was observed in 26 colonies. *Aenictus laeviceps* morphotypes L1 and L2 were the dominant species (53% of the total colonies in 2003 and 55% in 2005). *Aenictus inflatus*, *A. camposi*, *A. hottai*, and *A. cornutus* were not detected in the primary forests, and *A. gracilis* was observed only in the isolated primary forest (Table 1a). All of the *Aenictus* colonies detected in this study were on raid and no emigrating colony was observed. The number of *Aenictus* colonies differed significantly among forest types (repeated ANOVA: F = 6.42, df = 4, P = 0.004; Fig. 1a), with the highest number of colonies found in the primary forest, an intermediate number found in young and old secondary forests, and the lowest number in new fallow (Tukey-Kramer HSD: P < 0.05; Fig 1a). No significant differences were found between years (repeated ANOVA: F = 0.006, df = 1, P = 0.93) or for the interaction between year and forest type (repeated ANOVA: F = 2.08, df = 4, P = 0.13; Fig 1a).

For *Leptogenys*, we detected six species (36 colonies) in 2003 and four species (22 colonies) in 2005 (Table 1b). In contrast with *Aenictus*, differences in encounter rates with *Leptogenys* were not significant among forest types, although there was a weak tendency for more *Leptogenys* to be encountered in primary forests (repeated ANOVA: F = 2.43, df = 4, 14, P = 0.10; Fig 1b). No significant differences were found between years or for the interaction between year and forest type (F = 2.82, df = 1, 1, P = 0.12 for year; F = 0.25, df = 4, 14, P = 0.90 for interaction; Fig 1b).

Discussion

When *Aenictus* was used as a bioindicator, traditional swidden agriculture was shown to have a serious impact on biodiversity in the tropical rain forest of Sarawak. Once an area was farmed using swidden agriculture, the effect of the disturbance lasted more than 20 years, although some Dipterocarp trees recovered at old secondary forests (Momose et al., unpublished data). Vasconcelos (1999) suggested that ground-dwelling ant fauna recovered in as few as 25 years when the intensity of the disturbance was low, so it seems that the impact of traditional swidden agriculture on biodiversity is more severe than was previously expected. It is possible that a longer fallow period would increase the abundance of *Aenictus*. However, no *Aenictus* was detected in old secondary forests (>100 years after abandonment). Thus, it seems to be unrealistic to expect that biodiversity will be maintained by extending the fallow period.

Some *Aenictus* colonies were observed in young and old secondary forests, although in smaller numbers than in the primary forest. All of the secondary forests in which army ants were observed, except one, were located proximate to continuous primary forest. This means that remnant primary forest may have contributed to the maintenance of biodiversity in the surrounding area. In terms of managing forest usage to sustain biological diversity, our study suggested that preserving enough primary forest would be more effective than extending the fallow period after traditional swidden agriculture.

Four *Aenictus* species (*A. inflatus, A. camposi, A. hottai,* and *A. cornutus*) were observed only in secondary forests. All four species have previously been detected in a continuous primary forest (Yamane and Hashimoto 1999; Yamane, unpublished data). Therefore, it is unlikely that segregation of the *Aenictus* group occurred between forest types.

In contrast to *Aenicitus*, the number of colonies of *Leptogenys* did not differ among forest types. *Aenictus* preys exclusively on immature social insects (Gotward 1976), whereas the diet of *Leptogenys* is much broader (Maschwitz and Mühlenberg 1975; Suzzoni et al. 2000; but see Mashwitz and Schönegge 1983). Using *Eciton burchelli* and *Labidus praedator,* who prey on almost all kinds of arthropods (Rettenmeyer 1963a,b), Roberts et al. (2000) showed that the number of colonies of army ants did not differ significantly between a primary forest and a traditional shady coffee plantation. Future research is required about the relationship between the breadth of diet and the strength of tolerance to artificial disturbance among army ant groups.

Table 1a. List of *Aenictus* species encountered during the census in each forest type in 2003 (upper) and 2005 (lower)

2003		*Aenictus*								
Forest type	total	*A. laeviceps morpthotype L1*	*A. laeviceps morpthotype L2*	*A. gracilis*	*A. dentatus*	*A. inflatus*	*A. camposi*	*A. hottai*	*A. sp5 of sky*	*A. cornutus*
NF (n=3)	0	0	0	0	0	0	0	0	0	0
YSF (n=3)	0	0	0	0	0	0	0	0	0	0
OSF (n=5)	1	0	0	0	0	1	0	0	0	0
IPF (n=6)	9	3	2	2	1	0	0	0	0	1
CPF (n=2)	5	2	1	0	1	0	0	0	1	0

2005		*Aenictus*								
Forest type	total	*A. laeviceps morpthotype L1*	*A. laeviceps morpthotype L2*	*A. gracilis*	*A. dentatus*	*A. inflatus*	*A. camposi*	*A. hottai*	*A. sp5 of sky*	*A. cornutus*
NF (n=3)	0	0	0	0	0	0	0	0	0	0
YSF (n=3)	2	0	0	0	0	1	1	0	0	0
OSF (n=5)	2	1	0	0	1	0	0	0	0	0
IPF (n=6)	4	1	1	0	0	1	0	1	0	0
CPF (n=2)	3	2	1	0	0	0	0	0	0	0

NF, YSF, OSF, IPF, CPF designated new fallow, young secondary forest, old secondary forest, isolated primary forest, and continuous primary forest, respectively. See M&M for the definition of each forest type.

Table 1b. List of *Leptogenys* species encountered during the census in each forest type in 2003 (upper) and 2005 (lower)

2003	*Leptogenys*						
Forest type	total	*L. processionalis*	*L. diminuta*	*L. sp39 of sky*	*L. sp 6 of sky*	*L. mutabilis*	*L. chalybaea*
NF (n=3)	5	4	1	0	0	0	0
YSF (n=3)	1	0	0	1	0	0	0
OSF (n=5)	10	5	1	4	0	0	0
IPF (n=6)	11	2	5	3	1	0	0
CPF (n=2)	9	3	3	1	0	1	1

2005	*Leptogenys*						
Forest type	total	*L. processionalis*	*L. diminuta*	*L. sp39 of sky*	*L. sp 6 of sky*	*L. mutabilis*	*L. chalybaea*
NF (n=3)	2	2	0	0	0	0	0
YSF (n=3)	1	0	1	0	0	0	0
OSF (n=5)	5	2	2	1	0	0	0
IPF (n=6)	7	2	3	2	0	0	0
CPF (n=2)	7	3	2	1	0	0	1

NF, YSF, OSF, IPF, CPF designated new fallow, young secondary forest, old secondary forest, isolated primary forest, and continuous primary forest, respectively.
See M&M for the definition of each forest type.

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References

Aummeeruddy Y, Sansonnens B (1994) Shifting from simple to complex agroforestry systems: an example for buffer zone management from Kerinci. Agrofor Ayst 28:113–141

Coomes OT, Grimard F, Burt G (2000) Tropical forests and shifting cultivation: secondary forest fallow dynamics among traditional formers of the Peruvian Amazon. Ecol Econ 32:109–124

Cyranoski D (2007) Logging: the new conservation. Nature 446:608–610

Freeman JD (1955) Iban agriculture: a report on the shifting cultivation of hill rice by the Iban of Sarawak. HMSO, London

Gotward WHJr (1976) Behavioral observations on African army ants of the genus *Aenictus* (Hymenoptera: Formicidae). Biotropica 8:59–65

Ichikawa M (2002) Studies on uses of ecological resources at an Iban village in Bakong river basin, Sarawak. Ph D Thesis Kyoto University (in Japanese)

Inoue T, Yumoto T, Hamid AA, Seng LH, Ogino K (1995). Construction of a canopy observation system in a tropical rainforest of Sarawak. Selbyana 16:24–35.

Lanly JP (1982) Tropical forest resources. FAO Forestry Paper 30, FAO, Rome

Maschwitz U, Mühlenberg M (1975) Zur Jagdstrategie einiger orientalischer *Leptogenys-Arten* (Formicidae: Ponerinae). Oeocologia 20:65–83 (in German with an English summary)

Maschwitz U, Schönegge P (1983) Forage communication, nest moving recruitment, and prey specialization in the oriental ponerine *Leptogenys chinensis*. Oecologia 57:175–182

Myers N (1988) Tropical deforestation and climatic-change. Environ Conserv 15:293–298

Noss RF, Quigley HB, Hornocker MG, Merrill T, Paquet PC (1996) Conservation biology and carnivore conservation in the Rocky Mountains. Conserv Biol 10:949–963

Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? Tr Ecol Evol 15:473–475

Rettenmeyer CW (1963a) The behavior of Thysanura found with army ants. Ann Entomol Soc Am 56:170–174

Rettenmeyer CW (1963b) Behavioral studies of army ants. Univ Kan Sci Bull 44:281–465

Roberts DL, Robert JC, Petit LJ (2000) Use of premontane moist forest and shade coffee agroecosystems by army ants in Western Panama. Conserv Biol 14:192–199

Salafsky N (1993) Mammalian use of a buffer zone agroforestry system bordering Gunung Palung National Park, West Kalimantan, Indonesia. Conserv Biol 7:928–933

Schmitz OJ, Hamback PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. Am Nat 155:141–153

Schmitz OJ, Suttle KB (2001) Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081

Suzzoni JP, Schatz B, Dejean A (2000) Essential and alternative prey in a ponerine ant: variations according to the colony cycle. Life Sciences 32:1003–1008

Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodivers Conserv 8:407–418

Western D (1989) Conservation without parks: wildlife in a rural landscape. In: Western D, Pearl MC (eds) Conservation for the twenty-first century. Oxford University Press, New York, pp 158–165

Yamane S, Hashimoto Y (1999) A remarkable new species of the army ant genus *Aenictus* (Hymenoptera, Formicidae) with a polymorphic worker caste. Tropics 8:427–432

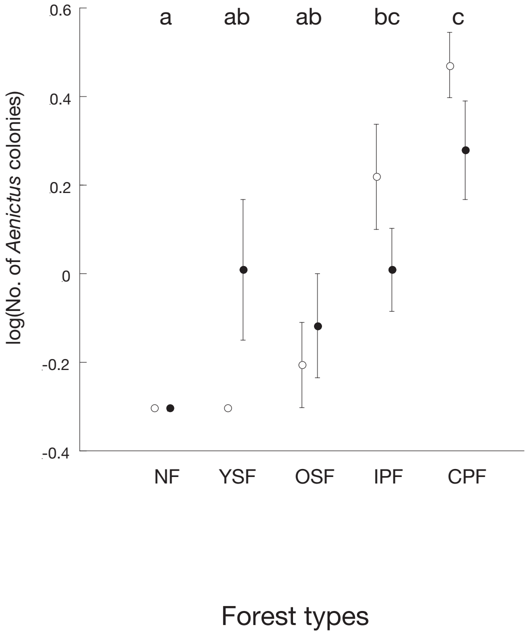

Figure 1a. Mean (±S.E.) of log-transformed encounter rates with *Aenictus* species within each forest type in 2003 (open circle) and 2005 (solid circle). Different letters among circle designated significant difference among forest types. NF, YSF, OSF, IPF, CPF designated new fallow, young secondary forest, old secondary forest, isolated primary forest, and continuous primary forest, respectively. See M&M for the definition of each forest type.

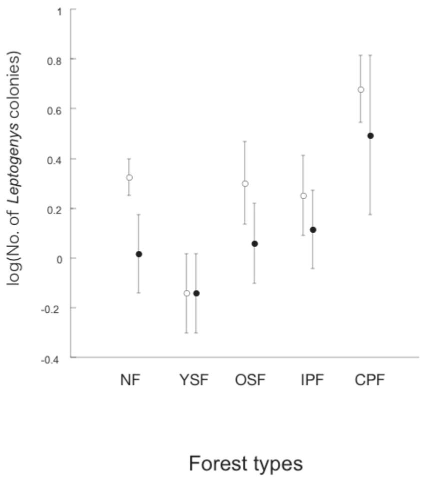

Figure 1b. Mean (±S.E.) of log-transformed encounter rates with *Leptogenys* species within each forest type in 2003 (open circle) and 2005 (solid circle). NF, YSF, OSF, IPF, CPF designated new fallow, young secondary forest, old secondary forest, isolated primary forest, and continuous primary forest, respectively. See M&M for the definition of each forest type.

Effects of Land-Use Changes on Bat Diversity in and around Lambir Hills National Park, Sarawak, Malaysia

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Introduction

Tropical forest landscapes are changing rapidly because of human activities. Approximately half of the potential tropical closed-canopy forest has already been removed and converted to other uses (Wright 2005). The effects of these anthropogenic changes on mammals have been studied across several taxonomic groups. Among these groups, bats (Chiroptera) are thought to be one of the most vulnerable taxa. Major threats to bat populations include the loss or reduction in quality of foraging habitat and habitat fragmentation (Racey and Entwistle 2002).

The order Chiroptera is divided into two suborders: the Megachiroptera, with a single family (Pteropodidae, ca. 163 species) and the Microchiroptera, with 17 families (ca. 814 species in total; Corbet and Hill 1992). Megachiropterans are known as Old World fruit bats and are distributed across Africa, tropical Asia, India, Australia, and their surrounding oceanic islands. Megachiropterans are relatively large (20 - 1500 g) and feed exclusively on plants (fruits, nectar, pollen, flowers, and leaves). In contrast, microchiropterans are found on every continent except Antarctica, are relatively small (1.5 to 150 g), and exhibit more diverse feeding habits (e.g., insectivorous, frugivorous, nectarivorous, ichthyophagous, and sanguivorous; Altringham 1996).

Recent studies have indicated that many bat species play important roles in tropical rain forests. Pollination by bats is a phenomenon restricted to the tropics and subtropics. Megachiropterans visit at least 141 plant species, including a number of commercially important plants (e.g., *Durio, Ceiba,* and *Parkia*) for nectar or pollen (Fujita and Tuttle 1991). Megachiropterans feed upon 145 genera of fruits and presumably disperse the seeds of the majority of the fruits they consume (Marshall 1985). In addition, approximately 70% of extant bat species are insectivorous and prey on a diverse range of insects (e.g., Lepidoptera, Diptera, Coleoptera, and Hemiptera; Jones and Rydell 2002).

Southeast Asia has the highest deforestation rate of any major tropical region, and currently, more than 50% of the land area in Asia is used for agricultural purposes (Zhao et al. 2006). The conversion of forests to cash-crop plantations (e.g., oil palm, rubber, and cocoa) is thought to be one of the major causes of the current high deforestation rates in the region (Primack and Corlett 2005). Such anthropogenic changes can create mosaics of fragmented vegetation, thereby greatly affecting the diversity, abundance, and feeding behavior of bats. Megachiropterans that inhabit these mosaic landscapes are expected to feed on crops because some agricultural plants may serve as food sources, and the bats can fly long distances from mosaic to mosaic. However, little is known about the effects and extent of the impacts of these anthropogenic changes.

The area surrounding a primary forest of the Lambir Hills National Park in Borneo is a typical example of such a mosaic landscape, including various agricultural lands and fragmented primary and secondary forests. In this study, we investigated the bat community in the mosaic landscape. Specifically, we explored differences in the density and diversity of megachiropterans between primary forests and agricultural lands within the landscape.

Methods

We conducted our research in and around the Lambir Hills National Park (LHNP), Sarawak, Malaysia (Fig. 1; 4°2'N, 113°50'E; ca. 150 m a.s.l.). One characteristic of the site was the high heterogeneity of vegetation. We selected four types of vegetation for bat censuses: primary forests, secondary forests, orchards, and oil palm plantations. The primary forests were intact lowland mixed dipterocarp forests within the LHNP. The park covers an area of 6949 ha and the height of emergent trees sometimes exceeds 70 m. Shanahan and Debski (2002) recorded 10 species of bats (five megachiropterans and five microchiropterans) in the park. The secondary forests were young forests that developed after slash-and-burn agriculture had been conducted by Iban villagers. Census points were established in three forests of varying ages: a 7-year-old forest dominated by *Vitex pinnata*, an approximately 30-year-old forest dominated by *Artocarpus elasticus*, and a >60-year-old forest dominated by A. *elasticus* (Nakagawa et al. 2006). Forest height varied among census points (2 - 25 m). These forests were surrounded by ponds, paddy fields, isolated intact forests, and rubber (*Hevea brasiliensis*) forests. The orchards were small (<5 ha) areas with many cultivated plants (e.g., *Durio kutejensis*, *Nephelium lappaceum*, *Carica papaya*, *Cocos* sp., *Musa* sp., *Parkia* sp., *Artocarpus integer*, *Lansium domesticum*, *Piper* sp., and *Saccharum* sp.) established by Iban villagers. Tree height ranged from 1 to 10 m. The orchards were located near villagers' houses and were surrounded by ponds, paddy fields, rubber forests, and bamboo groves. The oil palm plantations were large-scale (ca. 4000 ha) continuous plantations of mature African oil palm (*Elaeis guineensis*) managed either by a corporation or by Iban villagers. Vegetation consisted of a complete monoculture, and the heights of oil palms were 10 to 20 m. The plantations shared borders with the primary and secondary forests.

Censuses were conducted four times between April 2005 and August 2006. We set mist nets on the ground along trails in the forests or forest edges. In the primary forests, we also set nets on canopy walkways (at a height of 15 to 35 m) for five nights. There were no significant differences between data from the ground and the walkways so the data were combined. We used two to four nets (24- to 36-mm mesh; 6 to 12 m long; 6.0 m high; eight shelves) per night and occasionally harp traps (The Austbat Harptrap, Faunatech and Austbat, Australia; 4.2 m2 in area; four nights in the primary forests and two nights in the orchards). Traps were set at sunset and checked at 15-min intervals. Sampling continued until 2300 hours unless it rained, since bat activities are usually very low in the rain. We recorded age, sex, morphological measurements, and reproductive state of the captured bats. Age class was determined by the degree of fusion of the epiphyseal plates on the phalanges, which can be determined without harming the bats (Kunz 1988). Bats with unfused epiphyseal plates were regarded as juveniles. The number of census points and sampling effort varied among vegetation type: 14 179 m2h (area of traps [m2] × sampling time [h]) in the primary forests (six census points), 8707 m2h in the secondary forests (three census points), 6526 m2h in the orchards (three census points), and 3382 m2h in the oil palm plantations (five census points).

We identified bat species according to Payne and Francis (1998). Because some studies have suggested the presence of two cryptic species within *Cynopterus brachyotis* that differ significantly in genetic and morphological characteristics as well as habitat preferences (Francis 1990; Abdullah et al. 2000; Abdullah 2003), we divided the species into two categories (C. *brachyotis* I and C. *brachyotis* II). We classified individuals of C. *brachyotis* based on their forearm length: in adult C. *brachyotis* I (the larger form), the forearm length ranged from 60 to 66 mm, whereas for adult C. *brachyotis* II (the smaller form), the forearm length was approximately 55 mm but always less than 60 mm (M.T. Abdullah, UNIMAS, pers. comm.). If individuals of the species were juveniles and their forearm lengths were less than 60 mm, they were recorded as "C. *brachyotis* (unidentifiable)".

A chi-squared test (Sokal and Rohlf 1973) was used to compare the number of captures of megachiropterans, microchiropterans, and each individual species among the vegetation types. In the chi-squared tests, the observed and expected numbers of captures were compared. The expected number of captures was calculated based on the assumption that the capture rate was equal for each vegetation type.

Simpson's index of diversity (Simpson 1949) was calculated for each vegetation type. Unidentifiable individuals of C. *brachyotis* (see above) were assigned to C. *brachyotis* I and C. *brachyotis* II based on the proportion of the two forms in the community.

Results

The total sampling effort (32 795 m2h) resulted in the capture of 495 bats representing 28 species in five families. The capture rate of megachiropterans differed significantly ($P < 0.001$) among the four vegetation types and was particularly high in the oil palm plantations and orchards compared to the primary and secondary forests (Table 1). The capture rate of microchiropterans also differed significantly ($P < 0.001$) among vegetation types and was lower in the oil palm plantations compared to the other three plant communities (Table 1).

For the eight bat species with relatively large sample sizes (>20 individuals), capture rate varied among vegetation types (Table 1). The capture rates of *Balionycteris maculata*, *Penthetor lucasii*, and *Hipposideros cervinus* were the highest in primary forests. Capture rates were lower in secondary forests than in primary forests for all species except *C. brachyotis* I and II. In the orchards, the capture rates of *Eonycteris spelaea*, *Macroglossus minimus*, and *Glischropus tylopus* were very high compared to those in the other three vegetation types. In contrast, *B. maculata* and *P. lucasii* were not observed in the orchards. In the oil palm plantations, the capture rate of *C. brachyotis* I was notably higher than in the other vegetation types. However, the capture rates of other bat species were low or zero in the plantations.

Cynopterus brachyotis I was the most common and abundant species in all vegetation types, except for primary forests. This species accounted for 44% of all bats in the secondary forests, 41% in the orchards, and 72% in the oil palm plantations. In the primary forests, the dominant species was *H. cervinus* (24% of all bats), and *C. brachyotis* I accounted for only 4% of bats.

Simpson's index of diversity also varied among plant communities (Table 2). Simpson's index for megachiropterans was highest in primary forests, lower in secondary forests and orchards, and lowest in the oil palm plantations.

Discussion

To our knowledge, ours is the first study to demonstrate clear differences in the diversity and abundance of bats among forests and agricultural lands within a single landscape in Southeast Asia. The study showed that the diversity and abundance of bats are strikingly different among different vegetations in spite of a relatively small study area. In addition, the observed movements and feeding habits demonstrated potential effects of agricultural lands on nearby forests or other vegetation.

Relative to primary and secondary forests, the number of megachiropteran species was somewhat low in orchards and notably low in the oil palm plantations. In addition, the capture rates of two frugivorous bats (*B. maculata* and *P. lucasii*) clearly differed among the four vegetation types, and the two species were not recorded in the orchards or the oil palm plantations. These results indicate that megachiropteran species rarely use agricultural lands for feeding; thus, the vegetation is not suitable for maintaining a diversity of megachiropterans. Moreover, there may be no species unique to agricultural lands because those species for which more than two individuals were captured were also recorded at least once in the primary or secondary forests. Megachiropteran diversity in natural forests is thought to be maintained by various factors, including the diversity of food sources (Hall et al. 2004; Hodgkison et al. 2004a), the availability of roosts for tree-roosting bats (Zubaid 1993), and the heterogeneity of forest structure (Hall et al. 2004; Hodgkison et al. 2004b). The oil palm plantations clearly lacked these characteristics.

The capture rate of megachiropterans differed significantly among vegetation types, with high rates in the oil palm plantations and orchards and low rates in the secondary and primary forests. This trend was nearly opposite to the pattern of bat diversity; diversity was quite low in plantations, low in orchards and relatively high in the secondary and primary forests. The observed high capture rate and low species diversity of megachiropterans in agricultural lands were similar to the pattern reported by Hall et al. (2004), although their sampling sites were scattered across Southeast Asia and the crop species studied differed from those in our study. In the Philippines, Heaney et al. (1989) also measured high capture rates and low diversity of megachiropterans in agricultural lands relative to lowland forests. Thus, these patterns may be common throughout Southeast Asia. Similar patterns have also been found in the Neotropics. For example, Medellin et al. (2000) observed both low species richness of phyllostomid bats and high dominance of particular bat species in agricultural lands (shaded cacao plantations and cornfields with other crops) compared to adjacent rainforests. Phyllostomid bat diversity was also low in coffee plantations relative to small fragmented forests (Numa et al. 2005).

Microchiropterans showed a pattern quite different from megachiropterans. The capture rate of microchiropterans was lower in the oil palm plantations but did not differ among the other three vegetation types. One possible cause of the strikingly low capture rate of microchiropterans in the oil palm plantations may have been the low abundance of insects. Although studies concerning the abundance of prey insects in this vegetation type are rare, Chung et al. (2000) reported low beetle abundance and diversity in oil palm plantations compared to logged and primary forests in Sabah, Malaysia.

The drastic increase of *C. brachyotis* I in the oil palm plantations was a particularly intriguing result. The population size of *C. brachyotis* I in the oil palm plantations may indeed be large, considering that its capture rate was extraordinarily high and the plantations cover a vast area (ca. 388,500 ha in Sarawak as of 2004; Brown and Jacobson 2005). High capture rates and dominance of *C. brachyotis* in agricultural lands have been reported repeatedly in other regions (Abdullah et al. 1997; Hall et al. 2004). For example, Abdullah et al. (1997) measured a very high capture rate of *C. brachyotis* (570 individuals per 10,000 m^2h) in *Cocos* and *Musa* plantations in Indonesia, where *C. brachyotis* accounted for 93% of total captures. We collected seeds of forest plants from individuals captured in the plantation. The results indicate that the species move into, and affect, adjacent forests, although the intensity of the effects is unknown.

References

Abdullah MT. 2003. Biogeography and variation of Cynopterus brachyotis in Southeast Asia. PhD thesis. The University of Queensland, Australia.

Abdullah MT, Moritz C, Grigg GG, Hall LS. 2000. Evidence of cryptic species within Cynopterus brachyotis using mtDNA sequence. In: Yaacob Z, Moo-Tan S, Yorath S (eds) Proceedings of the international conference on in-situ and ex-situ biodiversity conservation in the new millennium. Yayasan Sabah, Kota Kinabalu, pp. 403–408

Abdullah MT, Siswanto H, Widiyanto A, Setiabudi A, Firmansyah. 1997. Abundance, diversity and distributional records of bats in disturbed habitats in Kalimantan Barat, Indonesia. Sarawak Mus J 11:75–84

Altringham JD. 1996. Bats: biology and behaviour. Oxford University Press.

Brown E, Jacobson MF. 2005. Cruel oil: how palm oil harms health, rainforest and wildlife. Center for Science in the Public Interest. Washington, DC.

Chung AYC, Eggleton P, Speight MR, Hammond PM, Chey VK. 2000. The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. Bull Entomol Res 90:475–496

Corbet GB, JE Hill. 1992. Order Chiroptera. In: Corbet GB, Hill JE (eds) The mammals of the Indomalayan region. Oxford University Press, Oxford, pp. 54–161

Francis CM. 1990. Trophic structure of bat communities in the understory of lowland dipterocarp rain forest in Malaysia. J Trop Ecol 6:421–431

Fujita MS, Tuttle MD. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. Conserv Biol 5:454–463

Hall LS, Grigg GG, Moritz C, Ketol B, Sait I, Marni W, Abdullah MT. 2004. Biogeography of fruit bats in Southeast Asia. Sarawak Mus J 80:191–284

Heaney LR, Heideman PD, E. Rickart A, Utzurrum RB, Klompen JSH. 1989. Elevation zonation of mammals in the central Philippines. J Trop Ecol 5:259–280

Hodgkison R, Balding ST, Zubaid A, Kunz TH. 2004a. Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. Biotropica 36:522–533

Hodgkison R, Balding ST, Zubaid A, Kunz TH. 2004b. Habitat structure, wing morphology, and the vertical stratification of Malaysian fruit bats (Megachiroptera: Pteropodidae). J Trop Ecol 20:667–673

Jones G, Rydell J. 2002. Attack and defense: interactions between echolocating bats and their insect prey. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp. 301–345

Kunz TH. 1988. Age determination in bats. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., pp. 47–58

Marshall AG. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. Zool J Linn Soc 83:351–369

Medellin RA, Equihua M, Amin MA. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforest. Conserv Biol 14:1666–1675

Nakagawa M, Miguchi H, Nakashizuka T. 2006. The effects of various forest uses on small mammal communities in Sarawak, Malaysia. For Ecol Management 231:55–62

Numa C, Verdú JR, Sánchez-Palomino P. 2005. Phyllostomid bat diversity in a variegated coffee landscape. Biol Conserv 122:151–158

Payne J, Francis CM. 1998. A field guide to the mammals of Borneo. The Sabah Society, Kota Kinabalu, Sabah, Malaysia.

Primack R, Corlett R. 2005. Tropical rain forests: an ecological and biogeographical comparison. Blackwell Publishing, Oxford.

Racey PA, Entwistle AC. 2002. Conservation ecology of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 680–743
Shanahan M, Debski I. 2002. Vertebrates of Lambir Hills National Park, Sarawak, Malaysia. Malaysian Nat J 56:103–118
Simpson EH. 1949. Measurement of diversity. Nature 163:688
Sokal RR, Rohlf FJ. 1973. Introduction to Biostatistics. W. H. Freeman and Company, San Francisco and London. Wright SJ. 2005. Tropical forests in a changing environment. Trends Ecol Evol 20:553–560
Zhao S, Peng C, Jiang H, Tian D, Lei X, Zhou X. 2006. Land use change in Asia and the ecological consequences. Ecol Res 21:890–896
Zubaid A. 1993. A comparison of the bat fauna between a primary and fragmented secondary forest in Peninsular Malaysia. Mammalia 57:201–206

Table 1 Capture rate of bats (individuals per 10,000m2h). Data for species with small sample sizes (<20 individuals) are not shown. The rightmost column presents results of the Chi-squared test: *P < 0.05, **P < 0.01, ***P < 0.001, –: impossible to test due to small sample size.

	Primary forests	Secondary forests	Orchards	Oil palm plantations	Significance
Megachiropterans	55	86	208	272	***
Microchiropterans	40	26	49	6	**
Each species					
Megachiroptera					
Balionycteris maculata	16	2	0	0	-
Cynopterus brachyotis I	4	49	106	201	***
C. brachyotis II	8	11	6	9	-
Eonycteris spelaea	4	1	44	12	***
Macroglossus minimus	5	3	31	0	***
Penthetor lucasii	13	3	0	0	-
Microchiroptera					
Hipposideros cervinus	23	13	11	3	*
Glischropus tylopus	4	1	31	0	-

Table 2 Simpson's index of diversity in the four vegetation types. (N: number of individuals, S: number of species, 1/D: Simpson's index of diversity). 1/D was not calculated for microchiropterans in oil palm plantations due to the small sample size.

		Primary forests	Secondary forests	Orchards	Oil palm plantations
Megachiropterans	*N*	78	75	136	92
	S	8	10	6	3
	1/*D*	5.00	2.09	2.54	1.19
Microchiropterans	*N*	57	23	32	2
	S	11	8	5	2
	1/*D*	2.95	3.50	2.24	
All bats	*N*	135	98	168	94
	S	19	18	11	5
	1/D	7.86	3.38	3.65	1.24

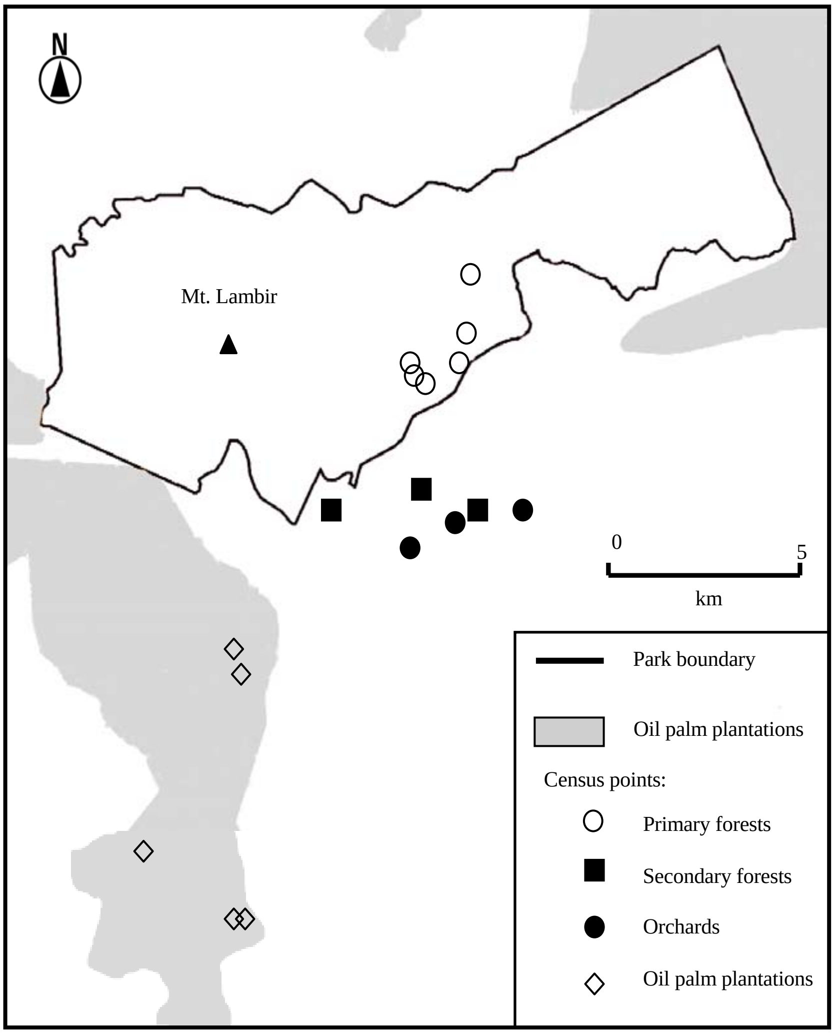

Figure 1. Study area and location of census points.

Effect of Forest Use on Community Structures and Trophic Levels of Small Mammals in Sarawak, Malaysia

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Introduction

In terrestrial forest ecosystems, anthropogenic effects on biodiversity and ecosystem function are a global concern. Tropical rain forests in Southeast Asia are characterized by extremely high plant diversity (Whitmore 1984); however, these forests have been exposed to drastic and rapid deforestation because of an increasing human population and a developing economy. The effect of altering habitats in tropical forests on the biodiversity of wild animals is an urgent subject for species conservation and proper forest management. Much research has been conducted on the effects of deforestation or forest use on changes in wildlife species composition or abundance, such as that for logged forests (Willott et al. 2000), fragmented forests (Harrington et al. 2001), and fallows (Medellín and Equihua 1998). In reality, however, a landscape is a complex assemblage of these forest types. To clearly understand the effects of forest use on the community structure in a region, we must asses a complex assemblage of these diverse vegetation types. The alternation of plant species composition and tree size in degraded forests may also be accompanied by changes in food resource availability for wild animals, resulting in changes in their food intake (Panasci and Whitacre 2000). The analysis of stable nitrogen isotopes ($\delta15N$) in organisms is a powerful tool with which to investigate trophic positions within a food web.

Our objective was to analyze the distribution patterns and levels of $\delta15N$ in small mammals in fragmented primeval forests, abandoned fallows at three different developmental stages, and rubber plantations, as compared with the distribution patterns and $\delta15N$ levels in primary forests to determine the effects of human forest use on small mammal communities and trophic levels in Sarawak, Malaysia. Because small mammals play an important role as seed dispersers in forest ecosystems and form the base of the mammalian food chain (Shine et al. 1998; Shanahan and Compton 2000), understanding the effects of forest uses on small mammals is needed to determine proper forest management strategies.

Materials and Methods

Study site

A field survey was conducted during August–September 2003, June – July 2004, and January–March 2005 in and around Lambir Hills National Park (LHNP), Sarawak, Malaysia (4°2’N, 113°5’E). The study site contained 20 plots (each 10×100 to 10×200 m) in six forest types: primary forests (two plots), fragmented primeval forests (six plots), abandoned fallows at three different developmental stages (new, young, and old: three plots each), and rubber plantation (three plots). Light conditions on the forest floor were determined by quantifying the percent canopy openness using a digital camera with a fisheye lens (Cool Pix 910, Nikon).

Small mammal trapping and litter sampling

Small mammals were live-trapped for five consecutive days and nights using wire-mesh live cage traps (15×12×30 cm). One trapping series was conducted in each study plot during each field survey for a total of three trapping series. Traps were baited with banana and sweet potato and covered with a sheet of transparent plastic to exclude rainfall. We checked all traps once a day in the morning (0700–1100 hours). Captured individuals were identified according to Payne et al. (1985) and marked by toe clipping with a unique number at the site of capture. After marking and recording sex, weight, reproductive condition, and capture point, individuals were released. Nomenclature follows that of Payne et al. (1985). The clipped toes were immediately returned to the laboratory, stored in a freezer at –20°C, oven-dried at 50°C for 48 h, and kept dry until analysis.

Leaf litter samples were hand-collected from ten 15×15 cm quadrats at 10-m intervals within each plot. These were oven-dried at 50°C for 72 h and ground to fine powder after removing sand and fungi from the leaves, twigs, and petioles.

Isotope analysis

For the δ15N analysis, samples from 144 individuals, representing 19 species in 3 families (treeshrews, squirrels, and rats or mice) were folded into tin capsules. The level of δ15N was measured using a mass spectrometer (Delta S or Delta plus XP, Germany) coupled with an Elemental Analyzer (Flash EA 111). The natural abundance of ^{15}N is expressed in per mil (‰) deviation from an international standard: $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1000$, where R is $^{15}N/^{14}N$. Atmospheric N was used as the N standard.

Data analysis

We conducted detrended correspondence analysis (DCA) on the species abundance data ($N \geq 5$) to identify gradients in the small-mammal assemblages over the 20 study plots. Less common species (N of captures <5) were excluded from the DCA. To correct for differences in the δ15N of primary production among sites, we calculated the average $\delta^{15}N$ of 10 leaf litter samples from each plot and estimated the corrected $\delta^{15}N$ of small mammals as: $\delta^{15}N_{\text{corrected}} = \delta^{15}N_{\text{small mammal}} - \delta^{15}N_{\text{leaf litter}}$, where $\delta^{15}N_{\text{small mammal}}$ is the directly measured $\delta^{15}N$ of a small mammal at a particular site and $\delta^{15}N_{\text{leaf litter}}$ is the average $\delta^{15}N$ of 10 leaf litter samples from that plot. DCA was performed using CANOCO 4 (ter Braak and Smilauer 1998) and all other statistical analyses were performed using JMP 4.0 (SAS Institute 2000).

Results

Community structures of small mammals

In total, we captured 283 individuals of 22 species from four families: Tupaiidae, Muridae, Sciuridae, and Erinaceidae. DCA extracted two axes that cumulatively accounted for 45.7% of the variation in the small mammal species abundance data. The first axis (DC1) was significantly correlated with the abundance of *Niviventer cremoriventer*, *Sundamys muelleri*, and *Leopoldamys sabanus*, whereas the second axis (DC2) was significantly correlated with the abundance of *Tupaia minor*, *T. gracilis*, and *Rattus rattus*; both correlations were positive. DC2 was also significantly negatively correlated with the abundance of *Maxomys rajah*. The DCA showed two distinctive groups: new fallow and other forest types (Fig. 1). The three new fallow plots had a high abundance of two species of treeshrew and house rat (*R. rattus*). However, there was no obvious partitioning among the other five forest types.

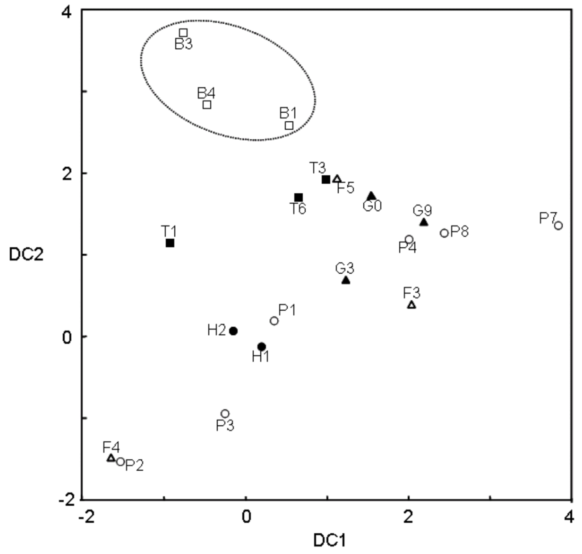

Fig. 1 Plot of the first two axes of the detrended correspondence analysis of the small mammal community species-abundance data (N ≥ 5) from 20 study plots. Symbols indicate the forest type: solid circle, primary forest; open circle, fragmented primeval forest; solid square, young fallow; open square, new fallow; solid triangle, rubber plantation; and open triangle, old fallow; after Nakagawa et al. (2006).

Trophic levels of small mammals

Differences in the $\delta^{15}N$ of leaf litter among the forest types were small and not significant. The $\delta^{15}N_{\text{corrected}}$ of rats and mice differed significantly among forest types (ANOVA, $F = 10.83$, $P < 0.0001$); those in forests that had been used relatively recently, such as new and young fallow and rubber plantations, had significantly higher levels of $\delta^{15}N_{\text{corrected}}$ than did those in primary or fragmented forests and old fallow (Fig. 2). In contrast, we found no significant differences in levels of $\delta^{15}N_{\text{corrected}}$ for treeshrews and squirrels among forest types. Canopy openness differed significantly among forest types (ANOVA, $F = 8.32$, $P < 0.001$) and was highest in new fallow. For the squirrel *Callosciurus notatus* and two rat species, *M. rajah* and *N. cremoriventer*, canopy openness and $\delta^{15}N_{\text{corrected}}$ were significantly and positively correlated (Fig. 3); such a pattern was not found for lesser (*T. minor*) or large (*T. tana*) treeshrews.

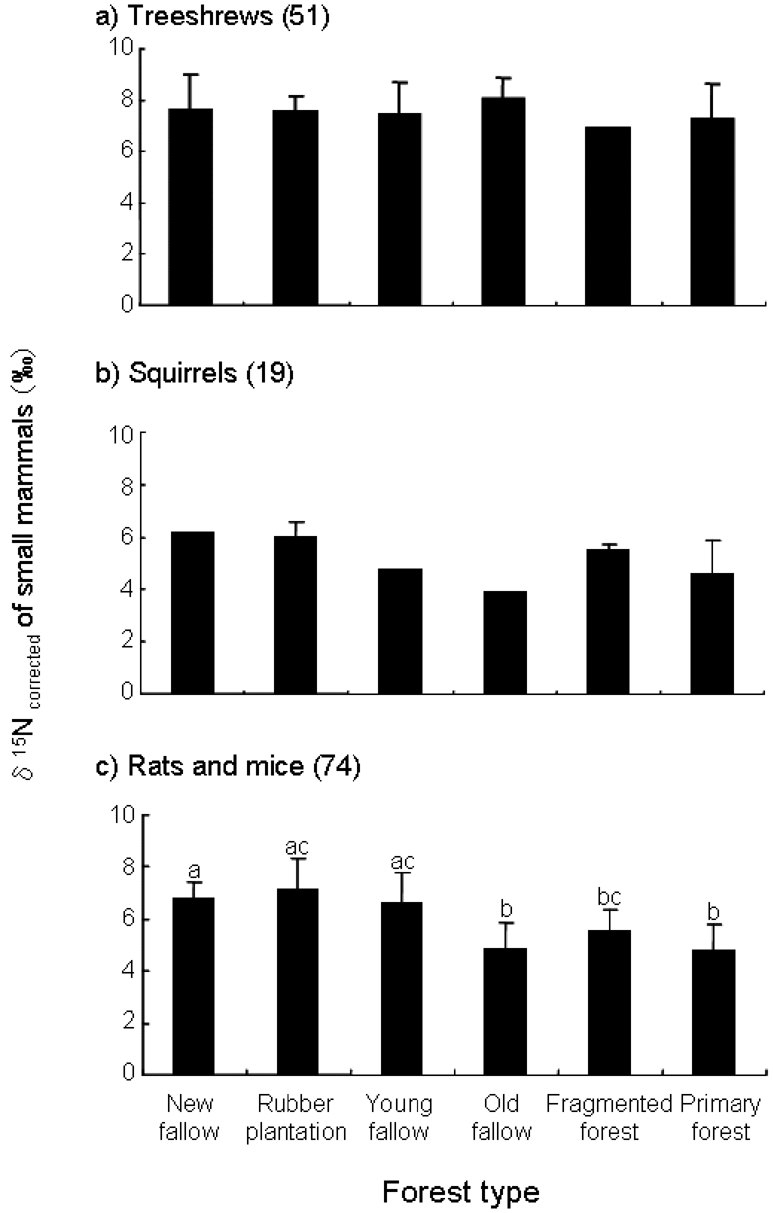

Fig. 2 $\delta^{15}N_{\text{corrected}}$ of (a) treeshrews, (b) squirrels, and (c) rats and mice among six forest types. Bars sharing any letters are not significantly different among the forest types (Scheffe's multiple comparison, $P < 0.05$). No significant differences were detected in treeshrews and squirrels. Sample sizes are indicated in parentheses; after Nakagawa et al. (2007).

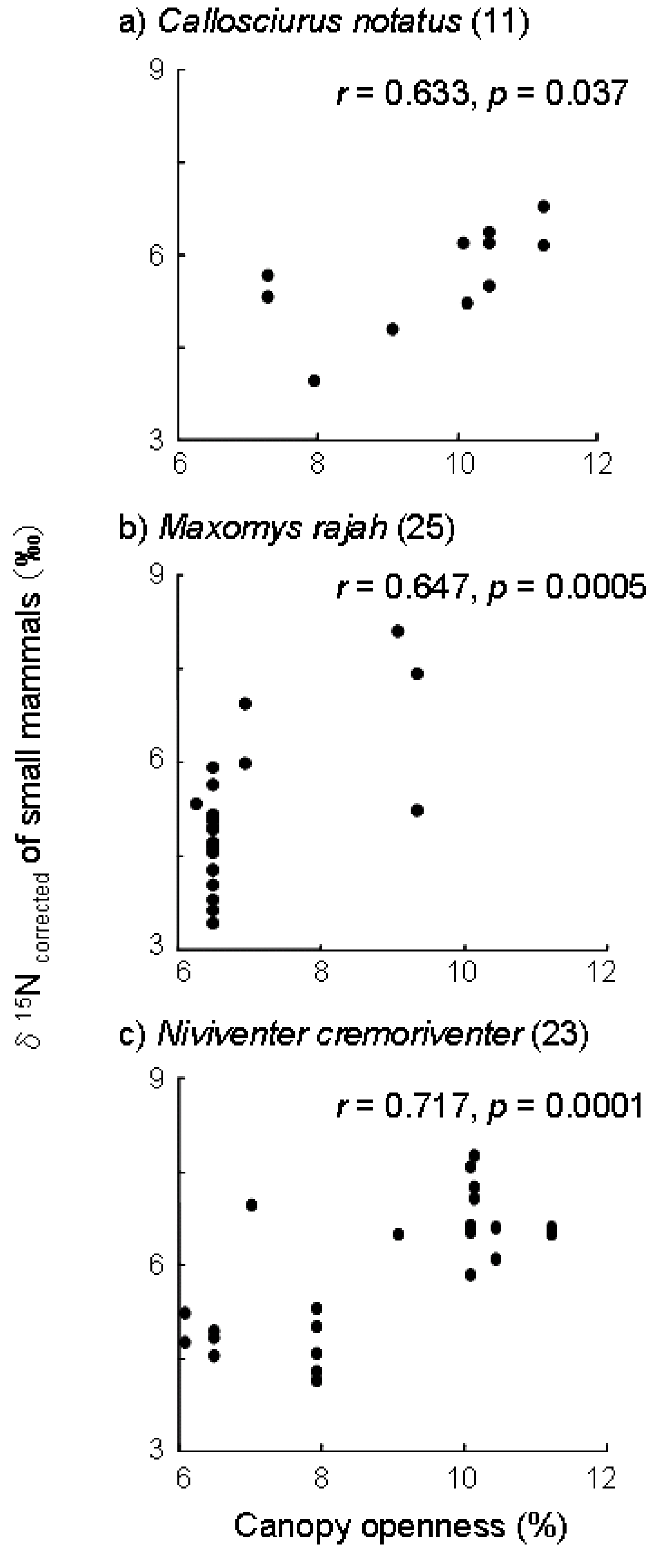

Fig.3 Correlations between canopy openness and the $\delta^{15}N_{\text{corrected}}$ of (a) *Callosciurus notatus*, (b) *Maxomys rajah*, and (c) *Niviventer cremoriventer*. Sample sizes are shown in parentheses; after Nakagawa et al. (2007).

Discussion

The analysis of small mammal species abundance among forest types indicated two distinct groups. Small mammal communities in new fallow had comparatively more house rats and lesser and slender treeshrews. The house rat is a human-associated species that is adapted to disturbance (Lynam and Billick 1999). The high occurrence of rats in new fallow, where disturbance had recently occurred and recovery from the disturbance had not yet advanced, is not unexpected. Lesser and slender treeshrews occur in gardens and plantations, as well as in forests (Payne et al. 1985), suggesting that they could be adaptable to disturbed habitats. Our results also indicate that small mammal communities could recover from the disturbance relatively quickly, that is, within several years after slash-and-burn agriculture. Although the species composition of young fallow was not entirely similar to that of primary forest, the plots in young fallow were included in the same group as primary forest; moreover, these plots contained some interior forest specialists or dominant species in the primary forest, such as Muller’s rat and brown spiny rat, which showed significant correlations with the DCA axes.

Rats and mice in highly degraded forests (e.g., new and young fallow and rubber plantation) were more enriched in 15N compared to those in primary forests or somewhat degraded forests (e.g., old fallow and fragmented primeval forest). This result indicates that rats and mice in highly degraded forest are likely to feed on more consumers such as invertebrates rather than on plant organs compared with rodents in primary or somewhat degraded forests. On the other hand, the δ15N of treeshrews did not differ among forest types, suggesting that their diet was not affected by forest uses. This result indicates that treeahrews that normally prefer to consume insects may be less affected by insect abundance as a result of changes in forest uses. The trend was also supported at the species level, except for treeshrews. Two species of rat and one species of squirrel showed significantly higher δ15N in forests with high compared to low canopy openness, suggesting an increase in consumers in their diets. In disturbed forests, which have high canopy openness, insects such as flies and butterflies were abundant (Willott et al. 2000; Horn et al. 2005). Rats and mice in the region are thought to consume a wide range of fruits or seeds, as well as insects (Payne et al. 1985; Kitamura et al. 2006). When insects are abundant, they may be easy to capture as a food resource. Direct quantification of diet or gut contents analysis of small mammals in a future study would clearly support our hypothesis.

Given the variation in the food supply and changes in vegetation cover that accompany habitat disturbances, dietary flexibility would be crucial for survival in degraded forests. The dietary flexibility of rats and squirrels may be the reason why community structures of small mammals are similar among various forest types examined in this study (except for new fallow). However, changes in the feeding activity of small mammals associated with forest uses may affect the distribution or survival of insects through higher predation pressure, as well as the regenerating patterns of plants through decreased predation and dispersal of fruits.

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References

Harrington GN, Freeman AND, Crome FHJ (2001) The effects of fragmentation of an Australian tropical rain forest on populations and assemblages of small mammals. J Trop Ecol 17:225-240

Horn S, Hanula JL, Ulyshen MD, Kilgo JC (2005) Abundance of green tree frogs and insects in artificial canopy gaps in a bottomland hardwood forest. Am Midl Nat 153:321-326

Kitamura S, Suzuki S, Yumoto T, Poonswad P, Chuailua P, Plongmai K, Maruhashi T, Noma N, Suckasam C (2006) Dispersal of Canarium euphyllum (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand. J Trop Ecol 22:137-146

Lynam AJ, Billick I (1999) Differential responses of small mammals to fragmentation in a Thailand tropical forest. Biol Conserv 91:191-200

Medellín RA, Equihua M (1998) Mammal species richness and habitat use in rainforest and abandoned agriculture fields in Chiapas, Mexico. J Appl Ecol 35:13-23

Nakagawa M, Miguchi H, Nakashizuka T (2006) The effects of various forest uses on small mammal communities in Sarawak, Malaysia. For Ecol Manage 231:55-62

Nakagawa M, Hyodo F, Nakashizuka T (2007) Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes. Can J Zool 85:472-478

Panasci T, Whitacre D (2000) Diet and foraging behavior of nesting roadside hawks in Petén, Guatemala. Wilson Bull. 112:555-558

Payne J, Francis CM, Phillipps K (1985) A Field Guide to the Mammals of Borneo. The Sabah Society, Kota Kinabalu, Malaysia

SAS Institute (2000) JMP user's guide. SAS Institute, Cary, NC, USA

Shanahan M, Compton SG. (2000) Fig-eating by Bornean tree shrews (Tupaia spp.): evidence for a role as seed dispersers. Biotropica 32:759-764

Shine R, Harlow PS, Keogh JS, Boeadi (1998) The influence of sex and body size on food habits of a giant tropical snake, Python reticulates. Func Ecol 12:248-258

ter Braak CJF, Smilauer P (1998) CANOCO reference manual and user's guide to Canoco for windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York, USA

Whitmore TC (1984) Tropical rain forests of the Far East. 2nd ed. Clarendon, Oxford

Willott SJ, Lim DC, Compton SG., Sutton SL (2000) Effect of selective logging on the butterflies of a Bornean rainforest. Conserv Biol 14:1055-1065

Community Structure of Aphyllophoraceous Fungi and Impacts of Human Forest Use in Sarawak, Malaysia

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Introduction

Fungi play important roles as decomposers and symbionts of plants in forest ecosystems and should contain enormously diverse species. Hawksworth and Mueller (2005) estimated the number of fungal species to be between 600 000 and 1 500 000 and suggested that there are hot spots of fungal diversity in the tropical region. Pegler (1997) also pointed out that Southeast Asia has possibly the greatest species diversity of fungi. However, information on the fungal community structure in the tropical forest is almost limited to that of Aphyllophorales in the neotropical region (Ferrer and Gilbert 2003; Schmit 2005; but see Hattori and See 2003). In addition, natural forests, which would support high fungal species diversity, are disappearing at an annual rate of 1.4% in Southeast Asia (Sodih et al. 2004). Thus, reliable and rapid evaluation of fungal community structures under undisturbed conditions in Southeast Asia is greatly needed.

It is well known that fungal flora and their species diversity are affected by forest environmental factors (e.g., Yamashita and Hijii 2006). Human uses of the forest affect the composition and diversity of macrofungi, such as Agaricales and Aphyllophorales in temperate and boreal zones (e.g., Penttilä et al. 2004; Sippola et al. 2004). Forest use in tropical regions is also expected to affect fungal community structure, although studies on the effect of forest use on the fungal community structure in this region are rare.

Although long-term study is needed to adequately characterize the fungal flora (Mueller et al. 2004), rapid assessments are still helpful for monitoring and managing rapidly changing tropical forests. Because fruiting bodies of bracket fungi and shelf fungi (Aphyllophorales, Basidiomycetes), which mainly utilize fallen logs, twigs, and other woody materials as their substrates, are long-lasting, year-to-year variation in species composition is smaller than that of ephemeral fungi, such as agaric mushrooms (Berglund et al. 2005). Aphyllophorales has also been taxonomically well described; thus, it provides suitable candidates of environmental indicators that could be used to examine the effects of forest use in tropical regions.

In this study, we conducted field survey and estimated the number of fungal species to reveal the community structure of aphyllophoraceous fungi in the primary forest. We compared fungal species density and species composition among five forest types (rubber plantation, land left fallow after rice cultivation for less than 10 years, land left fallow after rice cultivation for more than 30 years, isolated and fragmented primary forest, and primary forest) to reveal the effects of human forest use on the aphyllophoraceous fungal community

Methods

The study area is located in and around Lambir Hills National Park, Sarawak, Malaysia (4º20'N, 113º50'E). Aphyllophorales is a taxonomically polyphyletic group, but almost all species are pathogenic or saprotrophic fungi. We focused on polypores, hydnoid fungi, and stereoid fungi, but we excluded clavarioid and corticioid fungi because it is very difficult to identify species in these two groups. After identifying the fungi to the species or morphospecies level, we collected fruiting bodies and preserved them as dried specimens at the Sarawak Forestry Corporation (Forest Research Center) in Kuching, Sarawak, Malaysia.

To reveal the aphyllophoraceous fungal community structure in the primary forest, we established twelve 100×10 m transects which is divided into forty 5×5 m quadrats in the park. We collected all fruiting bodies of Aphyllophorales in these transects in June and December 2006. At the same time, we recorded the diameter and decay stage of the coarse woody debris (CWD) on which the fruiting bodies appeared. Because the number of fruiting bodies does not always correspond to the number of fungal individuals, we used the number of CWD on which almost all species occurred as that of individuals. For fruiting bodies of *Amauroderma subrugosum* and other fungi which appeared directly from the ground, we treated the number of 5×5 m quadrats as the number of individuals. We estimated the number of aphyllophoraceous fungal species using three estimators: Chao 1, Chao 2, and Jackknife 1.

To reveal the effects of forest use on the fungal community, we established 10 plots in and around the park. Two plots were established for every forest type: rubber plantation, land left fallow after rice cultivation for less than 10 years, land left fallow after rice cultivation for more than 30 years, isolated and fragmented primary forest, and primary forest. In a primary stand in the park, two study plots were established. The other plots were established around the park. In each plot, we established one long band transect (10 m wide and 100 m long) and recorded tree composition, soil water potential, the degree of canopy openness, and the mass of forest-floor leaf and branch litter (Yamashita et al. in press). Perpendicular to each long transect, we established four shorter band transects (5 m wide and 40 m long) at intervals of 25 or 50 m, in which we recorded the number of CWD pieces. We collected all fruiting bodies that appeared in the short band transects from 17 June to 6 September 2005. We used the number of branch transects in which these species occurred because the number of fruiting bodies does not always correspond to the number of fungal individuals.

We used canonical correspondence analysis (CCA) to reveal the relationships between fungal community composition and the environmental variables (Jongman et al. 1995). We performed preliminary principal-components analysis (PCA) for plant species composition so that we could use the PC axes as factors related to plant species composition. The PCA revealed that plant species composition in the rubber plantation and the young fallow forest differed conspicuously from each other and from that in the other forest types. Differences in the composition of CWD among plots were also evaluated by using the PCA scores, and the PCA results for CWD composition showed no clear grouping. We used the degree of canopy openness, soil water potential, the scores for PC-1 and PC-2 for the composition of CWD, the total number of pieces of CWD, the dry weight of litter, the scores of PC-1 and PC-2 for plant species composition, and the total basal area of the plot as environmental variables in the CCA.

Results

Fungal community structure in the primary forest

A total of 721 individuals from 101 species was collected from the 1.2 ha of transects. The estimated numbers of species were 155 (Chao 1), 161 (Chao 2), and 147 (Jackknife 1). Almost half of these species were singletons. Dominant species were *A. subrugosum*, *Ganoderma austrael*, *Microporus xanthopus*, and *Microporus affinis* (> 40 individuals in total). *Ganoderma australe* tended to appear on large fallen trunks, whereas *M. xanthopus* and *M. affinis* appeared on fallen branches.

Effects of forest use on the fungal community

The environmental variables are shown in Table 1. Canopy openness ranged from 6.1 to 10.5%, soil water potential from -586 to -23 kpa, number of pieces of CWD from 13 to 533 per ha, leaf and branch litter from 0.54 to 1.16 kg dry wt./m^2, and basal area from 11.5 to 74.6 m^2/ha.

A total of 155 samples from 67 species of polypores, hydnoid fungi, and stereoid fungi was collected during the study period. *Amauroderma subrugosum* and *Trametes* cf. *mimites* were dominant species in the study stands. Twenty-eight aphyllophoraceous species appeared in more than two transects, whereas 39 species were singletons.

The species density (number of species per 200 m^2) differed significantly among forest types ($P < 0.05$) but not among site positions ($P > 0.05$), and the interaction between forest type and site position was not significant ($P > 0.05$; Fig. 1). More than four species per 200 m^2 appeared in the rubber plantation, isolated primary forest, and primary forest. The fungal species density increased significantly with increasing number of pieces of CWD in the short band transect (Pearson's correlation coefficient; $r = 0.842$, $P < 0.05$), but it decreased significantly with increasing PC-2 scores for plant species composition ($r = -0.803$, $P < 0.05$).

In the CCA ordination, the first axis explained 23.1% of the total variance versus 17.4% for the second axis (Fig. 2). Automatic forward selection revealed that only the number of pieces of CWD significantly affected the fungal species composition (Monte Carlo permutation test, $P < 0.05$). The occurrences of *Flabellophora licmophora* (*Flic*), *Coriolopsis retropicta* (*Cret*), *Microporus vernicipes* (*Mver*), and *A. subrugosum* (*Asub*) were positively correlated with the number of pieces of CWD.

Fungal flora in the young fallow forest near the park and the old fallow forest near the village were clearly different from those in the other plots. The other eight plots were clustered at the central part of the diagram. Young fallow forest near the park and old fallow forest near the village were associated with *Podoscypha nitidula* (*Pnit*) and *Podoscypha* sp. 1 (*Psp1*), respectively.

Discussion

Four of the world's 25 biodiversity hot spots for plants and vertebrates are in Southeast Asia (Myers et al. 2000), and the study area is famous for its diverse plant species. Our study revealed that primary forest in this region maintains a high species diversity of Aphyllophorales compared with temperate and boreal zones

(10 to 89 species; Schmit 1999; Penttilä et al. 2004).

Community structures of living organisms other than fungi are affected by anthropogenic forest use in tropical regions (Waltert et al. 2003; Yasuda et al. 2003). Schulze et al. (2004) revealed that almost all the species groups or guilds of plants, birds, and insects could not accurately predict the biodiversity of other groups. A previous study at our study site revealed that the diversity of small mammals did not differ clearly among forest types (Nakagawa et al. 2006). Conversely, except at the rubber plantation (which had a high amount of CWD), our study showed that human forest use negatively affected aphyllophoraceous fungal diversity. This suggests that fungal diversity could indicate some aspects of a forest's environmental condition, such as the quantity of CWD. In boreal and temperate regions, the community structure of both ectomycorrhizal fungi (Visser 1995) and wood-inhabiting fungi (Penttilä et al. 2004) were strongly affected by forest management. Iwabuchi et al. (1994) showed that the species diversity of macrofungi increased as successional changes occurred in plant species composition. Hence, the response of the species diversity of macrofungi to forest disturbance appears to not differ greatly among regions.

Recently, studies of the community structure of decomposers have stressed the importance of management of CWD to maintain species richness of saproxylic fungi and other living organisms (Jonsson and Kruys 2001; Lindhe et al. 2004; Jonsson et al. 2005) because the abundance of CWD is positively correlated with the species richness of both rare and common wood-inhabiting fungi (Penttilä et al. 2004). Our results also showed that the abundance of CWD affected the species richness and composition of aphyllophoraceous fungi in the stands. This suggests that overuse of CWD in tropical regions, such as harvesting it for fuel, would negatively affect the fungal community that develops on CWD, with consequences such as a loss of species diversity and of functional groups.

Species diversity of the Aphyllophorales reflected forest conditions, especially the quantity of CWD, but species diversity might not be the best indicator of forest conditions in very different habitats. In our study, tree composition differed between rubber plantations and the other types of forest, but the number of fungal species was similar to those in isolated primary forests and primary forests. Some species, such as *A. subrugosum*, which appeared mainly in primary and isolated primary forests and was one of the dominant species in the primary forest, could be good indicators of forest condition. Both species diversity and the presence of indicator species have shortcomings, and further study is needed to elucidate good indicators of forest condition.

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References

Berglund H, Edman M, Ericson L (2005) Temporal variation of wood-fungi diversity in boreal old-growth forests: implications for monitoring. Ecol. Appl. 15:970–982

Ferrer A, Gilbert GS (2003) Effect of tree host species on fungal community composition in a tropical rain forest in Panama. Divers. Distrib. 9:455–468

Hattori T, See LS (2003) Community structure of wood-decaying Basidiomycetes in Pasoh. In: Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC (Eds) Pasoh; Ecology of a lowland rain forest in Southeast Asia. Springer, Berlin, pp. 161–170

Hawksworth DL, Mueller GM (2005) Fungal communities: Their diversity and distribution. In: Dighton J, White JF, Oudemans P (Eds) The fungal community — Its organization and role in the ecosystem. Taylor & Francis, Boca Raton, USA, pp. 27–37

Iwabuchi S, Sakai S, Yamaguchi O (1994) Analysis of mushroom diversity in successional young forests and equilibrium evergreen broad-leaved forests. Mycoscience 35:1–14

Jonsson BG, Kruys N (2001) Ecology of woody debris in boreal forests. Ecological Bulletins, Lund, Sweden

Jonsson BG, Kruys N, Ranius T (2005) Ecology of species living on dead wood — lessons for dead wood management. Silva Fenn. 39:289–309

Jongman RHG, ter Braak CJF, van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK

Lindhe A, Åsenblad N, Toresson HG (2004) Cut logs and high stumps of spruce, birch, aspen and oak — nine years of saproxylic fungi succession. Biol. Conserv. 119:443–454

Mueller GM, Bills GF, Foster MS (2004) Biodiversity of Fungi: Inventory and monitoring methods. Elsevier, London, UK

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nakagawa M, Miguchi H Nakashizuka T (2006) The effects of various forest uses on small mammal communities in Sarawak, Malaysia. For. Ecol. Manage. 231:55–62

Pegler DN (1997) The larger fungi of Borneo. Natural History Publications, Kota Kinabalu, Malaysia

Penttilä R, Siitonen J, Kuusinen M (2004) Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol. Conserv. 117:271–283

Schmit JP (1999) Macrofungal diversity of a temperate oak forest: a test of species richness estimator. Can. J. Bot. 77:1014–1027

Schmit JP (2005) Species richness of tropical wood-inhabiting macrofungi provides support for species-energy theory. Mycologia 97:751–761

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shahabuddin, Veddeler D, Mühlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. Ecol. Appl. 14:1321–1333

Sippola AL, Similä M, Mikkönen M, Jokimäki J (2004) Diversity of polyporous fungi (Polyporaceae) in northern boreal forests: effects of forest type and logging intensity. Scand. J. For. Res. 19:152–163

Sodih NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Tends Ecol. Evol. 19:654–660

Visser S (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. 129:389–401

Waltert M, Mardiastuti A, Mühlenberg M (2003) Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv. Biol. 18:1339–1346

Yamashita S, Hijii N (2006) Spatial distribution of the fruiting bodies of Agaricales in a Japanese red pine (*Pinus densiflora*) forest. J. For. Res. 11:181–189

Yamashita S, Hattori T, Momose K, Nakagawa M, Aiba M, Nakashizuka T (2008) Effects of Forest Use on Aphyllophoraceous Fungal Community Structure in Sarawak, Malaysia. Biotropica. In press.

Yasuda M, Ishii N, Okuda T, Hussein NA (2003) Small mammal community: habitat preference and effects after selective logging. In: Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC (Eds) Pasoh; Ecology of a lowland rain forest in Southeast Asia. Springer, Berlin, pp. 533-546

Table 1 Environmental variables for each study plot.

Plot	Position	Canopy Openness (%)	Soil Water Potential (Kpa)	CWD (pieces/ha)	Litter (g dry wt./ m^2)	Basal Area (m^2/ha)
R	Near park	10.5	-582	415	0.98	52.4
	Near village	7.0	-73	295	0.54	54.8
YF	Near park	9.1	-53	165	0.90	11.5
	Near village	9.7	-156	13	0.73	24.7
OF	Near park	7.8	-240	283	0.95	54.2
	Near village	7.7	-545	150	1.16	74.6
IP	Near park	6.1	-586	438	1.08	70.9
	Near village	7.0	-323	305	1.11	74.7
P1	-	6.8	-84	403	1.14	73.4
P2	-	6.9	-23	533	1.16	64.2

Sample statistics except for basal area are means, where number of samples of canopy openness and water potential was 10, that of CWD was 4, and that of litter was 5. After Yamashita et al. (in press).

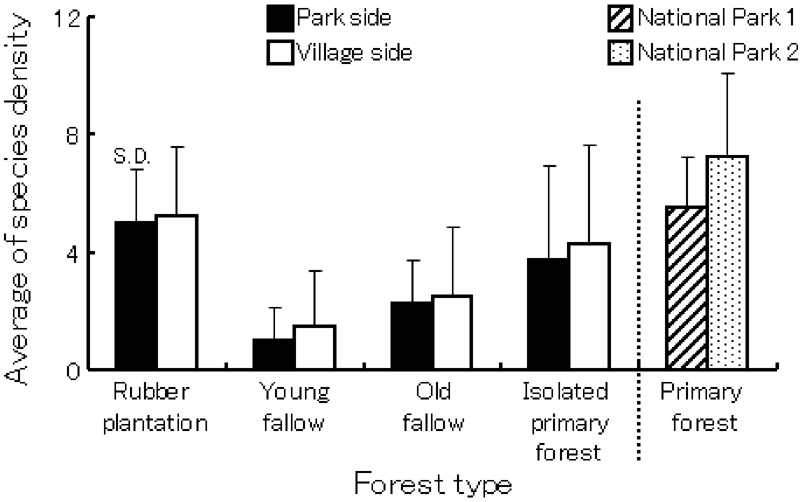

Fig. 1 The average of aphyllophoraceous species density per 200m^2 found in each plot ($n = 4$ short band transects). Species density differed significantly differed among forest types ($P = 0.007$) but not among site positions (park vs. village), and there was no significant site-forest type interaction (two-way ANOVA). The species density in P2 was significantly higher than those in young fallows (one-way ANOVA, Tukey-Kramer's HSD test, $P < 0.05$). After Yamashita et al. (in press).

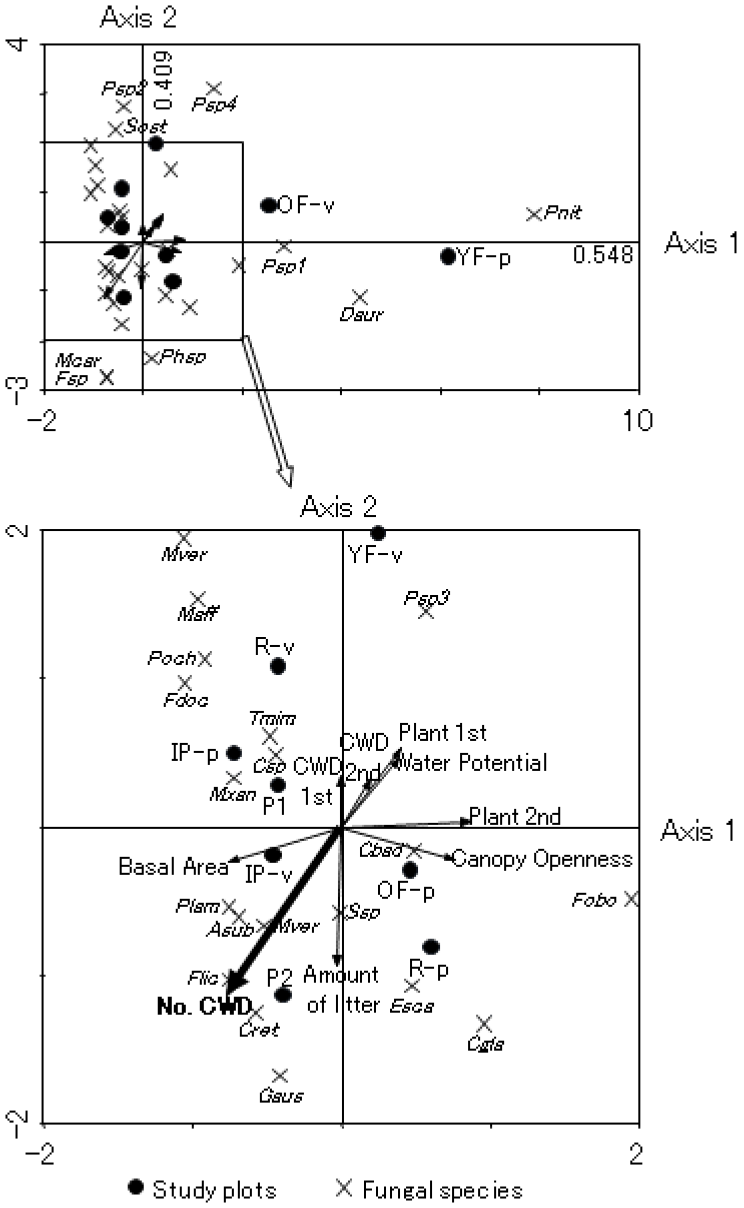

Fig. 2 The results of a canonical correspondence analysis ordination for the site scores of the study plots and the correspondence positions of the aphyllophoraceous species. The upper graph shows all plots and species; the lower graph shows plots and species that lie within 2units on either side of the origin. Environmental variables are shown by arrows. Numbers on the axes are eigenvalues. Variables with a significant effect are shown in bold (Monte Carlo Permutation test, $p < 0.05$). -v, near village; -p near park. After Yamashita et al. (in press).

Stand Structure, Floristic Composition and Diversity of Tropical Lowland Rain Forests in Sabah, Malaysia under Different Managements

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Introduction

Timber exploitation, which accelerated from the 1950s to 1970s by the introduction of mechanized methods, has been altering the tropical lowland forests of Sabah, Malaysian Borneo (Sabah Forestry Department 1989). For sustainable production of low-volume, high-quality and high-priced timbers, reduced-impact logging (RIL), a low impact logging technique of timber harvesting, was introduced in Sabah in 1989 (Lagan et al. 2007). It is believed that RIL is an adequate method for the sustainable management of tropical forests, because RIL can reduce the damages to the forests compared to the conventional logging method. However, there are relatively limited data to justify the sustainability of RIL in terms of full recovery of species composition, diversity and biomass after timber harvest (Pinard and Putz 1996; Bertault and Sist 1997; Sist and Nguyen-The 2002; Bischoff et al. 2005). Can the tropical forests after RIL approach the pre-harvest, old-growth status in the course of secondary succession? To answer this question, we compared the recovery processes of logged-over forests subjected to RIL and to a conventional method (high-impact logging) in terms of structure, floristic composition and diversity.

Materials and Methods

Eleven research plots of 0.2 ha area (100 m x 20 m or 50 m x 40 m, depending on the availability of similar topography) were established in Deramakot Forest Reserve (DFR) and the neighboring Tangkulap Forest Reserve (TFR), Sabah, Malaysian Borneo (5°N 117°E), under different forest managements (Table 1). DFR and TFR had been selectively logged in the 1950s-1980s with similar overall intensity. The minimum trunk diameter for harvesting was 60cm, but this rule does not appear to be necessarily followed. This resulted in very heterogeneous condition of remaining forests at the small spatial scale. After this period, DFR was selected as a focal site for the application of RIL in 1989, while TFR receives persistent pressure of conventional logging. In DFR, we established two plots in each of following four groups of forest management in May 2003. (1) Residual primary forest that appeared to be unaffected by logging,

(2) old-growth forest that was not logged after 1980s, (3) forests logged by RIL in 1995-1997, (4) forests logged by RIL in 1999-2000. The distinction between groups (1) and (2) was based on the proximity to logging roads or skid trails and on the presence or absence of stamps in the plot. Forests of groups (3) and (4) were identified by the management record of DFR (Lagan et al. 2007). In TFR, in May 2003, we established two plots in the forest that had been intermittently logged by the conventional method, and added one more plot in the same forest in March 2005. In the following analyses and discussion, we used three broad categories of forest management status as follows. Old-growth forests including (1) and (2), forests harvested by RIL including (3) and (4), and forests harvested by conventional logging (5).

All plots were divided into contiguous twenty 10-m x 10-m subplots. The location and altitude of the plots were measured by using a portable receiver of global positioning system (GPS III plus, Garmin, Olathe, USA). All living trees larger than 30 cm in trunk girth at 1.3 m above ground were measured first in May 2003 and re-measured in March 2005. Diameter at breast height (DBH) was calculated as girth divided by 3.14 (thus minimum DBH was 9.6 cm). Dead trees were checked at the tree census in March 2005. For comparison among the three categories of forest management, we incorporated the 2005 data to increase the sample size of the forest logged by conventional method. Buttressed or stilt-rooted trees were measured for trunk diameter at above the protrusions but not at 1.3m above the ground. Multiple trunks were separately recorded for DBH. Leaf area index (LAI), which is defined as the sum of leaf area per unit ground area, was measured at five plots using LAI-2000 Canopy Analyzer (LI-COR, Lincoln, USA) in June 2003. The five plots were PRI-1, 80s-2, RIL00-2, RIL05-1, and CV-1 (see Table 1 for the abbreviation of the plot). LAI was estimated based on ten measurements at corners of 10-m x 10-m subplots in each plot. This was repeated three times in different parts of the plot, from which the mean LAI was calculated.

Above-ground biomass (AGB, kg) of individual stem was estimated by using the following equations obtained by Brown (1997) and Chave et al. (2005) as:

$$\mathrm{AGB} = \exp(-2.134+2.530 \ln(\mathrm{DBH})), \qquad (1)$$

and

$$\mathrm{AGB} = \rho \times \exp(-1.499 + 2.148 \ln(\mathrm{DBH}) + 0.207(\ln(\mathrm{DBH}))^2 - 0.0281(\ln(\mathrm{DBH}))^3), \qquad (2)$$

respectively, where ρ is wood density (g cm^{-3}). The stand-level AGB density (kg m^{-2}) was derived by the summation of individual stem biomass divided by plot area. For equation (2), the use of stand-level average was recommended by Chave et al. (2005) if species-specific wood density was unavailable as in our case. Brown (1997) reported that mean wood density for 428 Asian tropical tree species was 0.57 g cm^3. If this value was used, biomass estimates by equation (2) was almost identical to those by equation (1). For simplicity, we reported the results based on equation (1) only.

To identify species, we collected leaves for voucher specimens, using a clipper and a catapult for tall trees. Species identification was based on the leaf specimens and bark characters. Voucher specimens were stored at the laboratory in DFR. We have not yet finished the matching of species between plots, so that floristic comparison among plots was done at the genus level. Four and 18 stems (0.3 and 1.4% of total number of stems) could not be identified to family and genus, respectively, and these were excluded from the calculation of number of taxa. Floristic diversity of each plot was evaluated by numbers of family, genus and species. Logged forests may have smaller numbers of taxa simply because stem density is reduced by logging. To allow for this, an index that represents diversity in terms of number of species relative to number of stem was calculated:

$$S = \alpha \ln (1+N/\alpha),$$

where S is the number of species, N is the number of stems, and α is a constant known as Fisher's diversity index (Fisher et al. 1943). To take into account the equitability of species abundance, Shannon's indices of diversity and evenness were also calculated (Magurran 2004). For floristic comparison among plots, detrended correspondence analysis (DCA) was conducted using relative basal area of genus in 2005, which was log (x+1) transformed before analysis (ter Braak & Smilauer 2002). The method of detrending used was by segments.

Dipterocarpaceae trees are dominant climax species in tropical lowland forest in Southeast Asia, and this family is well known as important commercial timber (Whitmore 1984). On the other hand, most of observed *Macaranga* (Euphorbiaceae) species were characterized as a gap-dependent species in regeneration (Slik et al. 2003). Their regeneration requires large canopy opening, and is abundant on disturbed soils (Whitmore 1984). Thus, we examined the dominances of the Dipterocarpaceae and *Macaranga* as indicators for disturbance.

Results

Stem density (number of stems per plot) and mean DBH was not significantly different among the three broad categories of forest management, although stem density tended to be lower in the forests harvested by conventional method than those in the other categories (Tukey multiple comparison tests, both $P > 0.05$, Fig. 1). Basal area, maximum DBH and AGB density were smaller in the forests harvested by conventional logging than in the rest ($P < 0.05$), while those of the old-growth forests and the forests harvested by RIL did not differ statistically from each other. AGB density of old-growth forests exceeded 48 kg m^{-2}, that of the forests harvested by RIL ranged from 31.8 to 48.1 kg m^{-2}, and that of the forests harvested by the conventional method from 9.6 to 28.4 kg m^{-2}. LAI was greater in old-growth forests than in the other categories, although this difference could not be tested statistically due to small sample size. DBH distribution of the forests harvested by RIL and the old-growth forests showed clearly L-shaped pattern (Fig. 2). DBH distributions of the forests harvested by conventional method showed the lack of larger trees (> 80 cm DBH) due to logging.

A total of 339 species belonging to 146 genera and 52 families (excluding unidentified stems) were found among 1333 stems ≥ 9.6 cm DBH, although the number of species may be reduced if matching of species in different plots was completed. The numbers of the observed taxa (families, genera and species) in the old-growth forests and the forests harvested by RIL were similar to each other, and were higher than those of the forests harvested by conventional method (Tukey multiple comparison tests, all $P < 0.05$; Fig. 3). The index of species richness of Fisher's α in the old-growth forests and the forests harvested by RIL was higher than that in the forests harvested by the conventional method (all $P < 0.05$). The α of the old-growth forests and the forests harvested by RIL overlapped greatly, all being greater than 50, while that of the forests harvested by conventional method was less than 40. The maximum value of α was 119.3 in the old-growth forest at PRI-1 and the minimum value was 17.6 in the forest harvested by conventional method at CV-3. Both of Shannon's indices of species diversity and evenness showed similar trends as number of taxa and Fisher's α̃.

The first and second axes of DCA cumulatively explained 24.4% of variance (eigenvalues, 0.34 and 0.21, respectively). Floristics of the three forest categories evaluated by genus composition clearly differentiated along the axis 1 (Fig. 4). The ranges of axis 1 scores of old-growth forests and the forests harvested by RIL partly overlapped, but the forests harvested by conventional logging were separated from the other two categories. Therefore, a most striking difference in species composition was found between the forests harvested by the conventional method and the rest. Among four abundant genera, two (*Dipterocarpus* and *Shorea*) that belong to Dipterocarpaceae were biased towards old-growth forests. Two genera of Euphorbiaceae showed contrasting patterns: *Macaranga* were abundant in disturbed sites while *Mallotus* were so in well-developed forests.

Old-growth forests and the forests harvested by RIL were dominated by Dipterocarpaceae trees, while the forests harvested by conventional method were by *Macaranga* trees (Fig. 5). According to the pattern of DBH distribution, Dipterocarpaceae contained many small-diameter trees in both the old-growth forests and the forests harvested by RIL, indicating a good regeneration (Fig. 2). On the other hand, *Macaranga* trees regenerated well in the forests harvested by the conventional method.

Discussion

Our results suggest that RIL is an efficient method to reduce logging impacts on forest structure, floristic composition and diversity compared with the conventional logging method. Commercially-logged forests occupy large tracts in tropical regions where human impacts are becoming increasingly greater, yet they have a high potential to protect biodiversity if managed properly (Cannon et al. 1998). The size of canopy opening by logging (i.e. creation of canopy gap) affected regeneration patterns and species composition elsewhere (Denslow 1980; Pickett and White 1985). RIL operation regulates the amount of logged trees and their size (DBH), location, and transportation of harvested logs (Sabah Forestry Department and European Union 2000). Consequently, RIL operation creates a smaller number of canopy gaps probably with a smaller mean size than the conventional logging does. Shade-tolerant trees can regenerate under a darker light condition. Therefore, these trees could have regenerated under small-sized canopy gaps in the forests harvested by RIL due to their physiological tolerance for reduced light. In contrast, the regeneration of shade-intolerant trees requires a sunnier condition (Turner 2001). Response to light condition associated with the difference in gap sizes caused a greater similarity of species composition and diversity between the old-growth forests and the forests harvested by RIL, and facilitated the regeneration of dipterocarp trees in the forests harvested by RIL (Sist and Nguyen-The 2002; Bischoff et al. 2005).

Differences of forest managements were related to the differences in the disturbance regime and regeneration patterns. For example, bulldozers heavily disturb topsoils by pulling out logged trees on the forest floor in the forests harvested by conventional method (Pinard et al. 2000). In our study, the forests harvested by conventional method were dominated by pioneer species of the genus *Macaranga*. *Macaranga* trees are known to regenerate under large canopy gaps often with disturbed soil conditions (Davies et al. 1998; Davies 2001). Moreover, an operation of the conventional method would have left a greater damage to the surrounding trees. On the other hand, RIL operation is gentle to forest with a minimum damage to soils and surrounding trees. This was achieved by both pre-harvest and harvest operations, including careful planning and construction of skid trails or skylines, directional felling, and appropriate skidding and landing (Sabah Forestry Department and European Union 2000). Our analysis dealt with two to three decades of a secondary succession only, and whether the species composition and structure of the forest including shrubs and herbs (that we do not include in our current analysis) can fully recover to a pre-harvest condition is still not known. To confirm the sustainability of the structure and floristic composition of tropical rain forests in DFR managed by RIL, long-term ecological monitoring is needed.

References

Bertault JG, Sist P (1997) An experiment comparison of different harvesting intensities with reduced-impact and conventional logging in East Kalimantan, Indonesia. For Ecol Manage 94:209-218

Bischoff W, Newbery DM, Lingenfelder M, Schnaeckel R, Petol GH, Madani L, Ridsdale CE (2005) Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. For Ecol Manage 218:174-192

Brown S (1997) Estimating biomass and biomass change of tropical forests. A primer. FAO, Rome.

Cannon CH, Peart DR, Leighton, M (1998) Tree species diversity in commercially logged Bornean rainforest. Science 281:1366-1368.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira K, Lescure JP, Nelson BW, Ogawa H, Puig H, Riera B, and Yamakura T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87-99.

Davies SJ (2001) Tree mortality and growth in 11 sympatric Macaranga species in Borneo. Ecology 82:920-932

Davies SJ, Palmiotto PA, Ashton PS, Lee HS, Lafrankie JV (1998) Comparative ecology of 11 sympatric species of Macaranga in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. J Ecol 86:662-673

Denslow JS (1980) Patterns of plant species diversity during succession under different disturbance. Oecologia 46: 18-21

Fisher RA, Corbert AS, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. J Animal Ecol 12:42-58

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Ecol Res 22:414-421.

Magurran AE (2004) Measuring biological diversity. Blackwell, Malden

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, Orland

Pinard MA, Putz FE (1996) Retaining forest biomass by reducing logging damage. Biotropica 28:278-295

Pinard MA, Barker MG, Tay J (2000) Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. For Ecol Manage 130:213-225

Sabah Forestry Department (1989) Forestry in Sabah. Sabah Forestry Department, Sandakan

Sabah Forestry Department and European Union (2000) RIL: operation guide book, specifically for crawler tractor use, 2nd ed. Sabah Forestry Department and European Union, Sandakan and Brussels

Sist P, Nguyen-The N (2002) Logging damage and the subsequent dynamics of a dipterocarp forest in East Kalimantan (1990-1996). For Ecol Mange 165:85-103

Slik JWF, Kessler PJA, van Welzen PC (2003) *Macaranga* and *Mallotus* species (Euphorbiaceae) as indicators for disturbance in the mixed lowland dipterocarp forest of East Kalimantan (Indonesia). Ecol Indicators

2:311-324

ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca

Turner IM (2001) The ecology of trees in the tropical rain forest. Cambridge University Press, Cambridge

Whitmore TC (1984) Tropical rain forests of the Far East. Second Edition. Oxford University Press, Oxford

Table 1. Description of the research plots.

Plot name	Abbreviation	Plot size (m)	Altitude (m)	Management status
Old-growth unlogged since the 1980s				
Ecological trail	PRI-1	100 x 20	248	Primary forest
ET antenna	PRI-2	50 x 40	248	Primary forest
ET jauh	80s-1	50 x 40	248	Unlogged since the 1980s
C54	80s-2	50 x 40	195	Unlogged since the 1980s
RIL				
Mannan	RIL95-1	100 x 20	196	8-10 years after RIL
Domingo	RIL95-2	100 x 20	200	8-10 years after RIL
C63 bawah	RIL00-1	100 x 20	195	5-6 years after RIL
C63 atas	RIL00-2	100 x 20	221	5-6 years after RIL
Conventional method				
Tangkulap 1	CV-1	100 x 20	109	Conventional logging
Tangkulap 2	CV-2	50 x 40	76	Conventional logging
Tangkulap 3	CV-3	100 x 20	52	Conventional logging

RIL indicates reduced-impact logging, and the time after logging is as of 2005.

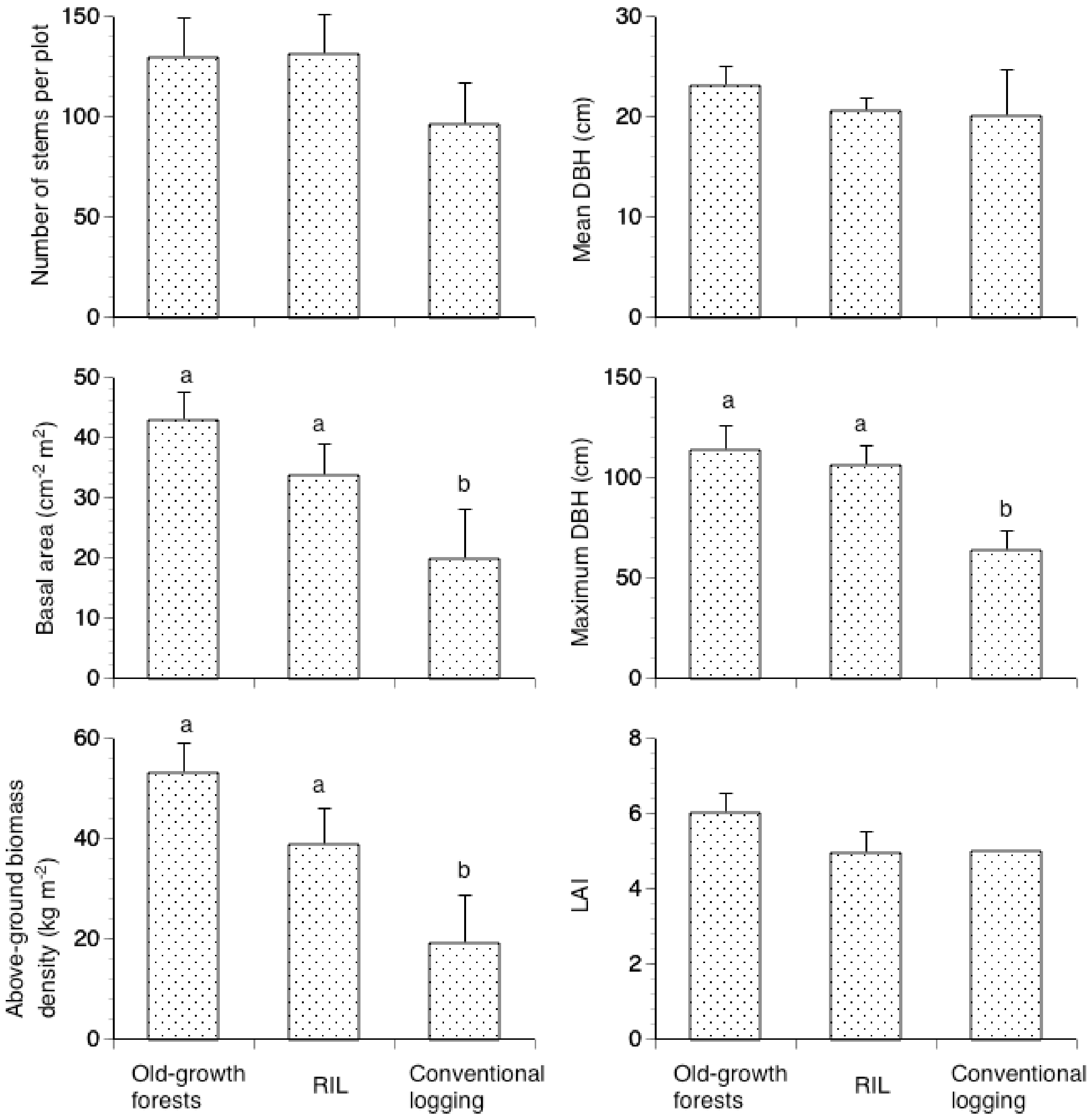

Figure 1. Stand structure in relation to management status in the tropical lowland forest in Deramakot, Sabah, Malaysia. RIL and conventional logging indicate the forests harvested by reduced-impact logging and by conventional logging, respectively. Forest categories that do not share the same letters differ at $P < 0.05$ by Tukey multiple comparison test. Vertical lines indicate standard deviation.

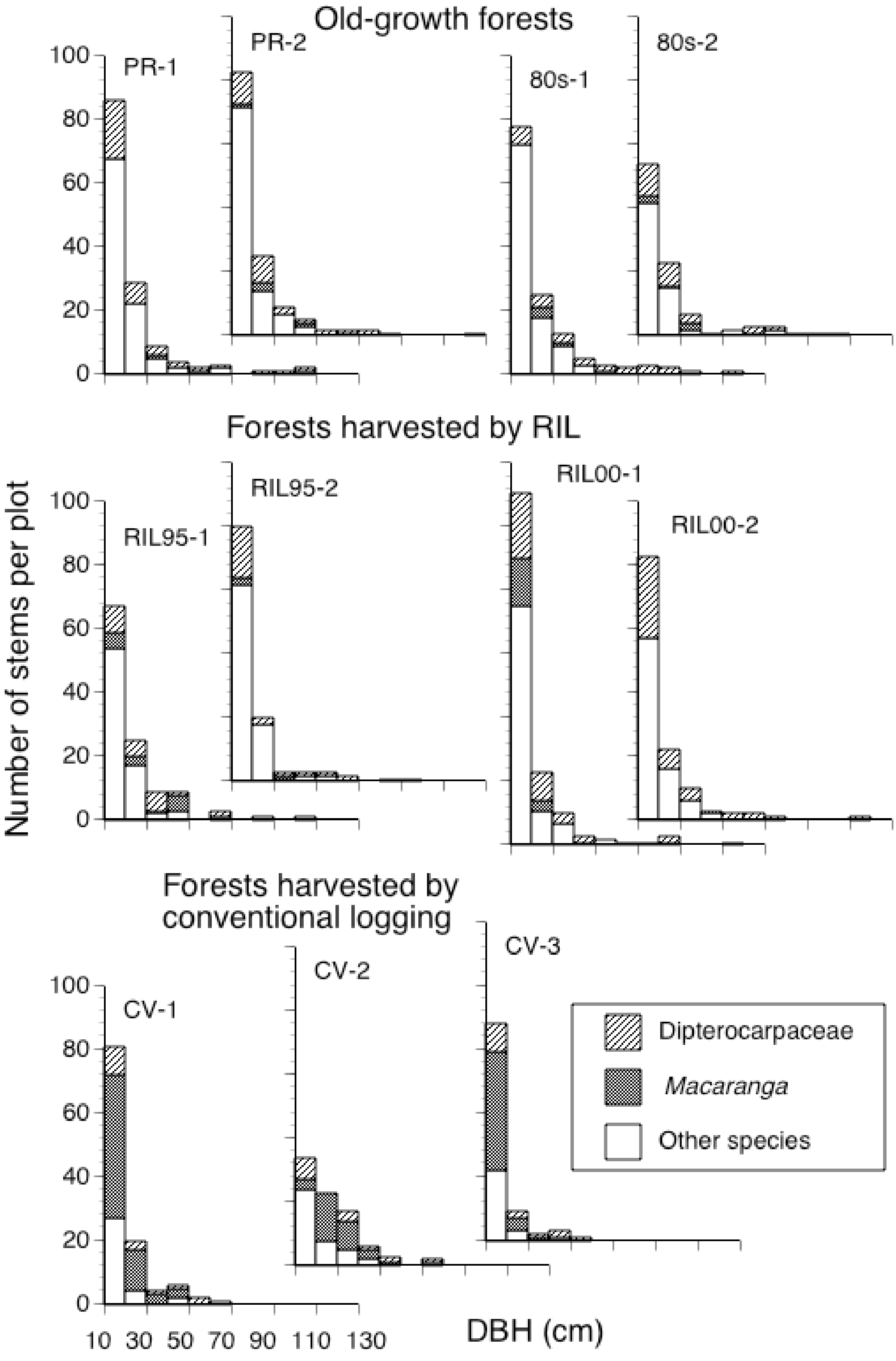

Figure 2. DBH distribution of trees in the 11 study plots, showing the fractions occupied by two dominant taxa, Dipterocarpacea and *Macaranga* (Euphorbiaceae). Stems < 10 cm DBH were excluded. See Table 1 for the plot abbreviations.

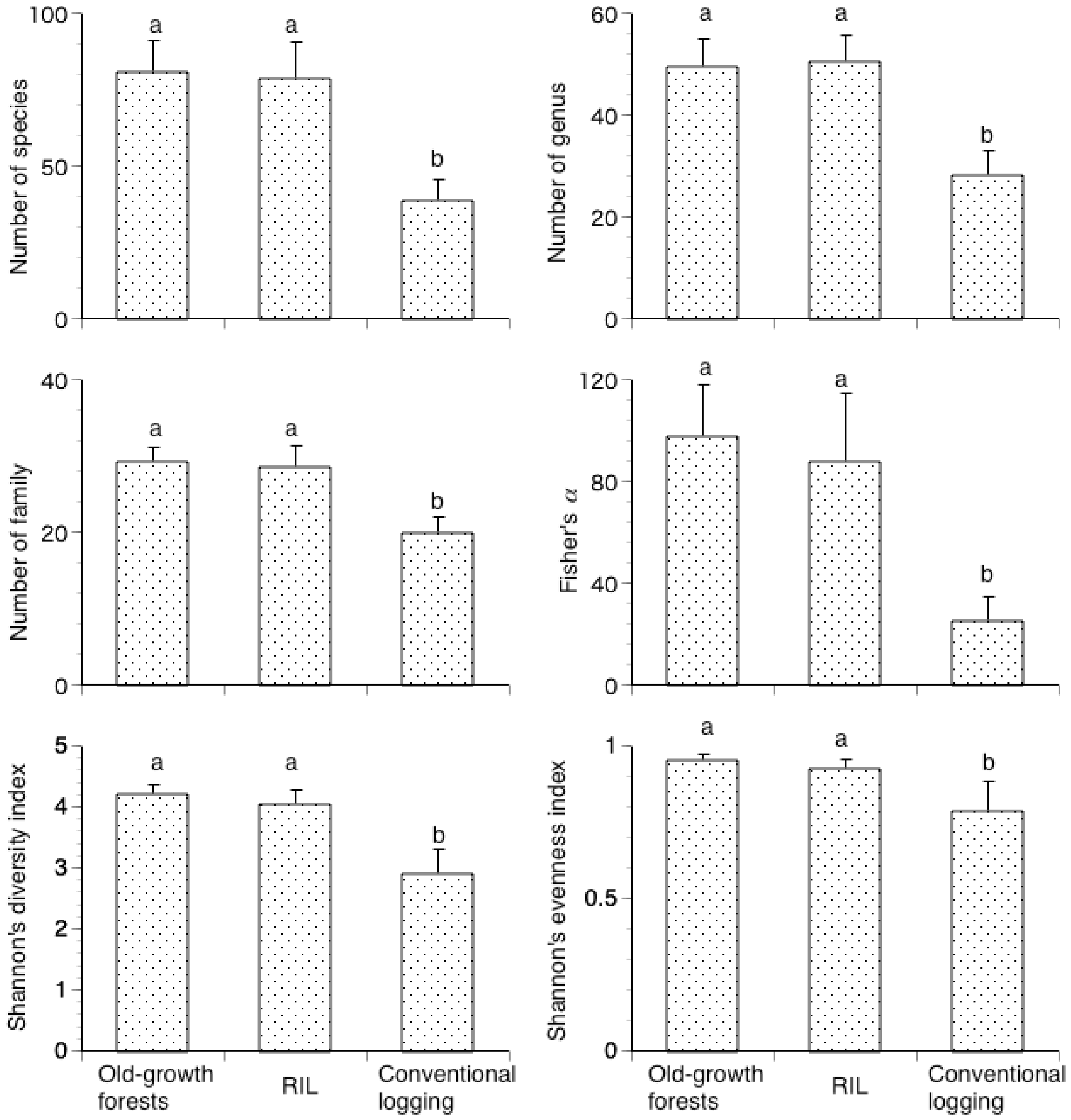

Figure 3. Tree diversity in relation to management status in the tropical lowland forest in Deramakot, Sabah, Malaysia. RIL and conventional logging indicate the forests harvested by reduced-impact logging and by conventional logging, respectively. Forest categories that do not share the same letters differ at $P < 0.05$ by Tukey multiple comparison test. Vertical lines indicate standard deviation.

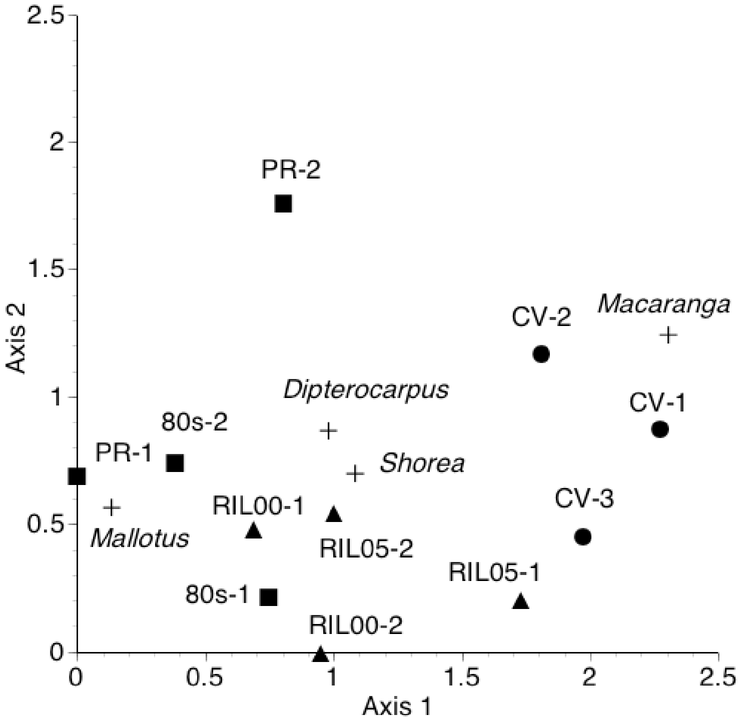

Figure 4. DCA diagram based on relative basal area of genus. Scores of four abundant genera were also shown. Square, old-growth forests; triangle, forests harvested by reduced-impact logging; circle, forests harvested by conventional method; cross, genus. See Table 1 for the plot abbreviations.

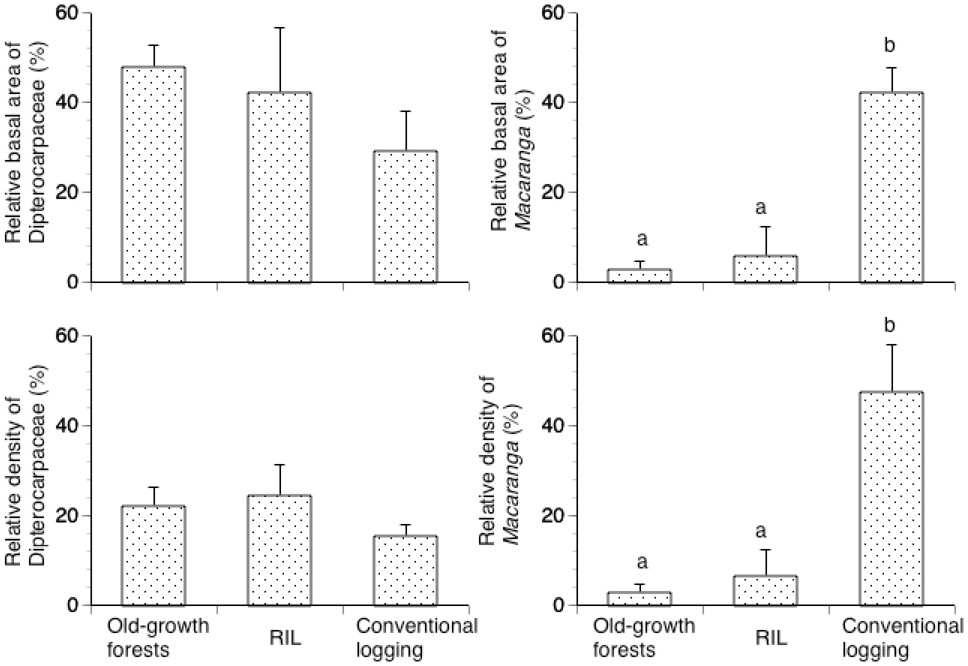

Figure 5. Dominance of Dipterocarpaceae and *Macaranga* (Euphorbiaceae) in terms of basal area and stem number in the three categories of forest management. RIL and conventional logging indicate the forests harvested by reduced-impact logging and by conventional logging, respectively. Forest categories that do not share the same letters differ at $P < 0.05$ by Tukey multiple comparison test. Vertical lines indicate standard deviation.

Effects of Logging on Forest Structure and Drosophilid Diversity in Tropical Lowland Forests of Sabah, Malaysia

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Introduction

Tropical forests are the most diverse and ecologically complex of the world’s ecosystems and their disappearance has been a major issue in conservation ecology since the 1980s (Bowles et al. 1998). The importance of both ecosystem services and the biological value of tropical forests has been emphasized by scientists and has caught the interest of citizens throughout the world. Sustaining biodiversity in tropical forests is a primary objective of conservation ecology. In addition, understanding the mechanisms of biodiversity degradation caused by logging disturbances in tropical forests is an important area of research in community ecology (Widodo et al. 2004).

In tropical forests that have regenerated after clearcut or that have been converted to plantations, insect diversity decreases from pre-disturbance levels (Eggleton et al. 1996). However, the effects of selective logging (i.e., a relatively moderate disturbance) on insect diversity remain unclear (Eggleton et al. 1996). In Sabah, Malaysia, a recently adopted logging method, i.e., reduced impact logging (RIL), has been launched to maintain sustainable forest use with minimal forest disturbance (Lagan et al. 2007). RIL was designed to limit forest disturbance and conserve large commercial trees as potential seed sources. Nevertheless, logging operations cause distinct changes in forest structure such as canopy destabilization and decreases in the density of trees or saplings (Hall et al. 2003).

The vertical distribution of the drosophilid community is closely related to the vertical foliage structure (Toda 1992; Tanabe et al. 2001). Specifically, drosophilid diversity tends to be higher in vertically complex than in simple forests (Tanabe et al. 2001). This difference in diversity can be explained in part by the “habitat heterogeneity hypothesis” whereby structurally complex habitats may provide more niches and more diverse ways of exploiting environmental resources and may thus increase species diversity (MacArthur and MacArthur 1961). Furthermore, drosophilid flies are useful indicators of biodiversity because their short lifespan (approximately 1 month) promotes rapid responses of their populations to environmental changes. In addition, their mobility allows quick relocation from unfavorable to favorable habitats (van der Linde and Sevenster 2002).

To test the habitat heterogeneity hypothesis, we investigated the effects of forest structural changes caused by various logging intensities on the species diversity of the drosophilid community. In addition, we discuss the relationship between biodiversity conservation and forest use by humans.

Material & Methods

Study plots

To assess the effects of various logging intensities on forest structure and the drosophilid community, we chose five study plots that experienced different disturbance regimes in the Deramakot Forest Reserve (DFR), Sabah, Malaysia. The disturbance regimes were characterized by two factors: the logging method [RIL or conventional (i.e., non-RIL) methods (CV)] and the time elapsed after logging. The five plots were differentiated according to the disturbance regimes (Table 1): “PRI” (primary forest with no logging), “80s” (harvested in the 1980s by CV), “RIL95” (harvested in 1995 by RIL), “RIL00” (harvested in 2000 by RIL), and “CV” (harvested continuously by CV).

Forest structure

In March 2005, the three-dimensional forest structure was measured using a portable lidar system. Details of the system were described by Parker et al. (2004). To measure vertical forest profiles, each plot was separated into lattices of each square 10-m on a side. Measurements were conducted at 2-m intervals along each separated line. For each 10-m section, vertical foliage densities were calculated at 1-m height intervals using the MacArthur–Horn method (MacArthur and Horn 1969) by combining data (i.e., height differences between the lidar system and the nearest foliage) from five measurement points.

Insect sampling

We used a bait (fermented banana) trap designed specifically for collecting drosophilid flies (Toda 1977). We selected 1–2 trees adjacent to each plot (within 5 m) for the placement of traps. Traps were set vertically from the understory to the canopy at each trapping site, with the lowest trap set at 0.5 m above the ground surface. The next trap was placed at 1.5 m aboveground, and remaining traps were set at 5-m intervals up into the canopy. The top traps varied in height depending on the canopy height of the forest (Table 1). Several (up to four) upper traps were suspended from the same rope using a pulley that was hung from a branch of the selected tree, and the lowest two traps were tied directly to the trunk of the same or a nearby tree (Table 1). We sampled four times in July–August and October–November 2003, and January–February and April–May 2004. During each sampling period, trapped insects were collected and trap baits were renewed three times at 10-day intervals. Samples from the most productive (determined from the sum of drosophilid flies across all plots) 10-day period during each season were selected for analyses. Flies were identified to species or morphospecies of Drosophilidae.

Data analyses

Forest structure

To estimate the vertical complexity of foliage, the foliage height diversity (FHD) was measured using the Shannon–Wiener index (Tanabe et al. 2001) for each 10-m section, and the mean FHD was calculated for each plot. Because of differences in plot shape (Table 1) and limited access caused by large fallen trees, the number of 10-m sections differed among plots (30 at PRI, RIL95, and RIL00; 24 at 80s; and 29 at CV). As an additional measure of foliage structure, the horizontal variance of the vertical foliage profile (HVF) was calculated as follows: the coefficient of variance for foliage densities at each 1-m height interval across all

10-m sections within each plot was calculated, and then the coefficients were averaged for all 1-m height intervals. Heights with no foliage across all 10-m sections were omitted from the calculations.

Differences in FHD or HVF were tested using one-way ANOVA. When a significant difference was detected among plots, multiple comparisons were performed using Tukey's honestly significant difference (HSD) test.

Diversity of the drosophilid community

The species richness and several diversity indices were calculated for each plot during each sampling period. Because the number of collected individuals and thus the number of species may have been biased by the number of traps, which varied among plots, species richness was estimated using sample rarefaction (Heck et al. 1975), based on the plot containing the lowest number of individuals in each season. Alpha, beta, and gamma diversity were calculated according to the concept of "additive partitioning of species diversity"; i.e., gamma (total) diversity can be partitioned into alpha and beta diversity (Levins 1968, Tanabe et al. 2001, Veech et al. 2002). Gamma diversity was calculated using the Shannon-Wiener formula, based on summed data for all traps in each plot. Alpha (intra-trap) diversity was estimated as the average Shannon-Wiener diversity calculated for each trap. Beta (inter-trap) diversity caused by species' compositional differences among traps was calculated as the difference between gamma and alpha diversity (gamma – alpha). As a measure of equitability, interspecific variation in the number of individuals was measured using Pielou's *J'*, based on gamma diversity and the observed number of species in each plot.

Generalized linear models in R (R Development Core Team 2004) were used to estimate the effects of forest structure. Separate analyses were conducted for species richness and each diversity index of the drosophilid community. Species richness was assumed to be Poisson distributed, whereas the diversity indices were assumed to be Gaussian distributed. The link functions were set as logarithmic. In addition, the four sampling periods were incorporated into the analyses as a categorical variable (the sampling period July–August was incorporated into the intercept). From all possible model combinations (including the null model with no variables) that incorporated the covariates (FHD and HVF) and one cofactor (season), the best model was selected using the Akaike information criterion (AIC; Akaike 1973). The deviance improvement was evaluated for the selected model. The percentage improvement compared to the deviance of the null model was used to estimate the relative explanatory power of the selected model.

Results

Forest structure

FHD was highest in the undisturbed plot of PRI and lowest in the most disturbed plot of CV. The moderately disturbed plots (80s, RIL00, and RIL95) were intermediate in FHD, between PRI and CV (Fig. 1). FHD differed significantly among plots (ANOVA, $P < 0.01$). PRI was significantly different from all the other plots (Tukey HSD, $P < 0.01$), but no other plots were significantly different from each other. Thus, all logging operations (even RIL) clearly affected forest structure by reducing FHD.

The mean HVF also differed significantly among plots (ANOVA, $P = 0.014$). This was primarily driven by the difference between PRI and RIL95 (Tukey HSD, $P = 0.039$; Fig. 1). HVF tended to be higher in the moderately disturbed plots.

Changes in drosophilid diversity with respect to forest structure and season

In total, 20883 individuals representing 80 species of drosophilid fly were identified (PRI: 5149 individuals, 52 species; 80s: 4348, 45; RIL00: 4398, 49; RIL95: 4344, 44; CV: 2644, 45). All of the diversity measures, with the exception of equitability, fluctuated significantly among seasons (Fig. 2). In particular, the variation in species richness was largely explained by season (76.07% deviance improvement; Table 2). The number of species, gamma diversity, and alpha diversity were lowest in May and highest in January. Throughout the four seasons at DFR, the most rainy days occurred in December–January, whereas the least rain fell in April–May. Because most drosophilid species are vulnerable to desiccation, moisture conditions are a key factor for drosophilid survival. Of the two measures of forest structure, only FHD positively affected beta diversity (Table 2). Equitability was not affected by either season or forest structure.

Discussion

Effects of logging disturbances on forest structure

Logging disturbances decreased the vertical heterogeneity of foliage density. Logging in DFR targets mature Dipterocarpaceae trees (diameter at breast height > ca. 60 cm) and has removed several large foliage crowns from the canopy and/or emergent layers. These losses of canopy foliage reduce the complexity of the vertical foliage structure and promote the growth of subcanopy and/or pioneer trees (Okuda et al. 2003). As this gap regeneration proceeds, the vertical foliage structure slowly recovers. However, our results indicate that the effects of logging remain prevalent in the vertical foliage structure of forests harvested by both conventional logging as early as the 1980s and by RIL in 1995.

In contrast, the horizontal heterogeneity of foliage density tended to be higher in moderately disturbed forests. According to theories addressing light acquisition by subcanopy trees, the foliage distribution is predicted to be stratified in mature forests with a closed canopy (Terborgh 1985), thus forming a horizontally continuous structure of dense and sparse foliage layers. The selective removal of large trees from the canopy layer and the subsequent gap regeneration may disturb this horizontal constancy of the foliage structure. However, at the most strongly disturbed plot (CV), the horizontal foliage heterogeneity was relatively low. This may be attributed to the disappearance of virtually all trees in the top layer by heavy logging, as well as the concomitant growth of subcanopy and pioneer trees.

Relationship between drosophilid diversity and forest structure

Species richness was independent of forest structure and fluctuated significantly among the four seasons. The stability of equitability throughout the seasons suggests that seasonal changes in gamma and alpha diversity were caused by seasonal changes in species richness. In contrast, beta diversity (representing the degree of vertical habitat segregation in the drosophilid community) was positively affected by FHD. These results are consistent with the habitat heterogeneity hypothesis, which predicts that structurally complex habitats usually accommodate more species than homogeneous habitats by providing a greater variety of microhabitats. Paradoxically, in forests with less obviously stratified standing trees, weakened habitat segregation may strengthen resource competition within the drosophilid community if component species use similar food resources (Shorrocks 1977; Tanabe et al. 2001). This strengthened competition may accelerate the extinction of species and may ultimately decrease local species richness.

In DFR, decreases in FHD caused by forest logging were related to decreases in beta diversity, but not to changes in species richness. Selective logging, especially RIL, in DFR has been operated to minimize the widespread effects of logging, thus reserving forest stands with diverse mosaics of foliage structure. Although species richness may decrease through strengthened competition in poorly stratified forest stands, adjacent stands with sufficient foliage stratification may function as regional sources of species to compensate for the local depletion of species richness. This seeding effect would be especially strong for highly mobile organisms such as flying insects and may thus serve as a reason why drosophilid species richness did not significantly vary among the study plots that differed in vertical foliage structure.

From a conservation ecology standpoint, we conclude that logging operations in DFR appear to be successful in terms of the conservation of drosophilid biodiversity. However, we caution against the generalization of our results to other organisms that may vary in mobility and in their responses to different sizes of habitat patchiness.

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References

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Proceedings of the second international symposium on information theory. Budapest, Hungary, pp. 267-281

Bowles IA, Rice RE, Mittermeier RA, da Fonseca GAB (1998) Logging and tropical forest conservation. Science 280: 1899-1900

Eggleton P, Bignell DE, Sands WA (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Philos Trans R Soc London, Ser B 351: 51-68

Hall JS, Harris DJ, Medjibe V, Ashton PMS (2003) The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. For Ecol Manage 183: 249-264

Heck KLJ, van Belle G, Simberloff D (1975) Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459-1461

van der Linde K, Sevenster JG (2002) Drosophila diversity over a disturbance gradient. Proceedings Experimental and Applied Entomology 13: 51-56

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Ecol Res 22: 414-421

Levins R (1968) Evolution in changing environments, some theoretical explorations. Princeton University Press, Princeton

MacArthur RH, Horn H (1969) Foliage profile by vertical measurements. Ecology 50: 802-804

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42: 594-598

Okuda T, Suzuki M, Adachi N, Quah ES, Hussein NA, Manokaran N (2003) Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. For Ecol Manage 175: 297-320

Parker GG, Harding DJ, Berger ML (2004) A portable LIDAR system for rapid determination of forest canopy structure. J Appl Ecol 41: 755-767

R Development Core Team (2004) R: a language and environment for statistical computing.

http://www.R-project.org (R Foundation for Statistical Computing: Vienna Austria.)

Shorrocks B (1977) The distribution and abundance of woodland species of British *Drosophila* (Diptera: Drosophilidae). J Anim Ecol 44: 851-864

Tanabe S, Toda MJ, Vinokurova AV (2001) Tree shape, forest structure and diversity of drosophilid community: Comparison between boreal and temperate birch forests. Ecol Res 16: 369-385

Terborgh J (1985) The vertical component of plant species diversity in temperate and tropical forests. Am Nat 126: 760-776

Toda MJ (1977) Two new 'retainer' bait traps. Drosophila Inf Serv 52: 180

Toda MJ (1992) Three-dimensional dispersion of drosophilid flies in a cool temperate forest of northern Japan. Ecol Res 7: 283-295

Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity: recent revival of an old idea. Oikos 99: 3-9

Widodo ES, Naito T, Mohamed M, Hashimoto Y (2004) Effects of selective logging on the arboreal ants of a Bornean rainforest. Entomol Sci 7: 341-349

Table 1 The disturbance regime, shape, canopy height, and trapping profile of each study plot.

Plot name	Abbreve	Disturbance regime	Plot size (m x m)	Canopy height (m)	Tree species at trap-sites	Trap heights (m)
Ecological trail	PRI	No impact of logging	20 x100	31.5-36.5	*Polygclaccae affine* *Shorea exelliptica*	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5, 31.5, 36.5
C54	80s	Harvested in the 1980s by CV	40 x 50	26.5-31.5	*Lithocarpus* sp. *Shorea macroptera*	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5, 31.5
C63 bawah	RIL00	Harvested in 1995 by RIL	20 x 100	26.5-31.5	*Shorea* sp.	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5
Mannan	RIL95	Harvested in 2000 by RIL	20 x 100	26.5-31.5	*Dipterocarpus* sp. *Dorio* sp.	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5
Tangkulap 1	CV	Continued intermittent harvest by CV	20 x 100	21.5-26.5	*Shorea parviforia*	0.5, 1.5, 6.5, 11.5, 16.5, 21.5

Abbrev; Abbreviation

Table 2 Parameter estimates and percentage deviance improvement of the selected models explaining the spatio-temporal variation in species richness and diversity indices of the drosophilid community.

	Intercept		FHD		HVF		January		May		October		(%)[#]
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	
Species richness	2.986	0.100	NS*		NS		0.408	0.130	-0.238	0.151	0.159	0.139	76.07
Equitability	-0.560	0.039	NS		NS		NS		NS		NS		0.00
Gamma diversity	0.597	0.077	NS		NS		0.180	0.100	-0.203	0.122	0.073	0.105	44.60
Alpha diversity	0.408	0.084	NS		NS		0.181	0.110	-0.230	0.135	-0.027	0.121	41.93
Beta diversity	-2.721	0.769	0.646	0.309	NS		0.217	0.214	-0.054	0.242	0.455	0.197	46.37

Est: Estimate, *NS: not selected, [#];Deviance improvement

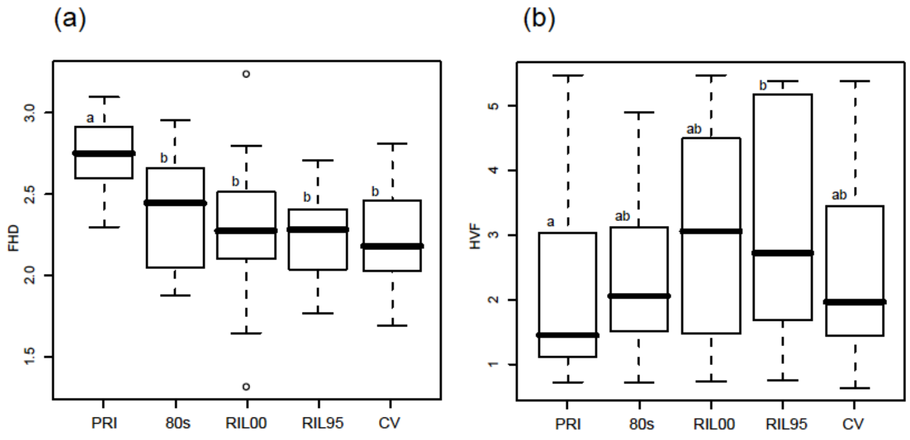

Fig. 1 Box-plots indicating the median (bold solid line), lower and upper hinges, extreme lower and upper whiskers, and outliers of (a) foliage height diversity (FHD) and (b) horizontal variance of foliage (HVF) within each plot. Different letters indicate statistically significant differences ($P < 0.05$) according to Tukey's HSD.

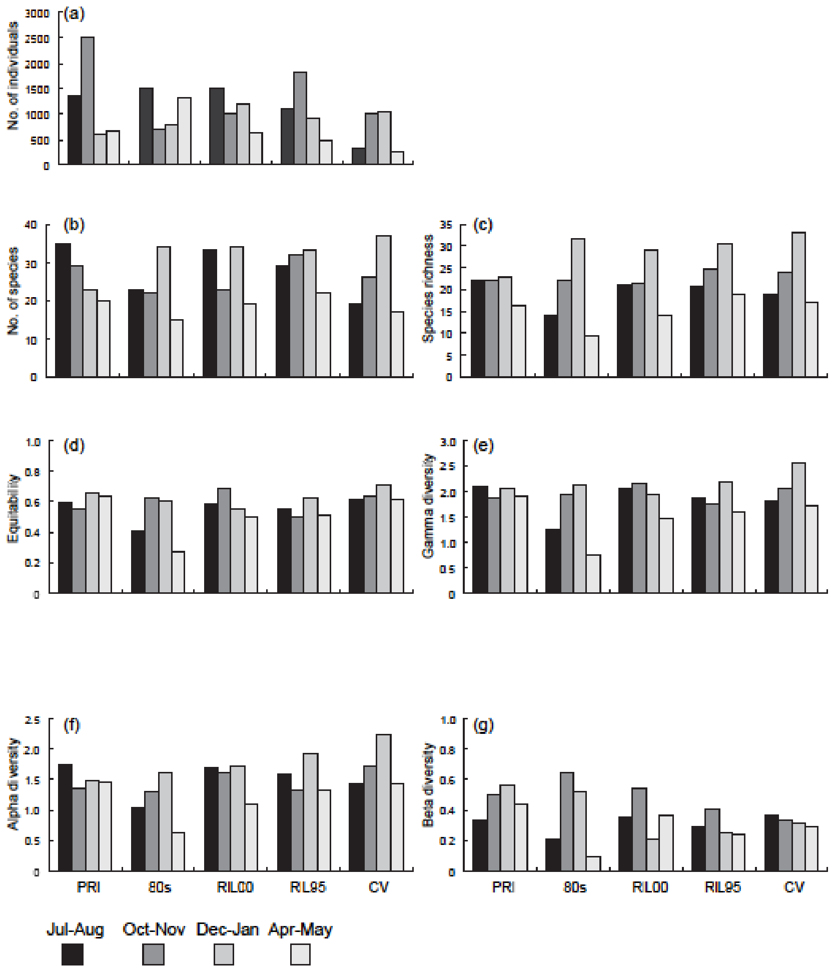

Fig. 2 Seasonal and among-plot variation in the (a) number of collected individuals, (b) number of collected species, (c) species richness estimated by rarefaction, (d) equitability, (e) gamma diversity, (f) alpha diversity, and (g) beta diversity.

Logging Effects on Soil Macro- and Meso-Faunas in the Rain Forests of Deramakot Forest Reserve, Sabah, Malaysia

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Introduction

Soil animals play important roles in every forest ecosystem in the world. Their abundance and diversity are considered to be a good indicator of forest healthiness. In Borneo, the effects of forest management have been investigated on moths (Chey 4et al. 1997), canopy arthropods (Chey et al. 1998), butterflies (Wilott et al. 2000) and beetles (Chung et al. 2000), but less frequently documented on soil animals except for termites (Eggleton et al. 1999). On the other hand, many studies which were carried out in the temperate zones of Europe, North America and East Asia revealed that forest clear-cutting caused substantial changes in soil fauna.

The purpose of our study is to detect the effects of different forest management schemes on soil fauna in tropical rain forests and to ultimately recommend a sound scheme for biodiversity conservation there.

Materials and Methods

Study sites

Ten sites were selected from forest stands under different management schemes in and around Deramakot Forest Reserve (DFR). The ten sites were grouped into three categories of management schemes: “unlogged” category including two primary-forest (PRI) sites and two sites which experienced a modest harvest by selective logging in the 1980s (80s), “RIL (reduced-impact logging)” category including two sites which were harvested by RIL in 1995 (RIL95) and two sites which were harvested by RIL in 2000 (RIL00), and “CV (conventional)” category including two sites which were continuously harvested by conventional selective logging until the time of our analysis.

Soil macrofauna

Sampling of soil macrofauna was conducted at five quadrats (each 25 × 25 cm) set at 10 m intervals along a line (40 m) in each site. Litter layer and topsoil (15 cm deep) were collected at each quadrat. The weight of litter layer and the water content were measured by drying the samples. Soil animals were immediately picked up from the soil and litter by hands in the field and preserved in 80 % ethanol. They were sorted to the groups listed in Table 1 under a stereo-microscope in the laboratory, and the sorted taxonomic groups were classified into four functional groups. Lavelle et al. (1995) recognized two important functional groups, ecosystem engineers and litter transformers. The former develops mutualism with internal microorganisms and can digest litter directly. Therefore, they affect nutrient cycling and/or soil formation, and are important in ecosystem functioning. Earthworms and termites are typical ecosystem engineers. Litter transformers such as Isopoda, Diplopoda, Blattodea and Diptera contribute to the decomposition of litter in association with external microorganisms. Predators such as Araneae, Pseudoscorpiones, Opiliones, Geophilomorpha, Symphylla and Lithobiomorpha have some roles in structuring soil animal communities. Ants act in various ways for ecosystem functioning, some as predators, others as decomposers and so on. In this study, we treated them together as one category “ants” because of the lack of information on their ecology.

Soil mesofauna

A 100 ml soil sample (20 cm^2 × 5 cm in depth) including litter layer was taken by a cylindrical core sampler at each of the ten points set at 5 m intervals along another line (45 m) in each site. The samples were put on Tullgren funnels within a few hours after sampling. Soil mesofauna was extracted for three days under irradiation of 40W electric bulbs and preserved in 80% ethanol. Among them, Collembola and oribatid mites were identified to specific level and counted under a microscope in the laboratory. Collembolan species were classified into three feeding groups, detritus feeders, fungal feeders and sucking feeders (Hasegawa 2006).

Statistical analyses

The variations in soil animal density among the forest management schemes and among the sites of each scheme were analysed by two-level nested ANOVA (group = management category, subgroup = site), separately for the total macrofauna, each functional group of macrofauna and each feeding group of Collembola. Canonical correspondence analysis (CCA) was used to examine the relation between environmental variables and the composition of the taxonomic groups of macrofauna in the study sites (ter Braak 1986). The following environmental variables were used in the analysis: the attributes based on vegetation data for all trees with DBH (maximum diameter at breast height) ≥10 cm were tree density, total basal area, above-ground biomass, the number of tree families, the number of tree species, Shannon-Wiener’s diversity index, Fisher’s alpha diversity index, the basal area percentage of Dipterocarpaceae, the basal area percentage of Euphorbiaceae, and the basal area percentage of Macaranga (Seino et al. 2006); soil environmental variables were the weight of organic matter and the water content in litter layer. Among them, significant variables ($p < 0.05$) were chosen by the forward selection.

Results and Discussion

Soil macrofauna

The mean densities of soil macrofauna in each of the ten sites are shown in Table 1. The mean density of total soil macrofauna was significantly higher in the unlogged sites than in the RIL sites ($p<0.05$, nested ANOVA; Fig. 1). This was primarily driven by ants, of which density was significantly higher in the unlogged sites than in the RIL and CV sites ($p<0.05$, nested ANOVA; Fig. 2). The number of orders or equivalent taxonomic groups of macrofauna was similar across the sites of three management categories (Table 1). The density of litter transformers was significantly higher in the CV sites than in the RIL and unlogged sites ($p<0.05$, nested ANOVA; Fig. 2). The density of predators was significantly higher in the CV sites than in the RIL sites ($p<0.05$, nested ANOVA; Fig. 2). The result of CCA demonstrated that the water content of litter layer and the basal area percentage of Dipterocarpaceae explained well the compositional variation of the soil macrofauna community among the sites (Fig. 3). The water content of litter and soil has been suggested as an important limiting factor for the survival of some soil animal groups (e.g., Lavelle et al. 2001). On the other hand, the dominance of Dipterocarpaceae, which has been detected as an environmental variable closely related to the structure of soil macrofauna community in tropical forests, probably reflects the forest maturity. Along the process of forest maturation, changes in a number of associated environmental factors would govern the dynamics of soil macrofauna community.

Soil mesofauna

The density and the species richness of total Collembola and oribatid mites did not differ so distinctly among the ten sites (Table 2). As for the functional groups of Collembola, detritus feeders and fungal feeders did not show significant differences in density among the management categories (Fig. 4), but the density of sucking feeders was significantly higher in the unlogged sites than in the other sites ($p<0.05$, nested ANOVA; Fig. 4). Hasegawa (2006) suggested that sucking feeders decreased in clear-cut sites and that their species composition was well related to the changes in vegetation. Sucking feeders feed on bacteria and/or the organic matter in free soil water, and therefore may be sensitive to a drought on the forest floor, which is often caused by a decrease of vegetation cover in logged sites. These results suggest that the density and the species richness of the total mesofauna were not so much affected by logging within the magnitude of current harvest schemes applied in DFR. However, the composition of Collembolan feeding groups was affected by logging, regardless of RIL or CV.

In DFR, we did not find distinct effects of logging on the density and the number of taxonomic groups in soil macrofauna (excluding ants) and mesofauna. However, the composition of functional and/or taxonomic groups varied among the sites under different forest management schemes. Various degrees of logging disturbance caused by these managements must have differently affected the relative abundances of component soil animals through changes in the above-ground plant community and/or the water content of organic matter on forest floor. We suggest that the compositional structure of soil animal community can be a potential indicator for evaluating the soundness of various logging schemes in relation to ecosystem functioning and biodiversity conservation in tropical forests.

Acknowledgments

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References

Chey VK, Holloway JD, Hambler C, Speight MR (1998) Canopy knockdown of arthropods in exotic plantations and natural forests in Sabah, north-east Borneo, using insecticidal mist-blowing. Bull Ent Res 88:15-24

Chey VK, Holloway JD, Speight MR (1997) Diversity of moths in forest plantations and natural forests in Sabah. Bull Ent Res 87:371-385

Chung AYC, Eggleton P, Speight MR, Hammond PM, Chey VK (2000) The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. Bull Ent Res 90:475-496

Eggleton P, Homathevi R, Jones DT, MacDonald JA, Jeeva D, Bignell DE, Davies RG, Maryati M (1999) Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. Phil Trans R Soc Lond B 354:1791-1802

Hasegawa M, Fukuyama K, Makino S, Okochi I, Goto H, Mizoguchi T, Sakata T, Tanaka H. (2006) Collembolan community dynamics during deciduous forests regeneration in Japan. Pedobiologia 50: 117-126

Lavelle P (2001) Soil Ecology. Kluwer Academic Publishers, Dordrecht

Lavelle P, Lattaud C, Trigo D, Barois I (1995) Mutualism and biodiversity in soils. Plant and soil 170:20-33

ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179

Willott SJ, Lim DC, Compton SG, and Sutton SL (2000) Effects of selective logging on the butterflies of a Bornean Rainforest. Conserv Biol 14:1055-1065

Table 1 Mean densities (m^{-2}) of soil macrofauna in ten sites under different forest management schemes.

Numbers in fig. 3	Soil macrofauna group	Forest management category									
		Unlogged				RIL				CV	
		PRI-1	PRI-2	80s-1	80s-2	RIL00-1	RIL00-2	RIL95-1	RIL95-2	CV-1	CV-2
	Platyhelminthes	0	0	0	0	0	0	0	0	3.2	0
32	Gastropoda	3.2	0	0	0	0	0	0	0	0	0
31	Hirudinea	0	0	0	3.2	0	0	3.2	0	0	0
	Oligochaeta (Earthworm)	83.2	12.8	48	9.6	28.8	22.4	32	48	64	38.4
	Pseudoscorpiones	28.8	35.2	22.4	28.8	12.8	3.2	38.4	25.6	35.2	35.2
28	Opiliones	3.2	6.4	3.2	0	0	3.2	0	6.4	3.2	3.2
	Araneae (Spider)	25.6	57.6	57.6	25.6	16	35.2	60.8	60.8	64	70.4
	Prostigmata	9.6	9.6	3.2	6.4	3.2	3.2	35.2	16	12.8	0
	Gamasida	3.2	12.8	0	3.2	0	3.2	16	9.6	9.6	9.6
	Oribatida	32	16	3.2	3.2	0	3.2	9.6	0	16	6.4
	Isopoda	28.8	12.8	9.6	19.2	6.4	12.8	16	9.6	28.8	73.6
	Diplopoda	32	3.2	19.2	19.2	6.4	12.8	9.6	12.8	25.6	57.6
27	Symphyla	3.2	6.4	6.4	0	0	3.2	0	0	3.2	6.4
	Lithobiomorpha	0	6.4	0	16	6.4	6.4	9.6	3.2	9.6	25.6
	Geophilomopha	6.4	6.4	9.6	6.4	3.2	3.2	9.6	3.2	6.4	6.4
	Collembola	48	67.2	115.2	28.8	32	44.8	112	92.8	57.6	73.6
	Campodeidae	6.4	9.6	16	0	0	3.2	3.2	9.6	22.4	22.4
	Japygidae	12.8	0	0	0	0	0	3.2	3.2	6.4	16
29	Thysanura	3.2	0	3.2	0	0	0	3.2	9.6	0	6.4
	Isoptera (Termite)	688	12.8	70.4	6.4	0	0	3.2	99.2	22.4	0
23	Blattodea	9.6	3.2	0	6.4	0	3.2	9.6	0	9.6	12.8
30	Dermaptera	0	0	0	0	0	0	0	0	6.4	0
25	Other Orthopetra	16	0	6.4	0	0	3.2	0	0	3.2	6.4
7	Hemiptera	22.4	48	41.6	6.4	19.2	9.6	28.8	32	19.2	22.4
22	Lepidoptera (larva)	12.8	6.4	19.2	3.2	0	3.2	3.2	0	0	6.4
15	Pselaphinae	19.2	19.2	0	0	3.2	0	22.4	3.2	28.8	0
	Staphylininae	28.8	9.6	28.8	3.2	9.6	28.8	6.4	19.2	3.2	3.2
10	Other Coleoptera (adult)	32	22.4	16	9.6	28.8	9.6	32	19.2	3.2	28.8
11	Other Coleoptera (larva)	22.4	6.4	19.2	12.8	9.6	12.8	25.6	57.6	22.4	9.6
19	Diptera (larva)	19.2	3.2	6.4	16	0	3.2	12.8	6.4	3.2	0
	Hymenoptera (Ants adult)	5357	828.8	656	176	131.2	211.2	172.8	67.2	73.6	364.8
	Hymenoptera (Ants larva)	25.6	0	0	3.2	9.6	9.6	0	3.2	0	166.4
	Insecta (unidentified)	6.4	9.6	0	6.4	0	0	0	0	0	6.4
	Total	6589	1232	1181	419.2	326.4	454.4	678.4	617.6	563.2	1078
	Total – ants	1206	403.2	524.8	240	185.6	233.6	505.6	547.2	489.6	547.2
	Number of groups	27	24	21	21	14	22	24	21	26	23

Table 2 Mean densities and species richness of Collembola in ten sites under the three categories of forest management schemes.

Management category	Site	Density (m^{-2})		Species richness		
		Average	SE	Average (per core)	SE	Total (per site)
unlogged	PRI-1	11000	1809	9.8	1.1	29
unlogged	PRI-2	9150	1282	9.8	0.9	33
unlogged	80s-1	12250	1988	10.9	1.4	34
unlogged	80s-2	16350	4104	11.4	1.1	34
RIL	RIL95-1	14000	2976	12.1	1.2	35
RIL	RIL95-2	7100	1668	7.9	1.2	33
RIL	RIL00-1	9900	2226	8.2	1.0	27
RIL	RIL00-2	10150	1886	9.3	0.9	28
CV	CV-1	7850	1883	7.9	1.1	28
CV	CV-2	16750	3366	11.1	1.1	35

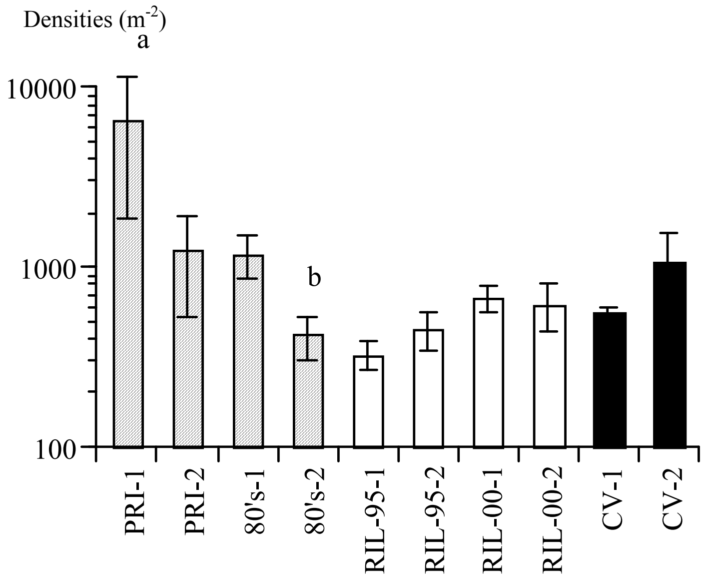

Fig. 1 Mean densities (bars: ±SE) of soil macrofauna in ten sites under the three categories of forest management schemes: "unlogged" (hatched), "RIL" (white), and "CV" (black).

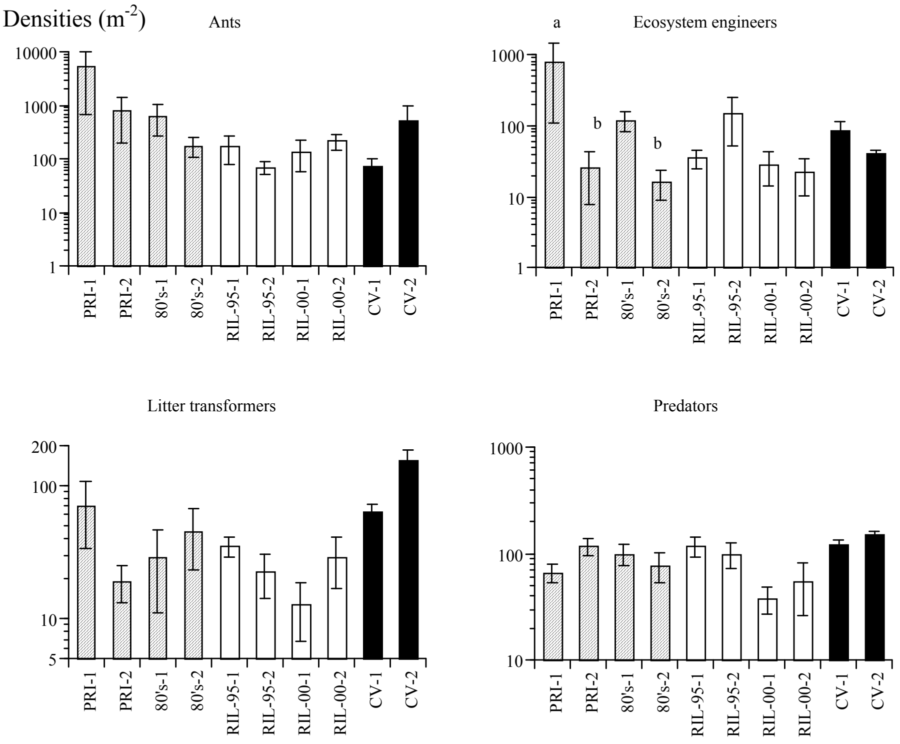

Fig. 2 Mean densities of four soil macrofauna functional groups (ants, ecosystem engineers, litter transformers and predators) in ten sites (see Fig. 1 for other explanations).

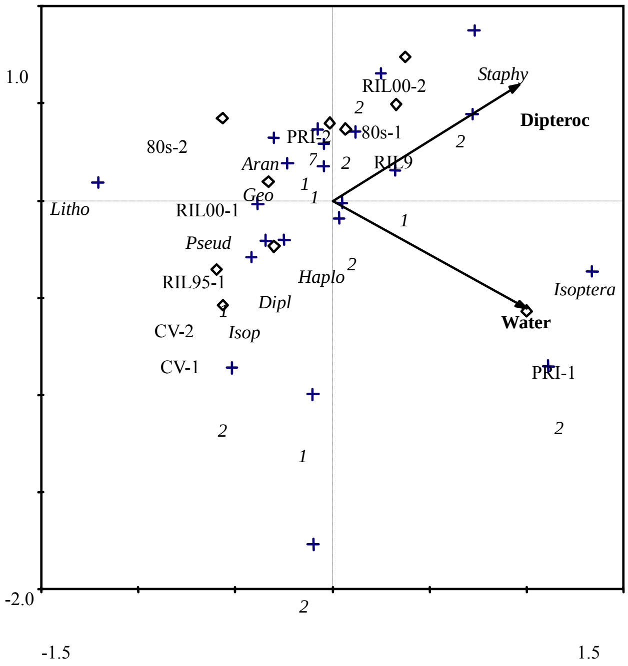

Fig. 3 Tri-plot ordination by CCA for soil macrofauna: sites (diamonds), taxonomic groups (crosses), and significant environmental variables (arrows). Dipteroc, relative basal area of Dipterocarpaceae; Water, water content in litter layer; Staphy, Staphylininae; Aran, Araneae; Litho, Lithobiomorpha; Pseud, Pseudscorpiones; Dipl, Diplopoda; Isopod, Isopoda; Haplo, Ologochaeta. Positions of other animal taxa are shown with numerals shown in Table 1.

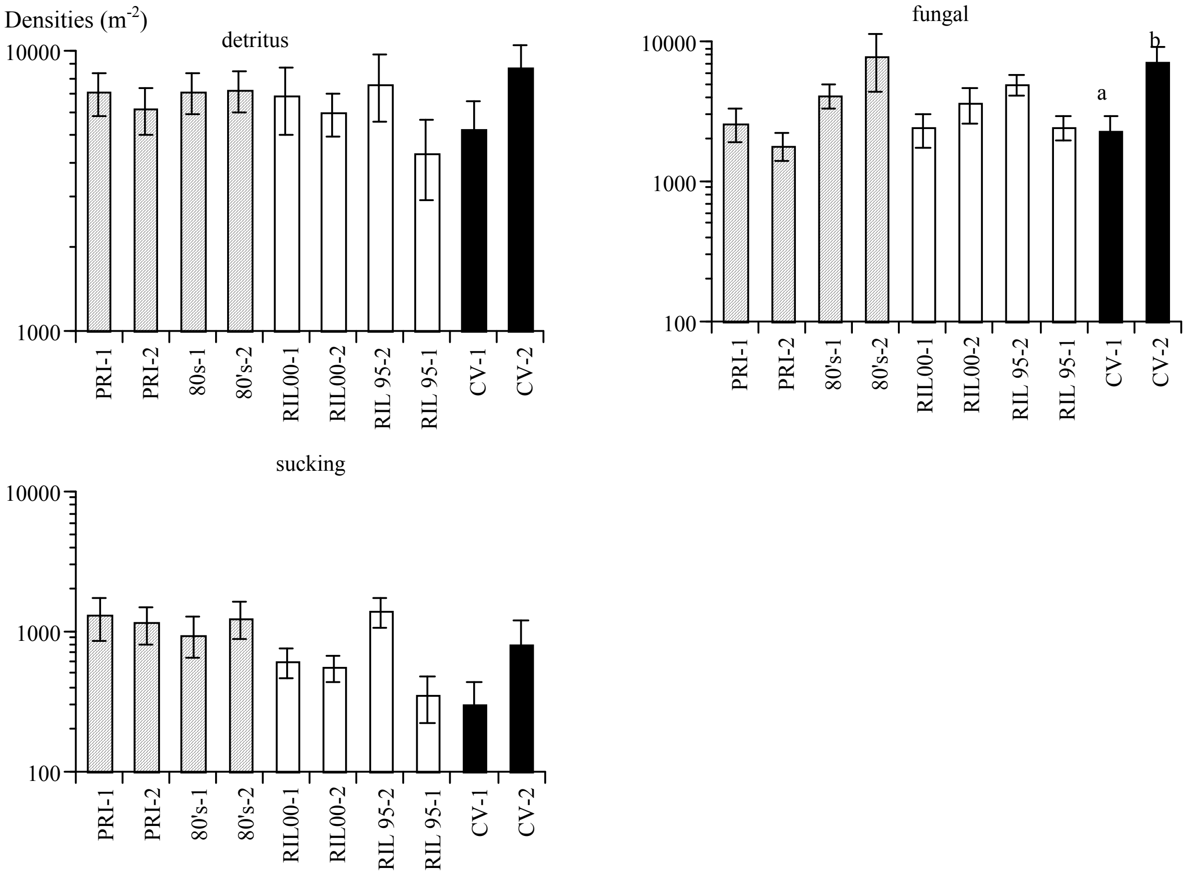

Fig. 4 Mean densities of three Collembolan feeding groups (detritus feeders, fungal feeders and sucking feeders) in ten sites (see Fig. 1 for other explanations).

Comparative Study on Mammalian Fauna in Different Harvesting Intensities with Reduced-Impact and Conventional Logging in Sabah, Malaysia

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Introduction

Habitat destruction including logging and forest clearing for agriculture has always been a major threat for most mammals in Southeast Asia and other parts of tropical regions (Cuaron 2000). Large proportion of tropical production forests (i.e. zoned for timber production) has already become logged-over forests, on which much of its biodiversity depends now (Frumfoff 1995). We must establish a strategy to conserve these threatened animals in production forests as well as those in primary forests (Frumhoff 1995; Johns 1997; Meijaard et al. 2006).

Selective logging is one of the most prevalent land uses in Southeast Asia and other tropical regions. The method is known to severely damage the residual stand and affect forest structure and biodiversity even though only a small proportion of the trees are often removed (Johns 1988; Cannon et al. 1994; Pinard and Putz 1996; Laurance and Laurance 1996).

There are several techniques for controlling and minimizing logging damage (e.g., Crome et al. 1992). One of such methods, reduced-impact logging (RIL), is a set of guidelines to reduce the physical impacts on the ground, remaining standing trees, streams and ecosystem as a whole with the combination of a pre-harvest census, carefully controlled felling and skidding, lowered allowable cut and regulated machinery use (Putz and Pinard 1993).

Some studies examined the effects of reduced-impact logging in retaining forest biomass and in damage reduction to forests in Southeast Asia and reported that reduced-impact logging reduced the damage or injury to residual stand by 18-27% (Pinard and Putz 1996; Bertault and Sist 1997; Sist et al. 1998). However, there is no study available on the mammalian responses to reduced-impact logging (Meijaard et al. 2006), although mammals have important ecological roles such as seed dispersal and/or pollination in the forests.

In this study, we examined the effects of reduced-impact logging on the mammalian fauna by comparing the diversity and the abundance in a reduced-impact logged forest and a conventionally logged forest in Sabah, Malaysia.

Materials and Methods

Study site

Our study was conducted in Deramakot Forest Reserve (55,083ha), a reduced-impact logged forest and adjacent Tangkulap Forest Reserve (27,550ha), a conventionally logged forest, in Sabah, Malaysian Borneo. The climate is humid equatorial with a mean annual temperature of about 26℃. Mean annual rainfall is about 3,500 mm (Huth and Ditzer 2001). The major vegetation of Deramakot is a mixed dipterocarp forest dominated by the family Dipterocarpaceae, while that of Tangkulap consists of abundant pioneer species of the genus *Macaranga* (Euphorbiaceae) (Seino et al. 2006).

Focal species and camera trap

Table 1 shows known middle- to large-sized mammal species in Deramakot (Matsubayashi et al. in press). We focused middle to large mammals because they are more likely to respond to landscape-level changes. Species of Chiroptera (bats), Dermoptera (colugo), small Insectivora (shrews), Scandentia (tree shrews), and small Rodentia (squirrels and rats) were excluded from this study. We follow the nomenclature by Payne et al. (1998).

A total of fourteen camera-traps were placed in the reduced-impact logged forest (7 traps) and the adjacent conventionally logged forest (7 traps) in February-March and August-September, 2006. In each forest, cameras were set up along animal trails at intervals of about 1km. We used automatic camera-traps (sensor camera Field note □, Marif, Yamaguchi, Japan) triggered by passive infrared motion sensors. All camera-traps were mounted on trees and set approximately 50cm from the ground, and were baited with durians or chicken, which were hung so high that animals could not consume them easily. All camera-traps operated 24 hours/day or until the film was fully exposed. We checked camera-trap sites every week to replace bait, and changed films and batteries if necessary. Day and time were recorded on each photograph.

We identified each photographed animal to species. As for genera *Muntiacus* (*Muntiacus atherodes* and *Muntiacus muntjak*) and *Tragulus* (*Tragulus napu* and *Tragulus javanicus*), we combined the congeneric species for each because they are indistinguishable on photographs. To exclude repetitive shots within a visit, we defined photographs of the same species within 60 minutes as 1 event. Number of camera-days was calculated for each camera trap. Since photographic rates correlate with animal density (Carbone et al. 2001), we used the number of independent photographs per camera-day as relative-abundance index (O'Brien 2003). In addition to camera-trap data, simultaneous field observations of larger mammals by night walking, driving census, and trace existence were also added to the species diversity list (Table 1).

We defined CNV/RIL ratio as the ratio between the relative-abundance index of each animal in the conventionally logged forest and that in the reduced-impact logged forest in order to discuss the relation between diet type and the persistence to heavy disturbance.

Differences in photographic rates between two forests were tested statistically using the Mann-Whitney *U* tests for each species recorded.

Results

Total study effort was 797 camera-days. Figure 1 shows species accumulation carves in each forest. Total 158 photographs were taken, of which 109 (396 camera-days) were from the reduced-impact logged forest and 49 (401 camera-days) were from the conventionally logged forest. In addition to the photographs of animals, there were 6 human records in conventionally logged forest.

Camera-trapped mammals consisted of 19 species, one Insectivora, three Primates, three Rodentia, eight Carnivora, and four Artiodactyla (Table 1). Of these 19 species, 18 species appeared in the reduced-impact logged forest and 11 in the conventionally logged forest (Table 1). Six species including sun bear and clouded leopard were recorded only in the reduced-impact logged site whereas only short-tailed mongoose was not detected in the reduced-impact logged forest.

The most numerous species trapped was mouse-deer *Tragulus* spp. (29 photos) followed by Malay civet *Viverra tangalunga* (27 photos), bearded pig *Sus barbatus* (24 photos), and pig-tailed macaque *Macaca nemestrina* (21 photos). Muntjac *Muntiacus* spp. and pig-tailed macaque *Macaca nemestrina* showed a significantly higher photographic rate in the reduced-impact logged forest ($p<0.05$; $p<0.05$), while no species were significantly more abundant in the conventionally logged forest. Total photographic rate was also significantly larger in the reduced-impact logged site ($p<0.05$). CNV/RIL was lower in frugivorous primates and higher in omnivorous pigs or carnivorous civets.

Discussion

Difference in mammalian fauna and abundance

The forest harvested by reduced-impact logging showed greater species richness than the forest logged conventionally (Table 1). However, the observed difference in the number of detected species may just reflect lower animal density in the conventionally logged forest but not the species number per se. Comparative studies of mammalian fauna in several paired sites of closely located logged and unlogged forests in Indonesia and Peninsular Malaysia showed that species presence was similar between logged and unlogged forests in some areas although slight differences were observed (Johns 1997; Laidlaw 2000; Wilson and Johns 1982).

The results suggest that forests exploited using reduced-impact logging is able to carry a higher density of the middle to large mammals compared with forests logged conventionally. A previous study also revealed that the density of Bornean orangutan *Pongo pygmaeus* in our focal reduced-impact logged site (Deramakot) was 1.50 individuals/km^2, which was more than twice as high as 0.62 individuals/km^2 in the site logged conventionally (Tangkulap) (Ancrenaz et al. 2005). Earlier studies have already documented that large mammals in Borneo often become less abundant in selectively logged forests (Felton et al. 2003; Heydon and Bulloh 1996, 1997).

Effect of difference in habitat quality and human presence

Table 2 shows the summary of results from current and another study in Deramakot and diet type for each species. Among the six species listed here, two primates are the most fruit-dependent animals, mouse-deer and muntjac are less dependent, and bearded pig and Malay civet are the least. CNV/RIL was lower in frugivorous primates and higher in omnivorous pigs or carnivorous civets. This tendency that frugivorous animals are more vulnerable to logging and omnivores or carnivores are tolerant indicates that heavy logging reduces fruit production in forest and reduces animal population consequently. It is known that primates' degree of frugivory negatively correlates with species' persistence to logging (Johns and Skorupa 1987). Logging activities reduce the availability of food resources for frugivores, even where timber trees are not themselves used by animals (Johns 1988; but see Ganzhorn 1995). Poor logging operation in the conventional method may cause the reduction in food resources and negatively affect the abundance of mammals.

In addition to food habitat, Marsh et al. (1987) suggested that the degree of territoriality could influence the adaptability of animals. Some primates and civets in Deramakot were strictly arboreal, although they were hardly recorded in this survey. Increased amount of canopy gap disrupts aerial pathway and arboreal species experience difficulties in locomotion (Johns 1997). Therefore, arboreal mammals can be more susceptible to logging.

Human activities accompanying logging practices can also affect mammals. It is known that hunting poses a great threat to large forest animals in many parts of the tropics (Linkie et al. 2003; Marshall et al. 2006). It can be even a greater threat to wildlife than timber harvesting in some cases (Bennet et al. 2002; Matthews and Matthews 2002; Walsh et al. 2003). In Deramakot and adjacent Tangkulap, hunting of wildlife is prohibited, but illegal hunting still occurs by villager and outsiders. Hunting pressure was higher in Tangkulap (conventionally logged area) because of easier access and insufficient prevention there. Therefore, Sabah Forestry Department has enforced regulation on the illegal hunting in Tangkulap area since 2005 (P. Lagan, Assistant District Forestry Officer, Deramakot, Sabah Forestry Department, pers. comm.).

Reduced-impact logging and the regulation of illegal hunting could maintain the food resources for mammals and secure their population. Further investigation is needed on the logging impact on the ecological functions of mammals in addition to that on the population density.

References

Ancrenaz M, Gimenez O, Ambu L, Ancrenaz K, Andau P, Goossens B, Payne J, Sawang A, Tuuga A, Lackman-Ancrenaz I (2005) Aerial surveys give new estimates for orangutans in Sabah, Malaysia. PLoS Biology, 3, 1-8.

Bennett EL, Milner-Gulland EJ, Bakarr M, Eves HE, Robinson JG, and Wilkie D S (2002) Hunting the world's wildlife to extinction. Oryx, 36, 328-329.

Bertault J, Sist P (1997) An experimental comparison of different harvesting intensities with reduced-impact and conventional logging in East Kalimantan, Indonesia. Forest Ecology and Management, 94, 209-218.

Caldecott JO (1986) An ecological and behavioral study of Pig-tailed Macaques. Karger, Basel, Switzerland.

Cannon CH, Peart DR, Leighton M, Kartawinata K (1994) The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. Forest Ecology and Management, 67, 49-68.

Carbone C, Christie S, Conforti K, Coulson T, Franklin N, Ginsberg JR, Griffiths M, Holden J, Kawanishi K, Kinnaird M, Laidlaw R, Lynam A, Macdonald DW, Martyr D, McDougal C, Nath L, O'Brien T, Seidensticker J, Smith DJL, Sunquist M, Tilson R, Wan Shahruddin WN (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation, 4, 75-79.

Crome FHJ, Moore LA, Richards GC (1992) A study of logging damage in upland rainforest in north Queensland. Forest Ecology and Management, 49, 1-29.

Cuaron AD (2000) A global perspective on habitat disturbance and tropical rainforest mammals. Conservation Biology 14: 1574-1579.

Davis DD (1962) Mammals of the lowland rain-forest of North Borneo. Bulletin of the Singapore Natural History Museum, 31, 1-129.

Felton AM, Engstrom LM, Felton A & Knott CD (2003) Orangutan population density, forest structure and fruit availability in a hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. Biological Conservation, 114, 91-101.

Frumuhoff PC (1995) Conserving wildlife in tropical forests managed for timber to provide a more viable complement to protected areas. BioScience 45: 456-464.

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology, 76, 2084-2096.

Heydon MJ, Bulloh P (1996) The impact of selective logging on sympatric civet species in Borneo. Oryx, 30, 31-36.

Heydon MJ, Bulloh P (1997) Mousedeer densities in a tropical rainforest: the impact of selective logging. Journal of Applied Ecology, 34, 484-496.

Huth A, Ditzer T (2001) Long-term impacts of logging in a tropical rain forest – a simulation study. Forest Ecology and Management, 142, 33-51.

IUCN (2006) IUCN Red List of Threatened Species. www.iucnredlict.org

Johns AD, Skorupa JP (1987) Responses of rain-forest primates to habitat disturbance: a review. International Journal of Primatology, 8, 157-191.

Johns AD (1988) Effect of “selective” timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. Biotropica, 20, 31-37.

Johns AG (1997) Timber production and biodiversity conservation tropical rain forests. Cambridge University Press, UK.

Kinnarird MF, Sanderson EW, O’Brien TG, Wibisono HT, and Woolmer G (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. Conservation Biology 17: 245-257.

Laidlaw RK (2000) Effects of habitat disturbance and protected areas on mammals of Peninsular Malaysia. Conservation Biology, 14, 1639-1648.

Laurance WF, Laurance SGW (1996) Responses of five arboreal marsupials to recent selective logging in tropical Australia. Biotropica, 28, 310-322.

Linkie M, Martyr DJ, Holden J, Yanuar A, Hartana AT, Sugardjito J, Leader-Williams N (2003) Habitat destruction and poaching threaten the Sumatran tiger in Kerinci Seblat National Park, Sumatra. Oryx, 37, 41-48.

Marsh CW, Johns AD, Ayres JM (1987) Effects of habitat disturbance on rain forest primates. In: Marsh CW, Mittermeier RA editors. Primate conservation in the tropical rain forest. Alan R. Liss, New York. Pp. 83-107.

Marshall AJ, Nardiyono, Engström LM, Pamungkas B, Palapa J, Meijaard E & Stanley SA (2006) The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. Biological Conservation, 129, 566-578.

Matsubayashi H, Lagan P, Majalap N, Tangah J, Sukor JRA, Kitayama K (in press) Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecological Research. DOI: 10.1007/s11284-006-0313-4

Matthews A, Matthews A (2002) Distribution, population density, and status of sympatric Cercopithecids in the Campo-Ma’an area, Southwestern Cameroon. Primates, 43, 155-168.

Meijaard E, Sheil D, Nasi R, Stanley SA (2006) Wildlife conservation in Bornean timber concessions. Ecology and Society, 11(1), 47

O’Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation, 6, 131-139.

Payne J, Francis CM, Phillipps K (1985) A field guide to the mammals of Borneo. The Sabah society with world wildlife fund Malaysia, Kota Kinabalu

Pinard MA, Putz FE (1996) Retaining forest biomass by reducing logging damage. Biotropica, 28, 278-295.

Putz FE, Pinard MA (1993) Reduced-impact logging as a carbon offset method. Conservation Biology, 7, 755-757.

Seino T, Takyu M, Aiba S, Kitayama K, Ong R (2005) Floristic composition, stand structure, and above-ground biomass of the tropical rain forests of Deramakot and Tangkulap Forest Reserve in Malaysia under different forest managements. In: Lee YF, Chung AY & Kitayama K editors. Proceedings of The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation in Tropical Rain Forests. DIWPA, Kyoto. Pp. 29-52.

Walsh PD, Abernethy KA, Bermejo M, Beyersk R, Wachter PD, Akou ME, Huijbregts B, Mambounga D, Toham AK, Kilbournk AM, Lahmq SA, Latourk S, Maiselsk F, Mbinak C, Mihindouk Y, Obiang SN, Effa EN, Starkeyk MP, Telfer P, Thibault M, Tutin CEG, Whitek LJT, Wilkiek DS (2003) Catastrophic ape decline in western equatorial Africa. Nature, 422, 611-614.

Wilson WL, Johns AD (1982) Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations, in East Kalimantan, Indonesia. Biological Conservation, 24, 205-218.

Table 1. Known middle – large mammals in Deramakot and summary of photographic records from the reduced-impact logged forest (RIL) and the adjacent conventionally logged forest (CNV).

Species [a]	Common names	Records/camera-day		IUCN 2006
		RIL	CNV	
INSECTIVORA				
Erinaceidae				
Echinosorex gymnurus	Moonrat	0.005	N/A	LC
PRIMATES				
Lorisidae				
Nycticebus coucang	Slow loris	N/A	N/A	LC
Tarsiidae				
Tarsius bancanus	Western tarsier	0.002	0.002	LC
Cercopithecidae				
Presbytis rubicunda	Red leaf monkey	N/A	N/A	LC
Presbytis cristata	Silvered langur	N/A	N/A	Not listed
Nasalis larvatus	Proboscis monkey	N/A	N/A	EN A2c, C1+2a
Macaca fascicularis	Long-tailed macaque	0.002	0.002	NT
Macaca nemestrina	Pig-tailed macaque	0.043 *	0.010	VU A1cd
Hylobatidae				
Hylobates muelleri	Bornean gibbon	N/A	N/A	NT
Pongidae				
Pongo pygmaeus	Orangutan	N/A	N/A	EN A2cd
PHOLIDOTA				
Manidae				
Manis javanica	Pangolin	N/A	N/A	NT
RODENTIA				
Hystricidae				
Trichys fasciculate	Long-tailed porcupine	0.005	N/A	LC
Hystrix brachyuran	Common porcupine	0.012	N/A	VU A1d
Thecurus crassispinis	Thick-spined porcupine	0.008	N/A	NT
CARNIVORA				
Ursidae				
Helarctos malayanus	Sun bear	0.010	N/A	DD
Mustelidae				
Martes flavigula	Yellow-throated marten	N/A	N/A	LC
Mydaus javanensis	Malay badger	0.005	0.002	LC
Aonyx cinerea	Oriental small-clawed otter	N/A	N/A	NT
Viverridae				
Viverra tangalunga	Malay civet	0.040	0.026	LC
Cynogale bennettii	Otter-civet	N/A	N/A	EN A1ce, C2a
Arctictis binturong	Binturong	0.008	0.005	LC
Arctogalidia trivirgata	Small-toothed palm civet	N/A	N/A	LC
Paguma larvata	Masked Palm civet	N/A	N/A	LC
Paradoxurus hermaphroditus	Common palm civet	0.010	0.007	LC
Hemigalus derbyanus	Banded palm civet	0.003	N/A	LC
Herpestidae				
Herpestes brachyurus	Short-tailed mongoose	N/A	0.002	LC
Herpestes semitorquatus	Collared mongoose	N/A	N/A	LC
Felidae				
Neofelis nebulosa	Clouded leopard	0.002	N/A	VU C2a(i)
Prionailurus planiceps	Flat-headed cat	N/A	N/A	VU C2a(i)
Prionailurus bengalensis	Leopard cat	N/A	N/A	LC

[a] Listed by Matsubayashi et al. (in press). *Arctogalidia trivirgata* was added. [b] Two species were pooled. * Significantly more abundant, $P < 0.05$IUCN status of each species is also given: EN-endangered; VU-vulnerable; NT-near threatened; LC-least concern; DD-data deficient

Table 1. Known middle – large mammals in Deramakot and summary of photographic records from the reduced-impact logged forest (RIL) and the adjacent conventionally logged forest (CNV).(*Continued*)

Species [a]	Common names	Records/camera-day RIL	Records/camera-day CNV	IUCN 2006
PROBOSCIDEA				
Elephantidae				
Elephas maximus	Asian elephant	N/A	N/A	EN A1cd
ARTIODACTYLA				
Suidae				
Sus barbatus	Bearded pig	0.040	0.019	LC
Tragulidae		0.050 [b]	0.025 [b]	
Tragulus javanicus	Lesser mouse-deer			LC
Tragulus napu	Greater mouse-deer			LC
Cervidae		0.025 * [b]	N/A	
Muntiacus atherodes	Bornean yellow muntjac			LC
Muntiacus muntjak	Red muntjac			LC
Cervus unicolor	Sambar deer	0.005	0.003	LC
Bovidae				
Bos javanicus	Tembadau / Banteng	N/A	N/A	EN A1cd+2cd, C1+2a
	TOTAL	0.277 *	0.105	

[a] Listed by Matsubayashi et al. (in press). *Arctogalidia trivirgata* was added. [b] Two species were pooled. * Significantly more abundant, $P < 0.05$IUCN status of each species is also given: EN-endangered; VU-vulnerable; NT-near threatened; LC-least concern; DD-data deficient

Table 2. Summary of mammalian density (as indexed by the relative-abundance index) in Deramakot and diet type

Survey method	Species	Density RIL	Density CNV	CNV / RIL	Diet type	% Frugivory (Source)
Camera-trapping [a]		records/camera-day				
	Mouse-deer	0.050	0.025	0.50	Frugivore/ Browser	
	Malay civet	0.040	0.026	0.65	Carnivore/ Insectivore	15% (Davis 1962)
	Bearded pig	0.040	0.019	0.48	Omnivore	
	Pig-tailed macaque	0.043	0.010	0.23	Frugivore	88% (Caldecott 1986)
	Muntjac	0.025	0.000	0	Frugivore/ Browser	
Aerial nest count [b]		individuals/km^2				
	Orangutan	1.50	0.62	0.41	Frugivore	100 - 21% (Knott 1998)

[a] Only species trapped > 9 times were listed.

[b] Data from Ancrenaz et al. (2005)

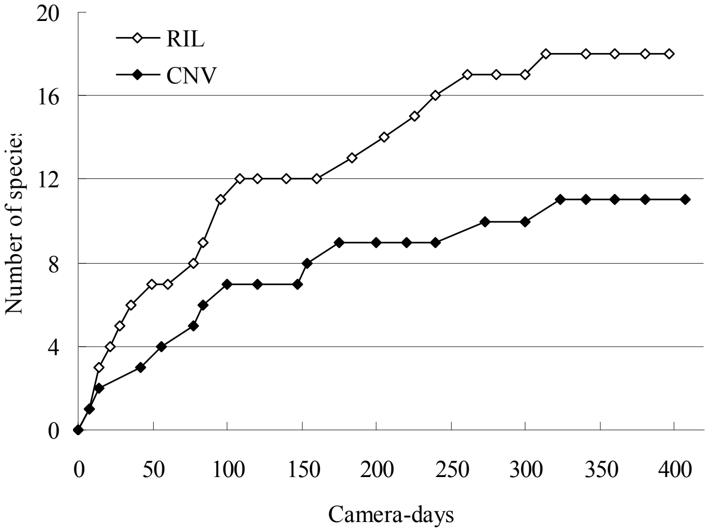

Fig. 1. Species accumulation carves in the reduced-impact logged forest (RIL) and the conventionally logged forest (CNV).

Tree Species Composition and Diversity in Relation to Forest Management in the Lowlands of Yakushima

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Introduction

We examined the effects of forest management on tree species composition and diversity in the lowland forests of Yakushima, an island in the south of Kyushu, Japan. Virtually all evergreen broad-leaved forests have been logged in Japan, but old-growth forests, which serve as a control treatment, still remain on Yakushima Island. Aiba et al. (2001) compared old-growth forests and secondary forests that were regenerating after the clear-cutting of old-growth forests on Yakushima Island over a range of altitude from 300 to 800 m above sea level. We performed a similar comparison, but restricted the altitude to lowland < 500 m to reduce the variation in environmental conditions, and included both conifer plantations and secondary forests that were regenerating after the clear-cutting of plantations. Conifer plantations have been converted from old-growth forests over the past 75 years or so and are currently one of the most dominant types of land use in the lowlands of Yakushima Island. In future, it may be desirable to reestablish natural forests after harvesting the plantations. However, little is known about what happens following the abandonment of plantations after harvesting (Sakai et al. 2006, Yamagawa and Ito 2006).

Materials and Methods

The study sites were located in the lowland forests (< 500 m above sea level) on Yakushima Island, Kagoshima Prefecture, Japan (30° N 130° E). The lowlands of Yakushima Island were once covered by old-growth evergreen broad-leaved forests. Most of the old-growth forests had been clear-cut by the early 1930s, and plantations of the evergreen conifer *Cryptomeria japonica* were established mainly on lower slopes (Fig. 1). Secondary forests also regenerated in clear-cuts that were not planted with *C. japonica*. Recently, these *Cryptomeria* plantations were again logged, but further afforestation was not conducted. In such areas, low-diversity forests strongly dominated by the deciduous broad-leaved tree *Aleurites cordata* regenerated. In addition to these silvicultural practices, topography affects the tree species composition in the lowland forests on Yakushima Island (Bellingham et al. 1996; Aiba et al. 2001, Tsujino et al. 2006), although *Cryptomeria* plantations and *Aleurites* forests are mainly restricted to lower slopes. We therefore established a total of 24 plots, with four in each of the following categories of forest: (1) old-growth forest on upper slopes, including ridges and steep mid-slopes; (2) old-growth forest on lower slopes, including valleys and gentle mid-slopes; (3) secondary forest on upper slopes; (4) secondary forest on lower slopes; (5) *Cryptomeria* plantation on lower slopes; and (6) *Aleurites* forest on lower slopes. The plot locations were selected in National Forests and privately owned forests using maps from the local Forestry Office and by interviewing local people, respectively.

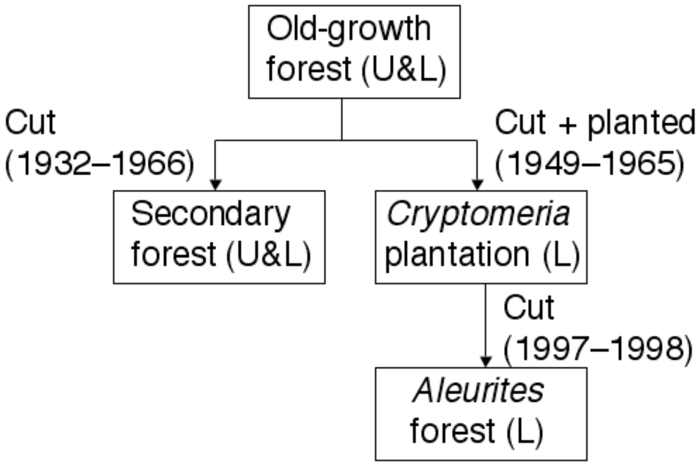

Fig. 1 The relationship among four forest types in relation to forest management in the lowlands of Yakushima Island. Year of logging for the study sites and the topography of each forest type (U, upper slope; L, lower slope) are also shown.

A tree census was conducted from 2006 to 2007. The plot area was 400 m^2 (10 × 40 m or 20 × 20 m), measured on the ground, depending on the availability of similar topography and the spatial extent of the forest type. All stems, including multiple stems, ≥ 2 cm in diameter at breast height (dbh, 1.3 m above the ground) were measured for dbh and identified to species. One old-growth plot on an upper slope, four secondary plots on upper slopes and two secondary plots on lower slopes had been established in 1984 (Kohyama 1988, 1989; Kohyama and Aiba 1997). Of these, two secondary plots on upper slopes and two secondary plots on lower slopes had an initial area of 100 m^2; these plots were expanded to 400 m^2 prior to the 2006–2007 census.

We conducted detrended correspondence analysis (DCA) to summarize the species composition (ter Braak and Smilauer 2002). We added 1 to the relative basal area of each species and log-transformed the input data. *Aleurites* forests (8–9 years old) were much younger than secondary forests (40–74 years old) in 2006–2007, but the secondary forests were 18–52 years old in 1984. We incorporated the 1984 data as well as the 2006–2007 data from the seven plots in the DCA to make the comparison between *Aleurites* forests and secondary forests more meaningful and to examine the temporal change in species composition over 22 years (all seven plots were recensused in 2006). We counted the number of species in each plot and computed Fisher's α, Shannon's index of diversity, and Pielou's index of evenness to evaluate species diversity; natural logarithms and stem numbers were used for the latter two indices (Magurran 2004). Fisher's α represents diversity in terms of the number of species relative to the number of stems, whereas Shannon's index is dependent on both the number of species and the evenness of species abundance.

Results and Discussion

Secondary stands showed forest structure similar to that of old-growth stands, except that the maximum dbh was significantly smaller on both upper and lower slopes and stem density was greater on upper slopes (Fig. 2), suggesting that forest structure had almost recovered to old-growth status 40–74 years after clear-cutting.

This is consistent with the results of Kohyama (1989) and Aiba et al. (2001). *Cryptomeria* plantations had a greater mean dbh than did the other forest types and tended to contain fewer stems per area. They also had a significantly greater basal area than did secondary forests of similar age on lower slopes (both approximately 40−50 years old). All of these differences likely reflect the effects of thinning management. *Aleurites* stands regenerating 8–9 years after the logging of *Cryptomeria* plantations had a significantly lower basal area (mean: 18.9 cm^2 m^{-2}) and maximum dbh (mean: 14.5 cm) than did other forest types. The basal area and maximum dbh of the six secondary forests for which long-term data were available were 39.9–53.9 cm^2 m^{-2} in 1984 (stand age 18–52 years old) and 15.3–39.1 cm, respectively. Therefore, the lower basal area of *Aleurites* forests may be characteristic of this forest type, but the smaller maximum dbh is probably a result of the younger age.

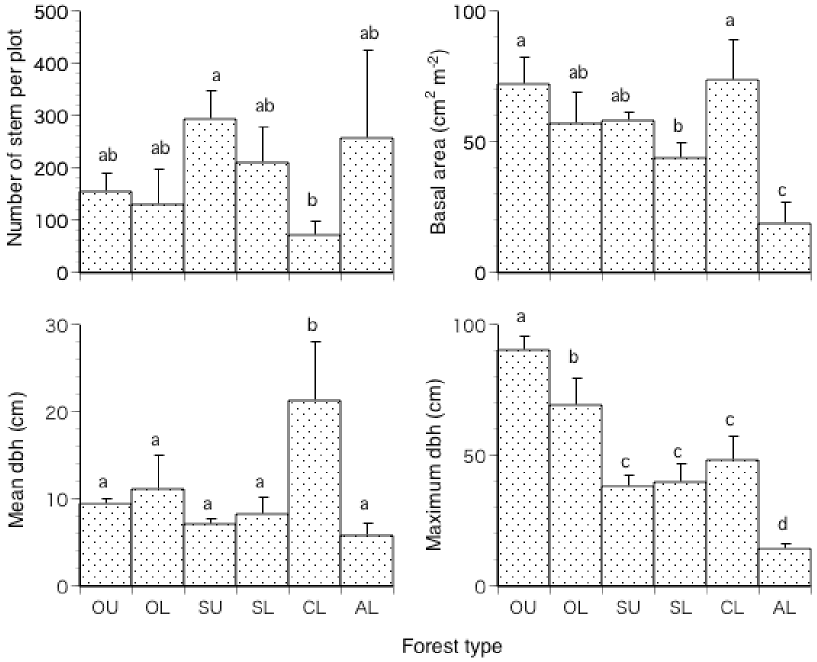

Fig. 2 Forest structure of the six forest-type categories in the lowlands of Yakushima Island.
The sample size was four plots in each forest-type category. Standard deviations are shown as vertical bars. Different letters indicate significant differences among plots at $P < 0.05$ using Tukey multiple comparisons (OU, old-growth forest on upper slope; OL, old-growth forest on lower slope; SU, secondary forest on upper slope; SL, secondary forest on lower slope; CL, *Cryptomeria* plantation on lower slope; AL, *Aleurites* forest regenerating on clear-cut *Cryptomeria* plantations on lower slope).

On upper slopes, both the old-growth and secondary plots had a high relative basal area (RBA >10%) of *Castanopsis cuspidata* var. *sieboldii*, which was the top dominant species in terms of basal area in three old-growth plots (RBA: 36–45%) and three secondary plots (36–69%). *C. cuspidata* probably regenerated from cut stamps in secondary forests, as suggested by the frequent occurrence of multiple-stemmed individuals. Other top dominants were *Quercus salicina* (RBA: 33%) in an old-growth plot and *Lithocarpus (Pasania) edulis* (36%) in a secondary plot. On lower slopes, no species showed consistently high RBA. The top dominants were *Q. salicina* (two plots, RBA: 23 and 51%), *Distylium racemosum* (27%), and *Schefflera octophylla* (23%) in old-growth plots, and *Aleurites cordata* (43%), *Ardisia sieboldii* (18%), *Fagara ailanthoides* (36%), and *Litsea acuminata* (31%) in secondary plots. As might be expected, plantations were strongly dominated by *Cryptomeria japonica*, exhibiting high RBA of 86–100%. One of the *Cryptomeria* plantations was well managed and contained only *C. japonica*. The other three plantations were less managed and contained other species, mainly in the understory. *Aleurites cordata* stands that developed after the logging of *Cryptomeria* plantations were strongly dominated by *A. cordata*, exhibiting high RBA of 42−100%.

We are aware of only two studies that have documented the natural vegetation regeneration after the clear-cutting of conifer plantations in the warm-temperate region of Japan. Yamagawa and Ito (2006) compared tree species composition before and after clear-cutting of *Chamaecyparis obtusa* plantations in Miyazaki Prefecture, Kyushu, and pointed out the importance of both advanced regeneration (surviving and resprouting stems) and new regeneration from seedlings; advanced regeneration reflected the abundant understory vegetation in the plantations. Sakai et al. (2006) found that evergreen oaks, including *C. cuspidata* and *Q. salicina*, successfully regenerated after clear-cutting of *C. japonica* and *C. obtusa* plantations in southern Shikoku and considered that this was caused by advanced regeneration. However, in the *Aleurites* forests of Yakushima, regeneration was very poor, probably because of poorly developed understory vegetation in the original plantation, where advanced regeneration appeared to be lacking. Only *Ardisia sieboldii*, which occurred as multi-stemmed individuals, had a potential for advanced regeneration by resprouting.

The eigenvalues of axes 1 and 2 of the DCA were 0.70 and 0.31, respectively, and cumulatively explained 27% of the variance. Along axis 1, three broad groups of forest were separated in order of increasing score (Fig. 3): (1) *Cryptomeria* plantations and *Aleurites* forests, (2) old-growth and secondary forests on lower slopes, and (3) old-growth and secondary forests on upper slopes. Along axis 2, further compositional differences were found between *Cryptomeria* plantations and *Aleurites* forests and between old-growth and secondary forests on lower slopes, but the difference between old-growth and secondary forests was unclear on upper slopes. Temporal changes in the species composition over 22 years were slight compared to the variation among the forest types *Aleurites* forests 8–9 years old were distinctively different from secondary forests both in 1984 (18–52 years old) and in 2006–2007 (40–74 years old).

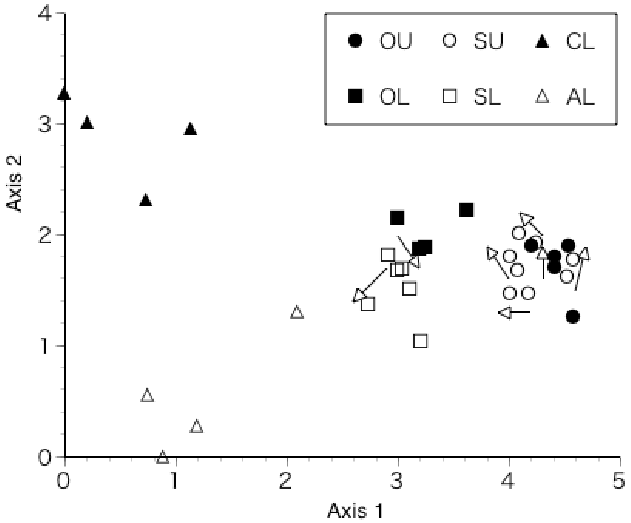

Fig. 3 DCA ordination diagram of plot scores. Arrows indicate the change in species composition from 1984 to 2006–2007 for seven long-term plots. Other plots were censused only in 2006–2007. See Fig. 2 for abbreviations of forest types.

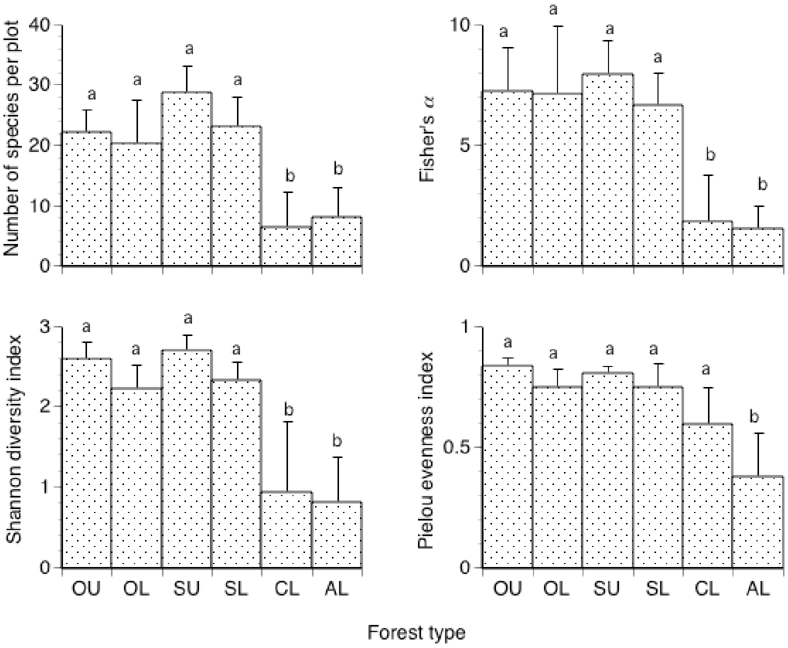

Fig. 4 Species diversity evaluated using various diversity indices for six forest-type categories. The sample size was four plots in each forest-type category, except for Pielou's index for *Cryptomeria* plantations for which n = 3 because one plantation plot contained only one species. Standard deviations are shown as vertical bars. Different letters indicate significant differences among plots at P < 0.05 using Tukey multiple comparisons. See Fig. 2 for abbreviations of forest types.

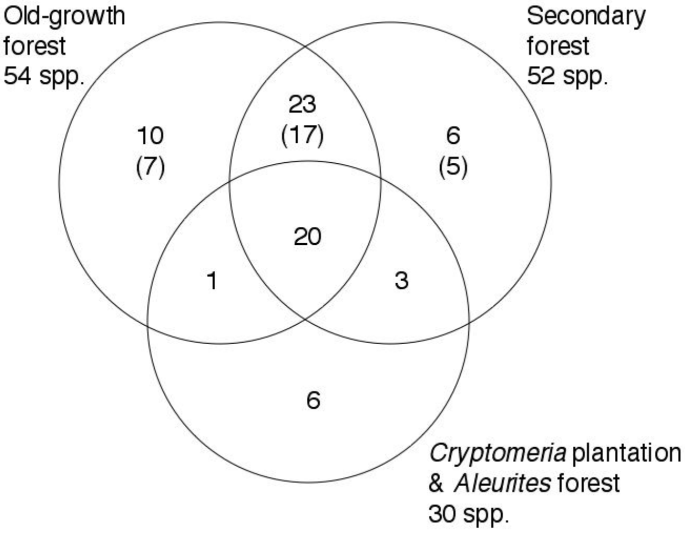

Fig. 5 Venn diagram of species occurrence in three forest-type groups, including old-growth forests on upper and lower slopes, secondary forests on upper and lower slopes, and *Cryptomeria* plantations and *Aleurites* forests (both on lower slopes). For species that are absent from the *Cryptomeria* and *Aleurites* forest group, the numbers of species that occurred on lower slopes are shown in parentheses.

Cryptomeria and *Aleurites* forests were less diverse than secondary and old-growth stands, although *Cryptomeria* plantations did not have significantly lower Pielou's index values than did old-growth or secondary forests (Fig. 4). One of the *Cryptomeria* plantations contained only *C. japonica*, and Pielou's index could not be calculated for this plantation. The differences between secondary and old-growth forests were unclear, which was consistent previous results (Aiba et al., 2001); the differences between upper and lower slopes were also unclear.

The 4484 stems ≥ 2 cm in dbh in the 24 plots (0.96 ha) censused in 2006–2007 comprised 69 species. We examined the distribution of species among three groups of forests: old-growth, secondary, and *Cryptomeria* plus *Aleurites*. As many as 39 (57%) of the 69 species were absent from the *Cryptomeria* plus *Aleurites* forest group (Fig. 5). Of these, 29 species occurred on lower slopes in old-growth or secondary forests or both, so that their absence from *Cryptomeria* and *Aleurites* forests was not entirely a result of habitat associations. Species that appeared to be unable to invade *Cryptomeria* or *Aleurites* forests included all three Fagaceae species (*Castanopsis cuspidata*, *Lithocarpus edulis*, and *Quercus salicina*) that bear large acorns and are dominant (RBA > 30%) in one or more plots of the old-growth and secondary forests. This indicates that dispersal limitation is partly responsible for the poor species diversity of *Cryptomeria* and *Aleurites* forests.

However, the *Aleurites* forests investigated were all located nearby (approximately 10–50 m) old-growth or secondary forests that can act as seed sources. Thus, dispersal limitation was not the primary reason for the poor species diversity of *Aleurites* forests. Poor advanced regeneration caused by intensive forest management such as thinning and weeding in the understory seemed to be an important factor. Post-harvest disturbance such as soil erosion and herbivory by sika deer may also be important (Sakai et al. 2006). Seeds of *A. cordata* are poisonous to humans, and the species' vegetative parts may also be toxic to mammals. Indeed, Tsujino and Yumoto (2004) did not find evidence of deer herbivory on *A. cordata* saplings in an old-growth lowland forest on Yakushima Island. A lack of herbivory by deer could explain the monodominance of *A. cordata* on clear-cuts of plantations.

References

Aiba S, Hill DA, Agetsuma N (2001) Comparison between old-growth stands and secondary stands regenerating after clear-felling in warm-temperate forests of Yakushima, southern Japan. Forest Ecol Manage 140:163–175.

Bellingham PJ, Kohyama T, Aiba S (1996) The effects of a typhoon on Japanese warm- temperate rain forests. Ecol Res 11:229–247.

Kohyama T (1988) A function describing all-sized trunk diameter distribution in warm-temperate rain forests. Bot Mag Tokyo 101:207–212.

Kohyama T (1989) Simulation of the structural development of warm-temperate rain forest stands. Ann Bot 63:625–634.

Kohyama T, Aiba S (1997) Dynamics of primary and secondary warm-temperate rain forests in Yakushima Islands. Tropics 6:383–392.

Magurran AE (2004) Measuring biological diversity. Blackwell, Malden.

Sakai A, Hirayama T, Oshioka S, Hirata Y (2006) Effects of elevation and postharvest disturbance on the composition of vegetation after the clear-cut harvest of conifer plantations in southern Shikoku, Japan. J For Res 11:253–265.

ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca.

Tsujino R, Yumoto T (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecol Res 19:291–300.

Tsujino R, Hino T, Agetsuma N, Yumoto T (2006) Variation in tree growth, mortality and recruitment among topographic positions in a warm temperate forest. J Veg Sci 17:281–290.

Yamagawa H, Ito S (2006) The role of different sources of tree regeneration in the initial stages of natural forest recovery after logging of conifer plantation in a warm-temperate region. J For Res 11:455–460.

Effects of Sika Deer and Conifer Plantations on the Density and Diversity of Current-Year Tree Seedlings in Lowland Forests on Yakushima Island, Japan

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Introduction

Sika deer populations have dramatically increased recently, producing increasing damage to forest vegetation in several areas in Japan (Takatsuki 1989; Takatsuki and Gorai 1994; Akashi and Nakashizuka 1999; Yokoyama et al. 2001; Tsujino et al. 2004). Grazing and browsing by high-density sika deer populations cause a loss of forest floor vegetation (Takatsuki and Gorai 1994; Tsujino and Yumoto 2004), a decrease of mature trees owing to bark stripping (Akashi and Nakashizuka 1999; Yokoyama et al. 2001), and an increase of some special plant species, which are not preferred by sika deer (Kaji and Yajima 1991). Large-scale logging and planting of commercial crops have also damaged ecological functions of forests and have eroded the public benefit provided by forests (Agetsuma 2007).

We should note first that most natural vegetation has already been disturbed by forest transformation (Agetsuma 2007). Thus in this study, we examined vegetation changes in the forest in relation to sika deer herbivory and human impacts such as conifer plantations. To clarify the effects of sika deer and conifer plantations on changes of forest vegetation, we established deer exclusion fences in three study sites, which showed differences in sika deer population density and percentage of area occupied by conifer plantations, and counted newly germinated and established current-year tree seedlings in summer and winter.

Methods

The study sites were located on Yakushima Island (30˚20' N, 131˚30' E), which has an area of ca. 503 km^2 and lies ca. 70 km south of Kyushu, Japan. The study area was in a warm-temperate forest at an altitude between 200 and 600 m on the western and northwestern part of Yakushima Island. The geology is granite. The forest consists mainly of broad-leaved evergreen trees of Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae (Tagawa 1980; Tsujino et al. 2006; Agetsuma et al. unpubl. data).

Three study sites with differences in the percentage of plantation area and sika deer population density were selected: the Seibu area (SE, ca. 250 m asl, Fig. 1), the Nagata area (NA, ca. 550 m asl, Fig. 1), and the Isso area (IS, ca. 500 m asl, Fig. 1). The estimated sika deer population density was greatest in SE and lowest in IS (Agetsuma et al. 2003; Agetsuma 2007), and the disturbance ranking, calculated as the percentage of total area occupied by conifer plantations, was IS > NA > SE (Hill et al. 1994).

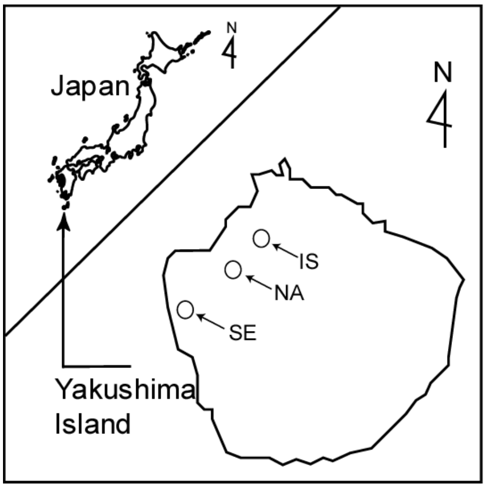

Fig. 1. Study sites on Yakushima Island, Japan. IS, NA, and SE indicate the Isso area (500 m asl), Nagata area (550 m asl), and Seibu area (250 m asl), respectively.

A subspecies of sika deer, *Cervus nippon yakushimae*, inhabits the whole area of Yakushima Island (Kagoshimaken Sizenaigo Kyokai 1981). The body weights of adult male and female *C. n. yakushimae* are 24–50 kg and 19–25 kg, respectively (Kagoshimaken Sizenaigo Kyokai 1994; Agetsuma et al. 2003; Komiya 2002). The deer population density on Yakushima Island may vary according to altitude, forest type, and degree of human impact. Natural predators of deer are absent. Deer were hunted in some areas on the island that suffered substantial damage to agriculture, but not in the study area. In broad-leaved evergreen forests in Japan, the leaves and fruits of evergreen and deciduous plants and graminoids are the primary food for sika deer (Takatsuki 1988; Takatsuki 1990; Asada and Ochiai 1996; Tsujino and Yumoto 2004; Agetsuma and Agetsuma-Yanagihara 2006).

Table 1. Numbers of seedling observation quadrats(1-m^2) at the three study sites.

	Number of Quadrats		
Study Site	Fenced	Unfenced	Total
Seibu Area	27	27	54
Nagata Area	17	22	39
Isso Area	22	22	44
Total	66	71	137

Six deer exclusion fences, each with a perimeter of ca. 80 m and an area of ca. 0.02 ha, were established and were duplicated at each site, at the Seibu and Isso areas in August 2003 and at the Nagata area in August 2004 (Table 1). An unfenced area of similar size was also selected in the vicinity of each fenced area. These study quadrats were divided into sub-quadrats of 5 × 5 m, and a total of 137 seedling observation quadrats (1 × 1 m) were established at the southwest corner of each sub-quadrat in fenced and unfenced quadrats in December 2003 (Table 1).

A seedling census was conducted for all living current-year tree seedlings in early summer (late May to early July) and winter (December to February). Most tree seedlings in this area germinated from April to June; the seedling growing season was summer to autumn; and seedling growth and mortality decreased in winter.

Thus, we defined current-year tree seedlings as seedlings less than 1 year old. We counted the number of current-year tree seedlings for each tree species in summer and winter, to compare seedling recruitment and establishment between fenced and unfenced quadrats and among study sites. We collected data four times at SE and IS in winter, three times at SE and IS in summer, three times at NA in winter, and two times at NA in summer. Thus, the replication numbers were 3 for SE, 2 for NA, and 3 for IS in summer, and 4 for SE, 3 for NA, and 4 for IS in winter.

A generalized linear model with a stepwise procedure was used to assess the relationship among the number of current-year tree seedlings (NSE), number of species (NSP), census season (SEA), study site (SIT), and fence treatment (FEN), starting from a full model with interactions:

Model 1

NSE ~ SEA + SIT + FEN + SEA:SIT + SEA:FEN + SIT:FEN + SEA:SIT:FEN

Model 2

NSP ~ SEA + SIT + FEN + SEA:SIT + SEA:FEN + SIT:FEN + SEA:SIT:FEN

where SEA (summer or winter), SIT (Seibu, Nagata, or Isso area), and FEN (fenced or unfenced quadrats) are categorical variables with two or three modalities. The colon indicates an interaction. We used Akaike's information criterion (AIC, Akaike 1973) for the model selection, with the minimum AIC as the best-fit estimator.

Results and discussion

A statistical analysis of the number of current-year tree seedlings selected the full model of the regression as that with the minimum AIC value (AIC = 4923.24). In both summer and winter, the mean number of seedlings per quadrat was greater in fenced quadrats than in unfenced quadrats (Fig. 2). In NA and SE, the high-density sika deer population probably grazed on newly germinated seedlings soon after germination, and the difference in seedling density between fenced and unfenced quadrats was great, especially in summer. On the other hand, newly germinated seedlings in IS were not browsed as much owing to the low density of sika deer in IS, and the difference in seedling density between fenced and unfenced quadrats was small. In winter, seedling establishment numbers were different between fenced and unfenced quadrats at each study site, probably because of feeding pressure and physical disturbance by sika deer.

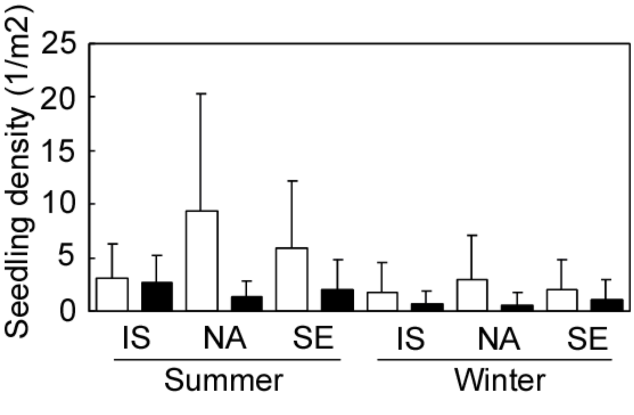

Fig. 2. Mean (mean + SD, white and black bars) numbers of current-year tree seedlings per 1-m^2 quadrat. White and black indicate fenced and unfenced quadrats, respectively. IS, NA, and SE indicate the Isso area, Nagata area, and Seibu area, respectively.

To identify the effects of sika deer and human impacts on tree seedling diversity in the forest, we compared the number of current-year tree seedling species among sites with different sika deer density and disturbance intensity. A statistical analysis of the number of species selected the full model with the minimum AIC value (AIC = 2896.95) (Fig. 3). The mean number of species per fenced quadrat was estimated to be greater at SE > NA > IS in summer and at NA > SE > IS in winter, and the difference between fenced and unfenced quadrats was estimated to be greater at SE > NA > IS in summer and NA > SE > IS in winter. This result indicates that human impacts, such as plantation areas, around the study sites limited the recruitment and establishment of current-year tree seedlings, especially in IS, probably because the conversion to conifer plantations decreased the natural forest area of seed sources. On the other hand, the mean number of species per unfenced quadrat was greater at IS > SE > NA in summer and in winter, with the difference between fenced and unfenced as above (SE > NA > IS in summer and NA > SE > IS in winter). This indicates that the feeding and/or physical disturbance owing to sika deer (Tsujino and Yumoto 2004) caused the decrease of seedling recruitment and establishment in unfenced quadrats, especially in SE and NA, and resulted in decreased seedling diversity.

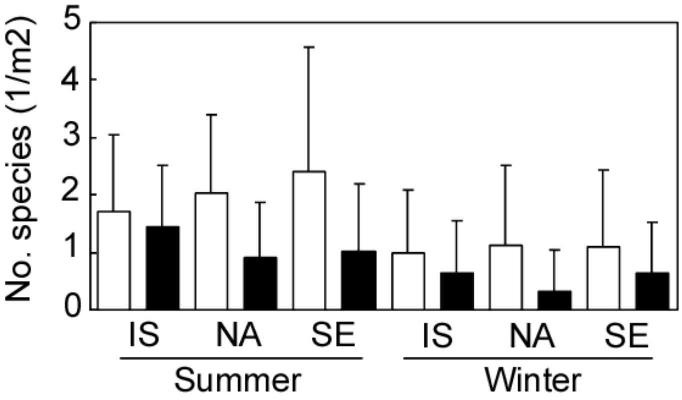

Fig. 3. Mean (mean + SD, white and black bars) number of species of current-year tree seedlings per 1-m^2 seedling observation quadrat. White and black indicate fenced and unfenced quadrats, respectively. IS, NA, and SE indicate the Isso area, Nagata area, and Seibu area, respectively.

In this study, we revealed two factors affecting tree seedling number and diversity: sika deer populations negatively affect both the number and diversity of current-year tree seedlings, and conifer plantations negatively affect the diversity of seedlings (Fig. 4). On the other hand, there is a negative relationship between sika deer population density and degree of human impact on the forest (Agetsuma 2007). We suggest that human impacts on a forest, such as conversion of natural forest to conifer plantation, have not only direct negative effects on tree seedling diversity, probably through a seed source effect, but also indirect positive effects by decreasing the sika deer density (Fig. 4). Thus, the effects of forest disturbances by humans are complex and include direct negative and indirect positive effects on tree seedling communities.

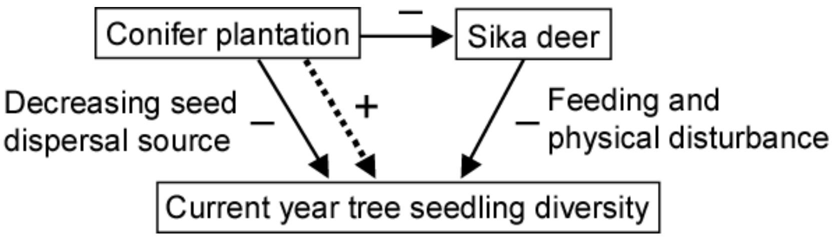

Fig. 4. Scheme showing the interactions among conifer plantations, sika deer, and current-year tree seedling diversity. Solid and broken lines indicate direct and indirect effects, respectively. Plus and minus signs beside arrows indicate positive and negative effects, respectively.

References

Agetsuma N, Sugiura H, Hill DA, Agetsuma-Yanagihara Y, Tanaka T. (2003) Population density and group composition of Japanese sika deer (*Cervus nippon yakushimae*) in ever-green broad leaved forest of Yakushima, southern Japan. Ecol Res 18: 475-483.

Agetsuma N. (2007) Ecological function losses caused by monotonous land use induce crop raiding by wildlife on the island of Yakushima, southern Japan. Ecol Res 22: 390-402.

Agetsuma N, Agetsuma-Yanagihara Y. (2006) Ecology of Yaku sika deer in the island of Yakushima (in Japanese). In: Ohsawa M, Tagawa H, Yamagiwa J (eds) World heritage, Yakushima. Asakura, Tokyo, pp 143–149.

Akashi N, Nakashizuka T.（1999）Effects of bark-stripping by Sika deer（*Cervus nippon*）on population dynamics of a mixed forest in Japan. Forest Ecol Manag 113: 75-82.

Asada, M. and Ochiai, K. (1996) Food habitats of sika deer on the Boso Peninsula, central Japan. Ecological Research 11: 89-95.

Hill DA, Agetsuma N, Suzuki S. (1994) Preliminary survey of group density of *Macaca fuscata yakui* in relation to logging history at seven sites in Yakushima Japan. Primate Research 10: 85-93.

Kagoshimaken Sizenaigo Kyokai. (1981) Yakusika no seisoku/bunnpu nikannsuru kinkyu chousa houkokusho. Kagoshimaken Sizenaigo Kyokai Chousahoukoku 5: 1-34 (in Japanese).

Kagoshimaken Sizenaigo Kyokai (1994) ‘Kendo Kamiyaku-Nagata-Yakusen Kairyoukeikaku Nitomonau Kankyoeikyo Monitoring’ Houkokusho. Kagoshimaken Sizenaigo Kyokai, Kagoshima (in Japanese).

Kaji K, Yajima T. (1991) Forage selection by introduced deer on Nakanoshima Island, and its effect on the forest vegetation. Proceedings of the International Symposium on Wildlife Conservation, in INTECOL 1990（ed. N.Maruyama *et al.*）pp. 52-55. Japan Wildlife Research Center, Tokyo.

Komiya T. (2002) Field Best Encyclopedia: Mammals in Japan. Gakken, Tokyo (In Japanese).

Takatsuki S. (1988) Rumen contents of sika deer on Tsushima Island, western Japan. Ecological Research 3: 181-183.

Takatsuki S. (1989) Effect of deer on plants and plant communities. Japanese Journal of Ecology 39: 67-80 (In Japanese).

Takatsuki S. (1990) Summer dietary compositions of sake deer on Yakushima Island southern Japan. Ecological Research 5: 253-260.

Takatsuki S, Gorai T.（1994）Effects of Sika deer on the regeneration of a *Fagus crenata* forest on Kinkazan Island, northern Japan. Ecological Research 9: 115-120.

Tsujino R, Yumoto T. (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecological Research 19: 291-300.

Tsujino R, Noma N, Yumoto T. (2004) Growth of sika deer (*Cervus nippon yakushimae*) population in the lowland forests of Yakushima Island, Japan. Mammal Study 25: 105-111.

Tsujino R, Takafumi H, Agetsuma N, Yumoto T. (2006) Variation in tree growth, mortality and recruitment among topographic positions in a warm–temperate forest. Journal of Vegetation Science 17: 281-290.

Yokoyama S, Maeji I, Ueda T, Ando M, Shibata E.（2001）Impact of bark stripping by sika deer, *Cervus nippon*, on subalpine coniferous forests in central Japan. Forest Ecology and Management 140: 93-99.

Changes in Insect Assemblages with Conversion from Old-Growth Evergreen Broadleaf Forests to *Cryptomeria japonica* Plantations on Yakushima Island, Japan

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Introduction

Recently, several studies have investigated the changes in insect assemblages after conversion from natural or secondary forests to plantations of conifers (primarily Japanese cedar, *Cryptomeria japonica*, and hinoki cypress, *Chamaecyparis obtusa*) in the temperate deciduous forests of Japan (e.g., Inada et al., 2006; Maeto & Makihara, 1999; Makino et al., 2007; Sayama et al., 2005; Sueyoshi et al., 2003). However, changes in insect communities in systems other than temperate deciduous forests in Japan have been less thoroughly examined (but see Maeto et al., 2002; Mizota & Imasaka, 1997). Thus, there is little information regarding shifts in insect assemblages in response to the conversion of evergreen broadleaf forests in Japan.

We examined the responses of insect assemblages to the conversion of an evergreen broadleaf forest to a *C. japonica* plantation. We compared the abundance and diversity of seven insect groups (tiger beetles, clerid beetles, longicorn beetles, leaf beetles, elephant beetles other than Curculionidae, hoverflies, and wasps) collected in old-growth evergreen broadleaf forests and *C. japonica* plantations in the lowlands on Yakushima Island, Japan.

Materials & Methods

1) Study sites

The study sites were located in lowland forests (150-250 m above sea level) on Yakushima Island, Kagoshima Prefecture, Japan. We selected two plantations of *C. japonica* (approximately 40 years old) in each of the eastern and western regions of the island and two old-growth evergreen broadleaf forests situated near the two plantations (Table 1). Each study site was located within a continuous stand at least 100 m from the boundaries of other forest types, although small patches of secondary stands of broadleaf forests were occasionally found in the vicinity of the plantations. Both old-growth sites are located in a National Forest, whereas both plantations are under private ownership. The forest floors of the plantations receive more light due to the process of tree thinning.

2) Sampling and identification

Townes-type, white Malaise traps (1.8 x 1.8 x 1.8 m) were used to capture insects. Within each site, three traps were haphazardly set, and the maximum distance between traps was < 100 m. Trapped insects were collected monthly from July to December 2006 and from March to May 2007. A mixture of 70 % ethanol and ethylene glycol was added as a preservative to the insect containers in the traps. Collected insects were morphologically identified to species.

3) Target insect groups

Five coleopteran groups [Tiger beetles (Cicindelidae), clerid beetles (Cleridae), longicorn beetles (Disteniidae and Cerambycidae), leaf beetles (Chrysomelidae), and elephant beetles other than Curculionidae (Anthribidae, Brentidae, and Rhynchophoridae)], one dipteran group [hoverflies (Syrphidae)], and one hymenopteran group [wasps (Vespidae)] were examined. These insect groups consist of several functional feeding types. Tiger beetles, clerid beetles, and wasps are predators, whereas longicorn beetles, elephant beetles, and leaf beetles are herbivores. Adult hoverflies are pollen feeders (herbivores), and the larvae consist of two feeding types in the species examined: members of the subfamily Syrphinae are aphid-feeders (predators), and members of the subfamily Eristalinae are decayed-wood feeders (herbivores). We based guild assignment of hoverflies on larval feeding habits.

4) Data analyses

Data for each taxonomic group were pooled for each site throughout the season, and species with sample sizes > 20 individuals were analyzed using chi-squared tests. Data were compared between the two forest types (all individuals collected in old-growth evergreen broadleaf forests versus *C. japonica* plantations). Expected values were calculated by multiplying the number of total captures for each species by 0.5, because the number of individuals of all target species combined was nearly identical between the two forest types.

We calculated the logarithm of the inverse Simpson's index as an index of species diversity, as follows:

$$\log (1/D) = \log \Sigma\ [N (N-1)] / [Ni (Ni-1)]$$

where N is the total number of individuals, and Ni is the number of individuals of the ith species.

Results & Discussion

We collected 431 individuals of 51 species of target insect groups in the *C. japonica* plantations and 447 individuals of 76 species in the old-growth evergreen broadleaf forests (Table 2). Indices of species diversity calculated for each insect group were lower in the *C. japonica* plantations than in the old-growth evergreen broadleaf forests (Table 2).

The total number of herbivorous species was much greater in the old-growth evergreen broadleaf forests (58 species) than in the *C. japonica* plantations (30 species). Herbivores depend directly on a wide variety of plants for food and shelter (Siemann, 1998). Therefore, the greater availability of more plant species in the old-growth evergreen broadleaf forests likely increased the species diversity of herbivores. In contrast, the total number of predator species did not significantly differ between the *C. japonica* plantation (21 species) and the old-growth evergreen broadleaf forest (18 species). These results suggest that the species diversity of predators was not greatly affected by the increased availability of plants in the old-growth evergreen broadleaf forest, because insect predators do not directly depend on a variety plants for food.

The numbers of trapped individuals of *Cicindela japonica*, *Stigmatium nakanei*, *Omadius nigromaculatus*, *Ceresium longicorne*, *Cryptocephalus perelegans*, and *Monolepta pallidula* were significantly greater in the old-growth evergreen broadleaf forest than in the *C. japonica* plantations (Tables 3-6). The recorded host plants of *C. longicorne* and *C. perelegans* are primarily broadleaf trees and do not include Japanese cedar (Kimoto and Takizawa, 1994; Takeda, 2007). These six species include three predators, *C. japonica*, *S. nakanei*, and *O. nigromaculatus*; thus, some predators may indeed be affected by the conversion of old-growth evergreen broadleaf forests to *C. japonica* plantations.

In contrast, the number of trapped individuals of Alticinae gen. sp., *Sipalinus gigas*, *Episyrphus balteatus*, and *Chalcosyrphus frontalis* were significantly greater in the *C. japonica* plantations than in the old-growth evergreen broadleaf forest (Tables 6-8). In addition, *Milesia oshimaensis* (28 individuals) were collected only in the *C. japonica* plantations (Table 8). Although the host plants of Alticinae gen. sp. and *C. frontalis* are unknown, the recorded host plants of *S. gigas* and *M. oshimaensis* include Japanese cedar (Ikezaki, 1976; Morimoto, 1984). *Episyrphus balteatus* is a predator that may indirectly depend on *C. japonica*.

As has been previously recorded in temperate deciduous forests (e.g., Makino et al., 2007), our results indicate that the conversion of evergreen broadleaf forests to *C. japonica* plantations causes shifts in insect assemblages. Such conversions may lead to the impoverishment of insect herbivores. Insect predators may also be affected by the disappearance of evergreen broadleaf forests. However, several insect species were rarely collected in the evergreen broadleaf forests and may appear and/or increase explosively in the *C. japonica* plantations.

References

Ikezaki Y (1976) Syrphidae from Tsushima. In: Nagasaki Biological Society (ed) Tsushima no Seibutsu (in Japanese). Nagasaki Biological Society, Nagasaki, pp 329-339

Inada T, Yunomura S, Maeto K (2006) The influence of forest management on the assemblage of longicorn beetles (in Japanese with English summary). J Jpn For Soc 88:446-455

Kimoto S, Takizawa H (1994) Leaf beetles (Chrysomelidae) of Japan (in Japanese with English summary). Tokai University Press, Tokyo

Maeto K, Makihara H (1999) Changes in insect assemblages with secondary succession of temperate deciduous forests after clear-cutting (in Japanese with English summary). Jpn J Entomol (NS) 2:11-16

Maeto K, Sato S, Miyata H (2002) Species diversity of longicorn beetles in humid warm-temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. Biodiv Conserv 11:1919-1937

Makino S, Goto H, Hasegawa M, Okabe K, Tanaka H, Inoue T, Okochi I (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan. Ecol Res 22:372-381

Mizota K, Imasaka S (1997) Comparison of flower-visiting beetle communities between natural and artificial forests in southern Kii Peninsula (in Japanese with English summary). Res Bull Hokkaido Univ For 54: 299-326

Morimoto K (1984) Rhynchophoridae. In Hayashi M (ed) The Coleoptera of Japan in color Vol. IV (in Japanese). Hoikusha, Osaka, pp 345-348

Sayama K, Makihara H, Inoue T, Okochi I (2005) Monitoring longicorn beetles in different forest types using collision traps baited with chemical attractants (in Japanese with English summary). Bull FFPRI 4:189-199

Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057-2070

Sueyoshi M, Maeto K, Makihara H, Makino S, Iwai T (2003) Changes in dipteran assemblages with secondary succession of temperate deciduous forests following clear-cutting (in Japanese with English summary). Bull FFPRI 2: 171-191

Takeda M (2007) Host plants. In: Ohbayashi N, Niisato T (eds) Longicorn beetles of Japan (in Japanese). Tokai University Press, Tokyo, pp 683-773

Table 1 Location and forest type of the investigated sites in Yakushima Island

Site	Forest type	Site position	Altitude (m)
CE	Plantation of *C. japonica* (40 yr.)	Eastern part	150
CW	Plantation of *C. japonica* (40 yr.)	Western part	220
OE	Old-growth evergreen broadleaf forest	Eastern part	170
OW	Old-growth evergreen broadleaf forest	Western part	250

Table 2 Comparisons of number of species, number of individuals, and diversity indices [logarithm of inverse Simpson's index, log(1/D)] between plantation of cedar and old-growth evergreen broadleaf forest in Yakushima

	Plantation of cedar			Old-growth evergreen broadleaf forest		
	No. of species	No. of individuals	log(1/*D*)	No. of species	No. of individuals	log(1/*D*)
Tiger beetles	1	5	0.00	2	47	0.20
Clerid beetles	5	35	0.31	7	98	0.40
Longicorn beetles	8	17	0.92	26	94	0.96
Leaf beetles	8	145	0.12	12	123	0.76
Elephant beetles	7	40	0.22	16	39	1.07
Hoverflies	15	170	0.59	7	21	0.80
Wasps	7	19	0.20	6	25	0.47
All target groups combined	51	431	0.87	76	447	1.34

Table 3 The number of tiger beetles collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 (CE+CW *vs* OE+OW)
Cicindelidae						
Cicindela japonica	2	3	9	27	41	23.43*
Therates alboobliquatus			1	10	11	

*$P<0.001$.

Table 4 The number of clerid beetles collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 (CE+CW *vs* OE+OW)
Cleridae						
Tillus igarashii				1	1	
Opilo carinatus		1	1	8	10	
Clerus postmaculatus				3	3	
Stigmatium pilosellum				1	1	
Stigmatium nakanei	2	22	25	34	83	14.75*
Stigmatium igai		2	1	7	10	
Omadius nigromaculatus		6	16	1	23	5.26**
Allochotes dichrous		2			2	

*$P<0.001$; **$P<0.05$.

Table 5 The number of longicorn beetles collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 (CE+CW *vs* OE+OW)
Disteniidae						
Distenia gracilis gracilis				1	1	
Cerambycidae						
Lepturinae						
Leptura ochraceofasciata ochraceofasciata		1	1		2	
Cerambycinae						
Allotraeus sphaerioninus			2		2	
Stenodryas clavigera clavigera				1	1	
?*Ceresium holophaeum*				6	6	
Ceresium longicorne		3		25	28	17.28∗
Ceresium sp.				2	2	
Comusia testacea				1	1	
Stenhomalus nagaoi				1	1	
Artimpaza setigera japonica				1	1	
Cleomenes takiguchii				4	4	
Callidiellum rufipenne	2				2	
Xylotrechus emaciatus		4	10	5	19	
Perissus kiusiuensis kiusiuensis			1	3	4	
Chlorophorus quiquefasciatus	1		2	1	4	
Chlorophorus muscosus			1	4	5	
Demonax transillis				2	2	
Anaglyptus arakawae kumagensis			2		2	
Clytini gen. sp.			1		1	
Lamiinae						
Mesosa longipennis			1		1	
Neosybra cribrella			1		1	
Sybra ordinata ordinata				3	3	
Pterolophia gibbosipennis subcristipennis				3	3	
?*Pterolophia kyushuensis*			1	1	2	
Uraecha bimaculata	1		2	2	5	
Xenicotela pardalina		1			1	
Mimectatina meridiana ohirai	1	3			4	
Rondibilis insularis			1		1	
Sciades fasciatus fasciatus				2	2	

∗$P < 0.001$

Table 6 The number of leaf beetles collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 （CE+CW *vs* OE+OW）
Chrysomelidae						
Cryptocephalinae						
Cryptocephalus perelegans		1	5	21	27	23.14∗
Eumolpinae						
Acrothinium gaschkevitchii			5	8	13	
Basilepta hirayamai		1	4	5	10	
Trichochrysea okinawana				1	1	
Lypesthes fulvus				7	7	
?*Lypesthes itoi*	9	3	1		13	
Hyperaxis fasciata		2	2	5	9	
Demotina fasciculata			1		1	
Demotina sp.			13	1	14	
Galerucinae						
Fleutiauxia armata		1			1	
?*Monolepta pallidula*		1	9	30	40	36.10∗
Alticinae						
Nonarthra cyanea				1	1	
?*Nonarthra tibialis*	1				1	
Alticinae gen. sp.	114	12		4	130	114.49∗

∗*P*＜0.001.

Table 7 The number of elephant beetles (excluging Curculionidae) collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 （CE+CW *vs* OE+OW）
Anthribidae						
Ozotomerus nigromaculatus				1	1	
Mecotropis kyushuensis			1		1	
Stiboderes impressus stibinus	1				1	
?*Dendrotrogus japonicus*			2		2	
Sintor bipunctatus			2		2	
Sympaector rugirostris			1		1	
Acorynus asanoi		2	5	3	10	
Litocerus kimurai				1	1	
Litocerus tokarensis insensibilis			1	1	2	
Litocerus multiguttatus		1		1	2	
?*Phaulimia confinis*				1	1	
Phaulimia aberrans				2	2	
Oxyderes fastigatus		1	2	3	6	
Aphaulimia debilis		1	2	4	7	
Habrissus unciferoides		3	2	2	7	
Brentidae						
Baryrhynchus poweri				1	1	
Rhynchophoridae						
Sipalinus gigas	31			1	32	28.12∗

∗*P*＜0.001.

Table 8 The number of hoverflies collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 (CE+CW *vs* OE+OW)
Syrphidae						
Syrphinae						
?*Allograpta iavana*				1	1	
Didea fasciata		1			1	
Episyrphus balteatus	42	25	3	4	74	48.64＊
?*Ischiodon scutellaris*				1	1	
?*Parasyrphus aeneostoma*		1			1	
?*Syrphus torvus*	1				1	
Allobaccha nubilipennis	3	3			6	
Baccha maculata		1			1	
Chrysotoxum sp.	1				1	
Platycheirus sp.	2	2			4	
Eristalinae						
?*Eumerus japonicus*		1	1	3	5	
?*Mallota yakushimana*		1			1	
Milesia oshimaensis	18	6			24	
Milesia undulata	1		3		4	
Takaomyia johannis		5	1	1	7	
Chalcosyrphus frontalis	25	23	3		51	39.70＊
Xylota sp.	6	2			8	

＊*P*＜0.001.

Table 9 The number of wasps collected with 3 Malaise traps in Yakushima

	CE	CW	OE	OW	Total	χ^2 (CE+CW *vs* OE+OW)
Vespidae						
Polistes rothneyi	1				1	
Parapolybia indica	1	6			7	
Vespa mandarinia	2			1	3	
Vespa ducalis	2	1	1		4	
Vespa analis	1	2		1	4	
Vespa similima	1	1	3	9	14	
Vespula flaviceps			1		1	
Vespula shidai		1		9	10	

Comparison of Food Availability and the Density of Japanese Macaques in Primary, Naturally Regenerated, and Plantation Forests

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Introduction

Japanese forests have changed considerably since the 1960s through ‘expansive afforestation,’ that is, through deforestation and replacement of broad-leaved trees with conifers, such as Japanese cedar *Cryptomeria japonica* and hinoki cypress *Chamaecyparis obtusa*. As a result, about 40% of Japanese forests have been converted to artificial coniferous forests. These tree species do not provide food for most indigenous vertebrate species, and are therefore believed to significantly affect Japanese wildlife. For example, crop raiding by Japanese macaques *Macaca fuscata* rapidly increased in the 1980s, and the area of damaged farmland has now reached 6000 ha. Agetsuma (1998) speculated that for about 10 yr after logging, food availability for the macaques did not decline because they foraged the grass vegetation in logged patches. However, as planted conifer stands developed, the grass was gradually replaced by tree plantations. In the 10–20 yr after logging, the planted forest became an artificial coniferous forest that provided little food for the macaques, leading them to raid crops. Damage to crops and forestry products by black bears (*Ursus thibetanus*), sika deer (*Cervus nippon*), Japanese serow (*Capricornis crispus*), Japanese hares (*Lepus brachyurus*), and wild boars (*Sus scrofa*) are also serious problems, which are suspected to be caused directly or indirectly by expansive afforestation (Takatsuki, 1996). In the 1990s, about 8000 Japanese macaques, 1200 Japanese serow, and 1500 black bears were killed annually as pests in Japan, even though some of these populations were endangered. Thus, to reduce damage to crops and to conserve wildlife, it is important to clarify and quantify the effects of expansive afforestation. In recent years, large-scale expansive afforestation has rarely been practiced due to the lack of adequate labor, and logged broad-leaved forests have often regenerated naturally with minimal human management. However, little empirical data exist on the disparate effects of these two regeneration systems on large, forest-dwelling mammals in Japan.

We compared food availability and group density of Japanese macaques on Yakushima Island, Japan, in three different forest types: primary forest, naturally regenerating forest, and artificially regenerating forest planted with *Cryptomeria japonica*. On this island, as in other parts of Japan, large-scale expansive afforestation was conducted in the 1960s and 1970s, and crop raiding by Japanese macaques became a serious problem in the 1980s. Now the annual cost of damage to crops is 10–40 million yen and more than 400 macaques are killed annually on Yakushima for pest control (Agetsuma, 1998). The goal of this study was to clarify differences among these forests types with respect to food availability and the density of Japanese macaques.

Methods

The study site was located in the western part of Yakushima at 700–1200 m above sea level. The primary vegetation here is transitional between a higher elevation coniferous forest and a lower elevation warm–temperate broad-leaved evergreen forest. The study area included both primary forest protected as national park and disturbed forest outside the park (Fig. 1a). The study in 2003 was conducted 7–27 yr after logging. For simplicity, we hereafter refer to the age of the regenerating forests in relation to the year 2003. The regeneration system changed in 1984. Before 1984, expansive afforestation was conducted: the forest was clear-cut, the felled areas were cleared, and 1000–2000 conifer saplings (*Cryptomeria japonica*) about 60 cm tall were planted per hectare. Weeding was conducted once a year for a few years after logging. Since 1984, no afforestation has occurred and clear-cut forests have been left to regenerate with little human management. We refer to the former stands as ‘plantation’ and the latter as ‘naturally regenerated.’

We established 5 × 5-m plots in primary and logged forests. In the primary forest, plots were randomly selected within a larger (0.75 ha) plot established in 1999. In the logged forest, we set each plot at the approximate center of each logged patch in 2002. We established 30 plots in primary forest, 10 in plantation forest (five in 19–22-yr-old and five in 23–27-yr-old forests) and 17 in naturally regenerated forest (seven in 7–10-yr-old, five in 11–13-yr-old, and five in 14–18-yr-old forests). In each plot, we recorded the species and diameter at breast height (DBH) of all trees taller than 1 m.

In early September of 2002 and 2003, we studied the fruit production of species eaten by macaques. This was carried out by a single observer counting the number of fleshy fruits on marked branches of each tree in each plot. The number of fruits in the tree was estimated by dividing the number of fruits on marked branches by the proportion of the branch relative to the total crown.

We censused Japanese macaques in August 2000, 2001, 2002, and 2003 using a point census with group follows (Hanya et al., 2003). We divided the 7.5-km^2 census area into 30 500 × 500-m grid squares (Fig. 1b). One observer was positioned in each grid square at a fixed point. Observers stayed at the points from 06:00 to 16:00. When they detected macaques by direct observation or vocalization, they recorded the time and approximate location, regardless of whether the animals were within or outside of the grid square. Whenever possible, 10–14 researchers followed groups that appeared in the census area. Group followers recorded the location of the center of the group every hour. Each point was censused for 6 days in 2000, 9 days in 2001, 7 days in 2002, and 5 days in 2003.

To estimate group density, we defined a group as a cluster of macaques whose spread was 500 m at maximum. At each point, we counted the number of groups detected each hour (e.g., 06:00–06:59) as follows. The number of groups detected each hour was averaged for each day, and then the day’s average value was averaged across all census days of the year for each point. We refer to this value, *n*, as the number of groups detected at a point. Because we followed some groups, it was possible to calculate the proportion of groups detected by point observers (detectability) at a given distance. We regressed the relationship between point-group distance *y* and detectability g(*y*) on a half-normal model: $g(y) = e^{-\lambda y^2}$ and calculated λ as the 'detectability constant.' Then, group density *D* was calculated as $D = \frac{\lambda n}{\pi}$ (Hanya et al., 2003).

Results

Fruit production was higher in young naturally regenerated forests than in primary forests (Fig. 2). However, the pattern varied among the four main fleshy-fruited species (Fig. 3), which comprised more than 95% of the fruit production. Fruit production was highest in 11–13-yr-old forests for *Eurya japonica* and 11–13-yr-old forests for *Symplocos myrtacea*. In the case of *Symplocos tanakae*, fruit production did not vary between primary and naturally regenerated forests in 2002 and was largely restricted to the 11–13-yr-old naturally regenerated forest in 2003. In contrast, *Cleyera japonica* fruited only in primary forest.

The density of macaque groups was higher in the youngest (7–10-yr-old) naturally generated forest than in the oldest (23–27-yr-old) plantation forest (Fig. 4).

Discussion

Food availability and group density of Japanese macaques were quite different between younger naturally regenerated forests and older plantation forests. In plantation forests 19 yr after logging, fruit production was negligible. The forest was composed mostly of *Cryptomeria japonica*, which offers male pollen cones as food only during the winter (Hanya, 2004). In contrast, in naturally regenerated forests, fruit availability was higher than in either primary or plantation forests for at least 7–18 yr after logging. Fruit availability is important because macaques in this region prefer fruits over other foods (Hanya, 2004), fruit availability is the principal determinant of the altitudinal variation in macaque density on Yakushima (Hanya et al., 2004), fruit production is known to affect reproduction in female Japanese macaques (Suzuki et al., 1998), fruit is high-quality food because of its high energy and low fiber content (Iwamoto, 1982), and fruit is generally a limited resource, whereas other foods, leaves in particular, are often superabundant (Janson & Chapman, 1999). Variation in the density of Japanese macaques was consistent with variation in food availability, at least for the plantation forest; macaque density was lowest in old plantation forests, where food availability was lowest.

In plantation forests, the macaques' food trees were cleared during logging. Even if they appear after logging, they are often cut to enhance the growth of *Cryptomeria japonica*. Once *Cryptomeria japonica* trees become large enough, short trees cannot reproduce under their shade. Our data indicate that these undesirable changes for frugivores, such as Japanese macaques, take place within 19 yr.

In young naturally regenerated forests, availability of food, and of fruit in particular, is higher than in primary and old plantation forests. Large fruiting trees are usually killed by clear-cutting, but this was not the case for the main sources of fruit for the macaques in this forest, as they are small trees. In cases of natural regeneration, felled areas are not cleared, and some small trees survive. When tall trees are cut, small trees receive more sunlight, which enhances their reproduction (Guariguata & Saenz, 2002). However, *Cleyera japonica* did not fruit in logged forest. The minimum DBH at which *Cleyera japonica* reproduced was 10 cm. This suggests that small *Cleyera japonica* in logged forests cannot reproduce like other species, even when light conditions are enhanced. Considering the observed interspecies variation in responses to logging, we propose that the effect of logging on frugivores varies with the flora. When large trees are the main source of fruit foods for frugivorous primates, their density and fruit availability are reduced by logging (Felton et al., 2003). When small trees offer a considerable amount of fruit, food availability for frugivores can be increased by logging (this study; Ganzhorn, 1995).

In conclusion, conversion of natural broad-leaved forest into monocultural *Cryptomeria japonica* forest is detrimental to the conservation of Japanese macaques. When small trees provide fruit for macaques, natural regeneration offers habitats of high fruit availability in the initial stage of regeneration, which lasts at least 7–19 yr after logging, and macaque density there is as high as in the primary forest.

References

Agetsuma N. (1998) Crop damage by wild Japanese monkeys on Yakushima Island, Japan. *Japanese Journal of Conservation Ecology* **3**: 43–55.

Felton A.M., Engstrom L.M., Felton A. & Knott C.D. (2003) Orangutan population density, forest structure and fruit availability in hand-logged and unlogged swamp forests in West Kalimantan, Indonesia. *Biological Conservation* **114**: 91–101.

Ganzhorn J.U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* **76**: 2084–2096.

Guariguata M.R. & Saenz G.P. (2002) Post-logging acorn production and oak regeneration in a tropical montane forest, Costa Rica. *Forest Ecology and Management* **167**: 285–293.

Hanya G. (2004) Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology* **25**: 55–71.

Hanya G., Yoshihiro S., Zamma K., Kubo R. & Takahata Y. (2003) New method to census primate groups: estimating group density of Japanese macaques by point census. *American Journal of Primatology* **60**: 43–56.

Hanya G., Yoshihiro S., Zamma K., Matsubara H., Ohtake M., Kubo R., Noma N., Agetsuma N. & Takahata Y. (2004) Environmental determinants of the altitudinal variations in relative group densities of the Japanese macaques on Yakushima. *Ecological Research* **19**: 485–493.

Iwamoto T. (1982) Food and nutritional condition of free ranging Japanese monkeys on Koshima Islet during winter. *Primates* **23**: 153–170.

Janson C.H. & Chapman C.A. (1999) Resources and primate community structure. In: *Primate Communities* (eds J.G. Fleagle, C.H. Janson & K.E . Reed), pp. 237–267. Cambridge University Press, Cambridge.

Suzuki S., Noma N. & Izawa K. (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. *Primates* **39**: 313–324.

Takatsuki S. (1996) Conservation of common species. In: *Conservation Biology* (ed H. Higuchi), pp. 191–220. University of Tokyo Press, Tokyo.

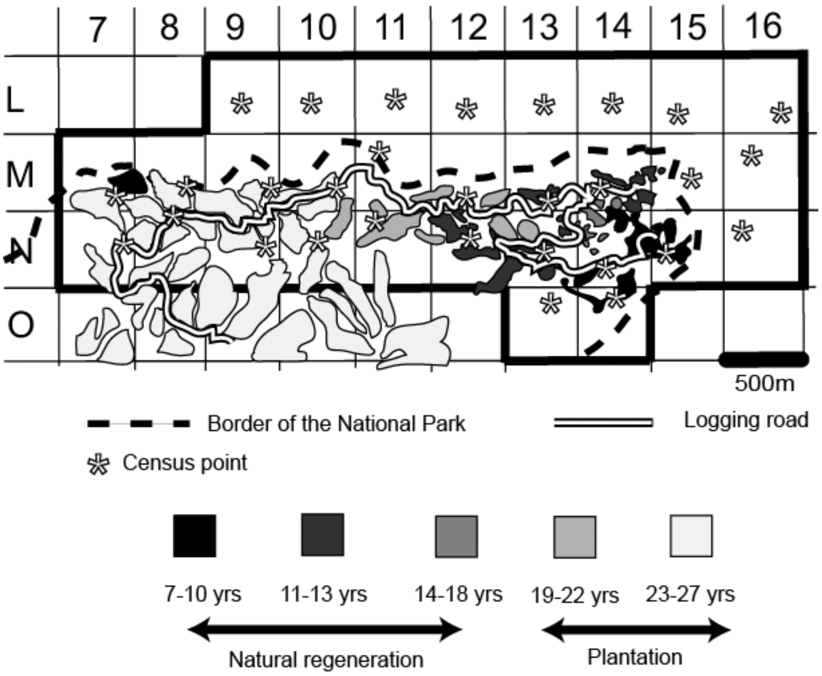

Fig. 1. Vegetation and the distribution of points where macaque groups were censused. Thick lines indicate the census area.

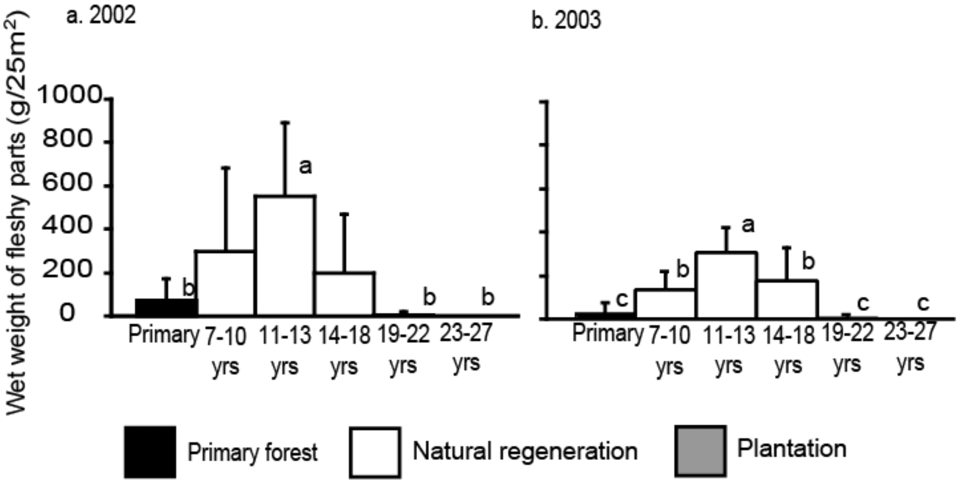

Fig. 2. Total annual fruit production. Means and standard deviations are shown.
Letters above the bars indicate significant differences between bars with different characters (in the order a > b > c).

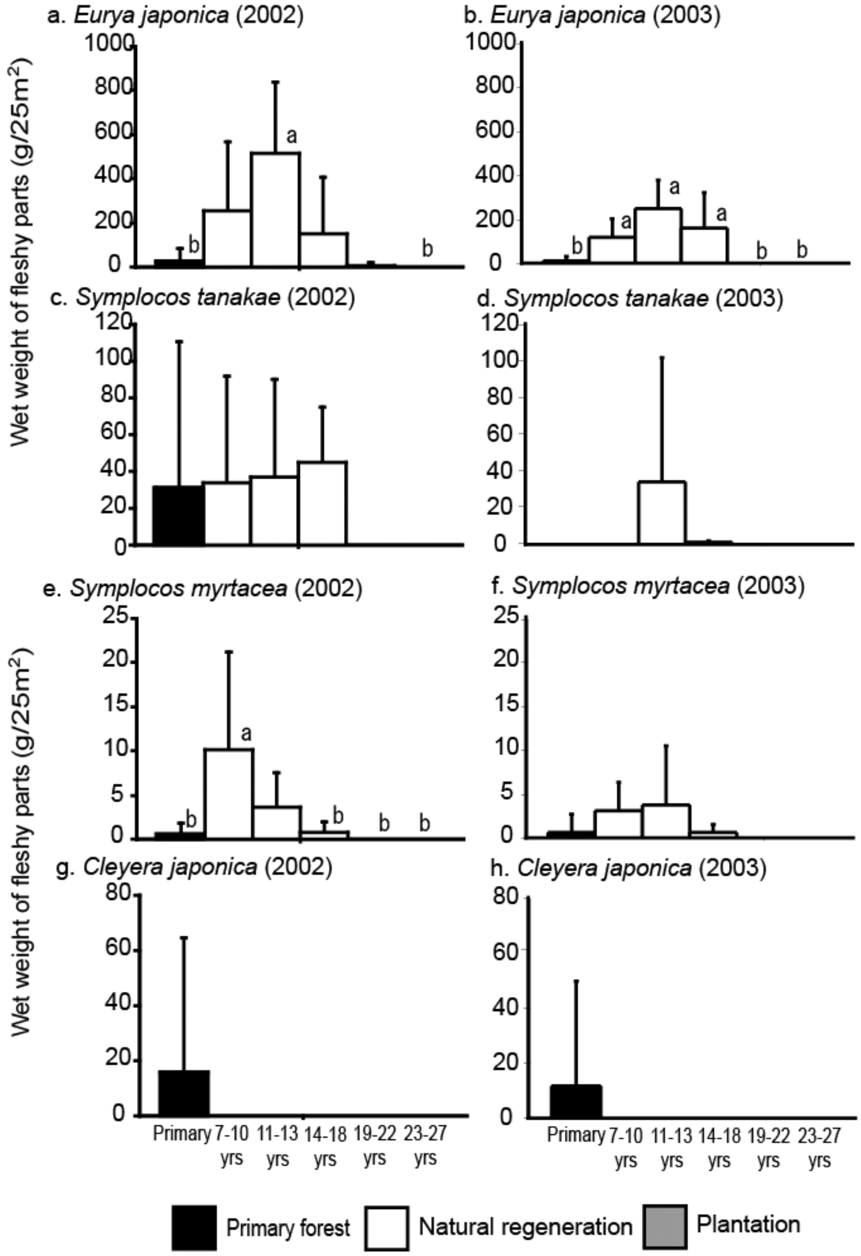

Fig. 3. Fruit production of the main species. Means and standard deviations are shown. Letters above the bars indicate significant differences between bars with different characters (in the order a > b > c).

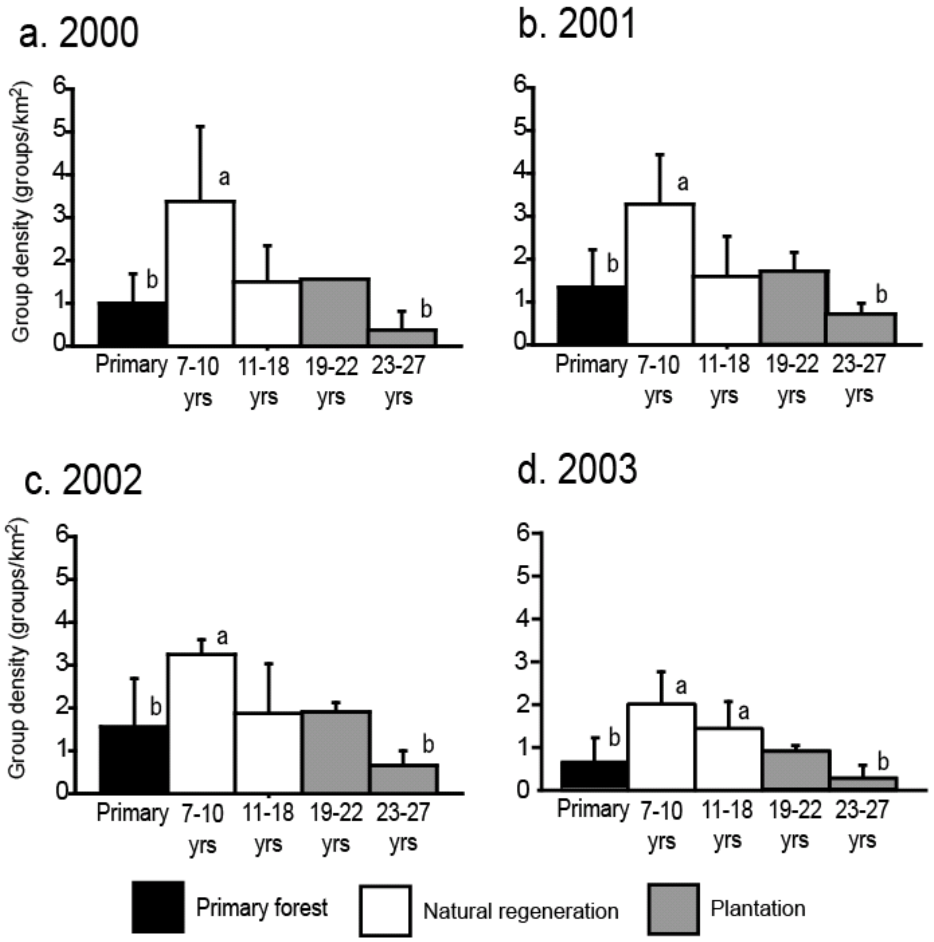

Fig. 4. Group density of Japanese macaques. Means and standard deviations are shown. Letters above the bars indicate that there are significant differences between bars with different characters, in the order of a>b>c

Changes in Plant Diversity after Conversion from Secondary Broadleaf Forest to *Cryptomeria* Plantation Forest: Chronosequencial Changes in Forest Floor Plant Diversity

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Introduction

The conservation of forest biological diversity is considered one of the most important criteria for ecologically sustainable forest management (Hunter 1999, Lindenmayer and Franklin 2002) because biological diversity is thought to be related to many ecological functions (Scherer-Lorenzen et al. 2005). This idea is still an open question. In addition to studies that focus on the relationships between biological diversity and ecological function, further information is required on the actual biological diversity of forested landscapes.

Conversions from primary broadleaf forests, coppice broadleaf forests, and semi-natural grasslands to conifer (sugi, *Cryptomeria japonica*, and hinoki, *Chamaecyparis obtusa*) plantations occurred after the 1940s in the mountainous areas of Japan, resulting in the replacement of a large portion of the natural and semi-natural vegetation of Japan by conifer plantations prior to the 1980s (Inoue 2003). Biological diversity sustained by traditional land use may have been negatively affected by the conversion of mixed stands to pure monocultures. Several studies have described the effects of such conversions on plant diversity in different regions and plantation forest types at the stand level (Nagaike 2002, Ito et al. 2003, 2004, Nagaike et al. 2005). However, few studies have investigated the dynamic chronosequential changes in plant diversity in both natural secondary forests and converted plantation forests (Nagaike 2003, Nagaike et al. 2006).

To sustainably manage a mosaic forest landscape composed of secondary broadleaf forests and conifer plantations, it is important to understand the plant diversity and how it changes with stand age of both forest types, as well as the contribution of each forest type to the maintenance of regional biodiversity. The appropriate zoning or spatial arrangement of stands for sustainable forest management depends on an understanding of the compositional characteristics of each forest type and age, as well as the dependence of plant species on forest type and age.

To obtain a scientific basis for plant diversity management and conservation, we addressed the following two specific questions. How does plant diversity change (recover) in both plantation and secondary natural forest stands after clear-cutting? How does conversion from deciduous broadleaf forest to evergreen conifer plantation affect species diversity? We used a chronosequence approach to compare sample stands of different ages scattered across a typical landscape.

Materials and methods

Study sites

The study was conducted in two areas located about 10 km apart: Ogawa and Satomi, Ibaraki Prefecture, central Japan. Both areas are located at the southern edge of the Abukuma Mountains (approximately 36º 50–56′ N, 140º 34–35′ E; 580–800 m above sea level). The annual mean temperature and precipitation in Ogawa are 10.7ºC and 1910 mm, respectively (Mizoguchi et al. 2002). The landscape of both areas is now mainly composed of deciduous broadleaf forests and plantations of *Cryptomeria japonica* (partly of *Chamaecyparis obtusa*), although the proportion of plantations is much higher in Satomi than in Ogawa (94% vs. 47% of the total forested area, respectively). In old-growth broadleaf forests, which are preserved only in Ogawa, the dominant canopy trees are *Quercus serrata*, *Fagus japonica*, and *F. crenata* (Masaki et al. 1992, Tanaka et al. in press). A large portion of the broadleaf forests in Ogawa, including the old-growth forests, has long been subjected to human activities such as burning, cattle grazing, and clear-cutting for fuel (Suzuki 2002). Small-scale (1–2 ha) clear-cutting with short intervals of ca. 30 years has been conducted repeatedly until now in the secondary broadleaf forests to make charcoal, produce pulp wood, and collect bed logs for mushroom culture. The conversion of pasture or secondary broadleaf stands to conifer plantations greatly increased the proportion of plantation forests in Japan after the Second World War (Inoue 2003). In addition, this land-use history resulted in a mosaic-like forest landscape in these areas, composed of secondary broadleaf stands and conifer plantations of various ages.

Field study

We examined the forest vegetation in 13 post-harvest secondary deciduous broadleaf forests (SB) and 26 conifer (*Cryptomeria japonica*) plantation forests (CP) along a chronosequence from just after clear-cutting to mature stands (70–80 years old). Four preserved old deciduous broadleaf forests (OG) were also studied as a reference for old-growth conditions. Plantation forests had been tended (i.e., weeded and thinned) according to the common schedule of the local governmental forest offices, but not so intensively managed as well-managed private plantations.

In each forest, we established a 10 × 100 m belt-shaped study plot at the center of each stand wherever possible to exclude the effects of neighboring stands of different management types. To minimize the influence of variation in site conditions, we selected stands located on gentle slopes, and the belt-shaped plots were designed to encompass the topographic variation in each stand (Iida and Nakashizuka 1995, Fukamachi et al. 1996, Nagaike 2002, Nagaike et al. 2003, 2006).

Each study plot was divided into 5 × 5 m quadrats, and a 1 × 1 m subquadrat was positioned in the corner of each quadrat. In total, we investigated 1060 quadrats and subquadrats:

160 in old-growth forests, 380 in secondary forests, and 520 in plantation forests. In each study plot, trees and woody vines > 2 m in height and with a diameter at breast height (dbh) > 5 cm were tagged, and their girth at breast height (gbh) was measured. Forest floor vegetation, i.e., < 2 m in height, was censused within each subquadrat using the Braun-Blanquet method. Standing dead stems > 5 cm in dbh were tagged and measured. We also recorded all woody plants > 2 m in height in each quadrat. Light conditions at the forest floor were measured in each subquadrat using hemispherical photographs taken 1 m above the ground.

A 200 × 300 m plot was established in the Ogawa Forest Reserve, and 2 × 2 m quadrats were placed at each intersection of a 10 × 10 m grid (651 quadrats in total) for the collection of additional data on forest floor vegetation in old-growth forests. The nomenclature follows Kitamura and Okamoto (1959), Kitamura et al. (1974, 1978), and Kitamura and Murata (1980).

Data analysis

To define understory vegetation species groups, the occurrence biases of species found in particular forests were tested using chi-square and Fisher's exact tests, based on the procedure of Nagaike et al. (2003). To include the vegetation data from the Ogawa Forest Reserve 2 × 2 m quadrats, we analyzed the pooled data from four 1 × 1 m subquadrats. In total, we investigated 1059 2 × 2 m subquadrats (691 in old-growth forests, 122 in secondary forests, and 246 in plantation forests) from four old-growth forests, 13 secondary broadleaf forests, and 26 plantation forests. We examined whether species occurred disproportionately in old-growth forests, secondary forests, or plantations. Species with no significant bias were classified as generalists, whereas those with occurrence frequencies ≤ 5 were classified as infrequent species. Thus, species were classified into five types according to their occurrence bias toward particular forest types. In addition, we classified the species listed in Numata and Yoshizawa (2002) as weed species, which are characterized as ruderal or disturbance-tolerant species (Bhuju and Ohsawa 1999, Kitazawa and Ohsawa 2002) and are usually considered undesirable from a management perspective. Species listed in the Red Data Book (Environment Agency of Japan 2000) did not occur in the study area.

To examine the differences between secondary forests and plantation forests in forest floor plant species abundance, analysis of variance (ANOVA) was performed for stands pooled into three age categories: young (3–10 years old), intermediate (10–40 years old), and mature (≥ 41 years old) stands (JMP, SAS Institute 2001). To test for compositional differences among forest types, cluster analysis and detrended correspondence analysis (DCA) were performed using PC-ORD (McCune and Mefford 1999). The species occurrence frequency in each plot was used for DCA. Correlations between the axis scores of DCA and stand structural and compositional variables reflecting management intensity were calculated using Kendall's τ (JMP, SAS Institute. 2001).

Results

Changes in stand structure and species diversity with stand age

As stand age increased, stand structural parameters such as basal area (BA) increased in both secondary forests and conifer plantations (Fig. 1). The BA was larger in plantation forests than in secondary forests (and old-growth forests) along the chronosequence (Fig. 1), although the maximum dbh was comparable in secondary forests and conifer plantations (data not shown).

Young stands (2–10 years after clear-cutting) had higher species richness of forest floor plant species (i.e., herbs and ferns) than did intermediate (11-40 years) and mature stands (>40 years) in both secondary and plantation forests (Tukey-Kramer’s HSD, $p < 0.01$; Fig. 2). The species richness of forest floor plant species was marginally higher in secondary forests than in plantation forests at each age category (ANOVA, $p = 0.05$; Fig. 2).

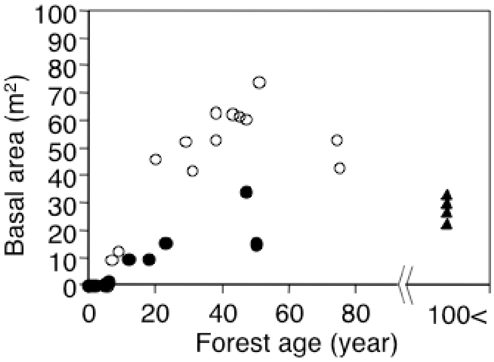

Fig. 1. Relationship between stand age and basal area (BA) of trees with diameter at breast height (dbh) > 5 cm. Open circle: conifer plantation; closed circle: secondary

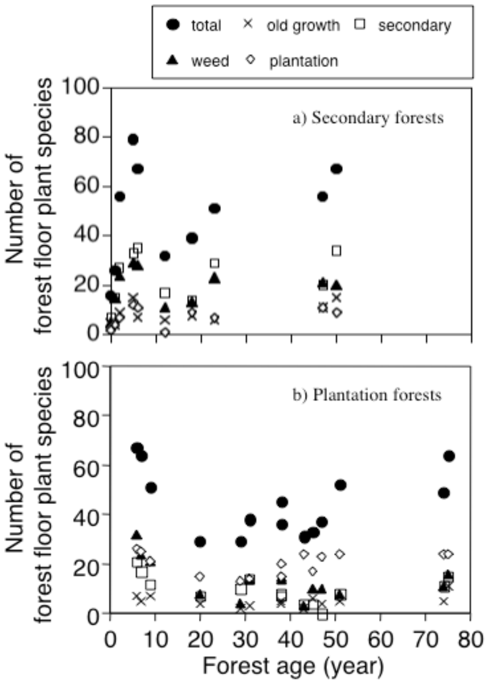

Fig. 2. Relationship between forest stand age and number of forest floor plant species in (a) secondary forests and (b) plantation forests.

Species diversity and composition in plantations and secondary forests

We recorded a total of 324 species (Fig. 3, Table 1). The three forest types appeared to contribute equally to the forest flora, although this result is based on restricted sampling (Fig. 3). According to the species occurrence biases, infrequent species (124 species, 38%) made up the highest percentage of species (Table 1). Secondary forest species (71 species, 22%) accounted for the second highest occurrence frequency, but plantation forest species accounted for nearly the same percentage (62 species, 19%). The secondary forest species group contained the highest percentage of weed species (41%). The old-growth forest species group contained the fewest weed species, but this was still a substantial percentage of the total species count (33 species, 10%).

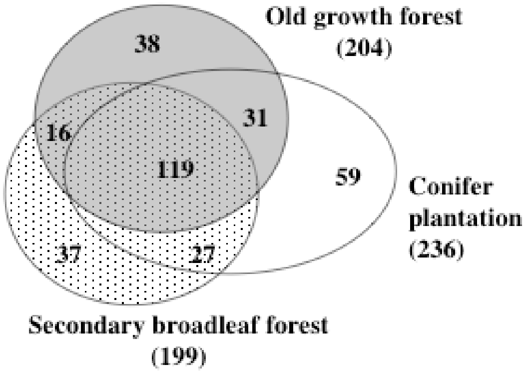

Fig. 3. Number of forest floor plant species in each forest type.

Table 1. Species groups classified with the distributional bias to the specific forest types.

Species group	No. of species	No. of weedy species (%)	Species
Old growth forest species	33	6 (18)	*Ainsliaea acerifolia* var. *subapoda*, *Pseudostellaria palibiniana*, *Salvia nipponica*, *Cynanchum magnificum*, *Viola eizanensis*, *Prenanthes acerifolia*
Secondary forest species	71	29 (41)	*Disporum smilacinum*, *Viola grypoceras*, *Hosta albo-marginata*, *Viola rossii*, *Luzula plumosa* var. *macrocarpa*, *Ixeris dentata*, *Carex lanceolata*, *Potentilla freyniana*
Plantation forest species	62	20 (32)	*Athyrium yokoscense*, *Oplismenus undulatifolius*, *Deparia conilii*, *Chloranthus serratus*, *Impatiens textori*, *Laportea bulbifera*, *Disporum sessile*, *Arachniodes borealis*
Others	158	39 (25)	
Common	34	7 (21)	*Carex sachalinensis* var. *alterniflora*, *Tricyrtis affinis*, *Elatostema umbellatum* var. *majus*, *Carex dolichostachya* var. *glaberrima*, *Arisaema serratum*, *Smilacina japonica*, *Cacalia farfaraefolia*, *Stellaria sessiliflora*
Infrequent species	124	32 (26)	*Caulophyllum robustum*, *Tulotis ussuriensis*, *Goodyera schlechtendaliana*, *Allium monanthum*, *Polygonatum involucratum*, *Chelidonium majus* var. *asiaticum*, *Scrophularia kakudensis*
Total	324	94 (29)	

Broadleaf (secondary and old-growth) and plantation forests were clearly distinguished by cluster analysis according to the forest floor plant species composition, although the difference between secondary forests and old-growth forests was not very distinct (Fig. 4). Broadleaf forests (secondary and old-growth forests) were also distinguished from plantation forests along axis 1 of the DCA ordination (Fig. 5). In addition, old-growth forests were distinguished from secondary forests along axis 2 (Fig. 5). According to the correlations between the DCA axis scores and forest age (Table 2), axis 2 was significantly positively correlated with forest age for both confer plantations and secondary forests. This is consistent with the placement of old-growth forests above secondary forests in the DCA ordination diagram (Fig. 2). For the plantation forests, the axis 1 scores were positively correlated with the proportion of plantation forest species and negatively correlated with the proportion of secondary forest species (Table 2). The axis 1 scores for secondary forests were negatively correlated with the proportion of secondary forest species (Table 2). The proportion of weed species was negatively correlated with axis 1 for secondary forests and axis 2 for plantation forests (Kendall's rank correlation, $p < 0.05$, Table 2).

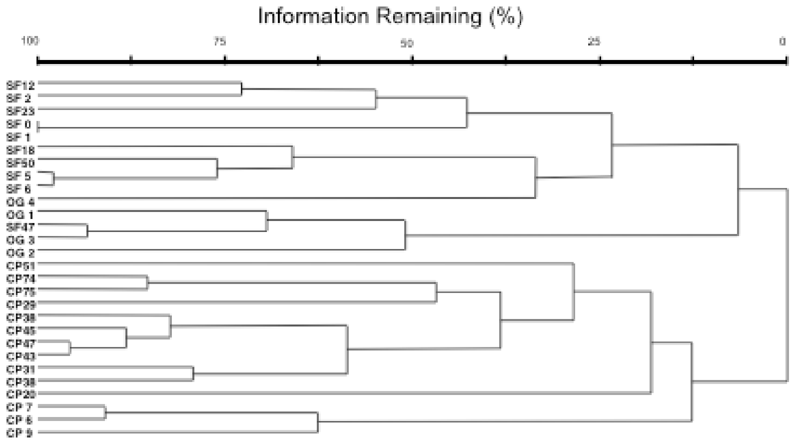

Fig. 4. Dendrogram showing the result of cluster analysis. Number in stand name indicates stand age.

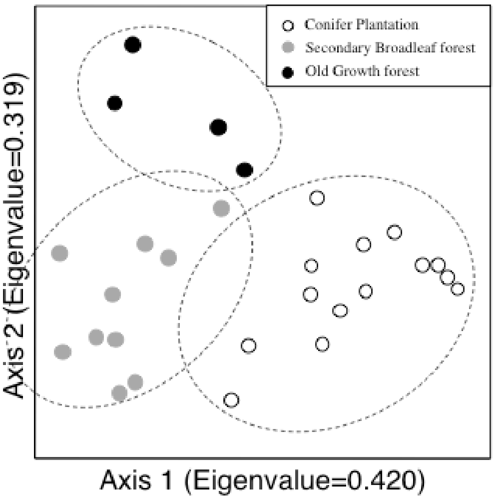

Fig. 5. Diagram of the results of detrended correspondence analysis (DCA). Each symbol indicates a stand.

Table 2. Correlation between the two axes of DCA and the forest age and the proportion of each species group (Kendall's rank correlation coefficient).

	Forest age	Proportion of old growth forest species	Proportion of secondary forest species	Proportion of plantation forest species	Proportion of weed species
Conifer plantation					
Axis 1	0.287	-0.022	-0.539**	0.473*	-0.275
Axis 2	0.729**	0.155	-0.407*	0.385□	-0.495*
Secondary broadleaf forest					
Axis 1	0.500□	0.389	-0.611*	0.222	-0.556*
Axis 2	0.556*	0.556*	-0.444	0.278	-0.389

*: $p < 0.05$, **: $p < 0.01$. †: marginally significant.

Ecological attributes of species in plantations and secondary forests

The proportion of weedy species was negatively correlated with stand age in both plantation and secondary forests (τb = –0.500, p = 0.061 for secondary forests; τb = –0.464, p = 0.021 for plantation forests; Fig. 6). The number of weedy species was highest approximately 5 years after clear-cutting in both secondary forests and plantation forests (Fig. 2). The proportion of secondary forest species was negatively correlated with stand age in plantation forests (τb = –0.420, p = 0.037; Fig. 6). The proportion of plantation forest species showed no significant correlation with stand age in either of the forest types (Fig. 6). The proportion of old-growth forest species showed a marginally positive correlation with stand age in secondary forests (τb = 0.444, p = 0.095; Fig. 6).

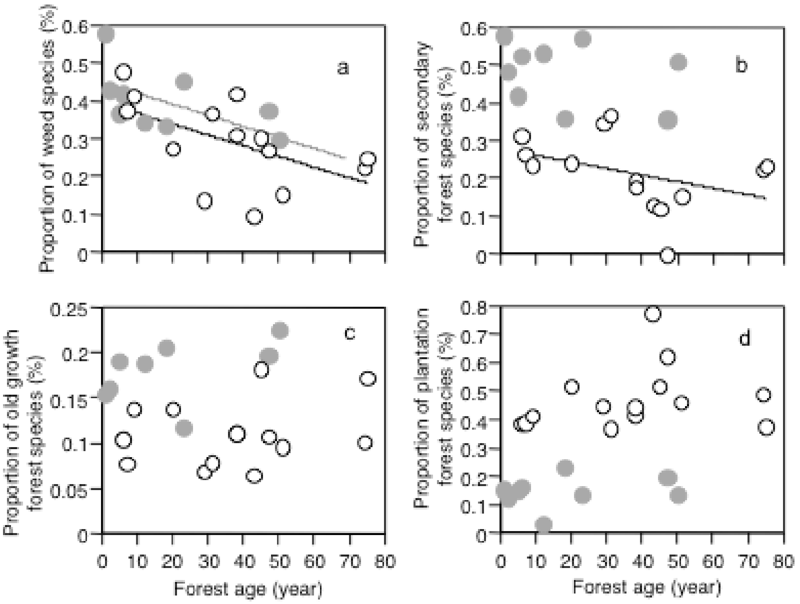

Fig. 6. Relationship between forest stand age and the proportion of four species types: (a) weed species, (b) secondary forest species, (c) old-growth forest species, and (d) plantation forest species.

Discussion

Although species richness differed only marginally between secondary and plantation forests along a chronosequence after clear-cutting and showed similar patterns of change along the chronosequence (Fig. 2), the conversion from secondary forests to plantation forests resulted in a distinctly different forest floor plant species composition (Figs. 4, 5). This difference is understandable because the conversion from deciduous broadleaf forest to evergreen conifer forest results in different microenvironments according to changes in canopy leaf composition and phenology (Ramovs and Roberts 2003). After canopy closure (ca. 10 years after clear-cutting), seasonal light, temperature, and moisture conditions are likely to be more temporally stable and spatially homogeneous in plantation forests than in secondary forests. Larger stem basal area in plantation forests relative to secondary forests (Fig. 1) may also contribute to the differences in forest floor microenvironments.

In both secondary forests and plantation forests, weeds accounted for a high percentage of species, suggesting the influence of severe disturbance; i.e., clear-cutting, in both forest types. The rather high percentage of weed species also found in old-growth forests may reflect the influence of large-scale disturbances, e.g., fire and grazing by horses and cattle, that frequently occurred in the past in this region (Suzuki 2002, Miyamoto and Sano 2007). The proportion of weed species decreased with stand age (time since disturbance) in both secondary and plantation forests (Fig. 6, Table 2). Colonization by a large number of weed species partly explained the high species diversity after clear-cutting (Fig. 2; Fahy and Gormally 1998, Bhuju and Ohsawa 1999, Nagaike 2000). Higher species richness in intensely managed stands has also been reported in many types of managed forest (Schoonmaker and McKee 1988, Brunet et al. 1996, Stapanian et al. 1998, Scherer et al. 2000).

Although the number and proportion of weed species decreased with stand age in both secondary and plantation forests, the results of DCA ordination and the relationships between the DCA axes and forest age suggest that the compositions of these forest types were not converging as stand age increased (Fig. 5). The proportion of secondary forest species in plantation forests decreased with stand age (Fig. 6). In contrast, the proportion of old-growth forest species did not change as stand age increased, even in secondary forests, suggesting that in the first 60 years post-clear-cutting in secondary that the abandonment of secondary coppice forests does not directly lead to the recovery of old-growth forest plant species (Ramovs and Roberts 2003). Thus, the preservation of the remaining old-growth forests is very important for the conservation of regional plant species diversity.

Relative to old-growth forests, both secondary forests and conifer plantations contributed substantially to local plant species diversity, although both contained large percentages of weed species (Fig. 3, Table 1). The plantation species included an abundance of ferns that may have taken advantage of the preferable environmental conditions of plantation forests (Table 1). Among the infrequent species, orchids were also found in plantation forests (Table 1). In contrast, most of the spring ephemerals such as *Erythronium japonicum* and *Anemone pseudo-altaica* were only found in deciduous broadleaf forests (secondary and old-growth forests). Plantation forests may contribute to local plant diversity, but cannot substitute for secondary and old-growth forests (Maeto et al. 2002, Inoue 2003).

To quantitatively evaluate the contribution of conifer plantations and secondary forests of different ages to the maintenance of local plant diversity, further understanding of the processes and mechanisms shaping species composition is necessary (Halpern 1989, Roberts and Gilliam 1995). In addition to the occurrence bias of forest floor plant species, information on the functional types (e.g., growth form, dispersal type, pollination type; Smith et al. 1997) of the component species will be important in understanding these processes and mechanisms.

References

Brunet J, Falkengren-Grerup U, Tyler G (1996) Herb layer vegetation of south Swedish beech and oak forests — effects of management and soil acidity during one decade. For Ecol Manage 88: 259–272

Bhuju D R, Ohsawa M (1999) Species dynamics and colonization patterns in an abandoned forest in an urban landscape. Ecol Res 14: 139–153

Environmental Agency of Japan (2000) Threatened wildlife of Japan—Red Data Book. Vascular plants. 2nd ed. Japan Wildlife Research Center, Tokyo.

Fahy O, Gormally M (1998) A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. For Ecol Manage 110: 263–273

Fukamachi K, Iida S, Nakashizuka T (1996) Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. Pl Ecol 124: 107–114

Halpern C B (1989) Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70: 704–720

Hunter Jr, M L ed (1999) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge

Iida S, Nakashizuka T (1995) Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan. For Ecol Manage 73: 197–210

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomol. Sci. 6: 151–163

Ito S, Nakagawa M, Buckley G P, Nogami K (2003) Species richness in sugi (Cryptomeria japonica D. Don) plantations in southeastern Kyushu, Japan: The effects of stand type and age on understory trees and shrubs. J For Res 8: 49–57

Ito S, Nakayama R, Buckley G P (2004) Effects of previous land-use on plant species diversity in semi-natural and plantation forests in a warm-temperate region in southeastern Kyushu, Japan. For Ecol Manage196: 213–225

Kitamura S, Murata G (1980) Colored illustrations of herbaceous plants of Japan (Choripetalae). Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Murata G, Hori M (1978) Colored illustrations of herbaceous plants of Japan (Sympetalae).

Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Murata G, Koyama T (1974) Colored illustrations of herbaceous plants of Japan (Monocotyledoneae). Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Okamoto S (1959) Colored illustrations of trees and shrubs of Japan. Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitazawa T, Ohsawa M (2002) Patterns of species diversity in rural herbaceous communities under different management regimes, Chiba, central Japan. Biol Conserv 104: 239–249

Lindenmayer D B, Franklin J F (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C.

Maeto K, Sato S, Miyata H (2002) Species diversity of longicorn beetles in humid warm-temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. Biodiv Conserv 11: 1919–1937.

Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashizuka T (1992) Community structure of a species rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98: 97–111

McCune B, Mefford M J (1999) PC-ORD: multivariate analysis of ecological data; version 4 [computer program]. MjM Software Design, Gleneden Beach, Oregon.

Miyamoto A, Sano M (2007) The influence of change in forest resource use on forest landscapes in Abukuma mountainous area in the past 90 years. this volume.

Mizoguchi Y, Morisawa T, Ohtani Y (2002) Climate in Ogawa Forest Reserve. Ecol studies 158: 11–18.

Nagaike T (2002) Differences in plant species diversity between conifer (Larix kaempferi) plantations and broad-leaved (*Quercus crispula*) secondary forests in central Japan. For Ecol Manage 168 (1): 111–123

Nagaike T, Hayashi A, Abe M, Arai N (2003) Differences in plant species diversity in *Larix kaempferi* plantations of different ages in central Japan. For Ecol Manage 183: 177–193

Nagaike T, Kamitani T, Nakashizuka T (2005) Effects of different forest management systems on plant species diversity in a *Fagus crenata* forested landscape of central Japan. Can J For Res 35: 2832–2841

Nagaike T, Hayashi A, Kubo M, Abe M, Arai N (2006) Plant species diversity in a managed forest landscape composed of *Larix kaempferi* plantations and abandoned coppice forests in central Japan. For Sci 52 (3): 324–332

Numata M, Yoshizawa N eds (2002) Weed flora of Japan. Zenkoku Noson Kyoiku Kyoukai, Tokyo. [In Japanese.]

Ramovs B V, Roberts M R (2003) Understory vegetation and environment responses to tillage, forest harvesting and conifer plantation management. Ecol Appl 13: 1682–1700

Roberts M R, Gilliam F S (1995) Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol Appl 5: 969–977

SAS Institute (2001) JMP user's guide. Version 5.0.1J, SAS Institute, Cary, North Carolina, USA.

Scherer G, Zabowski D, Java B, Everett R (2000) Timber harvesting residue treatment. Part II. Understory vegetation response. For Ecol Manage 126: 35–50

Scherer-Lorenzen M, Körner Ch, E.-D Schulze eds (2005) Forest Diversity and Function: Temperate and Boreal Systems, Springer Verlag, Berlin.

Schoonmaker P, McKee A (1988) Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. For Sci 34: 960–979

Smith T M , Shugart H H & Woodward F I eds (1997) Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge.

Stapanian M A, Sundberg S D, Baumgardner G A, Liston A (1998) Alien plant species composition and associations with anthropogenic disturbance in North American forests. Pl Ecol 139: 49–62

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. Ecol Studies 158: 25–41

Tanaka H, Shibata M, Masaki T, Iida S, Niiyama K, Abe S, Kominami Y, Nakashizuka T (2007) Comparative demography of three coexisting maples in gaps and under a closed canopy. J Veg Sci, in press

Understory Herbaceous Species Composition Depends on Tree Canopy Dynamics in an Old-Growth Forest, Ogawa Forest Reserve, Northern Japan

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Introduction

Forest biota are adapted to and maintained by natural disturbance within the forest (e.g., Attiwill 1994). Therefore, it is often considered that one option for ecologically sustainable forest management is to emulate the intensity, frequency, and period of natural disturbance (e.g., Seymour and Hunter 1999; Lindenmayer and Franklin 2002; Mitchell et al. 2002; Crow and Perera 2004). Studies of the effects of natural disturbance in maintaining species diversity have increased in frequency (e.g., Nakashizuka 2001). In particular, canopy gap creation, a major source of natural disturbance in forest canopies and the focal point for consequent natural regeneration of trees, has been studied in relation to gap size (e.g., Abe et al. 1995; Vandenberghe et al. 2006) and microsites after gap creation (e.g., Carlton and Bazzaz 1998). However, most studies have only examined the responses of canopy dynamics of tall tree species and few have applied the results to forest management (e.g., Emborg et al. 2000).

The major source of natural disturbance in Ogawa Forest Reserve in northern Japan is canopy gap creation (Nakashizuka 2002). Therefore, when considering forest management practices to match the intensity, frequency, and period of canopy dynamics in the region, one should consider the understory species involved in the canopy dynamics. Species classification according to canopy dynamics has mainly focused on shade tolerance (e.g., Abe et al. 1995). However, to emulate natural disturbance in a target region forest management should focus on several species traits, not only shade-tolerance but also disturbance tolerance, because logging always involves physical disturbance to forest dynamics. Few studies have focused on species with tolerance to disturbance. Hence, in this study we evaluated species canopy dynamics in an old-growth forest in the Ogawa Forest Reserve with special reference to specific habitat types of species in the landscape.

Study site and methods

Study site

This study was conducted in the Ogawa Forest Reserve and the surrounding forested landscape, in Ibaraki Prefecture, northern Japan. The landscape consists mainly of deciduous broadleaf old-growth forests, coppice forests, and coniferous plantations. We conducted vegetation surveys in these three major forest types. For the deciduous broadleaf old-growth forest (hereafter, “old-growth”), we studied the Ogawa Forest Reserve and the reserved belt that maintains features of an old-growth forest (e.g., well-developed stand structure and large maximum stem size). In the coppice forest (hereafter, “coppice forest’), some stands were actively managed for fuel and firewood, but some, in particular stands 30 or more years old, had been abandoned. *Cryptomeria japonica*, an evergreen conifer and important commercial timber species in Japan, is planted in the coniferous plantations. The plantation stands sampled for this study (hereafter, “plantation”) had a wide age range and management intensity, indicating the diverse management aims and motivations of forest owners or managers. For example, weeding and thinning were carried out on schedule in some stands, while other stands were almost abandoned, without any management occurring after planting.

Plant survey

A plot (200 × 300 m) was established and divided into a 10 × 10-m grid in the Ogawa Forest Reserve. A 2 × 2-m quadrat was set up at the intersection of each grid (651 quadrats in total). Beside the Ogawa Forest Reserve, 43 stands (old-growth: 4; coppice forest: 13; and plantation: 26) were examined. A belt 10-m wide and 100-m long was established in each stand. To exclude the effects of different management types in neighboring stands, study plots were set up at the center of each stand, where possible. The belt-shaped plots were designed to cover topographic variations in each stand and thus minimize variation in natural conditions (e.g., slope aspect and soil type) among the stands (Iida & Nakashizuka 1995; Fukamachi et al. 1996; Nagaike et al. 2005). Basically, each coppice forest and plantation, except for those less than 10 years old, had not been managed for at least 5 years. Coppice forest and plantation stand age ranged from 1 to 77 and from 4 to 76 years, respectively. Each belt-shaped plot was divided into 5 × 5-m grids; a 1 × 1-m quadrat was placed at the corner of every 5 × 5-m grid square. To analyze the different quadrat sizes (i.e., 2 × 2 m in Ogawa Forest Reserve and 1 × 1 m in belt-shaped plots), we transformed the data of four 1 × 1 m plots into 2 × 2 m in the belt-shaped plots.

The total number of quadrats investigated was 1059 (old-growth: 691; coppice forest: 122; and plantation: 246). All herbaceous species, including ferns, less than 2-m tall occurring in each 1 × 1-m quadrat were recorded. The survey was carried out twice (1991 and 2001) in the Reserve and once from 2001 to 2004 in the other stands.

Canopy dynamics

In the Ogawa Forest Reserve plot, canopy height above each quadrat (for 651 quadrats) was measured with a measurement pole in 1989 and 2001. We classified the canopy height in each survey into three categories: “gap”: $\leq$10 m; “development”: <10 m to $\leq$ 15 m; and “closed”: >15 m. The canopy dynamics are shown comparing the height of the canopy in 1989 and 2001.

Analysis

Frequency of species occurrence was summed for each forest type (old-growth, coppice forest, and plantation). To delineate the habitat types for each species, the occurrence biases of species found in particular habitats were analyzed using chi-square tests, based on procedures in Nagaike et al. (2003, 2005). All species were divided into three habitat groups, according to whether they occurred disproportionately in the old-growth forest (Old-growth forest species), coppice forest (Coppice forest species), plantation (Plantation species), or were without bias to a particular forest type or too infrequent for statistical analysis (Other species). We also examined whether a species is considered to be a weed (Numata & Yoshizawa 2002).

Results and discussion

We recorded a total of 353 species: 208 in old-growth forest, 206 in coppice forest, and 246 in the plantation. Of these 353 species, Other species (249 species, e.g., *Blechnum niponicum*, *Carex fernaldiana*, and *Smilax sieboldii*) made up the highest proportion, followed by Old-growth forest species (57 species, e.g., *Ainsliaea acerifolia* var. *subapoda*, *Pertya robusta*, and *Pseudostellaria palibiniana*). Coppice forest species and Plantation species accounted for 23 (e.g., *Carex lanceolata*, *Viola grypoceras*, and *Ixeridium dentatum*) and 24 (e.g., *Athyrium yokoscense*, *Deparia conilii*, and *Bidens frondosa*) species, respectively. The ratio of weed species to the number of species of each forest type was highest for Coppice forest (52%), followed by Plantation (38%), and Old-growth forest (16%).

In old-growth forest, "closed" canopy increased in frequency from 569 quadrats in 1989 to 596 quadrats in 2001. Consequently, both "development" and "gap" canopy types decreased in frequency (from 41 to 33 "development" quadrats and from 41 to 22 "gap" quadrats). In quadrats where "gap" changed to "closed" (i.e., gap closure) from 1989 to 2001, newly-occurring species were mainly Old-growth forest species (eight of 14 species). Lost species in the quadrats constituted 17 species, mostly Old-growth forest species (eight species). In quadrats where "closed" changed to "gap" (i.e., canopy gap creation), there were 14 newly-occurring species, of which eight were Old-growth forest species (Table 1). Four of the eight lost species were Old-growth forest species.

Fewer weed species, which were expected to be tolerant to severe disturbance, were found in old-growth forest, and more were found in coppice forest and plantations. This indicates that coppice forest and plantations suffered more severe disturbance than old-growth forest. Species that were new or that had disappeared from gap-created and canopy-closure quadrats were mainly Old-growth forest species. Therefore, we concluded that species adapted to old-growth forest canopy dynamics were native to old-growth forest, but differed from species which occurred after severe disturbance (i.e., Coppice forest and Plantation species). Consequently, we need to establish forest management procedures that maintain the diversity of Old-growth forest understory species.

References

Abe S, Masaki T, Nakashizuka T (1995) Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. Vegetatio 120: 21-32.

Attiwill PM (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. For Ecol Manage 63: 247-300.

Carlton GC, Bazzaz FA (1998) Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecol Monog 68: 99-120.

Crow TR, Perera AH (2004) Emulating natural landscape disturbance in forest management – an introduction. Landscape Ecol 19: 231-233.

Emborg J, Christensen M, Heilmann-Clausen J (2000) The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. For Ecol Manage 126: 173-189.

Fukamachi K, Iida S, Nakashizuka T (1996) Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. Vegetatio 124: 107-114.

Iida S, Nakashizuka T (1995) Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan. For Ecol Manage 73: 197-210.

Mitchell RJ, Palik BJ, Hunter Jr. ML (2002) Natural disturbance as a guide to Silviculture. For Ecol Manage 155:

315-317.
Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity – A comprehensive multiscaled approach. Island Press, Washington.
Nakashizuka T (2001) Species coexistence in temperate, mixed deciduous forests. TREE 16: 205-210.
Nakashizuka T (2002) Disturbance regimes. In: Nakashizuka T, Matsumoto Y. (eds) Diversity and interaction in a temperate forest community. Springer, Tokyo.
Nagaike T, Kamitani T, Nakashizuka T (2003) Plant species diversity in abandoned coppice forests in a temperate deciduous forest area of central Japan. Plant Ecol 166: 63-74.
Nagaike T, Kamitani T, Nakashizuka T (2005) Effects of different forest management systems on plant species diversity in a Fagus crenata forested landscape of central Japan. Can J For Res 35: 2832-2840.
Numata M, Yoshizawa N. (eds.) (2002) Weed flora of Japan. Zenkoku Noson Kyoiku Kyoukai, Tokyo (in Japanese).
Seymour RS, Hunter Jr. ML (1999) Principles of ecological forestry. In: Hunter Jr. ML (ed) Maintaining biodiversiry in forest ecosystems. Cambridge University Press, Cambridge.
Vandenberghe C, Frelechoux F, Gadallah F, Buttler A (2006) Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter? J Veg Sci 17: 481-488.

Table 1. The responses of plant species to changes in canopy dynamics in the Ogawa Forest Reserve

	From “gap” to close”		From “close” to “gap”	
Species types	Newly occurred species	Disappeared species	Newly occurred species	Disappeared species
Old-growth forest species	8	8	8	4
Coppice forest species	1		1	1
Plantation species		3	3	
Others	5	6	3	3
Total	14	17	14	8

Effects of Forestry Activities on Insect Biodiversity in Abukuma, Kanto Region, Temperate Japan

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Introduction

Forestry activities affect animal biodiversity in various ways and degrees by modifying forests and their surroundings that are inhabited by such organisms. As animals perform various functions in the forest ecosystem, forestry practices should be selected so as to retain, or at least not produce severe deterioration of, their biodiversity. However, it is often unclear how different animal groups respond to particular forestry practices in terms of their biodiversity.

In the Abukuma area, northern Kanto, temperate Japan, there have typically been two types of forestry practice: 1) small scale clear-cutting of deciduous broad-leaved trees, and 2) conversion of broad-leaved stands into coniferous plantations of Japanese cedar (*Cryptomeria japonica*) and hinoki cypress (*Chamaecyparis obtusa*). In order to learn how these practices have affected animal biodiversity, we investigated species richness and assemblage of insects in differently managed stands. Because insects not only have the greatest biodiversity among animals (e.g. Grimaldi and Engel 2005), but perform a wide range of ecosystem functions (Weisser and Siemann 2004), we consider them to be some of the best target animals for evaluation of effects of forestry activities on biodiversity.

In this report, we first show how species richness of insects changes with the age of regeneration stands after clear-cutting of broad-leaved trees, with special reference to differential responses among insect taxa (cf. Makino et al. 2006). Besides insects, some mites (Acari) were also monitored. Secondly, we compare insect assemblage as well as species richness between broad-leaved and conifer stands of various ages, focusing on longhorn beetles (Coleoptera, Cerambycidae) (cf. Makino et al. 2007). Longhorn beetles are useful indicators of forest conditions because they are mainly xylophagous in larval stages and frequently visit flowers as adults, thus are expected to be sensitive to changes in forest conditions. Finally, we briefly discuss effects of forestry on insect biodiversity in this region.

Materials & Methods

Study areas

This study was conducted in 2 areas, Ogawa and Satomi, Ibaraki Prefecture, central Japan. Both areas had plantations of *Cryptomeria japonica* and *Chamaecyparis obtusa*, though the percentage of plantation areas was much larger in Satomi than in Ogawa (94% vs. 47% of total forested area). Ogawa is located at the southern edge of the Abukuma Mountains in Kitaibaraki (approximately 36° 56' N, 140° 35' E, 580–800 m a.s.l.). In deciduous broad-leaved forests in the area, the dominant large trees are *Quercus serrata*, *Quercus mongolica* and *Fagus crenata*. Broad-leaved stands have repeatedly been clear-cut on a small scale to collect bed logs for mushroom culture, and this continues in the present. In addition, the number of conifer plantations converted from broad-leaved stands greatly increased after the Second World War. These practices have resulted in a mosaic-like landscape composed of secondary broad-leaved stands and conifer plantations of different ages. We selected 10 plots in broad-leaved stands to form a chronosequence from 1 to over 100 years after clear-cutting (Table 1). All plots were located within an approximately 30 km^2 area. Satomi (approximately 36° 50' N, 140° 34' E, 700-800 m a.s.l.) is about 10 km southwest of Ogawa area. We selected 8 plots of Japanese cedar plantations in an approximately 10 km^2 area in Satomi. The conifer plots also formed a chronosequence from 1 to 76 years after plantation.

Table 1. Study plots and the number of longicorn species collected in Ogawa (broad-leaved plots) and Satomi (conifer plots) (modified from Makino et al. 2007).

Area	Plot code	Age (year)	Area (ha)
Ogawa	O1	1	3
	O4	4	5
	O12	12	4
	O24	24	24
	O51	51	10
	O54	54	14
	O71	71	19
	O128	>100	98
	O174	>100	11
	O178	>100	10
Satomi	S3	3	4
	S7	7	6
	S9	9	5
	S20	20	5
	S29	29	14
	S31	31	12
	S75	75	3
	S76	76	3

Monitoring methods and target animals

Target animals were selected from a variety of taxa representing different ecological functions. All insects and mites were collected in the 10 broad-leaved plots in Ogawa in 2002; for longicorn beetles, additional collection was made in the 8 conifer plots in Satomi in 2003. Targets and collection methods are as follows. Insect traps, when used, were placed well inside the study plots to avoid possible edge effects.

Butterflies: One-hour transect counts were made twice a month from April to October between 9:00 and 15:00 (cf. Inoue, 2003). Species and number of butterflies sighted were recorded at each census. **Moths**: A single portable light trap (Okochi, 2002) was left overnight at each of the monitoring sites twice in August, and moths trapped inside were collected the following morning. All plots were censused on the same nights. **Ground beetles**: Pitfall traps were used, made from transparent plastic bottles (77 mm diameter, 158 mm height) with three small holes (about 5 mm in diameter) in the middle for drainage of rainwater. In each plot, ten pitfall traps were aligned in three parallel lines, with a distance of about 10 m between traps. Trapped insects were collected every two weeks from April to November. **Tube-renting bees and wasps**: Nesting traps, which were made of 16 bamboo stalks (approximately 8 to 16 mm in diameter) and four reeds (6 mm), were used. At each plot, nine traps were tied to tree trunks or wooden posts (where no substrate trees are available) at 1.5 m above the ground in April, and removed in November. Immatures found in the traps were reared until eclosion for identification. **Longicorn beetles, hoverflies and fruit flies**: Collection was made with Malaise traps (Golden Owl Publishers, 180 cm long, 120 cm wide, 200 cm high). Five traps were set in April at each plot at intervals of 10 m. Collection of trapped insects was made every two weeks as in pitfall traps. **Ants**: Litter sampling was made between July and August along a 100 m (or 200 m in a few sites) transect line in each plot, and ants were hand-sorted. Additionally, pitfall traps (disposable plastic cups) were set along the same line at 10 m intervals for a maximum duration of three days. **Oribatid mites and collembola**: A cylindrical core (25 cm^2 x 5 cm high) of soil was removed from eight divisions (4 x 2 m) of a quadrat (8 x 8 m) in April, August, and November; soil arthropods were later extracted with Tullgren funnels (cf. Hasegawa et al., 2004). **Mites associated with mushrooms**: Mushroom fruiting bodies were sampled in each plot once a month from April to November. Mites were hand-sorted from mushrooms and identified under a microscope.

Forest characteristics

In order to learn how forest characteristics affect insect biodiversity, we made plant censuses in the above plots. A 100 m line transect was established at each plot from September 2000 to October 2003. All trees and vines of at least 2 m in height and at least 5 cm in DBH were counted and their GBH (girth at breast height) was measured in a total of forty 5 x 5 m quadrats along both sides of the 100 m transect line mentioned above; the frequency of trees smaller than 5 cm in DBH in the 40 quadrats was also censused. Forest floor vegetation with a height of less than 2 m (forest floor plants) was censused following the Braun-Blanquet method for a 1 x 1 m subquadrat in each 5 x 5 m quadrat.

Analyses of longicorn assemblages

Canonical Correspondence Analysis (CCA) of longicorn beetles was performed with Canoco for Windows, Version 4.5 (ter Braak and Smilauer 2002). Only those species with a total count of at least 3 individuals were used in CCA. As environmental variables, we selected the following plant community indices: species richness of plants for 3 size classes (trees with DBH ≥ 5 cm, trees with DBH <5 cm, and forest floor plants), the density of trees with DBH ≥ 5 cm and maximum and average diameter of tress at breast height. In this analysis, the scores of the 1st and 2nd axes in Detrended Correspondence Analysis (DCA) for the plant community group ordination for the 3 size classes were also used, in order to investigate the effects of plant species compositions on communities of longicorns. In DCA of plants, species with at least 3 individuals in total were used, and population data were transformed using logarithmic transformation, log10(x+1). In DCA of trees with DBH ≥ 5 cm, the 1-year-old site (O1) and the 4-years-old site (O4) were excluded because there were no trees of this size class. Likewise, in the DCA of forest floor plants, the 1-year-old site was excluded. Population data were transformed using logarithmic transformation, log10(x+1). Environmental variables were tested using forward selection of variables with Monte Carlo test using 499 unrestricted permutations ($P < 0.05$).

Results

Insect species richness in relation to the age of broad-leaved stands

Species richness of insects in broad-leaved stands in Ogawa is shown in Figure 1, in which the number of species is represented as a proportional rather than absolute value. The response of species richness to the stand age was classified into the following three types. Type I (butterflies, hoverflies, fruit flies, tube-renting bees and wasps, and longicorn beetles): species richness was high in grasslands or in early stages of succession, while much lower in older forests. Type II (mites associated with mushrooms): species richness was low in early stages of succession, becoming greater as forests mature. The number of mushroom species showed a similar response to the mite. Type III (moths, ants, ground beetles, oribatid mites, and collembolas): species richness did not greatly vary with forest age. However, the taxa showing Type III response often had different community compositions among the plots (for soil animals, see Hasegawa et al. 2004). Therefore, uniform species richness did not mean a homogeneous species composition among ages of the stands.

Difference in longicorn assemblage between broad-leaved and conifer stands

A total of 106 longicorn species was collected in Ogawa and Satomi. The average number of species was larger in broad-leaved plots (35.8 SD7.7) in Ogawa than in coniferous ones (22.9 SD8.7) in Satomi (ANOVA, P=0.004). Both in Ogawa and Satomi, species richness was larger in young than in older stands (Fig. 1).

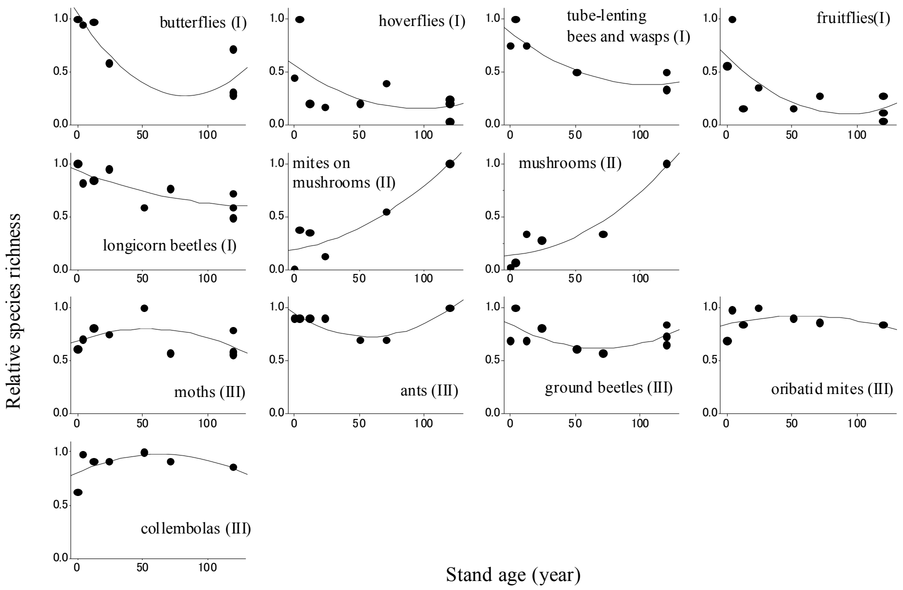

Fig. 1 Relationship between the species richness and the age of regeneration stands after clear-cutting in insects and other organisms in Ogawa, Abukuma area. The notation I, II, or III in parentheses stands for the type of response shown by the particular taxon. The species richness decreases with stand age in Type I, increases in Type II, and does not greatly change in Type III. Lines are quadratic polynomial approximations. Modified from Makino et al. (2006).

The CCA ordination divided the 18 plots into three groups (Fig. 2), which correspond to the following three stand types: initial stage stands, broad-leaved stands, and conifer stands. Species richness was largest in initial stage stands, followed by broad-leaved, and smallest in confer stands; the difference was significant among the three types (ANOVA, P<<0.001) as well as between any pair (corrected for multiple comparison with Bonferroni adjustment).

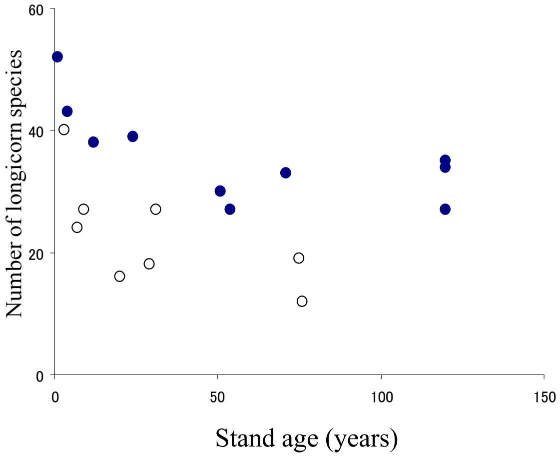

Fig. 2 The number of longicorn species collected with Malaise traps in stands of different ages. Solid and open circles stand for broad-leaved stands and conifer (*Cryptomeria japonica*) plantations, respectively.

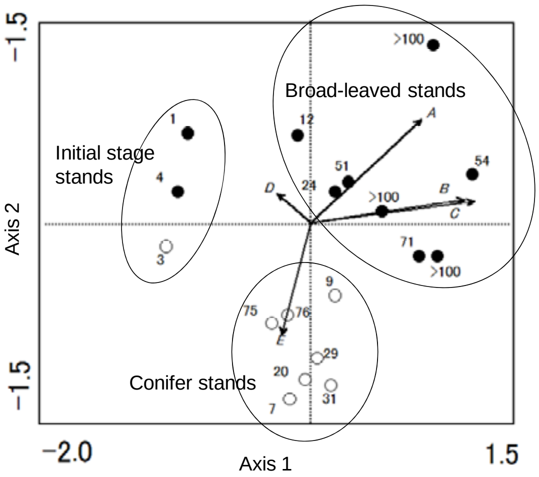

Fig. 3 Ordination of longicorn assemblages by canonical correspondence analysis (CCA). Three forest types are identified. Solid and open circles are as in Fig. 2, and figures show stand ages. Arrows with suffix A to E show variables of forest characteristics, which were significantly related with the division among the three forest groups. See text for more explanation. Modified from Makino et al. (2007).

The CCA analysis selected the following five variables of forest characteristics that are significantly related (P< 0.05) with longicorn species compositions: scores of DCA 2nd axis of forest floor plants (arrow

A in Fig. 3), the maximal DBH of trees (arrow B), the number of species of trees with DBH ≥ 5 cm (arrow C), species richness of forest floor plants (arrow D), and DCA 1st axis of trees with DBH ≥ 5 cm (arrow E). The arrows B and C, both representing the maturation process of forest growth, were nearly parallel to the 1st axis of the CCA diagram (Fig. 3), and explained the discrimination of longicorn species composition between the two older forest types (conifer stands and broad-leaved stands) and the young one (initiation plots). In contrast, the arrows A and E had more vertical directions, and explained the discrimination between broad-leaved and conifer stands. The arrow D representing the species richness of forest floor plants was short, indicating that its effect on the longicorn species composition is marginal.

Discussion

Effects of stand age on insect biodiversity

We showed that the effect of stand age on species richness was not uniform among the taxa monitored. This may be partly due to differential dependence on herbaceous plants. The taxa showing the Type I response, for example, are herbivores during the larval stage, and/or largely depend on flowers for carbohydrates as adults. Many butterfly species live in grasslands and utilize herbaceous plants as hosts. Even species whose larval hosts are trees visit herbaceous plants for nectar as adults (Inoue, 2003). Tube renting bees and wasps probably collect nectar and pollen, or hunt prey (for example, lepidopterous larvae, spiders, and grasshoppers) respectively, in grasslands or in very young and open stands. Although most longicorn beetles feed on dead trees during the larval period, adult insects frequently visit flowers. Then, for taxa showing Type I response, abundance of flowers may be an important factor that contributes to the high species richness observed in plots of early stages of succession. In contrast, those organisms which showed Type II or III responses (mites, soil animals, etc.: Fig. 1) do not seem to require or depend on as abundant a flower resource as do the Type I taxa.

Whatever the underlying mechanisms are, the different responses to the stand age among the taxa indicate that combinations of stands of various ages, or heterogeneously arranged stands, contribute to the maintenance of insect diversity at the landscape level. In Abukuma area, the traditional forestry utilizing regeneration stands by repeating a small-scale clear-cutting has produced open, grassland-like stands as well as middle-aged stands on the one hand, while retaining old forests on the other. This seems to have generally been giving a positive effect on insect diversity.

Effects of conifer plantation on longicorn diversity

The conifer stands, which were monocultures of Japanese cedars, had much smaller numbers of longicorn species than similar-aged broad-leaved stands, except for young plantations (Figs. 3, 4). Probably, the Japanese cedar is not an attractive host plant for longicorns. Kojima and Nakamura (1986) present host records of 468 Japanese longicorn species, of which 30 (6%) feed on (or emerge from) Japanese cedar. However, only two species are recorded as specialists of Japanese cedar or related conifers: the other species have wider host ranges including broad-leaved trees (Kojima and Nakamura 1986). This suggests that a great majority of Japanese longicorn species can live without Japanese cedar, which dominates forested areas in many parts of Japan. On the contrary, a significant decrease in broad-leaved forests and increase in cedar plantations may lead to impoverishment of longicorn faunas, because most species simply have hosts other than Japanese cedar.

An extensive conifer plantation may lead not only to impoverishment of longicorn diversity but to degradation of ecosystem functions that they possibly perform in pollination or in decomposition of dead trees. This is because longicorns frequently visit flowers as adults for pollen and/or nectar feeding, and they principally feed on dead or weakened trees as larvae thus facilitating decomposition by fungi or microorganisms. We urgently need to study the nature and magnitude of conifer plantation on ecosystem functions not only of longicorn beetles but insects in general.

References

Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, New York

Hasegawa M, Fukuyama K, Makino S, Okochi I, Goto H, Mizoguchi T, Sakata T, Tanaka H. (2004) Collembolan and oribatid mites community dynamics with the secondary succession of deciduous forests in Japan. Abstracts of XXII International Congress of Entomology

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomological Science, 6, 151-163.

Kojima K, Nakamura S (1986) Host tree records of Japanese longicorn beetles. Hiba-Kagaku Kyoiku Shinkosha, Shobara

Makino S, Goto H, Inoue T, Sueyoshi M, Okabe K, Hasegawa M, Hamaguchi, K, Tanaka H, and Okochi I. (2006) The monitoring of insects to maintain biodiversity in Ogawa Forest Reserve. Environmental Monitoring and Assessment, 120: 477-485

Makino S, Goto H, Inoue T, Hasegawa M, Okabe K, Tanaka H, Inoue, T, Okochi I. (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of Cryptomeria japonica (Taxodiaceae) in central Japan. Ecological Research, 22: 372-381

Okochi I (2002) A new portable light trap for moth collection. Bulletin of Forestry and Forest Products Research Institute, 1: 231-234

ter Braak CJF, Smilauer P (2002) CANOCO Reference Manual and Canodraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca

Weisser WW, Siemann E (2004) Insects and Ecosystem Function. Springer, Berlin

Coexistence of Tree Species Based on Structural Diversity

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Introduction

Structural characteristics of woody plants, such as plant height, leaf size, and biomass allocation to the aerial parts, are quite variable even among the species in a single community. Some structural variations that are linked to specific functions can be the basis for functional trade-offs and can therefore provide a chance for stable coexistence of plant species, which share many of the resources they consume (Westoby et al. 2002). Since the late 1980s, much effort has been made to elucidate the contribution of structural diversity to the stable coexistence of tree species. These studies have revealed that structural diversity contributes to stable coexistence in various ways. For example, the difference between structures that minimize biomass loss and structures that offer rapid growth is essential for niche differentiation along a spatial light gradient (Walters et al. 1993; Kitajima 1994). Another structural variation related to crown structure and trunk thickness is important in terms of the different strategies adopted by understory shrubs and canopy trees (Aiba and Kohyama 1997; Kohyama et al. 2003). However, past studies have had several weak points, and some critical questions remain unsolved. First, few of these studies have examined the potential for coexistence based on structural variations among ecologically or taxonomically related species, for which competitive exclusion is likely to operate. Second, differences in strategy at the sapling stage have been undervalued. In addition, phylogenetic constraints have rarely been considered in previous studies, even though these constraints could dramatically influence the results (Felsenstein 1985). Given these problems, we attempted to answer two questions: (i) Does the structural diversity of plant body lead to functional trade-offs and stable coexistence, even in taxonomically related late-successional species? (ii) How do structural variations in saplings, and especially variations in crown architecture (Kohyama 1987), contribute to stable coexistence? To do so, we focused on late-successional species in a Bornean rain forest with reference to their molecular phylogeny.

Materials and Methods

The study was conducted at Lambir Hills National Park, Sarawak, Malaysia (4°2′ N, 113°50′ E; 150 m a.s.l.). In the analysis focused on dipterocarp species, we measured the following structural traits: root mass, trunk mass, support-tissue mass, total leaf area, individual leaf area, crown projection area, plant height, and diameter at ground level. For non-dipterocarp species, we measured the same traits except for root mass. For the dipterocarp species, we also recorded the maximum net photosynthetic rates ($A_{\max}$) of saplings under the closed canopy and the wood density of mature trees. $A_{\max}$ was measured in the field in November 2003 and in March 2004 using a portable infrared gas analyzer (LI6400; LI-COR Inc., Lincoln, Nebraska, USA). The wood density of mature trees was obtained from the research literature on tropical timber (PROSEA 1994; Sudou 1970).

For 11 relatively abundant dipterocarp species, we analyzed their demographics using 5×5 m quadrats (248 in total) distributed in a regular matrix that covered 12 ha throughout two permanent sample plots in the park. In June 2003, all juvenile dipterocarps shorter than 2 m that occurred in the quadrats were numbered, their species was recorded, and their height was measured. In June 2004 (1 year after the first census), the quadrats were re-censused, and the status (i.e., living or dead) of all tagged individuals was verified.

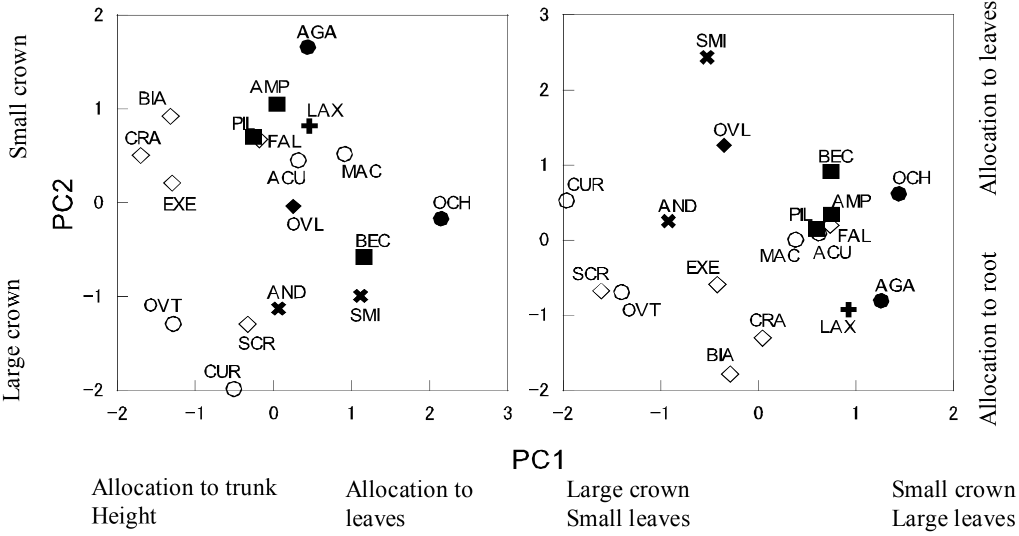
Allometric relationships among the parts of the individual plants were used to describe the structural characteristics of each species at two ontogenetic stages (i.e., with total dry masses of 5 and 30 g). Principal-components analysis (PCA) was performed on the log-transformed estimated values to clarify the constellations of traits by uniting parameters into principal components (PCs). Logistic regression and model selection using the stepwise Akaike information criterion were used to predict the survival rate of juveniles under certain conditions. Using the selected model, survival rates under a canopy openness of 5% at the two ontogenetic stages were estimated. Correlations between structural characteristics and indices of shade tolerance were calculated using the Pearson correlation coefficient for the raw data and, if required, for phylogenetically independent contrasts (Felsenstein 1985).

Results

Sapling structure and regeneration strategy in 18 Shorea species

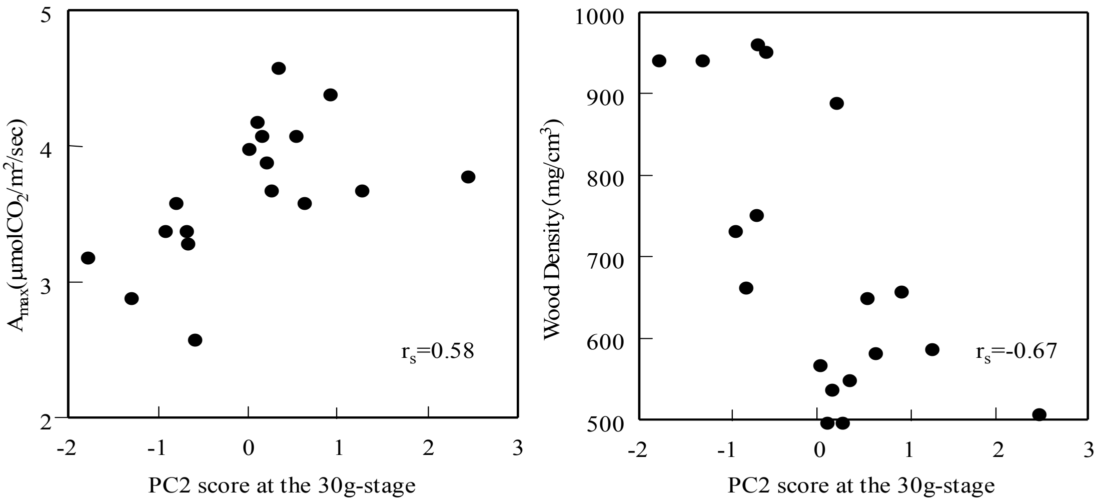
We tested whether the relationship between juvenile tree structure and function is robust among 18 functionally and taxonomically similar sympatric species of genus Shorea in a tropical rainforest in Borneo. The structural variation in saplings of the genus Shorea was as large as that found in sets of species with much more diverse origins. PCA showed that both crown architecture and the biomass allocation to leaves are major sources of structural variation in the 18 investigated species (Fig. 1). Of these two axes, allocation to leaves was significantly correlated with wood density and showed a limited correlation with

Fig.1 Two-dimensional scatter diagrams of ahistorical PCA on the predicted values of morphological traits at two ontogenetic stages. The symbols with plant species codes represent the section of the species; ●: Anthoshorea, ✖: Brachyptera, ○: Mutica, ◆: Ovalis, ■: Pachycarpae, ◇: Shorea.



photosynthetic rate, whereas crown architecture was significantly correlated with seed size (Fig. 2).

Fig.2 Correlation between PC2 score at the 30g-stage and two indices of shade tolerance



Variation in juvenile survival and related physiological traits among 11 late-successional dipterocarp species

To elucidate the environmental factors and physiological traits that most strongly determine the juvenile survival rate, we focused on 11 late-successional dipterocarp species in 248 quadrats distributed throughout a 12-ha area. We monitored the survival of juvenile (height < 2.0 m) individuals of these species for 1 year. The probability of survival for each species was expressed as a logistic function of plant height and three environmental factors: canopy openness, soil-water potential, and the density of conspecific individuals. Seven species exhibited increased survival under more open canopies, and one species exhibited increased survival and two species exhibited decreased survival at drier sites. Six species showed increased survival as the density of their conspecifics increased, whereas two species showed decreased survival under the same conditions. The magnitudes of the effects of the three environmental factors were similar. However, the interspecific difference in survival was most strongly determined by the dependence of small seedlings on their light environment. Survival under low light was positively correlated with root dry mass and negatively correlated with total leaf area of the juveniles. Species that sustained increased mortality under low light had a set of structural traits (i.e., a high root to leaf area ratio) that would potentially allow rapid growth under bright conditions.

Differences in the dry-mass cost of sapling height growth among 56 woody species co-occurring in a Bornean tropical rainforest.

	Cross-species analysis						
	R^2	Adult stature	Crown type	Interaction	Multiple comparison		
					Branched	Simple	Compound
M_W	0.80	**5.26***	1.12	0.55			
M_T	0.80	**8.56****	2.27	0.62			
M_L	0.76	0.96	**3.69***	0.94	ab	a	b
M_S	0.87	1.67	**10.8*****	0.25	a	b	a
M_C	0.74	0.63	1.54	0.71			
A_L	0.71	1.74	1.18	0.58			
A_C	0.71	0.25	1.08	0.49			
A_{IL}	0.94	0.03	**30.3*****	0.70	a	b	b
SLA	0.89	0.08	**5.15****	1.44	ab	a	b
LAI	0.62	1.77	**10.4*****	0.53	a	b	a
D	0.86	**8.59****	**3.63***	0.78	a	b	a
WDI	0.67	0.37	**5.54****	0.33	ab	a	b

Table 2. Summary of two-way ANOVAs with multiple comparisons to test the effect of adult stature and crown type on sapling structural traits. F-values are given for the two main effects and interaction. Degree of freedom of adult stature, crown type and the interaction were 1, 2 and 2. Degree of freedom for residuals were 50 for cross-species analysis. R^2 values were calculated for the model in which the effect of species was nested. Bold values are significant at $P < 0.05$; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. When significant differences were found among crown types, the results of multiple comparisons are also shown. Effects sharing the same letter were not significantly different at $P < 0.05$.

We analyzed the above-ground structure of saplings from 56 sympatric species in our study forest based on their phylogenetic background to elucidate interspecific variation in the dry-mass cost of height growth and its ecological consequences. The estimated extension cost (i.e., the total above-ground mass) for 1.5-m-tall saplings varied by up to 800% among the 56 species. However, no significant differences in extension cost were observed among saplings with three different crown types (branched, monoaxial simple-leaved, and monoaxial compound-leaved; Table 1), even though the monoaxial crown type has been considered to be an adaptation for achieving rapid height growth. The lack of differences have arisen because the advantages of monoaxial saplings in terms of the structural cost for displaying a given leaf area were unexpectedly small. Understory species had a significantly higher extension cost than canopy species because of their thicker (and consequently, heavier) trunks. For all 56 species combined, the trade-off between height growth efficiency and morphology that enhanced light interception (e.g., larger and more numerous leaves) was prominent. This trade-off, which makes efficient vertical growth incompatible with survival in the understory, potentially enables the stable coexistence of these species in a temporally heterogeneous light environment.

Discussion

Our analyses of the dipterocarp species showed that relatively shade tolerant species are characterized by structural traits that minimize biomass loss, such as a larger allocation to roots and a lower leaf mass per unit area, whereas relatively light-demanding species are characterized by structures that promote rapid growth, such as a large allocation to aerial parts and a high leaf area per mass ratio in both the seedling and the sapling stages. Thus, the light gradient can be partitioned by late-successional dipterocarp species even in the absence of canopy gaps based partly on the structural trade-offs, which is similar to the partitioning of the light gradient by pioneer species.

In the 18 Shorea species, structural variation in the saplings could be summarized by two independent axes, an axis for biomass allocation and an axis for crown architecture. This represents the first report that the variation in biomass, which has been discussed mainly for first-year seedlings, is independent of the variation in crown architecture at the sapling stage. In our analysis of 56 tree species, including non-dipterocarps, we revealed an eight-fold variation in extension cost along the axis for variation in crown architecture; therefore, this axis could be correlated with height growth rate. Whereas the variation in biomass allocation enables stable coexistence based on spatial heterogeneity in the light environment, the variation in crown architecture enables coexistence based on temporal heterogeneity in the light environment (Kohyama 1987; Kohyama and Hotta 1990).

The partitioning of spatial and temporal variation of light based on structural diversity and environment-dependent survival of ecologically or taxonomically similar tree species suggests that the community structure is rather stable and deterministic, which contrasts with the prediction of the unified neutral theory of biodiversity and biogeography (Hubbell 2001). Though only a few intensive comparisons of related species have previously been reported, a study of pioneer species in genus Macaranga at the same site also concluded that the coexistence of species was stable and deterministic and was based on interspecific variation in physiology and structure (Davies et al. 1998). Based on the results of our study, we believe that greater efforts to elucidate the mechanisms responsible for the coexistence of ecologically and taxonomically related species will be one of the most effective strategies for providing a thorough understanding of tropical forest communities.

References

Aiba S I, Kohyama T (1997) Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. J Ecol 85:611-624

Davies SJ, Palmiotto PA, Ashton PS, Lee HS, Lafrankie JV (1998) Comparative ecology of 11 sympatric species of Macaranga in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. J Ecol 86:662-673

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1-15

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419-428

Kohyama T (1987) Significance of architecture and allometry in saplings. Funct Ecol 1:399-404

Kohyama T, Hotta M (1990) Significance of allometry in tropical saplings. Funct Ecol 4:515-521

Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. J Ecol 91:797-806

PROSEA (1994) Plant resources of South-East Asia 5 (1) Timber trees: Major commercial timbers. Prosea Foundation/Pudoc-DLO, Bogor/Wageningen.

Sudou S (1970) Tropical timbers. Chikyu, Inc., Tokyo.

Walters MB, Kruger EL, Reich PB (1993) Relative growth-rate in relation to physiological and morphological traits for northern hardwood tree seedlings - species, light environment and ontogenic considerations. Oecologia 96:219-231

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: Some leading dimensions of variation between species. Ann Rev Ecol Syst 33:125-159

Leaf Morphological Distribution in 250 Tree Species in a Lowland Dipterocarp Tropical Rain Forest, Sarawak, Malaysia –Comparison of Homobaric and Heterobaric Leaves

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Introduction

Plant leaves show a range of morphological differences among species, including in their shape, size, and structure (Esau 1960). One important characteristic relates to the presence or absence of bundle-sheath extensions (BSEs) in the leaf (Wylie 1952): heterobaric leaves have BSEs, whereas homobaric leaves do not. BSEs are formed by parenchyma or sclerenchyma cells of the vascular bundle sheath, which extend to the epidermis on both sides of the leaf in heterobaric leaves. As a result, the mesophyll of heterobaric leaves is separated into many small "bundle-sheath extension compartments" by the BSEs (Terashima 1992). In contrast, homobaric leaves lack the BSEs and their internal structure is relatively homogeneous. These leaf types differ not only in their structural traits but also in their mechanical and functional characteristics. For example, BSEs in heterobaric leaves may provide mechanical support to the leaf blade (Wylie 1952), may act as a water conduit, or may cause non-uniform photosynthesis (Terashima 1992). Homobaric leaves, in contrast, exhibit larger lateral movements of gases in the leaf than is the case in heterobaric leaves (Pieruschka et al. 2006).

These morphological and functional differences may relate to a tree's growth environment and life form. Some authors have suggested that trees with heterobaric leaves will preferentially be found in deciduous forests, which have dry or cold seasons (Wylie 1952). In contrast, the proportion of trees with homobaric leaves may increase in wet or warm regions, which are usually dominated by evergreen species. This hypothesis is supported by the observation that many more evergreen tree species have homobaric leaves than is the case for deciduous tree species (Wylie 1952). Consequently, in the tropical rain forest, most tree species would be expected to have homobaric leaves, since the forest is humid throughout the year and consists mainly of evergreen trees.

In this study, we hypothesized that leaf type would be correlated with the growth environment or life form rather than with the forest biome, even in a tropical rain forest where most trees have evergreen leaves. The spatial distribution of microenvironmental factors such as light intensity, temperature, and relative humidity varies significantly even within a humid tropical rain forest. In particular, the upper canopy of the forest experiences significant desiccating conditions because of the high light intensities, high temperature, low humidity, and high wind speed, whereas the interior of the tropical rain forest is light-deficient, cooler (as a result of shading), and humid, and has lower wind speeds. Canopy gaps are drier and experience higher irradiance than the forest floor under a closed canopy. As a result of the frequent occurrence of water stress in the canopy and canopy gaps, heterobaric leaves may offer an adaptive advantage even in tropical rain forests. On the other hand, trees with homobaric leaves should be more abundant in forest understory species because of their more humid environment. If the proportion of species with each leaf type varies with the location in such heterogeneous forest environments, the distribution of the two types of leaves may influence stand-level photosynthesis and transpiration traits, which have been reported to differ between leaf types (Terashima 1992). However, only limited information is available on the distribution pattern of the two leaf types and their responses to different growth conditions. In the present work, we investigated the distribution of heterobaric and homobaric leaf types among 250 tree species in 45 families, with different life forms, in a tropical rain forest. In particular, we focused on the relationship between each leaf type and the corresponding life form type (e.g., emergent, canopy, sub-canopy, understory, and canopy gap species).

Materials and Methods

Study site The study was carried out in 2005 in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°12′N, 113°50′E; 150 to 250 m a.s.l.). The mean canopy height was about 30 to 40 m; some emergent trees reached heights of 50 to 70 m. The area has a humid tropical climate, with weak seasonal changes in rainfall and temperature. The mean annual precipitation and temperature were 2540 mm and 26.3 °C, respectively.

Plant material and leaf collection We collected the leaves of 434 individuals of 250 tree species from 127 genera in 45 families, from the forest understory to the emergent layer and in canopy gaps. Between two and five fully expanded and apparently nonsenescing leaves of each species were sampled for microscopic observation. Transverse slices were prepared and photographed under a light microscope. Based on these observations, all tree species were classified into heterobaric and homobaric leaf types (Fig. 1). However, some species displayed intermediate morphology. These leaves had BSEs only around the large veins, and the bundle sheath extension compartments were consequently very large compared with those in heterobaric leaves. In this study, these species were categorized as having homobaric leaves.

All tree species that we studied fell into five categories based on their mature tree height and their distribution bias (canopy gap vs. shaded). The height of mature trees of each species was determined by observation or obtained from the research literature (e.g., Sakai et al. 1999). The tree species were classified into four categories (Table 1) based on their mature height: forest understory (<12.5 m), sub-canopy (12.5 to 27.5 m), canopy (27.5 to 42.5 m), and emergent (>42.5 m). Tree species that grow mainly in canopy gaps were classified in a fifth category (canopy gap species), regardless of their height.

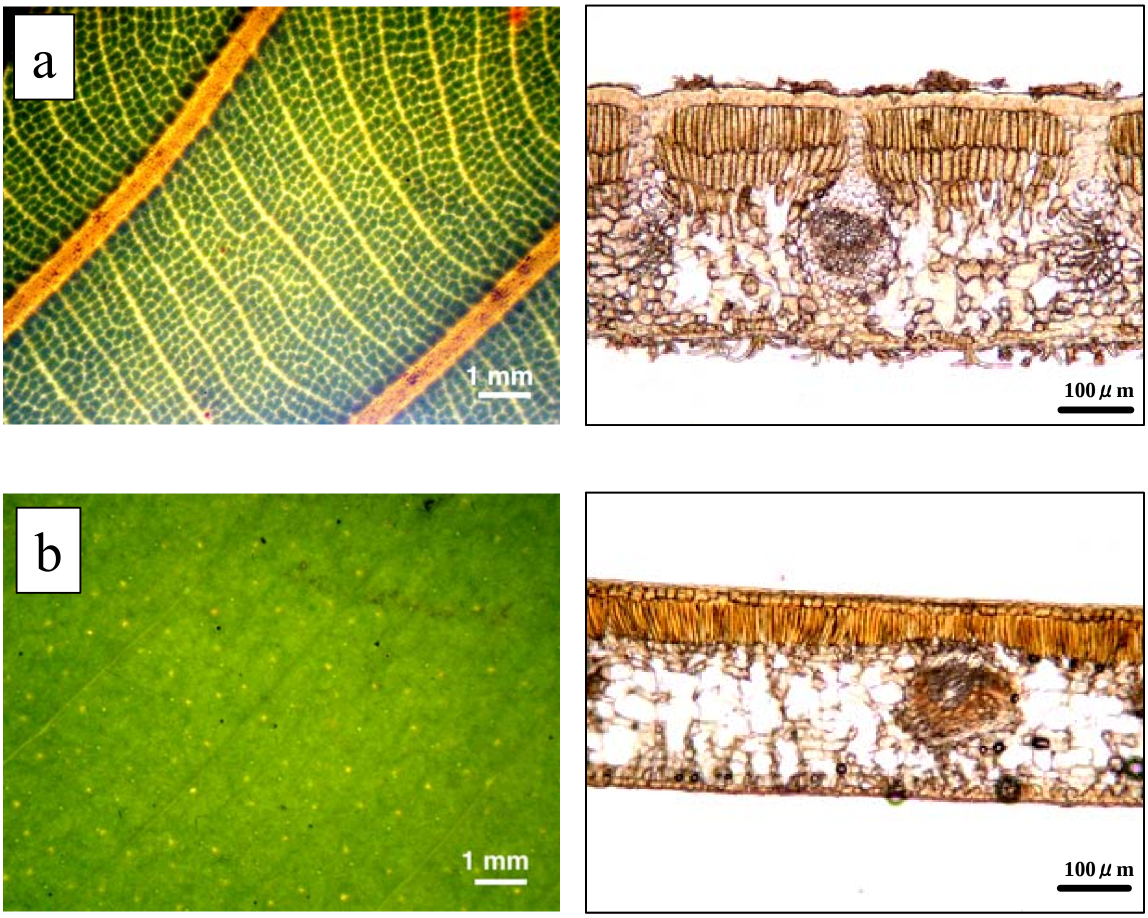

Fig. 1 Photographs of transmission and transverse sections of the leaves.
a: heterobaric leaf (*Lithocarpus luteus*), b: homobaric leaf (*Eugenia subrufa*)

Results

In total, 99 species (40% of the total) in 21 families displayed heterobaric leaves, and 151 species (60%) in 36 families had homobaric leaves (Table 1). The proportion of species with each leaf type differed significantly among life form categories ($P < 0.0001$, χ^2 test). The proportion of trees with heterobaric leaves was only 6% for understory species and 17% for sub-canopy species. The proportion increased to 43% for canopy species and reached 96% for emergent species. The proportion in the canopy gap species was also high (62%)

Table 1 Number of sampled tree species and tree proportion of heterobaric leaf among five life forms

Life form	No. of heterobaric leaf trees	No. of homobaric leaf trees	Total	Heterobaric leaf ratio (%)
Understory	3	46	49	6.1
Subcanopy	13	65	78	16.7
Canopy	23	30	53	43.4
Emergent	47	2	49	95.9
Canopy gap	13	8	21	61.9
Total	99	151	250	39.6

We also found a significant relationship between taxonomic group (family) and leaf type ($P < 0.0001$, df =

13, $N = 184$ species; χ^2 test for 14 families that included more than five species in the family). All species of Dipterocarpaceae, consisting mainly of canopy and emergent trees, were classified as heterobaric (see Kenzo et al. 2007). In contrast, species of Annonaceae and Rubiaceae, which appeared mainly in the forest understory, had only homobaric leaves. However, we found seven families (including the Euphorbiaceae and Sapotaceae) that had both leaf types. Species with different leaf types were found even in the same genus in these families: for example, this was true of genus *Macaranga* in the Euphorbiaceae and genus *Santiria* in the Burseraceae.

Discussion

The leaf type of a tree species (heterobaric or homobaric) may depend on its life form type in the tropical rain forest. In general, a greater proportion of evergreen tree species than deciduous species tend to have homobaric leaves (Wylie 1952). Nevertheless, upper canopy and gap species, and especially the most emergent species in the tropical rain forest, had heterobaric leaves, even at the small seedling stage (Table 1).

The difference in the distribution of leaf types as a function of mature tree height may be related to the steep microenvironmental gradient along the tree's height that occurs in a forest ecosystem. Under the canopy conditions of a tropical rain forest, tree leaves of emergent and canopy trees suffer strong desiccating conditions as a result of the higher vapor pressure difference (VPD), temperature, radiation, and winds compared with those in the understory layer (Yoda 1978). The presence of BSEs might confer an advantage to heterobaric leaves over homobaric leaves in the high-water-stress canopy environment. BSEs may be responsible for rapid stomatal response to drought signals, such as a reduction of water potential in the mesophyll or a higher concentration of abscisic acid (ABA), as a result of rapid transportation of these signals via the transpiration stream in BSEs (Terashima 1992). BSEs may also support and protect the leaf blade against collapse after severe dehydration or other stresses and may guide sunlight to thicker sun leaves (Nikolopoulos et al. 2002; Terashima 1992). The relatively high proportion of species with heterobaric leaves in the canopy gap and canopy species may also be related to their dry and sunny environment.

Conversely, the understory of a tropical rain forest is more suited to homobaric leaves, which may perform better than heterobaric leaves under shade. Light intensity in the tropical rain forest decreases significantly with decreasing height below the canopy, usually reaching only a few percent of the level of sunlight above the canopy at the forest floor (Yoda 1978). Under such conditions, the leaves of most plants that reproduce in the understory perform better in the shade. A lack of BSEs may improve the leaf's ability to utilize sunflecks because improved lateral CO_2 diffusion from shaded to illuminated areas of a homobaric leaf will enhance photosynthesis (Lawson and Morison 2006). Homobaric leaves can also increase their proportion of photosynthetically active leaf area. In a study of BSEs in 31 temperate heterobaric leaf tree species, Nikolopoulos et al. (2002) reported that photosynthetically active leaf area decreased from 91 to 48% as the density of BSEs increased. These characteristics of homobaric leaves could thus contribute to improved photosynthetic efficiency under limited light conditions.

The leaf types (heterobaric or homobaric) were also related to the taxonomic groups (family and genus), which usually reflect differences in life form types or growth habitats at or around maturity. Families that mainly appear in the canopy layer, such as Dipterocarpaceae, tend to have heterobaric leaves. In contrast, families that mainly appear in the forest understory, such as Annonaceae and Rubiaceae, tend to have homobaric leaves (see Kenzo et al. 2007). However, families such as Euphorbiaceae and Sapotaceae, which include tree species with a range of life form types from understory to emergent, included both heterobaric and homobaric species. Furthermore, some genera in these families, such as *Macaranga* (Euphorbiaceae), included species with different leaf types. The leaf type in a single species does not change throughout its growth stages or between individuals (Kenzo et al. 2007). These results suggest that the leaf type in each species depends on the growth habitats or life form types at maturity for each species, and these are, in turn, commonly related to the forest microenvironments at maturity.

In conclusion, we found a clear distribution pattern of the heterobaric and homobaric leaf types with respect to the growth environment and life form type of a species, and with respect to taxonomic groups, in a tropical rainforest. Our results suggest that tropical tree species might have adapted to a spatial gradient at maturity in various physical variables, such as light intensity and VPD, by developing different leaf types (heterobaric or homobaric) that offer different physiological and mechanical advantages.

References

Esau K (1960) Anatomy of seed plants. John Wiley and Sons, New York

Lawson T, Morison J (2006) Visualising patterns of CO_2 diffusion in leaves. New Phytol 169:641-643

Kenzo T, Ichie T, Watanabe Y, Hiromi T (2007) Ecological distribution of homobaric and heterobaric leaves in tree species of Malaysian lowland tropical rainforest. Am J Bot 94:764-775

Nikolopoulos D, Liakopoulos G, Drossopoulos I, Karabourniotis G (2002) The relationship between anatomy and photosynthetic performance of heterobaric leaves. Plant Physiol 129:235-243

Pieruschka R, Schurr U, Jensen M, Wolff WF, Jahnke S (2006) Lateral diffusion of CO_2 from shaded to illuminated leaf parts affects photosynthesis inside homobaric leaves. New Phytol 169:779-787

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am J Bot 86:1414-1436.

Terashima I (1992) Anatomy of non-uniform leaf photosynthesis. Photosynth Res 31:195-212

Wylie RB (1952) The bundle sheath extension in leaves of dicotyledons. Am J Bot 39:645-651

Yoda K (1978) Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. Malayan Nat J 30:161-177

Changes in Photosynthesis and Leaf Characteristics from Seedlings to Mature Canopy Individuals of Some Dipterocarp Species in a Tropical Rain Forest, Sarawak, Malaysia

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Introduction

Tropical rain forests have a complex and multilayered vertical structure. The crown surface of emergent trees in tropical rain forests usually experiences strong sunlight, whereas less than 1% of the solar radiation typically reaches the forest floor (Chazdon 1988). How do tree leaves respond to such drastic differences in light conditions at differing heights? It is well known that leaves in bright conditions (sun leaves) have greater nitrogen content and leaf mass per unit area (LMA), corresponding to a higher photosynthetic rate at light saturation ($A_{\max}$), than leaves in dark conditions (shade leaves). Shade leaves have a higher chlorophyll content and thinner leaf blade to maintain the dark respiration rate. Thus, the light compensation point (I_c) of shade leaves is smaller than that of sun leaves (Lambers et al. 1998). Carswell et al. (2000) and Rijkers et al. (2000) reported that the $A_{\max}$, LMA, and leaf nitrogen content increased significantly with tree height in some neotropical forest trees, although neither report gave much information about large canopy trees or emergent trees.

Does the photosynthetic capacity of canopy and emergent trees increase with height in the tropical rain forest? Some researchers have reported that the age- and/or size-dependence physiological traits showed an ontogenetic decrease in $A_{\max}$ with decreasing leaf nitrogen content and increasing of LMA in some canopy species (e.g., Thomas and Winner 2002). In general, this decline in leaf nitrogen content causes a reduction in $A_{\max}$ in tall trees (Niinemets 2002). It is well known that $A_{\max}$ may also depend on LMA (Thomas and Winner 2002), and an increase of LMA with tree size leads to an increase in resistance of CO_2 diffusion within the leaf and then a decrease of $A_{\max}$ (Terashima et al. 2001).

Tropical canopy and emergent trees may, however, realize a high $A_{\max}$ by developing a leaf mesophyll structure adjusted to the tropical canopy environment. Kenzo et al. (2004) reported that, in some canopy species with high $A_{\max}$ values (nearly 20 μmol CO_2 m^{-2} s^{-1}) in a Southeast Asian tropical rain forest, $A_{\max}$ had a higher positive correlation with leaf mesophyll structure, such as leaf palisade layer thickness and surface area of mesophyll cells per unit leaf area (A_{mes}/A_a), than with leaf nitrogen content and LMA. Alhough an increase in tree height is usually a known cause of declining physiological function of the hydraulic architecture for the transport of water from roots to leaves, we propose and test the hypothesis that tree height does not limit $A_{\max}$ for tropical canopy species in the tropical rain forest.

Our objective in the present study was to determine the effect of tree height on leaf photosynthesis, as well as on morphological and biochemical properties, in five dipterocarp species. To enable us to sample leaves from seedlings on the dark forest floor to mature canopy trees at the bright canopy layer, we used a canopy crane system that provided three-dimensional access to the forest.

Materials and Methods

Study site and plant material

Our study was conducted in an experimental plot (4 ha, 200×200 m) in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E; 150 to 250 m a.s.l.) in September 2001. In the study plot, the mean height of the canopy layer in the stand was about 30 to 40 m, and some emergent trees reached 50 m. The annual precipitation and temperature at the study site averaged 2429 mm and 26.3°C from 2000 to 2003, respectively.

We selected five dipterocarp species and 65 individuals, ranging from seedlings to mature trees (Table 1). The species examined were *Dipterocarpus globosus* Vesq. (DG), *Dryobalanops aromatica* Gaertn. f. (DA), *Shorea acuta* Ashton (SA), *S. beccariana* Burck (SB), and *S. macroptera* Dyer (SM). The height of selected trees ranged from 0.6 to 53 m, and the sample included small seedlings, pole-sized saplings, and emergent trees. The seedlings and saplings were chosen both from gaps and their periphery and under a closed canopy.

Gas exchange measurements

Leaf gas exchange rate was measured using a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE). All measurements were made in the morning between 0800 and 1100 in order to avoid the midday depression in photosynthesis (Kenzo et al. 2003). We selected three fully expanded and apparently non-senescing leaves taken from the top of the crown. The relation between the photosynthetic photon flux density and the carbon assimilation rate was determined. The light intensity, CO_2 concentration, and temperature in the chamber were controlled at 0 to 1800 μmol photon m^{-2} s^{-1}, 360 ppm, and 30°C, respectively. Based on the measurement data, we estimated A_{max} and I_c.

Leaf nitrogen content, chlorophyll determination, and leaf mesophyll structures

Following the gas exchange measurements, all leaves were sampled, and divided into three parts: one for measuring dry weight and nitrogen content, one for chlorophyll analysis, and the other for observation of mesophyll structure. Leaf nitrogen and carbon contents were determined by an NC analyzer (Sumigraph NC-900, Shimadzu). Chlorophyll was extracted with DMSO and was determined by a spectrophotometer (UV-1400, Shimadzu). The leaves used for observation of the mesophyll structure were fixed in FAA, and transverse slices were prepared. The thicknesses of the leaf blade and palisade layer were determined. The surface area of mesophyll cells per unit leaf area (A_{mes}/A_a) was estimated (Nobel 1999).

Results

Leaf photosynthetic, morphological, and biochemical properties in relation to tree height

Both within and across species, A_{max} and I_c increased significantly with tree height (Fig. 1A, B). We did not find significant interspecific differences in A_{max} and I_c with tree height (ANCOVA; $P > 0.05$), except for in the A_{max} of SB in the canopy individuals.

The leaf blade thickness and LMA increased significantly with tree height (Table 2, Fig. 1C). However, interspecific differences were found between SA and other species. SA had the thickest leaf blade and highest LMA among the species studied at all tree heights (ANCOVA; $P < 0.05$). The thickness of the palisade layer and the A_{mes}/A_a value also increased with tree height without interspecific differences (Table 2, Fig. 1D).

The relationship between nitrogen content per unit area (N_{area}) and tree height was similar to the other traits (Table 2); no significant interspecific difference was observed. The unit mass chlorophyll content (Chl_{mass}) and the chlorophyll to nitrogen (Chl/N) ratio decreased with height without interspecific differences (Table 2).

Leaf mesophyll structure and photosynthetic properties in the canopy

Leaf mesophyll structure significantly differed among species, suggesting a stronger effect on interspecific variation in canopy photosynthesis (Kenzo et al. 2004). In particular, SB leaves had the highest A_{max} (18 μmol m^{-2} s^{-1}) and the thickest palisade layer. Surprisingly, the palisade consisted of up to five or more layers (Fig. 2).

Leaf Amax and Ic in relation to leaf characteristics

Significant correlations were found between A_{max} and LMA and between A_{max} and N_{area} (Table 3; both $P < 0.001$). The highest correlation coefficients were observed between A_{max} and properties of leaf mesophyll structures, such as the thickness of the palisade cell layer and A_{mes}/A_a (Table 3; both $P < 0.001$).

Negative correlations were found between I_c and Chl_{mass} and between I_c and Chl/N (Table 3).

Discussion

Change of photosynthetic capacity and light compensation point with tree height

Photosynthetic capacity (A_{max}) was not limited by tree height in these tropical canopy tree species. For dipterocarp species, A_{max} bears a simple relation to tree height (Fig. 1A). Rijkers et al. (2000) also found a significant relation between A_{max} and tree height in four neotropical species. The slope and intercept of their linear regression line were very similar to those in our study. These facts may be important to estimate the capacity of CO_2 fixation in tropical forests, although further studies are needed in diverse tropical forests.

In contrast, at the dark forest floor, the lower I_c seems to contribute to maintaining a positive carbon assimilation rate (Fig. 1B). I_c was less than 10 μmol photon m^{-2} s^{-1} for most of the non-gap seedlings in this study. Many authors have reported that photosynthetic photon flux density below the closed canopy of tropical rain forests lies in the range of 5 to 20 μmol photon m^{-2} s^{-1} (e.g., Chazdon 1988). In regard to the low I_c for the seedlings, our study species may be well adapted to the low light conditions below the closed canopy of tropical rain forests.

Leaf photosynthetic traits in relation to leaf morphological and biochemical properties

Height-related differences in photosynthetic characteristics such as A_{max} and I_c are closely related to leaf morphological and biochemical traits. It is well known that A_{max} is strongly affected by various leaf characteristics, such as leaf thickness, leaf mesophyll structure (A_{mes}/A_a; Kenzo et al. 2004), and nitrogen content (Evans 1989). In general, age- and size-dependent decline of leaf nitrogen content seems to induce a reduction in A_{max} in tall trees (Koch et al. 2004). However, our results clearly showed that leaf nitrogen content increased with tree height in these tropical canopy species. Although high LMA may also limit A_{max} (Niinemets 2002), dipterocarp canopy trees had a well-developed leaf mesophyll structure, such as a thick palisade layer and high A_{mes}/A_a, which is responsible for reduced leaf internal resistance for CO_2 diffusion, together with high LMA. These results suggest that high leaf nitrogen and a developed mesophyll structure largely contribute to maintaining a high A_{max} in the upper canopy leaves.

The larger Chl_{mass} and Chl/N ratio in the leaves were related to the lower I_c value, permitting better acclimation under dark conditions in the small-tree stage (Table 2). There was a negative correlation between Chl_{mass} and I_c (Table 3), indicating that higher values of Chl_{mass} contribute to increased light harvesting efficiency at lower light availability (Lambert at al. 1998). In our study, the Chl/N ratio of all species increased with decreasing tree height, and the ratio was negatively correlated with I_c (Table 3); these attributes also contribute to improved light harvesting efficiency in darker conditions.

Conclusion

Our results suggest that A_{max} is not limited by tree height in tropical canopy tree species. We also found a simple and significant linear relation with tree height for both leaf photosynthetic characteristics (e.g., A_{max}) and leaf morphological and biochemical traits, which in turn affect photosynthetic traits (e.g., LMA and N_{area}), with some interspecific differences among dipterocarp species. Our study suggests that dipterocarp species can adapt their optimal photosynthetic ability to variable light conditions, from the seedling stage to large adult trees, by changing the morphological and biochemical properties of their leaves.

References

Carswell FE, Meir P, Wandelli EV, Bonates LCM, Kruijt B, Barbosa EM, Nobre AD, Grace J, Jarvis PG (2000) Photosynthetic capacity in a central Amazonian rain forest. Tree Physiol 20:179–186

Chazdon RL (1988) Sunflecks and their importance to forest understory plants. Advanced Ecol Res 18:1–63

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9–19

Kenzo T, Ichie T, Ninomiya I, Koike, T (2003) Photosynthetic activity in seed wings of Dipterocarpaceae in a masting year: Does wing photosynthesis contribute to reproduction? Photosynthetica 41:551–557

Kenzo T, Ichie T, Yoneda R, Kitahashi Y, Watanabe Y, Ninomiya I, Koike T (2004) Interspecific variation of photosynthesis and leaf characteristics in five canopy trees of Dipterocarpaceae in a tropical rain forest. Tree Physiol 24:1187–1192

Kenzo T, Ichie T, Yoneda R, Watanabe Y, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with height from seedlings to mature canopy trees in five dipterocarp species in a tropical rain forest. Tree Physiol 26:865–873

Koch GW, Sillett SC, Jennings GM, Davis SD (2004) The limits to tree height. Nature 428:851–854

Lambers H, Chapin III FS, Pons TL (1998) Plant physiological ecology. Springer-Verlag, New York, pp 540

Niinemets Ü (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rate with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. Tree Physiol 22:515–535

Nobel PS (1999) Plant Physiology 2nd Edn. Academic Press, NY, pp474

Rijkers T, Pons TL, Bongers F (2000) The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. Func Ecol 14:77–86

Terashima I, Miyazawa S, Hanba TY (2001) Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO_2 diffusion in the leaf. J of Plant Res 114:93–105

Thomas SC, Winner WE (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. Tree Physiol 22:117–127

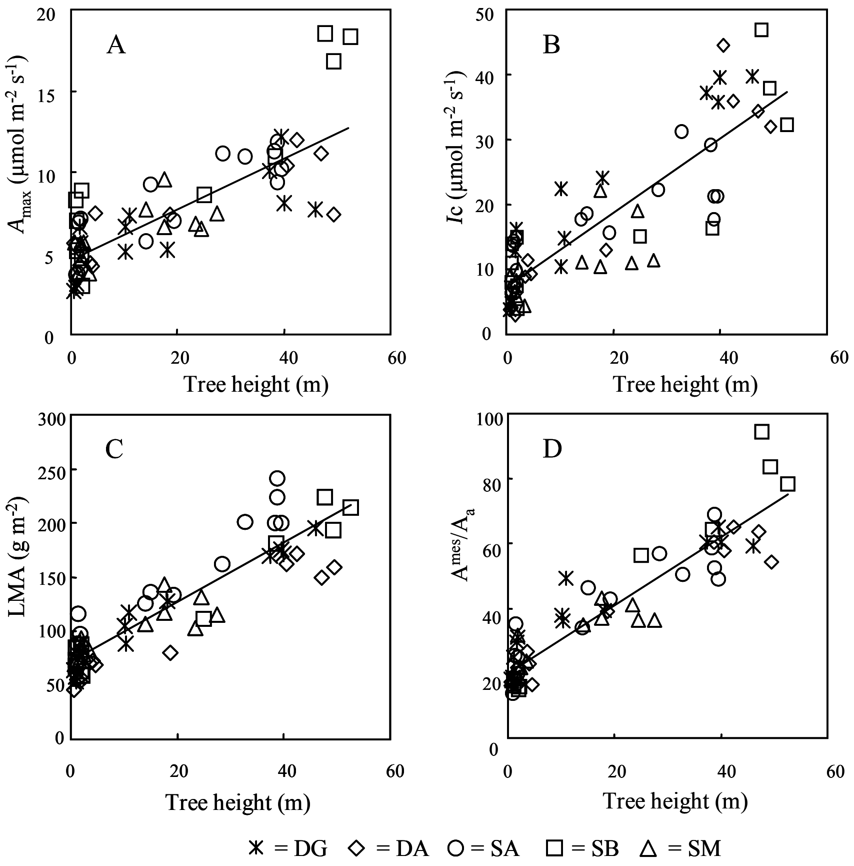

Figure1. Relation between tree height and: A_{max} (A), I_c (B), LMA (C) and A^{mes}/A_a (D) (Kenzo et al. 2006). Values are means for each individual across all replicate leaves. The regression lines are: A, $y = 4.69 + 0.16x$; $r^2 = 0.66$, $P < 0.001$. B, $y = 7.34 + 0.57x$; $r^2 = 0.74$, $P < 0.001$. C, $y = 69.7 + 2.76x$; $r^2 = 0.84$, $P < 0.001$. D, $y = 20.1 + 1.05x$; $r^2 = 0.86$, $P < 0.001$.

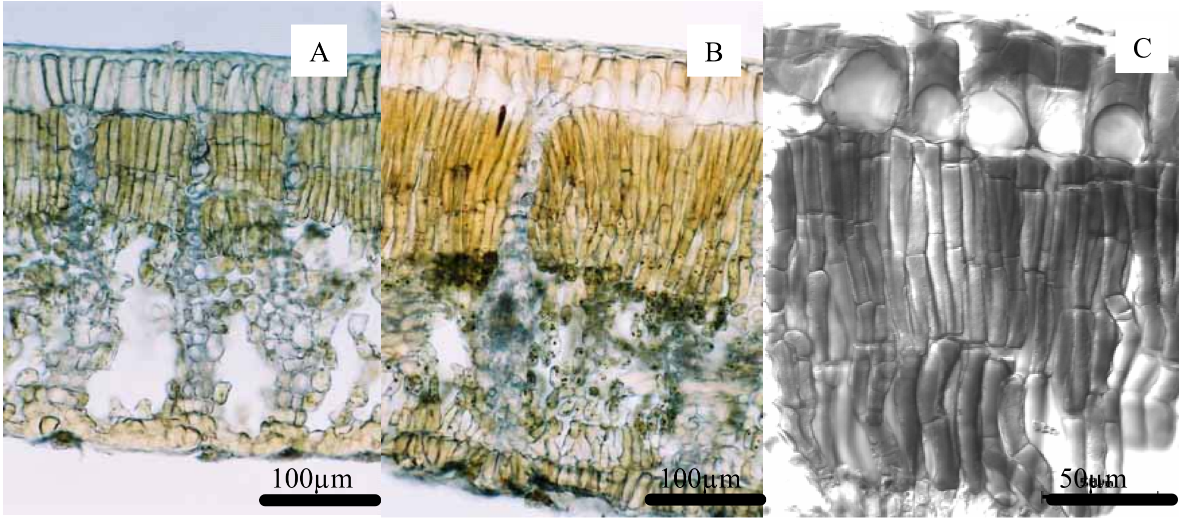

Figure 2. Light micrographs of transverse section of *Dryobalanops aromatica* (A) and *Shorea beccariana* (B). Photograph C is the palisade layer of SB at twice the scale (Kenzo et al. 2004).

Table 1. Tree species, species code, number of individuals, maximum (H_{max}) and minimum (H_{min}) tree height. (Kenzo et al. 2006).

Species	Code	Individual	H_{max} (m)	H_{min} (m)
Dipterocarpus globosus	DG	13	46.0	0.6
Dryobalanops aromatica	DA	12	49.4	0.6
Shorea acuta	SA	15	39.5	1.0
Shorea beccariana	SB	11	52.5	1.0
Shorea macroptera	SM	12	27.5	0.7

Table 2. Relation between tree height and leaf characteristics. Values are means for each individual across all replicate leaves (Data from Kenzo et al. 2006).

Leaf characteristics	Slope	Intercept	r^2	P
Leaf thickness (μm)	4.76	206	0.69	0.001
Palisade layer thickness (μm)	1.97	38.3	0.83	0.001
N_{area} (mol m^{-2})	0.0013	0.045	0.74	0.001
Chl_{mass} (mg g^{-1})	-0.05	3.48	0.49	0.001
Chl/N ratio	-0.06	5.4	0.48	0.001

Table 3. The light-saturated photosynthetic rate (A_{max}) and Light compensation point (I_c) in relation to leaf characteristics. Values are means for each individual across all replicate leaves (Data from Kenzo et al. 2006).

Variable 1	Variable 2	Slope	Intercept	r^2	P
A_{max} (μmol $m^{-2}s^{-1}$)	LMA (g m^{-2})	0.05	1.11	0.63	0.001
	N_{area} (mol m^{-2})	102.9	0.67	0.57	0.001
	Palisade layer thickness (μm)	0.08	1.67	0.76	0.001
	A^{mea}/A_a	0.15	1.85	0.72	0.001
I_c (μmol $m^{-2}s^{-1}$)	Chl_{mass} (mg g^{-1})	-6.98	35.5	0.51	0.001
	Chl/N ratio	-5.06	39.3	0.43	0.001

Functional Diversity of Tree Species in Warm-Temperate Rain Forest Communities of Yakushima Island

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Introduction

Natural plant communities are composed of many plant species sharing common traits as autotroph, or competing with each other for common limiting resources. Their coexistence has been examined in terms of differential requirement of multiple resources, spatio-temporal heterogeneity, disturbance-mediated non-equilibrium states and so on. In any situation, it is crucial to describe how species are similar to, or different from each other. From the view of community organization *via* interspecific trade-offs (Silvertown 2004), community response to natural and human disturbance is demonstrated by differential response of species thereby overall ecosystem functioning is maintained efficiently compared to single-species-dominated ecosystems.

We characterize plant species composing warm-temperate rain forests in lowland Yakushima Island from the view of ecomorphological and demographic traits. Yakushima Island located in south from Kyushu Island, Japan, is characterized by well-reserved primary warm-temperate rain forests at around 300-800 m altitude. We show how species differentiation in regeneration process contributes to the resilience of forest ecosystems to various types of perturbation. The within site, and within vegetation type comparison of traits will provide us basic information for among site/type comparison. We paid attention to leaf and seed characteristics in relation to regeneration traits in particular, where detailed examination of leaf longevity with Bayesian analysis is to be presented separately (Kubo, Ushihara and Kohyama, in preparation). In this report we focus on the relationship between seed size, seedling architecture and the choice of regeneration sites among co-occurring warm-temperate rain forest tree species.

Research Sites and Methods

Research sites were set on warm-temperate rain forests in southwestern part of Yakushima Island, mainly watersheds along River Segire, River Ohko and River Koyohji. The detail of the sites can be found in literature (Kohyama 1986, Kohyama and Grubb 1994, Aiba and Kohyama 1996). We use dataset first appeared in these papers.

Roadside census was carried out in the exposed, mountainside berm edge of the Ohko Forestry Road in Ohko Basin. We set two transects, ca. 35 m long and 55 m long with 1 m wide. All saplings taller than 50 cm and less than 2 cm diameter at breast height were monitored, just like the sapling census in nearby Segire River Basin (Kohyama 1986).

Allometry examination was first made at various sites on the southwestern side of Yakushima Island in early July 2006. The unique topography of the warm-temperate forest consists of uniform Miocene granite covering the entire mountain body. Fourteen commonest shade-tolerant tree species were previously studied in a mature closed canopy with no influences of tree-fall gaps (Kohyama and Grubb 1994). 6 tree species frequently seen along roadside banks, 3 of which also observed in shaded forest floors (*Eurya japonica*, *Rhododendron tashiroi*, and *Neolitsea aciculata*), were additionally selected for detailed study. Healthy, well-established seedlings with no breakage, resprouting, or root death, were then carefully excavated with a shovel for minimum root breakage in late October to early November 2006. Seedlings were defined as being less than 30 cm tall; shoot height ranging from 2-27 cm, excluding current-year seedlings. Total sample size summed up to 150 seedlings; 22 to 30 samples for each canopy and subcanopy species. Each seedling was carefully washed and dimensions measured. After dividing the plant into leaves, stems, and roots, each part was photocopied before being dried in an oven at 80 degrees Celsius for two full days. Although the root system was flattened for photocopying, the images were taken so that roots did not overlap with each other so that we could distinguish the actual root distribution. Seventeen species were sampled from habitats at two light conditions (forest floor and exposed road side).

Biomass allocation among root (below-ground) *versus* shoot (above-ground) and that within shoot dimensions (stem *versus* foliage) were analysed using a hierarchical Bayesian model for handling co-occurring all species at once. In this statistical model, factors affecting biomass allocation was categorized into two types— fixed and random effects. We set total seedling weight as the fixed effect that change the mean of the probabilistic distributions, leaving random effects to explain the change in variances dependent on unobservable factors such as unknown or individual seedling characteristics. Four parameters interpreting the fixed effects, deriving from prior distributions based on field data, were used in order to explain and infer the consequences of weight dependency and species difference in biomass allocation of shoot *versus* root and stem *versus* foliage dimensions. The Monte Carlo Markov Chain (MCMC) method was carried out using R2WinBUGS package on R 2.4.1 for acquiring the estimated posterior distributions of parameters. We assume that the probability biomass allocation to shoot p (thus root allocation is $1-p$) would follow the linear logistic model,

$$p = 1/[1+\exp(-z)], \tag{1}$$

where $z = \beta_1 + \beta_2$[log total biomass of seedling]. Equally, stem (q) *versus* foliage ($1-q$) biomass allocation were similarly presented,

$$q = 1/[1+\exp(-z')], \tag{2}$$

where $z' = \beta_3 + \beta_4$[log shoot biomass of seedling]. Each parameter contains a hierarchical structure consisting of a species-specific characteristic and a common characteristic among all 17 species.

Results and Discussion

Figure 1 shows the tendency across 14 shade-tolerant species, examined using dataset by earlier studies. Recruitment capacity is negatively correlated with maximum height (Fig. 1A), that is in accordance with the expected trade-off by the forest architecture hypothesis (Kohyama 1993). Density ratio of canopy gaps to closed stands is higher for shorter species (Fig. 1B), which supports the model implication that lower-layer species show the density spike at a younger stage of community development (T. Kohyama and T. Takada, in preparation).

Figure 2, summarizing the roadside species composition of saplings, suggests that the abundance there

(Fig 2B) is negatively correlated with seed size, but not for the sapling composition in forest gaps (Fig 2A). The two species, *Rhododendron tashiroi* (Rt) and *Eurya japonica* (Ej), are most abundant shade-bearing species in shallow-soil mountainside roadside. The occurrence of such shade-intolerant species *as Aleurites cordata* (Ac) and *Mallotus japonicus* (Mj) was restricted to valley-side road side with deep soil accumulation. When we plot maximum tree height against seed size among 14 shade-bearing species, there was a tendency that tall tree species have large seed size as compared to short tree species (Fig. 3). Such seed mass *versus* maximum adult size correlation is along general trends found in a wide diversity of land plants (Rees and Venable 2007). The dominance of short-stature species in gap-phase regeneration (Fig. 1B) may partly be explained by producing many regenerates (Fig. 1A) with small per-seed size.

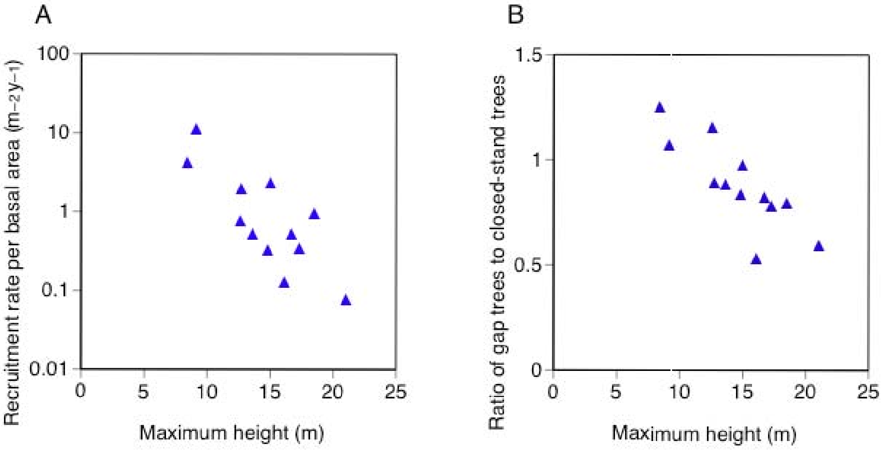

Fig. 1. Interspecific comparison of demographic performance among a dozen abundant shade-tolerant tree species in a primary warm-temperate rain forest in the Segire basin, Yakushima Island, southern Japan. (A) Recruitment rate per species basal area, and (B) ratio of tree densities at canopy gaps to those at closed-canopy stands, plotted against observed maximum height. Density and recruitment rate are defined above 2-cm trunk diameter at breast height. Based on census data of permanent plots monitored since 1981 (Kohyama 1986; Aiba and Kohyama 1996).

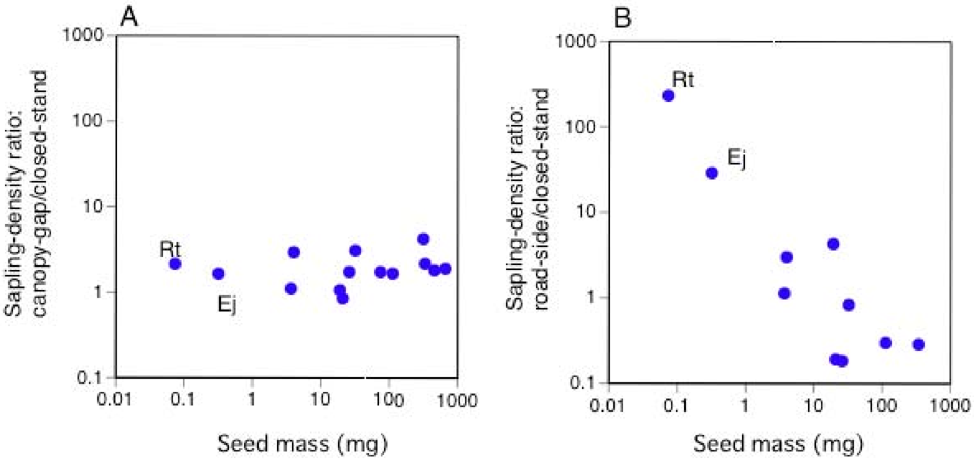

Fig. 2. Ratio in density of saplings (> 50 cm tall and < 2 cm dbh) between tree-fall gaps and closed stands (A), and that between roadside rocky banks and closed stands (B) for 14 abundant shade-tolerant species of warm-temperate rain forest in Yakushima, plotted against dry weight of seeds. Studied area is 2000 and 650 m^2 for closed stands and gaps (in Segire River basin), respectively, and is 90 m^2 for roadside banks (in Ohko River basin).

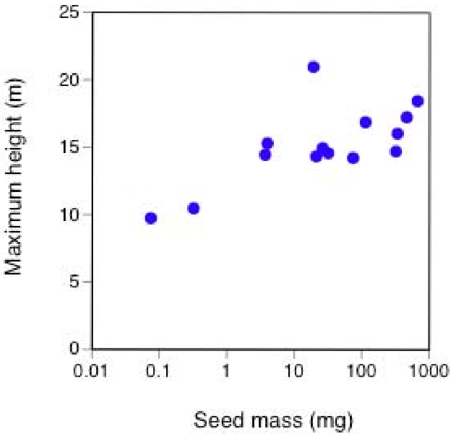

Fig. 3. Relationship between seed size and maximum attainable tree size of common 14 abundant shade-tolerant species in Segire River basin of Yakushima Island.

Two combinations of biomass allocation patterns among species were examined: (1) allocation patterns between root and shoot parts and (2) those within shoot, i.e. stem and foliage. In root versus shoot allocation, results showed that an average-sized individual, ignoring interspecific differences, would allocate resources to shoot biomass (Fig. 4). Species difference was found for eight species including large-seeded *Camellia sasanqua* (Cs) and small-seeded *Eurya japonica* (Ej), where significant species difference was recognized for those that do not include the mean of hyperspecies posterior distribution within the 95% confidence interval. When examining only the differences among species, *Eurya japonica* (Ej), *Cleyera japonica* (Cl), and *Litsea acuminata* (La) showed a positive response to shoot allocation within all 17species. *Stewartia monadelpha* (Sm), *Aleurites cordata* (Ac), *Camellia sasanqua* (Cs), *Neolitsea aciculata* (Na) and *Acer morifolium* (Am), on the other hand, showed root allocation to be more significant. Overall, there was no significant dependency on total dry mass allocation with change in seedling size.

When comparing stem to foliage allocation, as Fig. 5 shows, allocation in shoot dimensions showed to slightly invest in foliage biomass. *Eurya japonica* (Ej) and *Symplocos tanakae* (St) were “foliage-investing” species, while two deciduous, shade-intolerant species *Stewartia monadelpha* (Sm) and *Aleurites cordata* (Ac) were classified as “stem-investing” species. Results showed that stem-investing species allocated biomass in roots, while foliage-investing species *Eurya japonica* was a shoot-allocating species when root-shoot biomass allocation was compared. No species difference was found for foliage dry mass dependency in stem *versus* foliage biomass allocation.

A distinctive interspecific difference in biomass allocation and its dependency on total dry mass or shoot dry mass in root *versus* shoot and stem *versus* foliage allocation patterns, respectively, was not established from these results. However, architectural differences in species were visible among species from observations. *Rhododendron tashiroi*, for example, developing shallower horizontal roots compared to other shade-tolerant species, nevertheless it did not show a significant trait in biomass allocation patterns. It can thus be considered that factors other than biomass allocation would be involved with regulation in seedling architectural performance related to species diversity; even among root-allocating species, difference may occur between seedling height *versus* width dimensions. Results regarding biomass-allocating patterns would simply characterize one aspect of species' architecture; it would be insufficient in extensive comparison of species' architecture. Further analysis therefore, including architectural dimensions comparing above-ground and below-ground, such as depth *versus* height and crown *versus* root width, within above-ground and below-ground architectures will be necessary. It is also interesting to note that small-seeded species such as *Eurya japonica* and *Rhododendron tashiroi* and large-seeded species *Aleurites cordata* were both commonly seen along rocky roadside banks. While hypothesized that seedling architecture is correlated with seed size and its choices in sites for establishment, the classical proposal of the relationship between seed size and shade-tolerance may not directly apply for species studied here.

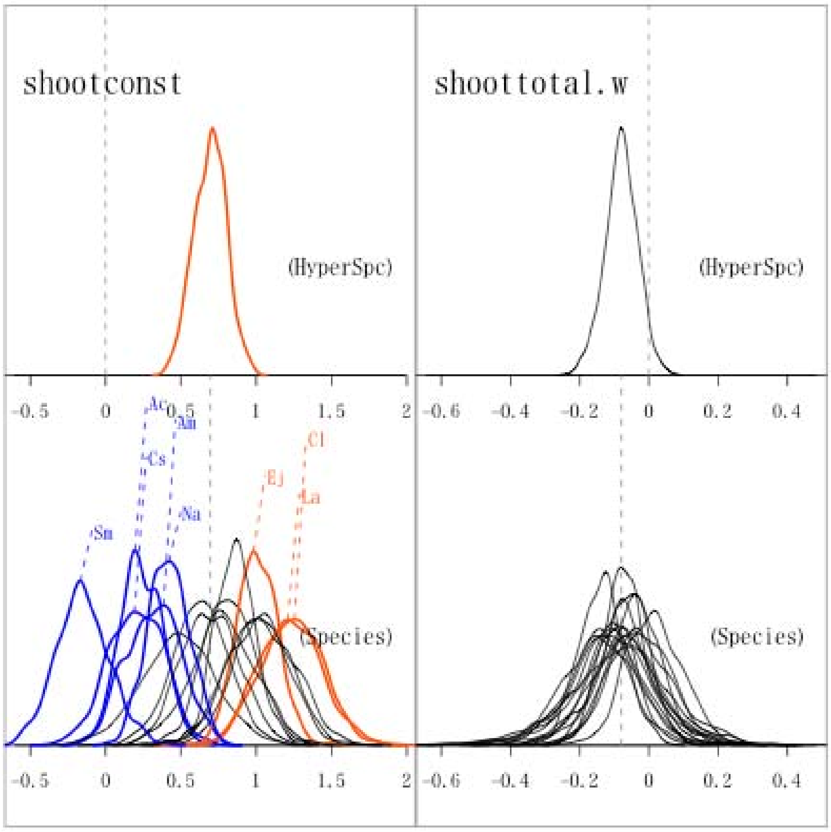

Fig. 4. Biomass allocation among root and shoot. The posterior distribution results of the hierarchical Bayesian model, each parameter expressed with 2 distribution panels. Vertical axes indicate frequency of distributions for posterior probabilities. Top panels, parameter distributions considering a common characteristic among all species (hyperspecies). Parameters which do not include a mean value of 0 within the confidence interval are shown in following colors; red as to those distributing in positive probabilities, blue for those in negative, black for those including the mean value within the confidence interval. Bottom panels, parameter distributions considering species difference, each line representing a species. Colors are sorted accordingly to the mean value derived from the posterior hyerspecies distribution. Panels on the left show results for constant term (β_1) for shoot *versus* root allocation patterns. Panels on the right show total mass dependency (β_2), in eqn (1).

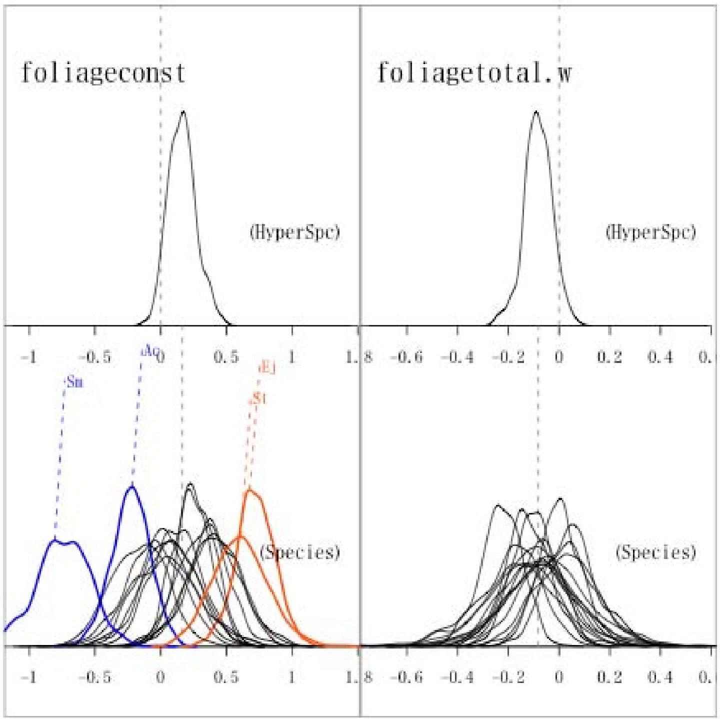

Fig. 5. Allocation patterns in stem and foliage. The posterior distribution results of the hierarchical Bayesian model, each parameter expressed with 2 distribution panels. Vertical axes indicate frequency of distributions for posterior probabilities. Top panels, parameter distributions considering a common characteristic among all species (hyperspecies). Parameters which do not include a mean value of 0 within the confidence interval are shown in following colors; red as to those distributing in positive probabilities, blue for those in negative, black for those including the mean value within the confidence interval. Bottom panels, parameter distributions considering species difference, each line representing a species. Colors are sorted accordingly to the mean value derived from the posterior hyerspecies distribution. Panels on the left show results for constant term (β_3) for foliage allocation patterns. Panels on the right show shoot mass dependency (β_4), in eqn (2).

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References

Aiba S, Kohyama T (1996) Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. J Ecol 84:207-218

Kohyama T (1986) Tree size structure of stands and each species in primary warm-temperate rain forests of southern Japan. Bot Mag Tokyo 99:267-279

Kohyama T (1987) Significance of architecture and allometry in saplings. Funct Ecol 1:399-404

Kohyama T (1993) Size-structured tree populations in gap-dynamic forest - the forest architecture hypothesis for the stable coexistence of species. J Ecol 81:131-143

Kohyama T, Grubb PJ (1994) Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperate rain forest. Funct Ecol 8:229-236.

Rees M, Venable DL (2007) Why do big plants make big seeds? J Ecol 95:925-936

Silvertown J (2004) Plant coexistence and the niche. Trends Ecol Evol 19:605-611

Reproductive Strategy of a Tropical Pioneer Shrub, *Melastoma malabathricum* (Melastomataceae)

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Introduction

Many studies of excess flower production (the production of more flowers than fruits) have been conducted. Holtsford (1985) described five categories of hypotheses to explain this phenomenon: male function, pollinator attractiveness, reproductive assurance, resource boom, and selective fruiting.

The resource boom hypothesis assumes that the amount of resources that will be available for fruit production is not predictable at the flowering stage and that high fruit set occurs only when the resources for fruit production are sufficient. Previous studies of this hypothesis dealt with the unpredictability of supra-annual environmental fluctuations (Holtsford 1985; Eriksson 1987; Gorchov 1988; Vaughton 1991; Nishikawa 1998). However, in tropical regions, some pioneer plants reproduce continuously (Momose et al. 1998; Sakai et al. 1999), and they are considered to be affected by environmental fluctuations over much shorter time scales.

Previously, the resource boom hypothesis has been tested under artificial environmental control (Coulter 1979; Willson and Price 1980; Lee and Bazzaz 1982; Holtsford 1985; Eriksson 1987; Gorchov 1988; Vaughton 1991; Nishikawa 1998). As a new approach to testing this hypothesis, we measured fluctuations in the demand and supply of resources under natural conditions in a species that reproduces continuously and clarified how plants adapt to those fluctuations through increasing the number of reproductive organs and aborting these organs when resources are insufficient.

Methods

Study site and plant materials

The study was conducted in Lambir Hills National Park (4°12′N, 114°02′E; ca. 100 m a.s.l.), Sarawak, Malaysia. The climate is almost aseasonal (Kato et al. 1995).

The study species, *Melastoma malabathricum* L., is a pioneer shrub that is abundant along the edges between natural and artificial habitats (e.g. beside roads, Corner 1988). These plants reproduce almost continuously throughout the year, and reproductive organs at various stages, including young flower buds and mature fruits, are almost always found on a given individual.

Size and dry weight

To estimate the dry weight of the reproductive organs attached to plants, we determined relationships between their size and weight. To create these relationships, we harvested and measured 94 buds, 21 flowers, and 71 fruits (parameters: fresh weight, dry weight, length, and width). From these samples, we performed multiple regressions to analyze the relationships between dry weight (the explained variable) and length and width (independent variables) and between the water content in the reproductive organs (water weight) and their size (length and width).

Growth of reproductive organs

From 5 June until 24 July 2004, we measured the lengths and widths of marked reproductive organs every day without damaging the organs. In total, we measured the growth of 90 samples from six plants. The abortion rate of reproductive organs (the proportion of organs originally present on one day that were no longer present on the next day) was obtained from these samples. The size growth of the reproductive organs was transformed into a dry weight growth using the multiple regression equations for dry weight as a function of size. We calculated water weight similarly.

Monitoring the number of reproductive organs

We monitored fluctuations in the number of reproductive organs on each individual between consecutive days. The number of reproductive organs was counted daily in each of seven categories based on their reproductive stage: bud (young, intermediate, large), flower, and fruit (young, intermediate, and large). These stages were defined for the reproductive organs according to their sizes and colors.

Respiration and transpiration of reproductive organs

Diurnal changes in respiration and transpiration were measured every hour during the day and every 3 hours at night using an LI-6400 portable photosynthesis meter (LI-COR, Lincoln, Nebraska) with a model 6400-05 conifer chamber. In total, 56 samples (nine individuals) from seven reproductive stages were measured on nine individual plants. Under natural light, each sample was measured for only 1 day, and then its dry weight was determined.

Photosynthesis of leaves

Diurnal changes in leaf photosynthesis were measured using the LI-6400 meter under natural light conditions. After the measurements, the area of each leaf was measured, and the area of each leaf was calculated.

Meteorological data

Solar radiation was measured at 10-minute intervals using a Pyranometer (MS-801, EKO Seiki) at a fixed open site. The plants in our study were assumed to receive approximately the same amount of solar radiation as the sensor because they were located at the roadside. Rainfall was measured every hour using a tipping-bucket rain gauge that collected 0.5 mm per tip (No.34-T, OTA).

Analysis

Based on the assumption that carbohydrates and water were demanded by reproductive organs and that their supply fluctuated in the short term, we analyzed the responses of plants as a function of these fluctuations.

Demand for carbohydrates was expressed as the increase in dry weight (g), and carbohydrate consumption was expressed as the respiration per reproductive organ per day (g $C_6H_{12}O_6$ day^{-1}). Similarly, demand for water was expressed as the increase in water weight (g) and water consumption of the transpiration per reproductive organ per day (g H_2O day^{-1}). The average demands for carbohydrates and water at each stage were thus obtained. The number of reproductive organs counted at each reproductive stage on each day was multiplied by the carbohydrate and water demands for that stage to produce an estimated total demand for carbohydrates and water for nine plants each day.

The resource supply was determined from our photosynthetic measurements and meteorological data. The relationships between photosynthetic photon flux density (PPFD) and photosynthetic rate were estimated from the gross photosynthetic rate, the maximum gross photosynthetic rate, the respiration rate, and PPFD (μmol m^{-2} s^{-1}; Boote and Loomis 1991). The relationship between total radiation and PPFD at our study site was provided by Megumi Yamashita (Kinki Surveyor School, personal communication). The radiation measured on each day from 31 May to 17 July 2004 was transformed into PPFD based on this conversion factor. The daily total photosynthetic productivity (g cm^{-2} day^{-1}) was estimated for each day as a function of the calculated PPFD values. The daily total rainfall was also calculated.

The daily abortion rate of the population on the next day was compared with the carbohydrate demand on the current day divided by the total photosynthetic productivity during the previous 1, 3, or 5 days and with the demand for water on the current day divided by the total rainfall during the previous 5 days. Spearman's rank correlation coefficient was calculated for each of these comparisons.

Results

The demand for resources (carbohydrates and water) was greatest during the flower stage (Table 1). The photosynthetic rates of leaves and PPFD both varied during the day. Because stomatal conductance decreased after 1000, we obtained separate relationships between PPFD and photosynthetic rate before and after this time. Maximum gross photosynthetic rates of leaves before and after 1000 were 11.0 and 7.3 μmol CO_2 m^{-2} s^{-1}, respectively. The respiration rate was 0.80 μmol CO_2 m^{-2} s^{-1}. The leaf transpiration rate averaged 376 mg cm^{-2} day^{-1}, and the mean area of a single leaf was 19.7 cm^2.

The daily abortion rates on the next day were significantly correlated with the carbohydrate demand on the current day divided by the total photosynthetic production per unit leaf area during the previous 1, 3, or 5 days (Table 2). However, the daily abortion rates on the next day were not correlated with the water demand on the current day divided by the total rainfall during the previous 5 days. That is, the daily abortion rates were correlated with the available carbohydrate resources but not with the available water resource.

Discussion

The daily abortion rates were correlated with the carbohydrate demand divided by the total photosynthetic production per unit leaf area during the previous 1, 3, or 5 days. The abortion of reproductive organs in *M. malabathricum* thus appears to represent an adaptation to environmental fluctuations at shorter time scales than previously reported in other plants.

Even in the absence of seasonal environment limitations, tropical climax species tend to reproduce at intervals of 1 year or longer (Momose et al. 1998; Sakai et al. 1999). This suggests that they reserve resources, and that the higher their photosynthetic production, the more their resource reserves increase (Yoneda et al. 2002). In contrast, tropical pioneer shrubs such as *M. malabathricum* reproduce continuously. When photosynthetic production is low, they abort their reproductive organs. Such a reproductive strategy, which minimizes the resources reserved for reproduction, can be explained by the typically high mortality of tropical pioneer species (Clark and Clark 1992, Shimano 2000).

Acknowledgments

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References

Boote KJ, Loomis RS (1991) The prediction of canopy assimilation. In: Boote KJ, Loomis RS (eds) Modeling crop photosynthesis – from biochemistry to canopy. Crop Science Society of America, Madison, Wisconsin USA, pp 109-140

Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62: 315-344

Corner EJH (1988) Wayside trees of Malaya 3rd ed. The Malayan Nature Society, Kuala Lumpur, Malaysia

Coulter MC (1979) Seed abortion in *Anagallis arvensis* on southeast Farallon Island, California. Madroño 26:101-102

Eriksson O (1987) Regulation of seed-set and gender variation in the hermaphroditic plant *Potentilla anserine*. Oikos 49:165-171

Gorchov DL (1988) Effects of pollen and resources on seed number and other fitness components in *Amelanchier arborea* (Rosaceae: Maloideae). Am J Bot 75:1275-1285

Holtsford TP (1985) Nonfruiting hermaphroditic flowers of *Calochortus leichtlinii* (Liliaceae): potential reproductive functions. Am J Bot 72:1687-1694

Kato M., Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T (1995) Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. Res Popul Ecol 37:59-79

Lee TD, Bazzaz FA (1982) Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. Ecology 63:1363-1373

Momose K, Ishii R, Sakai S, Inoue T (1998) Plant reproductive intervals and pollinators in the aseasonal tropics: A new model. Proc Roy Soc London B 265:2333-2339

Nishikawa Y (1998) The function of multiple flowers of a spring ephemeral, *Gagea lutea* (Liliaceae), with reference to blooming order. Can J Bot 76:1404-1411

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am J Bot 86:1414-1436

Shimano K (2000) A power function for forest structure and regeneration pattern of pioneer and climax species in patch mosaic forests. Plant Ecology 146: 207-220

Vaughton G (1991) Variation between years in pollen and nutrient limitation of fruit-set in *Banksia spinulosa*. J Ecol 78:389-400

Willson MF, Price PW (1980) Resource limitation of fruit and seed production in some *Asclepias* species. Can J

Bot 58:2229-2233

Yoneda R, Ninomiya I, Patanaponpaiboon P, Ogino K (2002) Carbohydrate dynamics on [sic] trees in dry evergreen forest, Thailand. I. Diel fluctuation of carbohydrates in a whole tree of *Hydnocarpus ilicifolius*. Tropics 11:125-134

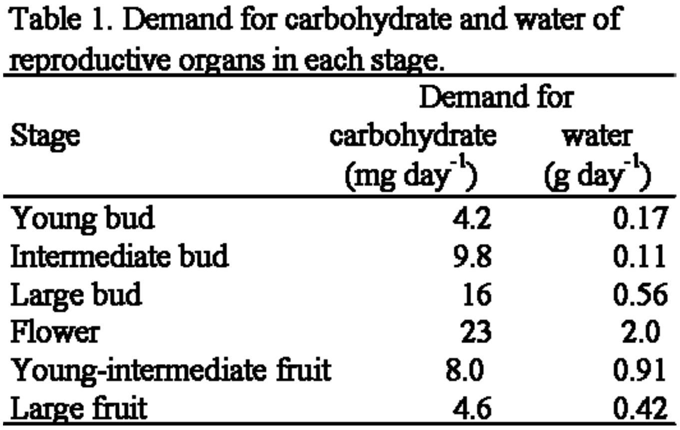

Table 1. Demand for carbohydrate and water of reproductive organs in each stage.

Stage	Demand for carbohydrate (mg day^{-1})	Demand for water (g day^{-1})
Young bud	4.2	0.17
Intermediate bud	9.8	0.11
Large bud	16	0.56
Flower	23	2.0
Young-intermediate fruit	8.0	0.91
Large fruit	4.6	0.42

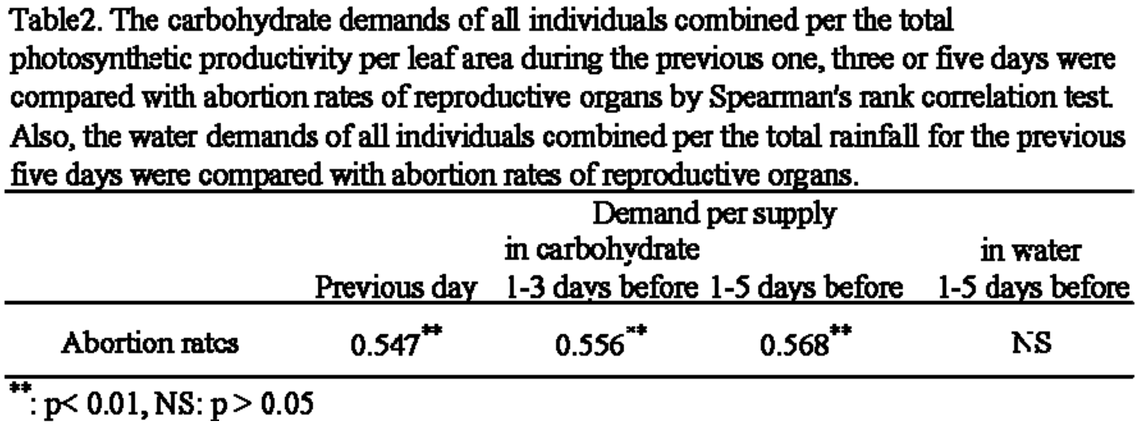

Table2. The carbohydrate demands of all individuals combined per the total photosynthetic productivity per leaf area during the previous one, three or five days were compared with abortion rates of reproductive organs by Spearman's rank correlation test. Also, the water demands of all individuals combined per the total rainfall for the previous five days were compared with abortion rates of reproductive organs.

	Demand per supply in carbohydrate: Previous day	Demand per supply in carbohydrate: 1-3 days before	Demand per supply in carbohydrate: 1-5 days before	Demand per supply in water: 1-5 days before
Abortion rates	0.547**	0.556**	0.568**	NS

**: $p < 0.01$, NS: $p > 0.05$

Variations in the Quantity of Attractants in Floral Odors and their Effects on Beetle Pollinator Arrivals in *Homalomena propinqua* (Araceae)

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Introduction

The Araceae represent one of the most diverse and abundant families in the humid tropics (Young 1986; Mayo et al. 1997), and their inflorescences are usually monoecious and protogynous (Bernhardt 2000). Beetle pollinators tend to arrive more frequently at the pistillate-phase inflorescences during the period of heat generation by the spadices than at the staminate-phase inflorescences, and this difference in timing can promote cross-pollination (Gibernau et al. 1999; Bernhardt 2000).

Homalomena propinqua (subfamily Aroidae) is a common understory herb found in lowland dipterocarp forests in Borneo, and two types of beetles (*Parastasia bimaculata* Guerin, Scarabaeidae; *Dercetina* sp., Chrysomelidae) are its main pollinators (Kato 1996; Momose et al. 1998; Kumano and Yamaoka 2006). Protogynous inflorescences of this species remain open for 3 days; the spathe is fully open by 0500 on the first day, and adhesive pollen begins to be shed on the morning of the second day. Beetle pollinators arrive at inflorescences mainly between 0700 and 1000, when the spadices generate endothermic heat (Kumano and Yamaoka 2006). Pollinators remain in the floral chamber with eating and/or mating, until the spathe closes tightly on the morning of the fourth day.

In our previous study (Kumano and Yamaoka 2006), we showed that the quantity of attractants released by the plant in the floral odors increased during the period of endothermic heat generation and proposed that the arrival of beetle pollinators may be affected by the increase in the quantity of these attractants. However, little information has been published about the attractiveness of floral odors even though beetle pollinators are attracted over long distances mainly by olfactory cues (Gottsberger and Silberbauer-Gottsberger 1991). In this study, we focused on variations in the quantity of attractants in floral odors to elucidate the relationship between quantity of attractants and arrivals of beetle pollinators in the *H. propinqua* pollination system. To do so, we first observed beetle pollinator arrivals during each floral stage, collected and analyzed floral odors, and then we conducted a bioassay of the main volatiles contained in these floral odors. We also investigated the relationships between variations in the quantity of attractants and the frequency of pollinator arrivals both during heat generation by the spadices and among floral stages. We use the results of these analyses to discuss the factors responsible for the reproductive success of *H. propinqua.*

Materials and Methods

Study site and materials

Our study was carried out in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20′N, 113°50′E; 150 to 250 m a.s.l.). We found two *H. propinqua* populations along small streams, located 100 m apart and separated by a ridge. All examinations were conducted using these two populations.

Observation of pollinator arrivals during each floral stage

To determine the frequency of beetle pollinator arrivals during each floral stage, we used unpollinated inflorescences (40 inflorescences on the first day of flowering, 44 inflorescences on the second day, and 19 inflorescences on the third day). All inflorescences were covered with polyethylene bags the day before flowering and remained covered until our observations began. Bags were removed at 0600, and pollinators were then free to arrive at the inflorescences. Thereafter, we caught pollinators inside the floral chambers at 1030 hours using polyethylene bags. Differences in pollinator arrivals were compared using a two-way ANOVA followed by Schéffe's multiple-comparison test.

Bioassays using the main compounds found in floral odors

Bioassays were conducted using laboratory standard chemicals for the five main components of floral odor in *H. propinqua*, which together represented 88% of the floral odors compositions by mass on the first day(Kumano and Yamaoka, 2006). To test their effectiveness, we added 100 μg per hour of each test compound on a Petri dish placed below a plant with no inflorescences. We recorded the species and the total number of pollinators that flew in a zig-zag pattern above the Petri dish or that landed on the dish between 0630 and 1030. As a negative control, we used an empty Petri dish placed beside the Petri dish containing the test compound. As a positive control (intact flowers), we counted the total number of beetles that remained in open flowers once per week when we conducted the bioassays. To confirm differences in attractiveness of pollinators between test compounds and positive controls (intact flowers), we transformed the number of individuals to log $(\chi + 1)$ scale and subjected the resulting data to a one-way ANOVA, followed by Dunnet's test.

Sampling of floral odors

To examine temporal variation in the quantity of attractants during the morning pollination period, we used eight unpollinated inflorescences per day from the first day to the third day of flowering. To confirm the variation in attractant quantities among floral stages, we used 10 unpollinated inflorescences and sampled consecutively from the first to the third day of flowering between 0700 and 0800 hours, when both of the main beetle pollinators visit most frequently (Kumano and Yamaoka, 2006). The methods used for collection and chemical analyses of the floral odors are described by Kumano and Yamaoka (2006). Temporal variations in the quantity of attractants were analyzed using the Kruskal-Wallis test combined with Scheffé's test. Differences among floral stages were tested using Friedman's test combined with a Steel-Dwass test.

Results

Observation of pollinator arrivals at each floral stage

The mean number of pollinator arrivals at each floral stage is shown in Fig. 1. The mean number of P. bimaculata arrivals decreased significantly from day 1 to day 3 (Schéffe's test, $P < 0.01$). On the other hand, the mean number of Dercetina sp. arrivals showed no significant differences among floral stages ($P > 0.05$).

In addition, the number of P. bimaculata arrivals on the third day was significantly lower than the number of Dercetina sp. arrivals at every floral stage (P < 0.05).

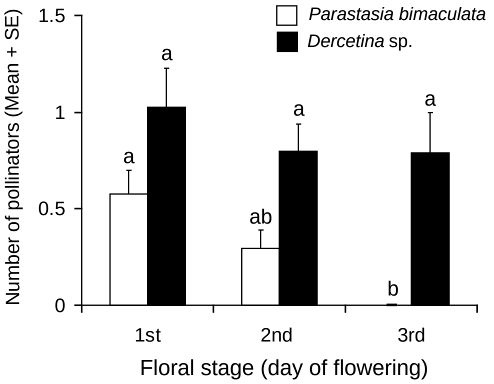

Fig. 1 Mean number (+ 1SE) of pollinators (*Parastasia bimaculata* and *Dercetina* sp.) arrivals on each floral stage inflorescence (the first day = 40 inflorescences, the second day = 40, the third day = 19). Different letters indicate significant differences (Sheffé test, P < 0.05). Open bars show *P. bimaculata*, and solid bars show *Dercetina* sp.

Table 1 Attractiveness of five main compounds in floral odors of *H. propinqua* and mixtures of them toward beetle pollinators (*Parastasia bimaculata* and *Dercetina* sp.).

Attractants [2]	Number of pollinator (mean ± SE)[1]	
	P. bimaculata	*Dercetina* sp.
α-Pinene (P)	0	0 *
2-Butanol (B)	0	0 *
2-Methyl-3-buten-2-ol (M)	0.13 ± 0 .13	0 *
2-Heptanol (H)	0	0 *
Veratrole (V)	0	1.71 ± 0.52
BP	0	0 *
BM	0	0.29 ± 0.18
BH	0	0.14 ± 0.14 *
BV	0.57 ± 0.30	2.29 ± 1.30
VM	0.29 ± 0.29	3.71 ± 1.43
VP	0	4.00 ± 1.09
VH	0	1.71 ± 0.47
BVP	0.29 ± 0.18	0.57 ± 0.20
BVM	0.14 ± 0.14	0.57 ± 0.20
BVH	0.86 ± 0.40	0.29 ± 0.18
BVPH	0.50 ± 0.31	1.20 ± 0.39
BVMH	0.13 ± 0.13	0.75 ± 0.25
BVPMH	0.60 ± 0.25	4.60 ± 1.44
Positive control (intact flowers	0.65 ± 0.15	2.70 ± 0.59

[1] Means in the same column with asterisk are significantly different between the positive control based on Dunnet test (P < 0.05). Each trial conducted on the separate day.

[2] Capital letters mean abbreviated names of five compounds. P: α-pinene, B: 2-butanol, M: 2-methyl-3-buten-2-ol, H: 2-heptanol, V: veratrole

Bioassays using the main components of the floral odors

The results of our bioassay are shown in Table 1. The positive controls (intact flowers) showed that *Dercetina* sp. arrived at inflorescences four times more frequently than *P. bimaculata*. No pollinators were attracted by empty Petri dishes (the negative controls). *Parastasia bimaculata* was attracted by 2-methyl-3-buten-2-ol (M), veratrole (1,2-dimethoxybenzene; V) plus M, and all mixtures containing 2-butanol (B) plus V thus the minimum components necessary for the attraction of *P. bimaculata* were M and BV. In contrast, *Dercetina* sp. was attracted by V, all mixtures containing V, and BM, which therefore appear to be the minimum components required for the attraction of *Dercetina* sp. Of these minimum components, BV and veratrole were the more efficient attractants for *P. bimaculata* and *Dercetina* sp., respectively.

Variations in the quantity of attractants in floral odors

Temporal variations in the quantity of the minimum components of attractants are shown in Table 2. On the first day of flowering, quantities both of BV and V increased significantly between the 0530 to 0630 period and the 0700 to 0800 period, then remained above the initial level (but not significantly) until the 10:00 to 11:00 period (Schéffe's test, $P < 0.05$). On the second day, the pattern was similar, but the quantity didn’t vary significantly among times for either attractant (Kruskal-Wallis test, $P > 0.05$). On the third day, the pattern was similar to that on the second day, but with a lower quantity of attractants, and quantities didn’t vary significantly among the five collection periods (Kruskal-Wallis test, $P > 0.05$). Variations in the

Table 2 Time variations in the quantity of attractants in floral odors of *H. propinqua* from 05:30 to 12:30 hours over the flowering periods (μg/ h / flower).

flowering day		Time				
		5:30-6:30	7:00-8:00	8:30-9:30	10:00-11:00	11:30-12:30
Attractants of *P. bimaculata*						
BV (2-butanol + Veratrole)						
1st	Median	**13.64** ^{a}	**97.54** ^{b}	**49.53** ^{ab}	**28.08** ^{ab}	**13.67** ^{a}
	Quatile	5.64 - 33.97	55.19 - 117.41	25.66 - 80.97	16.86 - 49.34	7.12 - 15.71
	Min - Max	2.38 - 57.92	52.26 - 194.08	11.88 - 141.39	13.54 - 80.62	6.33 - 63.25
2nd	Median	**41.32**	**77.76**	**41.76**	**38.69**	**11.7**
	Quatile	17.25 - 99.48	42.24 - 128.31	27.98 - 90.54	16.75 - 102.96	6.74 - 42.45
	Min - Max	2.38 - 456.27	29.23 - 172.37	22.89 - 121.78	5.28 - 106.98	2.73 - 85.00
3rd	Median	**11.89**	**12.36**	**14.53**	**15.51**	**3.66**
	Quatile	8.58 - 16.51	6.22 - 44.43	3.13 - 18.13	10.06 - 20.48	2.61 - 4.27
	Min - Max	2.69 - 23.93	7.89 - 163.61	0.81 - 19.85	1.74 - 23.82	1.21 - 4.78
Attractant compound of *Dercetina* sp.						
Veratrole						
1st	Median	**0.67** ^{a}	**16.29** ^{b}	**10.23** ^{ab}	**3.55** ^{ab}	**2.08** ^{a}
	Quatile	0.25 - 1.14	10.06 - 27.59	2.59 - 20.21	1.63 - 4.62	1.05 - 2.37
	Min - Max	0 - 6.06	5.50 - 29.55	1.78 - 34.95	1.49 - 5.34	0.46 - 5.40
2nd	Median	**6.46**	**18.02**	**8.06**	**4.44**	**3.9**
	Quatile	1.88 - 19.45	9.82 - 38.99	5.73 - 12.66	3.27 - 23.57	1.94 - 7.95
	Min - Max	0.29 - 205.95	2.51 - 53.19	2.10 - 21.93	2.86 - 25.50	0.91 - 18.25
3rd	Median	**1.66**	**7.02**	**4.05**	**1.91**	**1.88**
	Quatile	1.29 - 6.81	0.83 - 19.92	0.95 - 7.03	0.92 - 3.47	1.4 - 2.11
	Min - Max	0.21 - 15.73	0 - 141.25	0.11 - 9.28	0.14 - 3.87	0.13 - 2.63

Medians with different letter are significantly different among five collection times in each day (Sheffé test, $P < 0.05$).

quantity of attractants among floral stages are shown in Fig. 2. The quantity of BV decreased steadily over time, and the difference compared with the first day became significant on the third day (Steel-Dwass test, $P < 0.05$). The quantity of veratrole also decreased slightly from the first day to the third day, but the difference was not significant (Friedman's test, $P > 0.05$).

Discussion

In general, the pistillate phase (stigma receptivity) and the staminate phase (anther dehiscence) of protogynous Araceae inflorescences do not overlap, therefore obligate outcrossing seems to be the general rule (Mayo et al. 1997). Our results showed that *P. bimaculata* tended to arrive during the pistillate phase, when heat generation occurs; in contrast, *Dercetina* sp. arrived at inflorescences regardless of the floral stage (Fig. 1). To confirm the relationship between these behaviors and variations in the quantity of attractants, we examined the variations in quantities of BV and veratrole, and these were consistent with the frequency of arrivals of both insects during heat generation (Table 2) and among floral stages (Fig. 2). These results demonstrated that *P. bimaculata* is attracted by inflorescences that produce more BV when the volatilization of BV increases due to heat production by the spadices, whereas *Dercetina* sp. is attracted to even relatively small amounts of veratrole, and can thus arrive at inflorescences both during and after heat generation. Thus, *P. bimaculata* appears to have adapted to the protogynous *Homalomena* inflorescence. However, the number of *Dercetina* sp. arrivals was approximately four times that of *P. bimaculata* (Table 1, positive control), thus *H. propinqua* may be capable of attracting both specialized and general anthophagous pollinators to promote both the female and the male reproductive success.

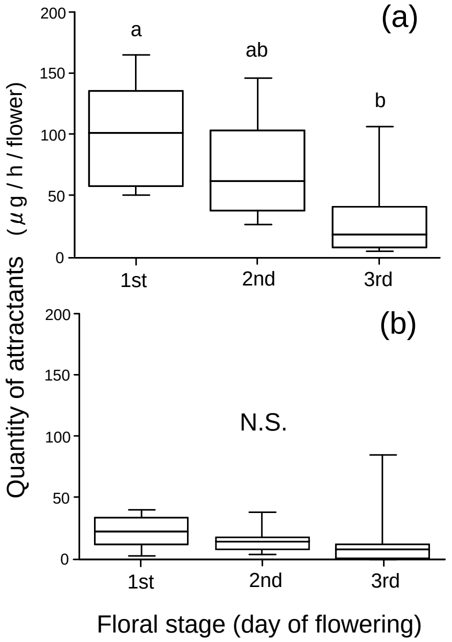

Fig. 2 Variations in the quantity of attractants among floral stages. Maximum and minimum values for each sample are shown at upper and lower ends of the vertical bars, respectively, and 75% and 25% points are given by the upper and lower ends of the box, respectively. The middle bar indicates median (each n = 10). Different letters indicate significant differences (Steel-Dwass test, $P < 0.05$). N.S. means no significant differences (Steel-Dwass test, $P > 0.05$). (a) BV (2-butanol + veratrole), (b) veratrole

References

Bernhardt P (2000) Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. Plant Sys Evol 222:293-320

Gibernau M, Barabé D, Cerdan P, Dejean A (1999) Beetle pollination of *Philodendron solimoesense* (Araceae) in

French Guiana. Int J Plant Sci 160: 1135-1143

Gottsberger G, Silberbauer-Gottsberger I (1991) Olfactory and visual attraction of *Eriscelis emarginata* (Cyclocephalini, Dynastinae) to the inflorescence of *Philodendron selloum* (Araceae). Biotropica 23:23-28

Kato M (1996) Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. Am J Bot 83:732-743

Kumano Y, Yamaoka R (2006) Synchronization between temporal variation in heat generation, floral scents and pollinator arrival in the beetle-pollinated tropical Araceae *Homalomena propinqua*. Plant Spec Biol 21:173-183

Mayo SJ, Bogner J, Boyce PC (1997) The genera of Araceae. Royal Botanical Gardens, Kew, UK.

Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD, Itioka T, Hamid AA, Inoue T (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. Am J Bot 85:1477-1501

Young HJ. (1986) Beetle pollination of *Dieffenbachia longispatha* (Araceae). Am J Bot 73:931-944

Spatial Distribution of Two Bumble Bee Species in an Agro-Forestry Landscape

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Introduction

Bumble bees are important contributors to the pollination of temperate plants, including herbs, shrubs, and trees (Heinrich 1979; Yumoto 1987). They are important pollinators in both forests and open lands around artificially managed landscapes (Kato and Miura 1996; Walther-Hellwig and Frankl 2000; Osada et al. 2003; Yamazaki and Kato 2003), although little is known about their spatial distribution, i.e., habitat use, in these landscapes (Bhattacharya et al. 2003).

Forestry has changed natural forests into artificially structured forest landscapes. *Satoyama* forest is an east-Asian traditional forestry ecosystem in which many different human-managed landscape units, including both forest units (secondary forests, conifer plantations, and sometimes old-growth forests) and open-land units (cutover lands) are intermixed (Tabata 1997; Fukamachi et al. 2001). Different plant species compositions have been reported from different *satoyama* forest landscape units.

Two bumble bee species, the short-tongued *Bombus ardens ardens* Smith (*B. ardens*) and the long-tongued *B. diversus diversus* Smith (*B. diversus*), coexist and are dominant in *satoyama* forests (Kato and Miura 1996; Osada et al. 2003). *B. ardens* visits the simple-structured flowers of trees and shrubs (Yumoto 1987; Katayama 1996; Osada et al. 2003), whereas *B. diversus* generally prefers the complex floral structures of herbs, such as long corolla tubes (Washitani et al. 1994; Dohzono and Suzuki 2002). The local extinction of *B. diversus* because of habitat loss might reduce the sexual reproduction of plant species pollinated by this bee (Washitani et al. 1994). Eusocial *Bombus* species visit flowers of many plant taxa within a season. The diversity of woody species with shallow flowers is high in forests, whereas the diversity of herbaceous species with complex flowers is high both on the forest floor and in open lands. Thus, we predicted that within a given landscape, *B. ardens* would inhabit forests and *B. diversus* would inhabit both forests and open lands. Landscape units that lack flowering plant diversity, such as conifer plantation monocultures, would be avoided by both bumble bee species.

We used window traps to examine the spatial distribution (i.e., among several landscape units) of the two *Bombus* species in a *satoyama* forest. We also investigated the diversity of insect-pollinated plant species in five landscape units around the study area. We discuss the relationships between flower preference and the spatial distribution of the two *Bombus* species. We also address the management of landscape units for the conservation of the bumble bee pollination system in *satoyama* in which the traditional forest management system has been changing.

Materials and methods

Bumble bee species

Bombus ardens is widely distributed in Japan and Korea, except for Hokkaido and the Ryukyu Islands. B. *diversus* is endemic to the Japanese islands. The average colony life span of the two species differs widely; B. *ardens* lives from early April to early July, whereas B. *diversus* lives from late April to mid-October (Katayama 1996; Nakamura and Toquenaga 2002).

Study area and landscape units

In 2003, we investigated five landscape units around Ogawa Forest Reserve (OFR; 36°56' N, 140°35' E; 610–660 m elevation), which is located in the southern part of the Abukuma Mountains near Kitaibaragi City, Ibaraki Prefecture, Japan. We investigated five landscape units in and around OFR; these consisted of four forest units and one open-land unit:

- Old-growth deciduous forest (>100 years old): The dominant tree species were *Quercus crispula, Q. serrata*, *Fagus crenata,* and *F. japonica* (all Fagaceae), *Carpinus* spp. (Carpinaceae), and *Acer* spp. (Aceraceae) (Nakashizuka and Matsumoto 2002);
- Remnant forest (>100 years old): This consists of a narrow belt (30–50 m wide) of old-growth forest preserved as a boundary or firebreak. The dominant species were similar to those of the old-growth forest;
- Secondary deciduous forest (11–24 years old): The four secondary forests that we investigated were used for the production of mushroom logs and wood chips (Suzuki 2002). The dominant species were *Q. crispula*, *Q. serrata,* and *Carpinus laxiflora* (Suzuki 2002);
- Conifer plantation (25–50 years old): Two Japanese cedar (*Cryptomeria japonica*) and two hinoki cypress (*Chamaecyparis obtusa*) stands were investigated;
- Cutover lands (secondary forest 5–7 years after clear-cutting): *Rubus* spp., *Aralia elata,* and *Stephanandra incisa* were abundant, with a vegetation height of 2–4 m.

Bumble bee collection

We used window traps to collect bumble bees. The bumbles tended to strike against plastic transparent panes (45 cm high x 36 cm wide) and drop into a tray filled with 2 L of water and a small amount of detergent (Inari 2003). At the OFR old-growth forest and remnant forest, we set up four trap sites ≥ 200 m apart. We also set up trap sites in four secondary stands, four plantations, and three cutover lands (two sites in one large stand and two sites in two small stands). In all, we set up 20 study sites within an area of approximately 90 ha.

At each forest site, we set three traps at different heights to cover different strata: forest floor, 0.5 m;

shrub layer, ~3 m; and under-canopy layer, 8–20 m above the ground, depending on forest height. Two traps per site were set at a height of ~1.5 m in the cutover lands. A total of 56 traps were used. All traps were set at least 15 m inside each landscape unit. The window traps were set once a month from April to October, and the bumble bees were collected 6 days later.

For statistical analyses, we pooled data from the cutover lands and the pasture because these landscape units had similar floras (Fig. 3). We compared the total numbers of *B. ardens* and *B. diversus* individuals collected among the landscape units using a chi-square test. The expected number of individuals was calculated assuming a uniform distribution among the traps (we considered the number of traps per landscape unit). The distribution pattern between castes (queens and workers) was analyzed for *B. diversus*. We also used the chi-square test to examine the vertical distribution of the two species among forest units (primary, remnant, secondary, and plantation forests).

Diversity of insect-pollinated plant species in the landscape units

We investigated the insect-pollinated (entomophilus) plant diversity in the old-growth OFR stand, the remnant forest, two secondary forests (12 and 24 years old), two conifer plantations (both 32 years old), cutover lands (5 and 6 years old), and two pastures near OFR. We delineated one 10 x 100 m plot in each stand, except in one secondary forest in which the plot was 10 x 90 m. We inventoried all tree stems ≥ 5 cm in diameter at breast height and identified all shrubs ≥ 200 cm in height in each 5 x 5 m subplot. We also laid out 40 1 x 1 m quadrats inside each plot (36 quadrats in the young secondary forest plot) and inventoried all herbaceous species within each quadrat. We counted the number of entomophilus tree, shrub, and herb species for each plot and further subdivided herbs into early bloomers (April–June) and late bloomers (July–October). The number of species in each category was compared among the landscape units.

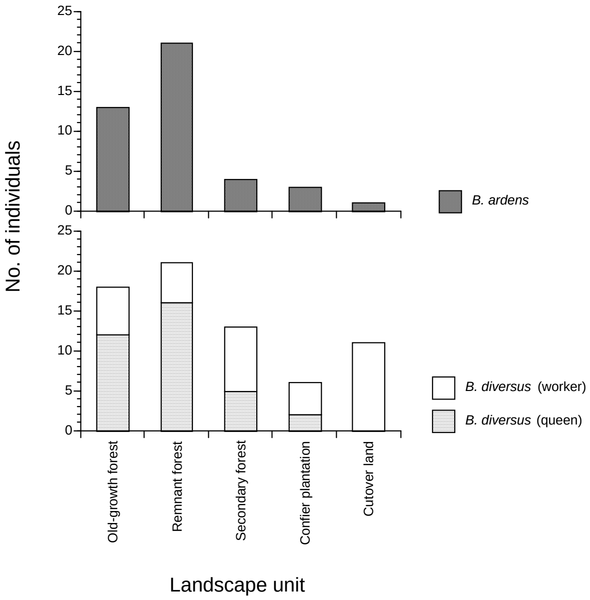

Fig. 1 Numbers of bumblebees collected in each landscape unit.
B. diversus individuals were divided into two groups: queens (shaded bars) and workers (open bars).

Results

Bumble bee collection using window traps

The total trappings for the year comprised 16 queens and 26 workers of *B. ardens*, 37 queens, 34 workers, and three males of *B. diversus*, and two queens and three workers of *B. hypocrita*. *B. ardens* queens were collected from April to June and workers from May to August. *B. diversus* queens were collected from April to June, whereas workers were collected from June to October (Fig. 1).

The number of *B. ardens* collected was significantly greater in old-growth and remnant forests than in other landscape units ($\chi^2 = 28.7$, d.f. = 4, $P < 0.001$; Fig. 1), the distribution pattern was not different between queens and workers. However, there was no significant difference in the total number of *B. diversus* collected among landscape units ($\chi^2 = 8.9$, d.f. = 5, $P > 0.05$; Fig. 1). *B. diversus* queens were caught more frequently in old-growth and remnant forests than in other units, but more workers were collected in cutover lands than in forest units (queens, $\chi^2 = 22.2$, d.f. = 5, $P < 0.001$; workers, $\chi^2 = 10.3$, d.f. = 5, $P < 0.05$; Fig. 1).

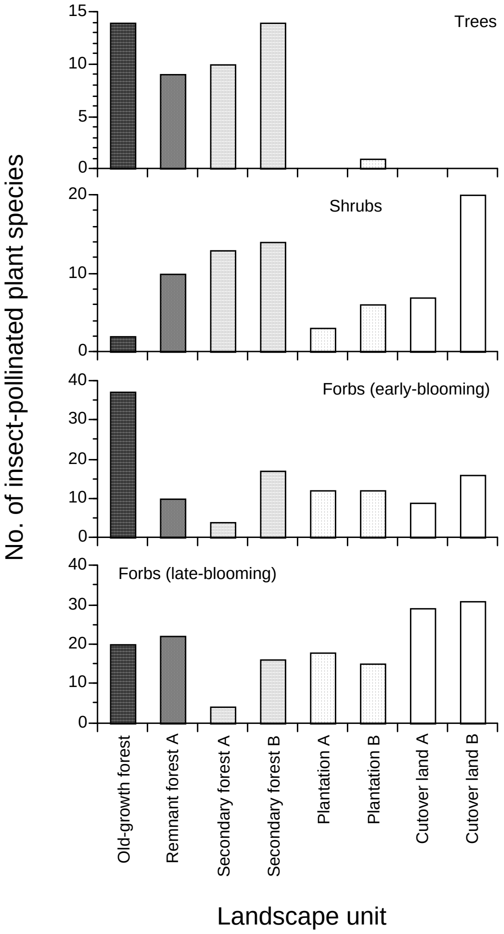

Fig. 2 Number of insect-pollinated plant species in five landscape types. Bumble bees were also trapped in the old-growth forest, remnant forest, secondary forest B, and cutover land A.

Diversity of insect-pollinated plant species in the landscape units

The diversity of entomophilus trees was high in old-growth, remnant, and secondary forests (Fig. 2). We rarely found entomophilus tree species in the canopy or subcanopy strata of plantations. Entomophilus shrub diversity was high in one cutover area and in secondary forests, but was relatively low in old-growth and remnant forests and plantations (Fig. 2). Among all the landscape units, the number of early-blooming herbs was largest in the old-growth forest (Fig. 2). Late-blooming herbs were more abundant in open-land units than in forest units (Fig. 2).

Discussion

Around OFR, most *B. ardens* queens and workers were caught in old-growth and remnant forests. We rarely collected *B. ardens* in secondary forests, conifer plantations, or cutover lands. We predicted that *B. ardens* inhabits forest vegetation in which woody species diversity is high. However, the diversity of woody species, i.e., trees and shrubs, was also high in secondary forests and cutover lands, respectively. Why was *B. ardens* not caught more frequently in these landscape units? The population dynamics of *B. ardens* are strongly affected by the abundance of tree flowers (Inari 2003). However, many trees in secondary forests and cutover lands were not large enough to flower. *B. ardens* may respond not only to woody diversity, but also to the abundance of flowers in trees.

As predicted, *B. diversus* was distributed in both forest and open-land units. Interestingly, we found a large difference in spatial distribution patterns between castes. Like *B. ardens* individuals, *B. diversus* queens were concentrated in old-growth and remnant forests, whereas the workers were more often trapped in open-land units. The rich diversity of early-blooming herbs on the floor of old-growth forests may attract the queens. However, why *B. diversus* queens were rarely caught in open-land units, where entomophilus herbaceous flower diversity is as high as that in old-growth, remnant, and secondary forests, is difficult to explain. Flowering individuals of spring ephemerals (e.g., *Erythronium japonicum*, *Corydalis lineariloba*, and *Viola* spp.) and shrubs (e.g., *Rhododendron obtusum* var. *kaempferi* and *Kerria japonica*) visited by *B. diversus* were not abundant in open-land units (A. Ushimaru personal observation). This scarcity of spring ephemeral flowers may be one reason that queens infrequently visit open-land units in the spring. In contrast, late-blooming herbs were found more frequently in open-land units than in forest units, suggesting that *B. diversus* queens forage on the flowers of forest herbs and shrubs until early summer, and workers spread into open lands to seek summer- and autumn-blooming herbs. Thus, the seasonal shift in the distribution of floral resources within the *satoyama* landscape results in inter-caste differences in spatial distribution.

We seldom collected bumble bees of either species in conifer plantations. During and after World War II, old-growth forests were widely replaced by conifer plantations (Nagaike et al. 2005). However, conifer plantations have not been extensively managed because of high costs. Infrequent logging and thinning has created a very dark forest floor, with consequent low understory plant diversity (Nagaike et al. 2005). Although forest-floor plants were not necessarily rare in plantations, we found very few flowering individuals because of low light conditions (A. Ushimaru, personal observation). This lack of flowers may account for the rarity of bumble bees.

Our results showed that old-growth stands are important habitat for both bumble bee species and for early-blooming insect-pollinated plants. In contrast, open lands play a significant role in the mutualism between *B. diversus* and late-blooming herbs. However, during the past decades, changes in official forest management policy have resulted in a rapid decrease in old-growth forests and cutover lands and an increase in conifer plantation monocultures (Fukamachi et al. 2001; Kato 2001; Inoue 2003; Nagaike et al. 2005). These landscape changes may have decreased the amount of habitat available for many plants and insects, including pollinators such as bumble bees (Tabata 1997; Kato 2001; Inoue 2003). The conservation of old-growth stands and the creation of new cutover lands by periodic logging are encouraged to conserve bumble bee–plant interactions.

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References

Bhattacharya M, Primack RB, Gerwein J (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? Biol Consev 109: 37-45

Dohzono I, Suzuki K (2002) Bumblebee-pollination and temporal change of the calyx tube length in *Clematis stans* (Ranunculaceae). J Plant Res 115: 355-359

Fukamachi K, Oku H, Nakshizuka T (2001) The change of a satoyama landscape and its causality in Kamiseya, Kyoto Prefecture, Japan between 1970 and 1995. Landscape Ecol 16: 703-717

Heinrich B (1979) Bumblebee Economics. Harvard University Press, Cambridge, Massachusetts

Inari N (2003) Seasonal changes in vertical distribution of bumblebees and their floral resources within a cool-temperate deciduous forest in northern Japan. In: Toda M (ed) Reports on pollination network in a cool-temperate deciduous forest. Hokkaido University, Hokkaido, pp 27-41

Inoue T (2003) Butterfly fauna in and near the Ogawa Forest Reserve. Bull Forestry Forest Prod Res Inst 2: 237-246.

Katayama E (1996) Survivorship curves and longevity for workers of *Bombus ardens* Smith and *Bombus diversus* Smith (Hymenoptera, Apidae). Jap J Entomol 64: 111-121.

Kato M (2001) ‘Satoyama’ and biodiversity conservation: ‘Satoyama’ as important insect habitats. Glob Environ Res 5:135-149.

Kato M, Miura R (1996) Flowering phenology and anthophilous insect community at a threatened natural lowland marsh at Nakaikemi in Tsuruga, Japan. Contr Biol Lab Kyoto Univ 29:1-48

Nagaike T, Yoshida T, Miguchi H, Kamitani T, Nakashizuka T (2005) Rehabilitation for species enrichment in abandoned coppice forests in Japan. In: Stanturf JA, Madsen P (eds) Restoration of boreal and temperate forests. CRC Press, London, pp 371-381

Nakamura H, Toquenaga Y (2002) Estimating colony locations of bumble bees with moving average model. Ecol Res. 17: 39-48

Nakashizuka T, Matsumoto Y (Eds) (2002) Diversity and interaction in a temperate forest community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo.

Osada N, Sugiura S, Kawamura K, Cho M, Takeda H (2003) Community-level flowering phenology and fruit set: comparative study of 25 woody species in a secondary forest in Japan. Ecol Res 18: 711-723

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. In Nakashizuka, T., Matsumoto, Y. (Eds) Diversity and interaction in a temperate forest community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo, pp 27-40

Tabata H (ed) (1997) Satoyama and its conservation (in Japanese). Hoikusha, Osaka

Walther-Hellwig K, Frankl R (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. J Appl Entomol 124: 299-306

Washitani I, Osawa R, Namai H, Niwa M (1994) Patterns of female fertility in heterostylous *Primula sieboldii* under severe pollinator limitation. J Ecol 82: 571-579

Yamazaki K, Kato M (2003) Flowering phenology and anthophilous insect community in a grassland ecosystem at Mt. Yufu, western Japan. Contr Biol Lab Kyoto Univ 29: 255-318

Yumoto T (1987) Pollination systems of a warm temperate evergreen broad-leaved forest in Yakushima Island. Ecol Res 2: 133-145

Effects of Local Density and Forest Fragmentation on Reproductive and Regeneration Success of *Shorea laxa* (Dipterocarpaceae)

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Introduction

Plant–animal interactions such as pollination, seed dispersal, and herbivory play pivotal roles in plant reproductive and regeneration processes (Ghazoul and McLeish 2001). The scale and intensity of these interactions are affected by the local density of host plants and their habitat area (Garcia and Chacoff 2007). Aggregation of host plants may enhance their pollination success, resulting in enhanced seed set, outcrossing, or escape from seed predation as a result of predator saturation. However, recent rapid deforestation, especially in the tropics, has severely reduced pollinator populations and species richness, decreasing the reproductive output of plants in remnant habitats and increasing inbreeding depression (Aizen and Feinsinger 1994; Young et al. 1996). Similarly, environmental change in the remnant forest also results in recruitment losses and rapid changes in species composition (Laurance et al. 2006).

In this study, we focused on the reproduction of *Shorea laxa* Slooten, one of the ecologically and commercially key dipterocarp species in the Southeast Asian tropical forest. We investigated whether reproductive success and seedling recruitment were affected by forest type (primary continuous forest versus fragmented forest, known locally as *pulau*) and local adult tree density in terms of (1) seed set, (2) seed predation by insects, (3) seed predation by vertebrates, (4) the selfing rate, and (5) seedling survival.

Materials and methods

Study site and species

We conducted our field study in and around Lambir Hills National Park (LHNP), Sarawak, Malaysia (4°2'N, 113°50'E; 150 to 200 m a.s.l.). We established a 80-ha study plots in LHNP, which contains continuous stands of primary forest. The fragmented forests resulted from traditional land use by local peoples and were located near LHNP (typically less than 1 km). These areas were originally primary forest, although some selective cutting of trees for house construction has occurred historically. One *pulau* was used for our study plot; it covered 5 ha, was located 200 m from the edge of the primary forest, was surrounded by secondary forests, and was located mainly in hilly terrain.

Shorea laxa (section Richetioides, Dipterocarpaceae) is commonly found in northeastern Borneo and becomes a canopy tree that reaches heights of 30 to 40 m. The mean density of mature stems in primary forest (diameter at breast height ≥ 30 cm) of *S. laxa* was 1.8 stems ha^{-1} (Takeuchi et al. 2005). The species flowers and produces seeds at irregular, supra-annual intervals. The fresh seed mass ± SD of *S. laxa* averages 18.3 ± 12.3 g (Takeuchi and Nakashizuka 2007). In LHNP, flowering occurred in early March 2005.

Census of flower and seed fate before seed dispersal, and seedling survival

Two seed traps (0.5 m^2 surface area) were placed beneath the crowns of 20 trees per plot in each type forest in early March 2005, just before flowering, and were monitored until late October 2005 to describe the patterns of seed fate and predation. Every week or two, we collected all seeds present in the seed traps. Seed traps were made of nylon cloth with a mesh size of 1 mm and were set 1 m above the ground. All collected seeds were counted, measured, and classified into four categories: sound, immature, attacked by insects, or attacked by vertebrates. Seeds that had holes on their surface or larvae or frass inside were categorized as having been attacked by insects. Seeds attacked by arboreal vertebrates were either broken into pieces or exhibited clear tooth marks. Seeds with insect damage rarely germinated; those that did were classified as sound (also see Nakagawa et al. 2005).

Seedling plots containing over 50 seedling individuals (ranging in size from 1×1 m to 1×5 m) were established beneath the canopy after seed dispersal in September 2005. Seedling survival was measured in 7 months later (i.e., in April 2006).

Environmental data

To characterize the light conditions at the forest floor, we measured the percent canopy openness using a digital camera with a fisheye lens (CoolPix 910, Nikon). Two or three images were taken beneath the canopy at each sampling site at ground level and at a 0.2-m height, and were analyzed using Gap Light Analyzer v2.0 (Frazer et al. 1999).

Under the canopy of each tree, we quantified the soil-water potential using the method of Deka et al. (1995). Soil samples were taken on the morning of 25 October 2006, after a relatively dry spell with no rain for 6 consecutive days. We extracted two 3-cm cores to a depth of 10cm beneath the canopy after removing the surface litter. Each soil sample was sealed in a plastic box for 8 days with filter paper (Whatman No. 42) placed in the soil. On 31 October 2006, the filter paper was weighed to within 1 mg after quickly removing soil with a small paintbrush, and the soil-water potential was calculated (Deka et al. 1995).

DNA analysis and estimation of selfing rate of seeds

Seed samples for estimating selfing rate were collected beneath the 14 focal trees in late August. Total DNA was extracted from the cotyledon (seeds) or cambium (adult trees) of each individual using the DNeasy Plant Mini Kit (Qiagen). Genotypes of DNA samples were scored using five to six pairs of microsatellite PCR primers that had been developed for *Dipterocarpus tempehes* Slooten (Isagi et al. 2002), *Shorea leprosula* Miq. (Lee et al. 2004), and *Shorea lumutensis* Sym. (Lee et al. 2006). For PCR, we used 10-µL reaction mixtures containing 1× PCR Buffer (Promega), 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 200 nM of each primer (one of each pair was fluorescently labeled), 1 ng of template DNA, and 0.25 to 0.50 units of *Taq* polymerase (Promega). PCR amplification was carried out for 5 min at 94°C, followed by 30 cycles of 30 s denaturing at 94°C, 30 s annealing at the optimized temperature, and 30 s extension at 72°C, with a final 3-min incubation at 72°C, using a GeneAmp^{TM} PCR System (Model 9700 and Model 2700; PE Applied Biosystems). The genotypes were determined using an ABI 3100 Genetic Analyzer and version 3.7 of the GeneScan^{TM} software (PE Applied Biosystems). To estimate whether the analyzed seed had been self-fertilized, we examined the genotype similarity between the seed and the presumed mother tree using Cervus 2.0 software (Marshall et al. 1998).

Nearest-neighbor index (PULAU)

We calculated a nearest-neighbor index (*NNI*) for each focal tree based on the proximity of conspecific trees:

$$NNI = \sum \left(\frac{1}{n_{ij}} \right)$$

where n_{ij} is the distance (m) between the focal tree*i* and the other conspecific tree*j* located within 200 m of the focal tree (Ghazoul and McLeish 2001). By summing the reciprocal of the distances, this index considers both the number of surrounding flowering trees and their distance, weighted more heavily for the nearest neighbors. Thus, a high index value indicates low isolation and the existence of many nearby neighbors.

Statistical analysis

Data were analyzed using the stepwise generalized linear mixed model (GLMM) techniques implemented in the R statistical software (http://www.r-project.org/) to test correlations between seed fate and *NNI*. For seedlings, we tested the effects of *NNI* and environmental variability across habitats (canopy openness and soil-water potential) on the seedling survival. The *NNI* values were ln-transformed, canopy openness values were arcsine-transformed, and water potential values (negative values, converted into positive values for analysis) were ln-transformed before the analysis.

Results

Effect of forest type

Large numbers of seeds fell before they had matured (97% or more, Table 1). The proportion of mature seeds was significantly higher in *pulau* than in primary forest (Table 1). The proportion of seeds >1 cm in diameter that were attacked by insects exceeded the proportion attacked by vertebrates in both forest types, but the difference was greater in *pulau*. Predation by vertebrates was significantly higher in the primary forest, but predation by insects did not differ significantly between forest types (Table 1). The selfing rate of mature seeds was significantly higher in primary forest than in *pulau* (Table 2).

Seedling survival did not differ significantly between primary forest and *pulau* (Table 3). *Pulau* had significantly more light (a greater canopy openness) and significantly less water (lower water potential) than the primary forest (Table 4). We found no interaction between light intensity and water potential (data not shown).

Table1 Number of focal tree, analyzed seeds and proportion of each seed fate.

Difference between forest type(primary vs. *pulau*) was tested by ANOVA.

Forest	No. of focal tree	Average no of total analyzed seeds±SD	Proportion of Mature seeds ±SD	Proportion of seed fate (＞1cm diameter) ±SD		
				Insect	Vertebrates	Sound
Total	20	2058.2 ±923.8	0.027 ± 0.012	0.262 ± 0.094	0.147 ± 0.092	0.590 ± 0.137
Primary	15	2152.9 ±1011.2	0.026 ± 0.012	0.276 ± 0.101	0.183 ± 0.076	0.540 ± 0.115
Pulau	5	1774.0 ±583.0	0.030 ± 0.013	0.220 ± 0.061	0.040 ± 0.012	0.740 ± 0.070
p			<0.05	n. s.	<0.01	<0.01

Table 2 Number of focal tree and selfing rate in both forest type.
Difference between forest type (primary vs. *pulau*) was tested by ANOVA.All analyzed seeds were mature.

Forest	No. of focal tree	Average no of total analyzed mature	Selfing rate ±SD
Total	14	42.93 ± 17.26	0.080 ± 0.125
Primary	9	42.33 ± 5.34	0.094 ± 0.147
Pulau	5	44.00 ± 30.14	0.054 ± 0.080
p			<0.01

Table 3. Number of focal tree and survival rate (after 8 month) of seedlings in both forest types. Difference between forest type (primary vs. *pulau*) was tested by ANOVA.

Forest	No. of focal tree	Average no of total analyzed seedlings±	Survival rate ±SD
Total	11	50.0 ± 13.05	0.665 ± 0.173
Primary	6	58.0 ± 7.78	0.699 ± 0.184
Pulau	5	40.0 ± 11.55	0.623 ± 0.173
p			n. s.

Table 4. Environment diffarence between primary forest and *pulau*.

	Water Potential(kPa)±SD	Canopy Openness (%) ±SD
Primary	-0.01 ± 0.01	5.90 ± 0.54
Pulau	-0.28 ± 0.29	7.40 ± 0.40
p	<0.05	<0.05

Effect of local host density

Seed mature rates (the proportion of mature seeds) were negatively correlated with *NNI* in both forest types; the correlation was significant in primary forest and marginally significant in *pulau* (Table 5). The proportion of seeds predated by insects was not significantly correlated with *NNI* in either forest type, but the proportion of seeds predated by vertebrates was marginally positively correlated with *NNI* in the primary forest. We also found a significant negative correlation between the proportion of sound seeds and *NNI* in primary forest. The selfing rate of mature seeds also showed a significant and negative correlation with *NNI* in the primary forest, which suggests that isolation promotes self-fertilization. The correlation between *NNI* and the rates of sound seed production and selfing was not significant in *pulau*.

Seedling survival 8 months after seedling establishment in the primary forest was significantly affected by *NNI* and light intensity. On the other hand, seedling survival in *pulau* was negatively correlated with both light intensity (marginally significant) and water potential (significant), but we found no significant correlation with *NNI* (Table 6).

Table5 Results of stepwise GLMM for seed fate.

	Primary			Pulau		
		coefficient	p		coefficient	p
Mature rate	AIC:6981			AIC: 2215		
	Intercept	−4.652	<0.001	Intercept	−3.819	<0.001
	NNI_ln	−0.709	0.049	NNI_ln	−0.629	0.087
Predation by insects	AIC: 1551			AIC: 374.5		
	Intercept	−1.003	<0.001	Intercept	−1.204	<0.001
Predation by vertibrates	AIC: 1235			AIC: 120.4		
	Intercept	−0.500	0.380	Intercept	−3.136	<0.001
	NNI_ln	0.817	0.060			
Sound	AIC: 1809			AIC: 403.1		
	Intercept	−0.973	0.025	Intercept	0.997	<0.001
	NNI_ln	−0.878	0.007			
Selfing	AIC: 200			AIC: 59.67		
	Intercept	−9.285	0.001	Intercept	−2.637	0.030
	NNI_ln	−5.310	0.023	NNI_ln	5.700	0.220

Table6 Results of stepwise GLMM for seedling survival.

	Primary			Pulau		
		coefficient	p		coefficient	p
Seedling survival after 8 months	AIC: 317.8			AIC: 195.5		
	Intercept	3.2	0.051	Intercept	2.724	0.114
	NNI_ln	−8.081	<0.001	Openness_arcsin	−41.364	0.071
	Openness_arcsin	−193.243	<0.001	Water potential_ln	−0.523	0.002

Discussion

Effect of forest type on reproductive and recruitment success of **Shorea laxa**

We observed a significantly higher seed maturation rate in *pulau* than in primary forest. This suggests that pollination might function better in *pulau* than in primary forest. However, seed predation by vertebrates was significantly lower in *pulau* whereas predation by insects did not differ significantly between forests. These results can be explained if forest fragmentation has a stronger effect on populations of canopy vertebrates than on populations of insects. This is consistent with the results of Nakagawa et al. (2006), who also reported decreased rodent populations in *pulau* compared with primary forest. These results suggest that vertebrates may be more vulnerable than insects to forest fragmentation.

On the other hand, these differences did not lead to significant differences between forest types in terms of seedling survival 8 months after seedling establishment. However, the higher light intensity and decreased soil moisture in *pulau* compared with primary forest (Table 4) suggests that forest fragmentation may degrade the environment, even if these results are not apparent in the short term (i.e., our results reflect survival after less than 1 year). Seedling survival was affected by environmental conditions (Table 6). The long-term effect of the environmental changes that result from forest fragmentation may thus affect the survival pattern of seedlings.

In this study, we found that the difference between the *pulau* environment and the primary forest environment had no strong negative effects on the reproductive and recruitment success of *S. laxa*, at least in the short term (Tables 1 and 2). In other words, the *pulau* forest type, which represents a traditional form of forest reserve, may offer a similar function to that of primary forest for *S. laxa*.

***Effect of local density on reproductive and recruitment success of* Shorea laxa**

Local host density affected the seed maturation rate and marginally the predation rate by vertebrates (Table 5). This suggests that aggregation of the study species had a negative effect on reproductive success in terms of both seed maturation and predation by vertebrates. It is not clear whether the decreased seed maturation rate results from seed abortion as a result of insect predation, which did not differ significantly among sites(Table 1), and/or inbreeding (selfing), which was significantly higher in primary forest(Table 2). The selfing rate of mature seeds decreased significantly with increasing local tree density, suggesting that tree isolation may increase the rate of pollination failure. The predation rate by vertebrates was marginally positively correlated with tree density in primary forest, suggesting that vertebrates respond to the local density of a food resource. On the other hand, we found that local host density did not affect insect predation in either forest type. This may result from differences in feeding behavior and range between insects and vertebrates.

Seedling survival was significantly correlated with *NNI* in primary forest. This indicates that predators, herbivores, and pathogens, which are a cause of seedling mortality in *S. laxa,* would exhibit density-dependent behavior.

In conclusion, our results show that *S. laxa* obtains advantages from low tree density in terms of seed maturation, avoidance of seed predation by vertebrates, and seedling recruitment. These results provide a possible explanation for why tropical trees tend to be sparsely distributed.

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References

Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine Chaco Serrano. Ecol Appl 4:378-392

Deka RN, Wairiu M, Mullins PWC, Mullins E, Veenendaal EM, Townend J (1995) Use and accuracy of the filter-paper technique for measurement of soil matric potential. Eur J Soil Sci 46: 233–238.

Frazer GW, Canham CD, Lertzman KP (1999) Gap light analyzer (GLA). Simon Fraser University, Burnaby, British Columbia, and Institute of Ecosystem Studies, Millibrook, New York.

Garcia D, Chacoff NP (2007) Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. Conserv Biol 21:400-411

Ghazoul J, McLeish M (2001) Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. Plant Ecol 153:335-345

Isagi Y, Kenta T, Nakashizuka T (2002) Microsatellite loci for a tropical emergent tree, *Dipterocarpus tempehes* V. Sl. (Dipterocarpaceae). Mol Ecol Notes 2:12-13

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, Giraldo JP, Lovejoy TE, Condit R, Chave J, Harms KE, D'Angelo S (2006) Rapid decay of tree-community composition in Amazonian forest fragments. Proc Nat Acad Sci USA 103:19010-19014

Lee SL, Ng KKS, Saw LG, Lee CT, Muhammad N, Tani NTsumura Y, Koskela J (2006) Linking the gaps between conservation research and conservation management of rare dipterocarps: A case study of *Shorea lumutensis*. Biol Conserv 131:72-92

Lee SL, Tani N, Ng KKS, Tsumura Y (2004) Isolation and characterization of 20 microsatellite loci for an important tropical tree *Shorea leprosula* (Dipterocarpaceae) and their applicability to *S. parvifolia*. Mol Ecol Notes 4:222-225

Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639-655

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. Biotropica 37:389-396

Takeuchi Y, Kenta T, Nakashizuka T (2005) Comparison of sapling demography of four dipterocarp species with different seed-dispersal strategies. For Ecol Manage 208:237-248

Takeuchi Y, Nakashizuka T (2007) Effect of distance and density on seed/seedling fate of two dipterocarp species. For Ecol Manage 247:167-174

Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends Ecol Evol 11:413-418

Direct Genetic Analysis of Single Pollen Grains in Pollination Studies

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Introduction

Habitat fragmentation is a major threat to the biodiversity of forest ecosystems. During plant reproduction, habitat fragmentation disturbs gene flow and affects both the genetic structure and genetic diversity of progeny. Because insects are sensitive to habitat disturbances (Aizen and Feinsinger 2002), the pollination of insect-pollinated plants is often negatively affected by fragmentation (Young *et al*. 1996, Ghazoul *et al*. 1998, Benítez-Malvido and Martínez-Ramos 2003). In contrast, Dick *et al*. (2003) reported that long-distance pollen movement was enhanced in a fragmented site. These results reflect the complex and unpredictable responses of animal pollinators to fragmentation.

The genetic diversity and genetic structure of plant progeny are directly affected by both the quality and quantity of pollen grains that are transported to the stigma. Despite a wealth of data concerning the quantity of pollen transported to flowers (e.g., Herrera 1987, Mayfield *et al*. 2001), no studies have directly analyzed the genetic quality of transported pollen. The determination of genotypes from pollen grains carried by insects can reveal the genetic structure and diversity of transported pollen as well as the movement patterns of flower-visiting insects. This method may also provide a novel approach for evaluating human impacts on forest ecosystems.

We developed a new method of multiple microsatellite genotyping to analyze the pollination of insect-pollinated plants. We confirmed the reliability of the method by analyzing the genotypes of pollen grains transported by flower-visiting insects.

Materials and Methods

Plant species

Magnolia obovata Thunb. (Magnoliaceae) is a large (up to 20–30 m in height), common deciduous tree species native to temperate forests in Japan. The standing density of adult trees is relatively low, with only a small number of trees per hectare (Isagi *et al*. 2004). Flowers of this species are hermaphroditic and protogynous. The primary pollinators of *M. obovata* are beetles (Kikuzawa and Mizui 1990, Isagi *et al*. 2004), which crawl through the flowers for long periods of time (Thien 1974). Bees, hover flies, and thrips also visit the flowers of *M. obovata* (Tanaka and Yahara 1998).

Study site

A field survey was conducted at the Ogawa Forest Reserve, Ibaraki Prefecture, central Japan (36˚56’ N, 140˚35’ E). The average annual mean air temperature and precipitation over 10 years (1986–1995) at a meteorological station in Ogawa (36˚54’ N, 140˚35’ E) were 10.7°C and 1910 mm, respectively (Mizoguchi *et al*. 2002). The area is covered by a deciduous broad-leaved forest, and the dominant woody species in the canopy are *Quercus serrata*, *Fagus japonica*, and *F. crenata*. Research in the reserve has included intensive studies of the structure and dynamics of the plant community (Nakashizuka *et al.* 1992) and the population dynamics of *Carpinus* (Shibata and Nakashizuka 1995), *Acer* (Tanaka 1995), and *Cornus* (Masaki *et al.* 1994) species. Several types of land use (e.g., conifer plantations, paddy fields, pastures) surround the forest reserve.

Sampling

During the flowering period of *M. obovata* in 2004 and 2005, fresh stamens and flower-visiting insects were collected from six adults of *M. obovata*. Each insect was collected immediately after visitation. Samples were stored at –30˚C prior to DNA analysis.

DNA extraction from a single pollen grain

For DNA extraction from a single pollen grain, we modified the extraction method described by Suyama *et al.* (1996). Extraction buffer (1 µL) containing 0.01% SDS, 0.1 µg/µL proteinase K (TaKaRa, Tokyo. Japan), 1× PCR buffer (containing 1.5 mM $MgCl_2$) of Ampli*Taq* Gold (Applied Biosystems, Foster City, CA) was placed into a 0.2 mL PCR tube. Under a stereomicroscope, a single pollen grain was removed from the stamen surface using a plastic pipette tip (for manipulating 0.5–10 µL of liquid) that had been stretched and cut to obtain a sharp end. One pollen grain was then placed into the buffer and crushed using a sterile plastic pipette tip (for manipulating 20–200 µL of liquid). The reaction buffer was incubated at 37˚C for 60 min and then at 95˚C for 10 min.

Determination of multiple microsatellite genotypes

Because a single pollen grain contains only a small amount of haploid nuclear material, it is impossible to divide template DNA into multiple reaction tubes to amplify multiple microsatellite loci. Therefore, to obtain multiple microsatellite genotypes from a single pollen grain, we had to either conduct whole genome amplification before microsatellite genotyping or genotype several loci simultaneously in a single reaction tube. We tested both methods for obtaining genotypes of multiple microsatellite loci from single pollen grains.

LL-DOP PCR for whole genome amplification

LL (long products from low DNA quantities)-DOP (degenerate oligonucleotide-primed) PCR (Kittler *et al.* 2002) is one method for whole genome amplification from a small amount of DNA. This method can generate long products from a small amount of template DNA with high fidelity (Kittler *et al.* 2002). The entire genomes of 16 pollen grains were amplified separately using the Expand High Fidelity PCR System (Roche, Basel, Switzerland) following the manufacturer's protocol. Using amplified DNA from a single pollen grain as a template, 11 microsatellite loci developed by Isagi *et al.* (1999) were amplified separately in 11 reaction tubes.

Multiplex PCR

The multiplex PCR method (Chamberlain *et al.* 1988) can amplify multiple loci simultaneously in a single reaction tube using a small quantity of DNA. Genotypes of nine microsatellite loci of 20 pollen grains were scored using a Multiplex PCR kit (Qiagen, Hilden, Germany) following the manufacturer's protocol.

Genotypes were determined using an ABI PRISM 3100 Genetic Analyzer, GENESCAN^{TM} analysis software version 3.7, and GENOTYPER^{TM} analysis software version 2.0 (all from Applied Biosystems). The genotypes of pollen grains were compared to those of the pollen parent from which the stamen was sampled.

Genotyping of pollen grains adhering to flower-visiting insects

Among the observed flower-visiting insects, bumblebees (Apidae, *Bombus*), flower beetles (Scarabaeidae, Cetoniinae), and small Coleoptera (Ligriidae, *Arthromacra*) were used to confirm the effectiveness of our analysis method. We removed 47–48 pollen grains (143 grains total) from the surfaces of a bumblebee (*Bombus diversus*), a flower beetle (*Protaetia cataphracta*), and a small beetle (*Arthromacra sumptuosa*). The genotypes of nine microsatellite loci of each pollen grain were determined using the multiplex PCR method. The pollen samples for which genotypes were determined for more than five microsatellite loci were used for analysis. The percentage of self-pollen (i.e., pollen transported within a tree) was calculated for each insect. The genetic diversity of transported pollen grains was expressed in terms of gene diversity (Nei 1973).

Results

LL-DOP PCR

Among 176 combinations of 11 loci and 16 pollen grains, 71 genotypes (40.0%) were successfully determined. The proportion of successful genotyping differed among the microsatellite loci (Fig. 1), ranging from 0.06 (locus: *M15D5*) to 0.94 (locus: *M6D1* and *M6D8*).

Multiplex PCR

Among 180 combinations of nine loci and 20 pollen grains, 163 genotypes (approx. 90.6%) were successfully determined, and all of the amplified alleles were consistent with those of the pollen parent from which the stamen was collected (Fig. 2). Although the proportion of successful genotyping differed among the microsatellite loci (Fig. 1), the variances were smaller than those of the LL-DOP PCR method.

Genotyping of pollen grains adhering to flower-visiting insects

In the analysis of pollen grains that adhered to flower-visiting insects, we were able to determine genotypes for more than five microsatellite loci of 134 pollen grain samples. The percentage of self-pollen in the pollen load was 93.6% on bumblebees, 12.5% on flower beetles, and 95.7% on small beetles. The gene diversity of pollen grains from bumblebees, flower beetles, and small beetles was 0.36, 0.79, and 0.47, respectively.

Discussion

Comparison of analysis methods

We compared two methods of PCR amplification for determining the genotypes of multiple microsatellite loci from a single pollen grain. The proportions of successful genotyping in the LL-DOP PCR method were lower than those in the multiplex PCR method. In addition, the variance in the success rate of each locus was high in the LL-DOP PCR method. Whole genome amplification methods do not always amplify the entire genome, and a portion of genome may often be lost (Wells *et al.* 1999). Therefore, it may be difficult to amplify multiple regions that include microsatellite loci from one copy of the haploid nuclear genome of a single pollen grain. Thus, we determined that the LL-DOP PCR method was unsuitable for the genetic analysis of pollen grains.

In contrast, the multiplex PCR method successfully genotyped a single pollen grain with high fidelity. Failed genotyping was unevenly distributed among individual loci, suggesting that these failures resulted from traits of each locus or the PCR primers. The multiplex PCR method is suitable for analyzing pollen grains because it amplified pollen DNA with high success rates and fidelity. In addition, this method can be completed in less time and at a lower cost than the LL-DOP PCR method.

Genotyping of pollen grains adhering to flower-visiting insects

Among the 143 pollen grains analyzed, the genotypes of 134 pollen grains (93.7%) were determined for more than five microsatellite loci. This result indicates that the method is practical and effective for detailed studies on pollination. We found large differences in the percentage of self-pollen and gene diversity among insect species, suggesting that the visitation behavior of insects varies with species. Differences in visitation behavior can result in varying effects on the reproduction and fitness of pollinated *M. obovata*. The present method of genetically analyzing a single pollen grain may facilitate more detailed pollination studies, including research on pollinator efficiency and human impacts on pollination systems.

References

Aizen MA, Feinsinger P (2002) Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. In: Bradshaw GA and Mooney HA (eds) How landscapes change: human disturbance and ecosystem fragmentation in the Americas. Springer, Berlin, pp 111–129

Benítez-Malvido J, Martínez-Ramos AM (2003) Impact of forest fragmentation on understory plant species richness in Amazonia. Conserv Biol 17: 389–400

Chamberlain JS, Gibbs RA, Ranier JE, Nguyen PN, Caskey CT (1988) Deletion screening of the Duchenne muscular dystrophy locus via multiplex DNA amplification. Nucleic Acids Res 16: 11141–11156

Dick CW, Etchelecu G, Austerlitz F (2003) Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforests. Mol Ecol 12: 753–764

Ghazoul J, Liston KA, Boyle TJ (1998) Disturbance-induced density-dependant seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. J Ecol 86: 462–473

Herrera CM (1987) Components of pollinator ‘quality’: comparative analysis of a diverse insect assemblage. Oikos 50: 79–90

Isagi Y, Kanazashi T, Suzuki W, Tanaka H, Abe T (1999) Polymorphic DNA markers for *Magnolia obovata* Thunb. and their utility in related species. Mol Ecol 8: 698–700

Isagi Y, Kanazashi T, Suzuki W, Tanaka H, Abe T (2004) Highly variable pollination patterns in *Magnolia obovata* revealed by microsatellite paternity analysis. Int J Plant Sci 165: 1047–1053

Kikuzawa K, Mizui N (1990) Flowering and fruiting phenology of *Magnolia hypoleuca*. Plant Species Biol 5: 255–261

Kittler R, Stoneking M, Kayser M (2002) A whole genome amplification method to generate long fragments from low quantities of genomic DNA. Anal Biochem 300: 237–244

Masaki T, Kominami Y, Nakashizuka T (1994) Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. Ecology 75: 1903–1910

Matsuki Y, Isagi Y, Suyama Y (2007) The determination of multiple microsatellite genotypes and DNA sequences from a single pollen grain. Mol Ecol Notes 7: 194–198

Mayfield MM, Waser NM, Price MV (2001) Exploring the ‘Most Effective Pollinator Principle’ with complex flowers: bumblebees and *Ipomopsis aggregata*. Ann Bot 88: 591–596

Mizoguchi Y, Morishita T, Ohtani Y (2002) Climate in Ogawa Forest Reserve. In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community. Springer, Tokyo, pp 11–18

Nakashizuka T, Iida S, Tanaka H, Shibata M, Abe S, Masaki T, Niiyama K (1992) Community dynamics of Ogawa Forest Reserve, a species-rich deciduous forest, central Japan. Vegetatio 103: 105–112

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70: 3321–3323

Shibata M, Nakashizuka T (1995) Seed and seedling demography of four co-occurring *Carpinus* species in a temperate deciduous forest. Ecology 76: 1099–1108

Suyama Y, Kawamuro K, Kinoshita I, Yoshimura K, Tsumura Y, Takahara H (1996) DNA sequence from a fossil pollen of *Abies* spp. from Pleistocene peat. Genes Genet Syst 71: 145–149

Tanaka H (1995) Seed demography of three co-occurring *Acer* species in a Japanese temperate deciduous forest. J Veg Sci 6: 887–896

Tanaka H, Yahara T (1988) The pollination of *Magnolia obovata*. In: Kawano S (eds) The world of plants, vol. 2. Kenkyusha, Tokyo, p 37

Thien LB (1974) Floral biology of *Magnolia*. Am J Bot 61: 1037–1045

Wells D, Sherlock JK, Handyside AH, Delhanty JDA (1999) Detailed chromosomal and molecular genetic analysis of single cells by whole genome amplification and comparative genomic hybridization. Nucleic Acids Res 27: 1214–1218

Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends Ecol Evol 11: 413–418

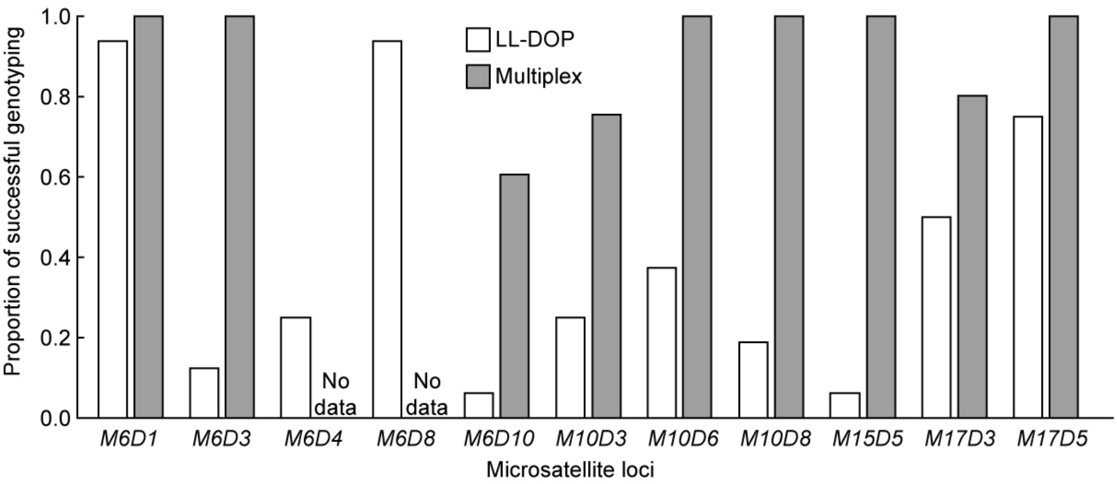

Fig. 1 The proportion of successful genotyping of microsatellite loci using the LL-DOP PCR and multiplex PCR methods. We examined 16 and 20 pollen grains using the LL-DOP PCR and multiplex PCR methods, respectively. Genotype determination was considered successful when the allele corresponding to the pollen parent was obtained. 1

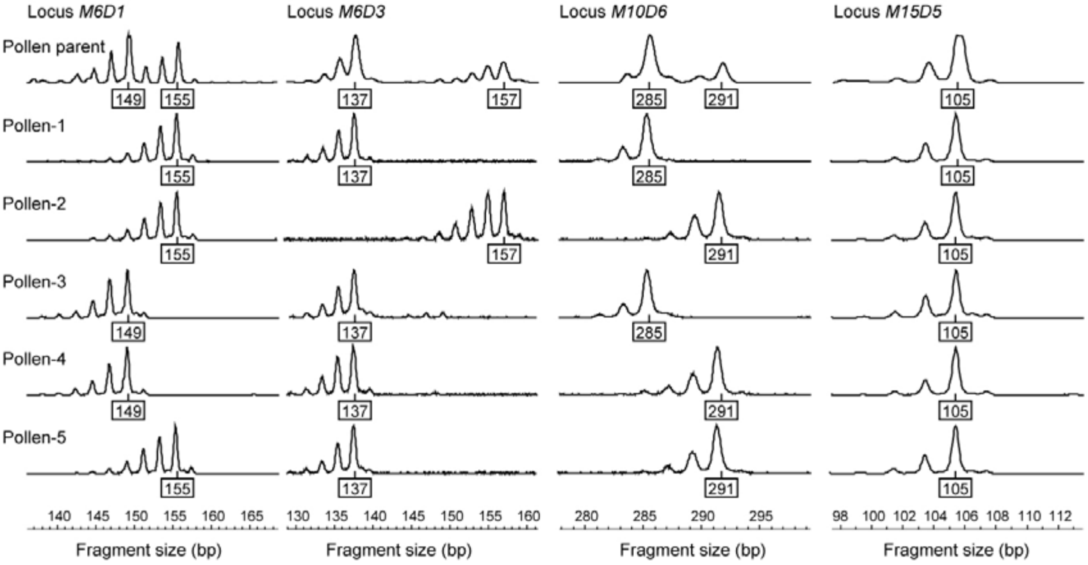

Fig. 2 Electropherograms of alleles at four microsatellite loci (*M6D1*, *M6D3*, *M10D6*, *M15D5*) of pollen parents and pollen grains amplified using the multiplex PCR method (modified from Matsuki *et al*. 2007).

The Effects of Forest Fragmentation on Population Structure and Reproductive Output in Populations of *Magnolia obovata*

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Introduction

Forest fragmentation caused by anthropogenic activity is a threat to the continuation of local populations and communities throughout the world, because it causes a decrease in the number of conspecific reproductive individuals, which can result in decreased reproductive output and, eventually, increased risk of extinction. Forest fragmentation also changes environmental conditions via edge effects, which can positively or negatively affect seedling establishment, growth, and reproductive output of trees. Animal-pollinated plant reproductive output can be influenced through changes in local animal assemblages, caused by changes in behavior and flight patterns, in response to fragmentation (Aizen and Feinsinger 1994; Didham 1996). Thus, forest fragmentation can directly and indirectly affect reproductive output; however, few studies have investigated the effect of forest fragmentation on population structure and reproductive output of tree species.

Many studies have examined reproductive output of herbaceous species and shrubs. However, few studies of reproduction in tall tree species have addressed reproductive processes by marking or sampling reproductive twigs, but it is laborious to estimate reproductive output at the individual level. In this study, we addressed whole plant reproductive output, including flowering, fertilization, and seed set.

The study species, *Magnolia obovata*, is ubiquitous in the cool temperate forests of Japan, but at a relatively low density. It is not clear how such sparse tree populations are maintained. This species has a large reproductive organ, which makes it easy to evaluate the reproductive output at the whole plant level throughout the reproductive process.

The aim of this study was to evaluate the effect of forest fragmentation on the population structure and reproductive output of *M. obovata*. We compared tree density, size distribution patterns, reproductive characteristics (flower number, fruit set, and seed number per fruit) at two nearby sites, one conserved and one fragmented, in the southern part of the Abukuma Mountains, Ibaraki Prefecture, central Japan, over a three-year period.

Materials and Methods

Study Site

The study was carried out in the Ogawa Forest Reserve and its surrounding area, in the southern part of the Abukuma Mountains, Ibaraki Prefecture, central Japan (36°56´N, 140°35´E; altitude 610–660 m above sea level). Mean annual air temperature and precipitation at a meteorological station in Ogawa (36°54´N, 140°35´E) during the study period were 10.7°C and 1910 mm, respectively (Moriguchi et al. 2002). The study area is covered by deciduous broadleaf forest, and the dominant woody species in the canopy are *Quercus serrata*, *Fagus japonica*, and *F. crenata* (Nakashizuka et al. 1992; Masaki et al. 1994).

The study site was about 2 km × 3 km, and included lands with various uses, such as conserved natural forest (98 ha), fragmented natural forest (29 ha), secondary forest, coniferous plantations, farmland, and pasture. The study was conducted in the conserved natural forest and the fragmented natural forest (Fig. 1).

The fragmented forest is shaped like a fish bone, and is located about 500 m from the conserved forest (Fig. 1). According to forest management notes and interviews with local people, forest fragmentation was caused by clear cutting of broadleaf forest and planting of coniferous trees in the 1970s. The vegetation of the conserved forest is thought to be similar to that of the fragmented forest. Secondary forests and coniferous plantations surround the conserved and fragmented forests. The secondary forests include several deciduous broadleaf species, such as *Quercus serrata*, and are used for charcoal production by the local people.

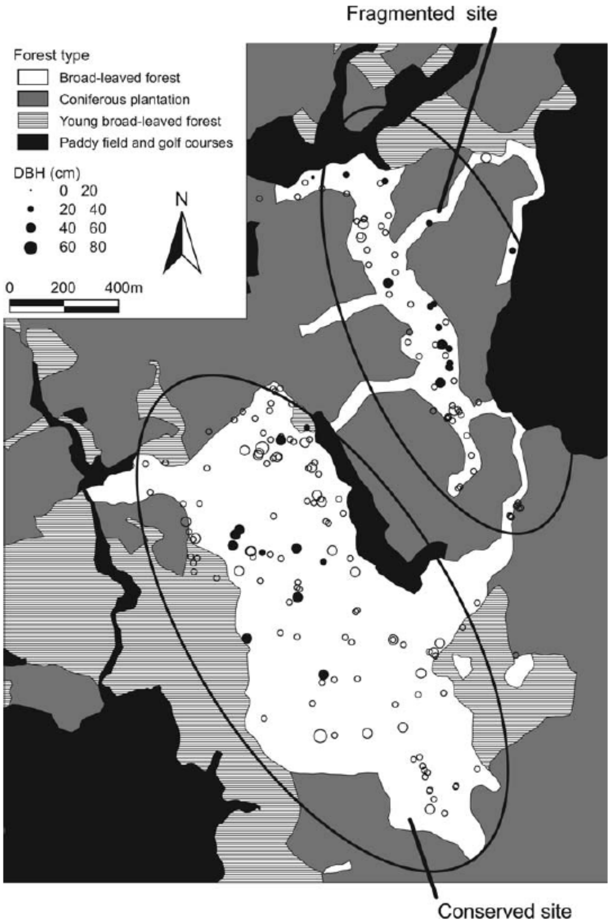

Fig. 1 The sizes and locations of reproductive *Magnolia obovata* trees in the conserved and fragmented forest sites. Filled circles: Adult trees from which fruits were collected (Isagi et al. 2007).

Study Species

The flower of *M. obovata* is one of the largest in the region, protogynous and without nectaries. The main pollinators of the flowers are beetles, bumble bees, and halictid bees (Tanaka and Yahara 1988; Tateno et al. personal observation). Although individual flowers last for 3–4 days, a tree flowers for up to 40 days, from late May to early July, in this study area (Tateno et al. unpublished data). Seeds reach maturity in mid-September at the study site and are dispersed by birds.

Field Study and Sampling

Reproductive *M. obovata* trees were identified and the location of each tree was determined with a portable GPS (eTrex Summit, Garmin, Kansas, USA). We measured diameter at breast height (DBH) of all trees and checked the flowering status of each tree.

Eight individuals (22.1–56.4 cm DBH) per forest type were selected for counting flower number and fruit number from the conserved and the fragmented forests. We accessed the canopy by ladder or climbing ropes, or both, and sketched almost all of the flowers or flower buds on a branch during the flowering period. We checked for fruit set in late September.

We selected fourteen individuals (18.0–56.6 cm DBH) for fruit sampling from the conserved forest and the fragmented forest. Five or more mature fruits were collected from each sampled tree; however, in non-fruiting years, we were unable to collect five fruits per individual. The numbers of ovules and mature seeds in each fruit were counted.

Results and Discussion

The density of trees was 1.3 trees/ha in the conserved forest and 1.9 trees/ha in the fragmented forest. Although there were no differences in size distribution patterns of large trees between the conserved and the fragmented forests, the number of small individuals (<40 cm DBH) was higher in the fragmented forest than in the conserved forest (Fig. 2). These small trees can establish in forest edges and roadsides at the time of clear-cutting of surrounding forests. According to the distribution map of individuals, some patches containing small individuals were located along the forest edge and roadside in the fragmented forest (Fig. 1). The percentage of reproductive trees increased with size, and all trees with DBH greater than 30 cm were reproductive (Fig. 2). These results suggest that, in the near future, the density of reproductive individuals should increase much more in the fragmented forest than in the conserved forest.

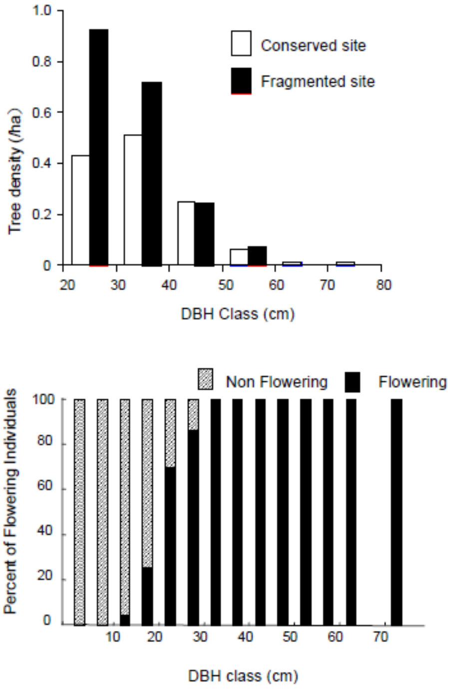

Fig. 2 Size distributions of *Magnolia obovata* trees and the percentage of flowering individuals.

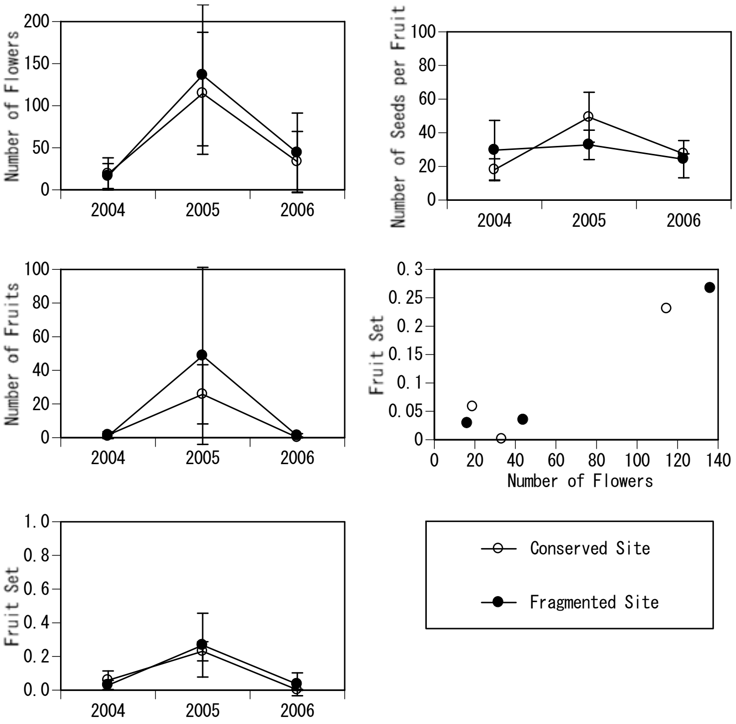

Fig. 3 Interannual changes in reproductive properties of *Magnolia obovata* in the conserved and fragmented forests.

The trees flowered and produced fruit every second year, and were synchronized between the conserved forest and the fragmented forest (Fig. 3). There was a clear positive correlation between flower number and fruit set (Fig. 3), suggesting that increased flower number results in increased fruit set in *M. obovata* of this site. Kikuzawa and Mizui (1990) showed significantly increased fruit set by self-pollination and concluded that populations of *M. obovata* were pollinator-limited in a deciduous broadleaf forest in northern Japan. In contrast to fruit set, seed number per fruit did not show clear inter-annual variation. Seed number per fruit varied widely among fruits. Isagi et al. (2004) found that outcrossing rate and number of pollen donors varied widely among fruits. Pollination is highly variable at the level of fruits and individuals, possibly because of high variability in pollinator behavior. Seed number per fruit may be affected by several other processes, such as seed predation and abortion.

Although the average reproductive output did not differ significantly between the conserved and fragmented forests, the responses of reproductive processes to the local density of reproductive individuals differed between the two sites. Isagi et al. (2007) reported that the fertilization of ovules and outcrossing were more dependent on density of reproductive individuals in the fragmented forest than in the conserved forest. Similarly, fruit set in this study was dependent on density of reproductive individuals in the fragmented forest; however, this relationship was not significant in the conserved forest (Tateno et al. unpublished data). These results suggest that compensatory mechanisms for the low density may operate in the conserved forest more effectively than in the fragmented forest. We speculate that foraging area of pollinators may be wider in the conserved forest because it may be easier for them to forage in the canopy of deciduous trees. In the fragmented forest, the canopy of deciduous trees was interspersed with coniferous plantations, farmland, and pasture, and pollinators may concentrate near trees growing in the congested areas of conspecific trees. A better understanding of pollinator foraging behavior will be important for predicting the effect of fragmentation on population dynamics of this species.

Forest fragmentation may favor *M. obovata* populations because of the increasing number of safe sites for seedling establishment, growth, and future reproduction. Currently, the reproductive outputs of the two forest sites were not significantly different, but in the future the density of reproductive trees will increase in the fragmented forest, which will weaken pollen limitation and increase reproductive output. However, the fragmented populations may suffer negative genetic effects, such as inbreeding depression, increased susceptibility to diseases and pests, fixation of deleterious alleles, and loss of self-incompatibility alleles. Future studies are required to predict the effects of forest fragmentation, both the ecological and genetic consequences, on *M. obovata* population dynamics.

Acknowledgments

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References

Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75:330–351

Didham RK, Ghazoul J, Stork NE & Davis AJ . (1996). Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11:255-260

Isagi Y., Kanazashi T., Suzuki W., Tanaka H., Abe T. (2004) Highly Variable Pollination Patterns in *Magnolia obovata* Revealed by Microsatellite Paternity Analysis *International Journal of Plant Sciences* 165:1047–1053

Isagi Y., Tateno R., Matsuki Y., Hirao A., Watanabe S. Shibata M.(2007) Genetic and reproductive consequences of forest fragmentation for populations of *Magnolia obovata*. Ecological Research 22:382-389

Kikuzawa K, Mizui N (1990) Flowering and fruiting phenology of *Magnolia hypoleuca.* Plant Species Biol 5:255–261

Masaki T, Kominami Y, Nakashizuka T (1994) Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. Ecology 75:1903–1910

Moriguchi Y, Morishita T, Ohtani Y (2002) Climate in Ogawa Forest Reserve. In: Makashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community. Springer, Tokyo, pp 11–18

Nakashizuka T, Iida S, Tanaka H, Shibata M, Abe S, Masaki T, Niiyama K (1992) Community dynamics of Ogawa Forest Reserve, a species-rich deciduous forest, central Japan. Vegetatio 103:105–112

Tanaka H, Yahara T (1988) The pollination of *Magnolia obovata*. In: Kawano S (eds) The world of plants, vol. 2. Kenkyusya, Tokyo, p 37

Analysis of Mating Patterns and Spatial Genetic Structure in *Acer mono* Using Microsatellite Genetic Markers in Conserved and Fragmented Forests

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Introduction

Acer mono Maxim. (Aceraceae) is a deciduous canopy tree widely distributed in eastern Asia, and one of the major components in deciduous cool-temperate forests of Japan. The genus *Acer* exhibits great variability in its reproductive systems, including monoecy, androdioecy, and dioecy, and *A. mono* shows heterodichogamy, as do most *Acer* species (de Jong 1994). Heterodichogamy, by definition, refers to a breeding system that involves two types of bisexual individuals (protandrous and protogynous individuals) in a population and has been reported from 11 families and 17 genera of flowering plants, including *Grayia* (Chenopodiaceae), *Juglans* (Juglandaceae), and *Acer* (Aceraceae). In heterodichogamous taxa in genus Acer, male individuals occasionally occur at a low frequency (heterodichogamous androdioecy, Gleiser & Verdú 2005).

Several previous studies addressing sex expression in these taxa have revealed the reciprocal and synchronous nature of two flowering types, and heterodichogamy is considered an effective mechanism to avoid selfing and to ensure outcrossing by promoting between-type mating (Gleeson 1982, Pendleton *et al*. 1988, Asai 2002, Sato 2002, Kimura *et al*. 2003, Bai *et al*. 2006). However, no empirical studies have explored the exact mating patterns of these taxa. Understanding mating systems and patterns in these taxa will provide important insight into the ecological role of this mating system.

Here we characterize microsatellite genetic markers for parentage analysis and examine mating patterns of *A. mono* within a natural forest stand. We address the following questions: (1) is flowering of the two mating types, protandry and protogyny, in *A. mono* reciprocal and synchronous? (2) Does heterodichogamy in *A. mono* effectively avoid selfing (3) and promote between-type mating? (4) What other factors affect mating patterns?

Another issue in this study is the effects of forest fragmentation on the mating system and gene flow in *A. mono*. However, we could not perform direct paternity testing on seeds in fragmented populations to compare with the above data from continuous populations because of our experimental restrictions. Here we employ indirect methods to estimate the levels of gene flow in conserved and fragmented populations based on the genetic structure of adult trees, and predict the possible effects of forest fragmentation on gene flow and genetic diversity.

Materials and Methods

The species

Acer mono Maxim. var. *marmoratum* (Nichols.) Hara f. *dissectum* (Wesmael) Rehder (hereafter *A. mono*) is a deciduous tree species that reaches a height of about 20 m and is one of the major components of cool-temperate forests in Japan. Sex expression in *A. mono* was first described in detail by Mitigami *et al.* (1989); males and two types of hermaphroditic (protandrous and protogynous) individuals were found in a population. This maple is known to be visited by various types of insects such as flies, hover flies, and small solitary bees of the Halictidae and Andrenidae (Matsui 1991) and is considered to have generalist pollination systems.

The field study and sampling

The field study was conducted in a 6-ha plot in Ogawa Forest Reserve (36˚56' N, 140˚35' E, 610-660 m above sea level) and in a neighboring fragmented forest site in Ibaraki and Fukushima Prefecture (Fig. 1). All trees with diameter at breast height (DBH) >5 cm in the 6-ha plot had been tagged and mapped, and DBH of each tree had been measured every four years.

All tagged individuals of *A. mono* in the 6-ha plot were checked for anthesis and flowering type (male, protandry, or protogyny) in 2003. In 2005, flowering phenology and sex expression of all flowering trees in the plot were examined; the sex of flowers in bloom was recorded for each flowering tree in the plot every 3-5 days from 5 to 20 May by collecting three to five inflorescences. Sex phases of flowering individuals at a given time were classified into three categories including female, male, and cosexual stages. The flowering rate of a single plant was estimated by the proportion of flowering shoots in its crown. Potential mating probability P(*i*, *j*), which refers to the degree of temporal overlap between the male stages of individuals with flowering type *i* and the female stages of those with flowering type *j*, was calculated following the methods of Sato (2002).

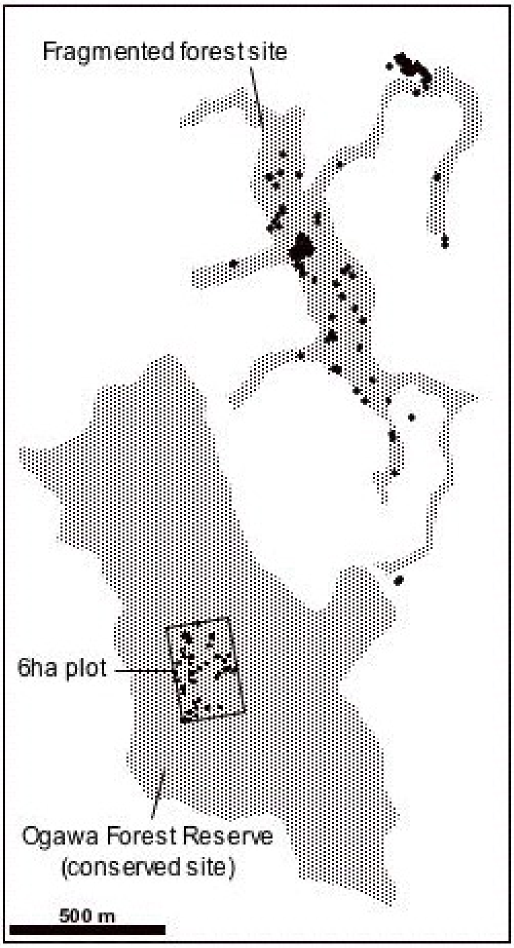


Fig. 1. Map of the study sites. The shaded area indicates natural forests in the conserved and the fragmented sites. Dots show the locations of sampled individuals of *A. mono*.

Leaf samples for genetic analysis were collected from all 46 flowering trees and eight non-flowering trees from the 6-ha plot, and from 130 flowering individuals from the fragmented forest site. Seeds for paternity analysis were collected in October 2003 from four maternal trees in the 6-ha plot, including one protandrous (tree number *PP6587*) and three protogynous (*PP4762*, *PP5249*, *PP6487*) individuals. To detect pollen flow from nearby areas outside the plot, additional leaf samples were collected from 33 flowering trees in the surrounding area with a width of 50 m outward from each side of the 6-ha plot.

Development of microsatellite markers in **Acer mono**

We characterized nuclear microsatellite markers in *A. mono* as described in Kikuchi & Shibata (in press). Microsatellites were developed from a genomic library enriched for (CT) dinucleotide repeats in *A. mono* Maxim. var. *marmoratum* (Nichols.) Hara and screened for PCR amplification and polymorphism using 34 individuals from the 6-ha plot. Thirteen polymorphic loci were characterized, with an average of 13.8 alleles per locus (Table 1).

Genetic analysis

Six (Am116, Am118, Am607, Am742, Am775, and Am909) of the developed microsatellite markers were employed in further analysis according to their robustness of PCR amplification, their reliability of allele scoring, and the low frequency or absence of null alleles. Moreover, we used two microsatellite loci, MAP09 (Pandey *et al.* 2004) and Aca24 (Terui *et al.* 2006), which have been reported in other *Acer* species (*A. pseudoplatanus* and *A. capillipes*, respectively).

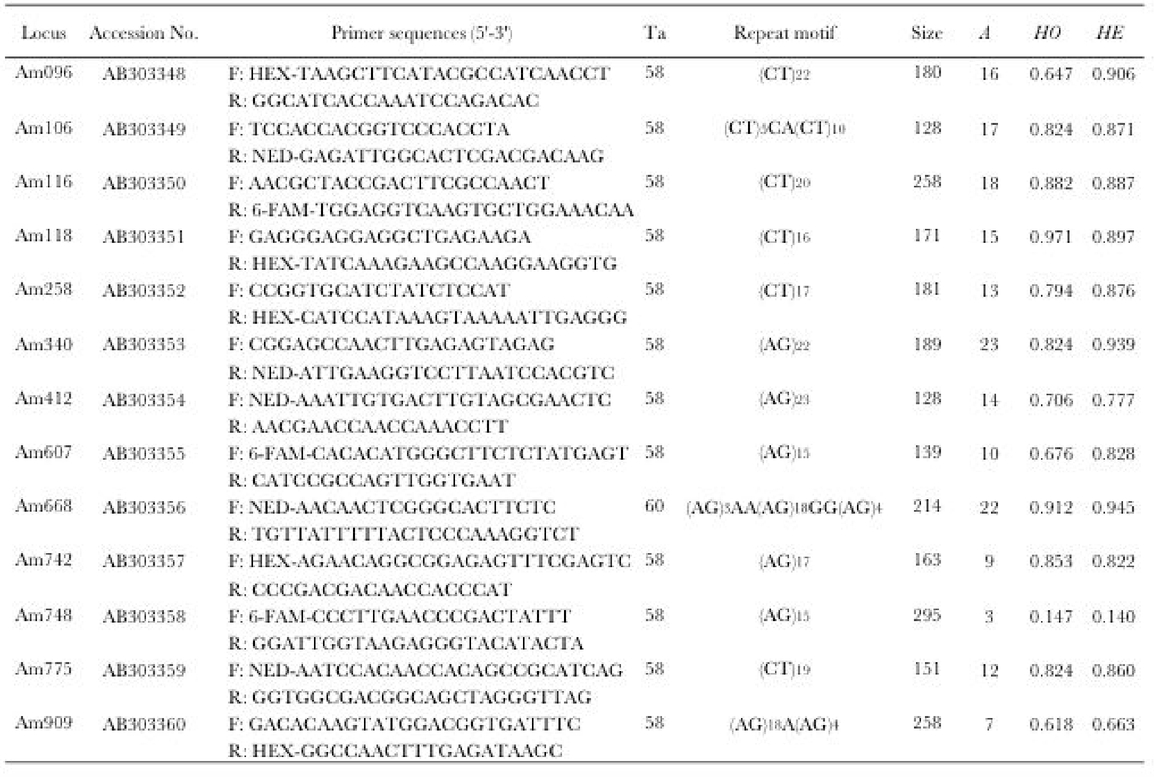
DNA samples of adult individuals were extracted from leaf tissues using the cetyltrimethylammonium bromide (CTAB) method described by Murray & Thompson (1980) and modified by Mukai & Yamamoto (1997). DNA from seeds was extracted using a DNeasy Plant Mini Kit (Qiagen). PCR amplifications were performed in a 6-μL reaction mixture consisting of approximately 1 ng of template DNA, 20 mM Tris-HCl (pH 8.4), 50 mM KCl, 1.5 mM MgCl2, 0.2 mM of each dNTP, 0.25 μM of each primer, and 0.25 U *Taq* polymerase. The PCR conditions included an initial denaturation step of 3 min at 94°C, followed by 35 cycles of 30 s at 94°C, 30 s at an annealing temperature of 50 to 60°C (for details see Table 1), and 30 s at 72°C, followed by a final extension step of 5 min at 72°C. Alleles were scored on an ABI 3100 automated sequencer, using the software GeneScan 3.7.1 and Genotyper 2.5 (Applied Biosystems).

Genetic data analysis

Estimators of microsatellite genetic diversity, measured as the number of alleles per locus (N_A) and expected heterozygosities (H_E), were computed for two groups of adult trees, one from the 6-ha plot and the other from the fragmented forest, using the program GenAlex (Peakall & Smouse 2006). The inbreeding coefficient F_{IS} and the fixation index F_{ST} were calculated according to Weir & Cockerham (1984) using FSTAT software (Gouldet 2001).

Genotype data of adult individuals from the 6-ha plot and the fragmented forest were also used to examine spatial genetic structure. We employed a spatial autocorrelation analysis between individuals based on multilocus genotypes. A relationship coefficient *r* (Wang 2002) was computed using SPAGeDi 1.2 software (Hardy & Vekemans 2002). Ten distance classes up to 303.7 m and 15 up to 1277.4 m were automatically set up at irregular distance intervals using SPAGeDi to allocate a relatively equal number of individual pairs to each distance class.

Table 1. Characteristics of 13 microsatellite loci in *Acer mono*. These include the locusname, DDBJ accession number, primer sequence, and annealing temperature (T_a). Repeat motif and expected product size are derived from the sequenced clone. Number of alleles (A) and observed (H_O) and expected (H_E) heterozygosity were based on 34 samples (cited from Kikuchi & Shibata in press).



Locus	Accession No.	Primer sequences (5'-3')	Ta	Repeat motif	Size	*A*	*HO*	*HE*
Am096	AB303348	F: HEX-TAAGCTTCATACGCCATCAACCT R: GGCATCACCAAATCCAGACAC	58	$(CT)_{22}$	180	16	0.647	0.906
Am106	AB303349	F: TCCACCACGGTCCCACCTA R: NED-GAGATTGGCACTCGACGACAAG	58	$(CT)_5CA(CT)_{10}$	128	17	0.824	0.871
Am116	AB303350	F: AACGCTACCGACTTCGCCAACT R: 6-FAM-TGGAGGTCAAGTGCTGGAAACAA	58	$(CT)_{20}$	258	18	0.882	0.887
Am118	AB303351	F: GAGGGAGGAGGCTGAGAAGA R: HEX-TATCAAAGAAGCCAAGGAAGGTG	58	$(CT)_{16}$	171	15	0.971	0.897
Am258	AB303352	F: CCGGTGCATCTATCTCCAT R: HEX-CATCCATAAAGTAAAAATTGAGGG	58	$(CT)_{17}$	181	13	0.794	0.876
Am340	AB303353	F: CGGAGCCAACTTGAGAGTAGAG R: NED-ATTGAAGGTCCTTAATCCACGTC	58	$(AG)_{22}$	189	23	0.824	0.939
Am412	AB303354	F: NED-AAATTGTGACTTGTAGCGAACTC R: AACGAACCAACCAAACCTT	58	$(AG)_{23}$	128	14	0.706	0.777
Am607	AB303355	F: 6-FAM-CACACATGGGCTTCTCTATGAGT R: CATCCGCCAGTTGGTGAAT	58	$(AG)_{15}$	139	10	0.676	0.828
Am668	AB303356	F: NED-AACAACTCGGGCACTTCTC R: TGTTATTTTTACTCCCAAAGGTCT	60	$(AG)_3AA(AG)_{18}GG(AG)_4$	214	22	0.912	0.945
Am742	AB303357	F: HEX-AGAACAGGCGGAGAGTTTCGAGTC R: CCCGACGACAACCACCCAT	58	$(AG)_{17}$	163	9	0.853	0.822
Am748	AB303358	F: 6-FAM-CCCTTGAACCCGACTATTT R: GGATTGGTAAGAGGGTACATACTA	58	$(AG)_{15}$	295	3	0.147	0.140
Am775	AB303359	F: NED-AATCCACAACCACAGCCGCATCAG R: GGTGGCGACGGCAGCTAGGGTTAG	58	$(CT)_{19}$	151	12	0.824	0.860
Am909	AB303360	F: GACACAAGTATGGACGGTGATTTC R: HEX-GGCCAACTTTGAGATAAGC	58	$(AG)_{18}A(AG)_4$	258	7	0.618	0.663

Paternity of seeds collected from four trees in the 6-ha plot was determined using the program Cervus version 3.0 (Marshall *et al*. 1998, Kalinowski *et al*. 2007). We used likelihood methods implemented in Cervus to find the most likely pollen parents. Cervus calculates likelihood ratios (the likelihood that the candidate parent is the true parent divided by the likelihood that the candidate parent is not the true parent) and LOD scores (the natural log of the product of the likelihood ratios at each locus). Paternity was assigned to an individual with the highest LOD scores and Delta values (difference in LOD scores between the most likely parent and the second most likely parent) exceeding the 90% confidence level. If none of the candidates in the 6-ha plot plus its surrounding area (a total of 12 ha) had positive LOD scores, seeds were scored as being sired by an individual outside the population. In any other case, paternity was identified as "not determined."

Results

Flowering phenology in **A. mono**

Forty-six out of 173 tagged trees of *A. mono* (DBH >5 cm in 2001) in the 6-ha area were found bearing flowers during the study period. Most (95.2%) of the trees with DBH >20 cm produced flowers, whereas none of the trees with DBH <15 cm flowered (Fig. 2; data based on Forestry and Forest Products Research Institute 2003). Sex expression of all flowering individuals in the plot was investigated in 2005, and 25 trees were found to be protandrous and 21 were protogynous. Male individuals were not found in the plot in 2005. Female and male flowering in the protogynous and the protandrous individuals, respectively, were at their peak in early May; female flowers of 17 (81%) protogynous individuals and male flowers of 20 (80%) protandrous individuals were in bloom from 5 to 12-13 May. The peak in male flowering of the protogynous individuals occurred from 16 to 17 May and was synchronized with the female-flowering peak of protandrous individuals (Fig. 3); during this period, 19 protogynous individuals had male flowers in bloom, of which two were in the cosexual stage, and 20 protandrous individuals were in the female stage (Fig. 3). The second male stage was observed in 12 protandrous individuals in mid to late May, after the female phase.

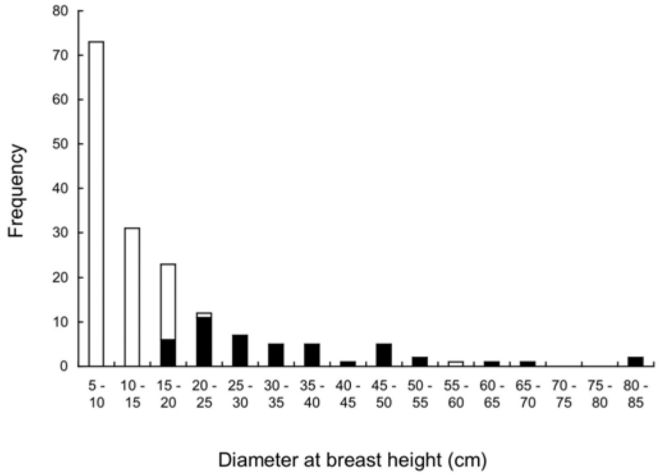


Fig. 2. Size-class distribution of *A. mono* trees with DBH >5 cm in the 6-ha plot, based on data collected in 2001 (Forestry and Forest Products Research Institute 2003). Filled and open bars indicate trees found bearing and not bearing flowers, respectively.

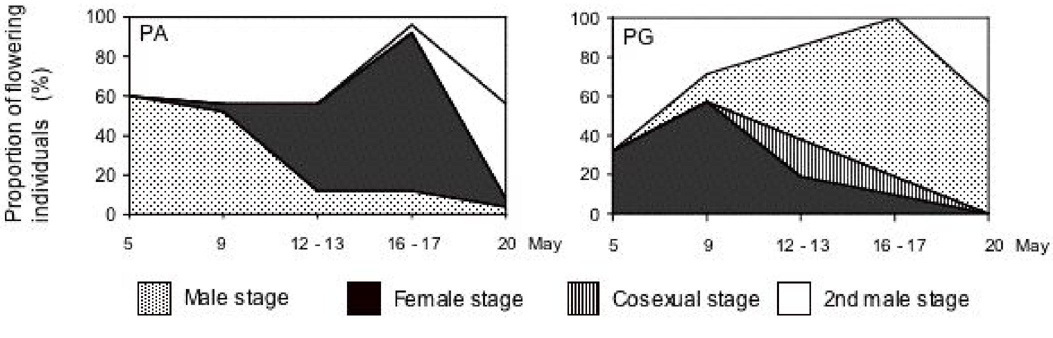


Fig. 3. The proportion of flowering individuals in each flowering phase at a given time of observation for protandrous (PA, above) and protogynous (PG, below) individuals.

The potential mating probability was 0.71 for between-type mating, 0.40 for P (PG, PA) and 0.31 for P (PA, PG), where PA and PG denote protandrous and protogynous individuals, respectively. The potential probability for within-type mating was 0.29, 0.10 for P (PA, PA) and 0.19 for P (PG, PG).

Genetic diversity and structure

Using eight microsatellites, 128 alleles were detected in 211 samples. An average of 13.25 alleles per locus were found in 81 samples from the 6-ha plot plus its surrounding area in the conserved site, whereas N_A was 14.25 in 130 samples from the fragmented site (Fig. 1). H_E was 0.801 and 0.781 in samples from the conserved and the fragmented sites, respectively. F_{IS} values were not significantly different from the null hypothesis in the former (F_{IS} = -0.007), but were significantly positive (F_{IS} = 0.031, $p < 0.05$) in the latter. F_{ST} was 0.029 (95% confidence interval of 0.013-0.047), suggesting low but significant genetic divergence between the two sites.

The relationship coefficient *r* was significantly positive for the four shortest distance classes (<101.7 m) and negative at six of the eight longest distance classes (>334.4 m) for the fragmented forest site at the 95% significance level. It was positive and negative only in the shortest (<44.7 m) and the longest distance classes (213.8-303.7 m) in the 6-ha plot (Fig. 4).

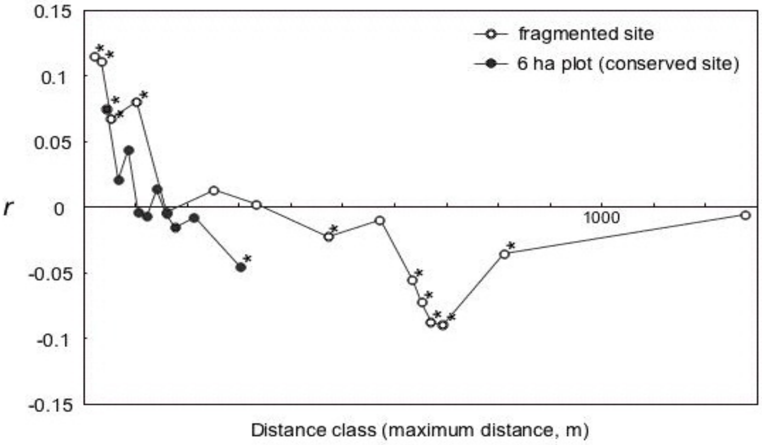


Fig. 4. The results of spatial autocorrelation analysis within the 6-ha plot in the conserved site (filled circles) and in the fragmented site (open circles). Asterisks indicate significant values for relationship coefficients *r* ($p < 0.05$) based on 1000 permutations.

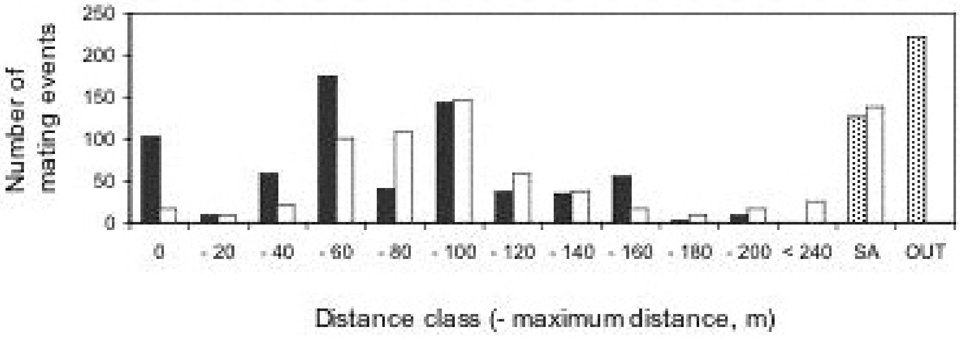


Fig. 5. Distribution patterns of mating distance inferred from parentage analysis. Filled and shaded bars indicate the number of mating events in each distance class. SA and OUT denote the frequency of seeds sired by individuals from the surrounding area and the frequency of seeds in which paternity was not decided, respectively. Open bars indicate expected values based on the number of individual pairs at a given distance class.

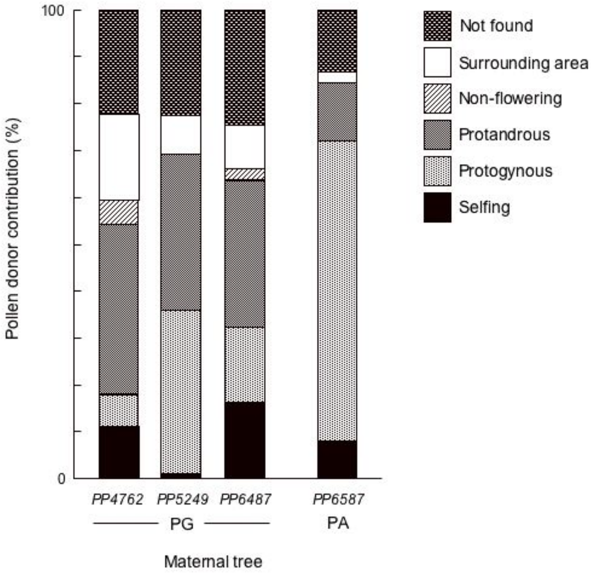


Fig. 6. The proportion of selfed seeds and outcrossed seeds sired by each type of pollen donor (protogynous and protandrous individuals, those not found bearing flowers in the plot [shown as "Non-flowering"], and those in the surrounding area). The proportion of seeds without a pollen parent among the sampled adults is indicated as "Not found."

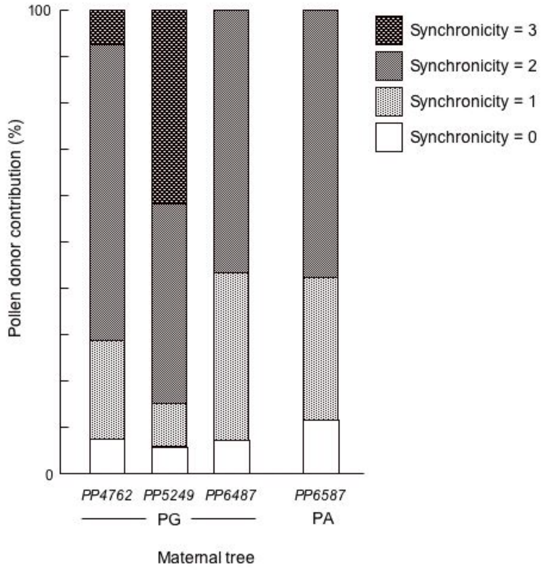


Fig. 7. The relative contribution of each type of pollen donor among the outcrossed seeds sired by flowering adults within the plot, in relation to flowering synchronicity between the male phase of pollen donors and the female phase of maternal trees.

Parentage analysis

A total of 1036 seeds collected from four mother trees were genotyped for paternity tests. Paternity was assigned to individuals within the plot in 60.6% of the seeds and to individuals in the surrounding area in 12.1% of seeds, and 21.4% were assumed to be sired by outside individuals. Paternity was not determined for only 0.29% of the seeds. The distribution of mating distance was illustrated in Fig. 5. Selfing rates ranged from 0.01% for the maternal tree *PP5249* to 15.6% for *PP6487* (Fig. 6). Of 554 outcrossed progenies sired by flowering trees in the plot, 396 were sired by trees of the reciprocal morph, significantly exceeding the number sired by the same heterodichogamous morph (p <0.0001, Chi-square test). However, between-type mating was largely superior to within-type mating for three of the maternal trees, *PP4762*, *PP6587* (p <0.001), and *PP6487* (p <0.01), but not for *PP5249*.

Next, we examined the effects of reciprocal flowering synchronicity between pollen donors and mother plants on mating patterns. The degree of reciprocal synchronicity between a maternal tree and each pollen donor was numerically scored from 0 to 3 based on the number of observations at which the female flowering of the maternal tree coincided with the male flowering of the pollen donor. Contribution of pollen donors with flowering synchronicity ≥1 (i.e., with male flowering period overlapping female flowering of the maternal tree for at least one observation) was disproportionately higher for all the maternal trees (p <0.001, chi-square test; Fig. 7).

To address the factors determining mating patterns in *A. mono*, the relative contribution of pollen donors was regressed with their flowering synchronicity to a maternal tree, mating distance, and their flower production. The relative flower production of each individual was roughly estimated from its crown size as determined from DBH and the proportion of flowering shoots in the crown. Here we applied a simple nonlinear power function model relating crown width (*CW*) and DBH of the congener *A. rubrum* (Bragg 2001):

$$CW = 1.64 + 0.249\ (\mathrm{DBH})^{0.876}.$$

The estimation of relative flower production was therefore obtained by multiplying (CW)*2π/4 and the proportion of flowering shoots. Pollen donor contribution was correlated with relative flower production (r = 0.550, p <0.001) and flowering synchronicity (r = 0.349, p <0.001), but not with mating distance (Fig. 8).

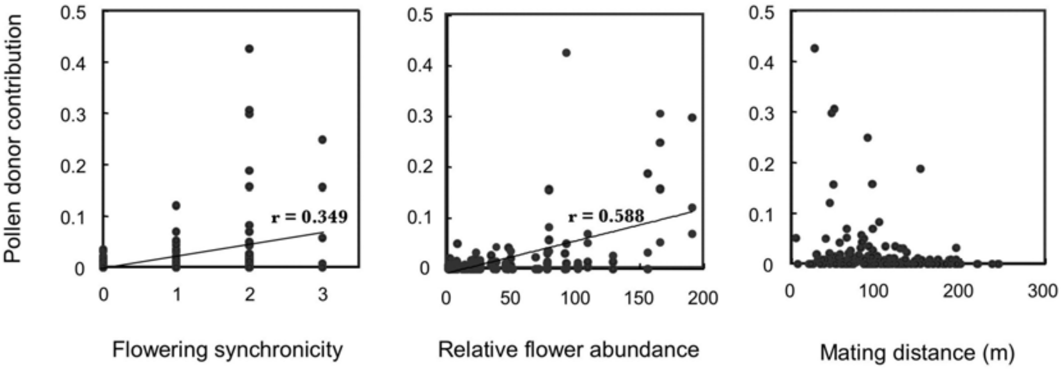


Fig. 8. Relationships between the contribution of pollen donors and their flowering synchronicity with the maternal tree, their flower abundance, and mating distance.

Discussion

Previous studies on flowering systems of heterodichogamous taxa have revealed reciprocal and synchronous flowering of protandrous and protogynous mating types within a population (Gleeson 1982, Pendleton *et al*. 1988, Asai 2002, Sato 2002, Kimura *et al*. 2003, Bai *et al*. 2006), and heterodichogamy has been considered an effective breeding system to avoid selfing and to ensure outcrossing by promoting between-type mating.

This study investigated exact mating patterns in *A. mono* and serves as an important empirical case addressing the ecological role of heterodichogamy in this maple.

In this study, flowering phases of the two mating types in *A. mono* were synchronous and reciprocal (Fig. 3). The potential mating probability, which was 2.4 times higher between the mating types than within the same type, is comparable with that of *A. japonicum* (Sato 2002). Temporal separation of male and female flowering within individual trees was apparent, but not perfect, with a cosexual stage in a few protogynous trees, as has been reported in previous studies (Pendleton *et al*. 1988, Sato 2002 and Kimura *et al*. 2003).

Paternity analysis using highly polymorphic microsatellites demonstrated high levels of outcrossing in *A. mono*. However, a certain amount of self-fertilization occurred in this natural population, suggesting no obligate self-incompatibility systems in *A. mono*. Self-compatibility is considered common in heterodichogamous taxa, including *Juglans* and *Acer* (reviewed by Renner 2001). Gabriel (1966) reported self-compatibility without a gametophytic or sporophytic incompatibility system in the heterodichogamous maple *A. saccharum* by experimental pollination, but also demonstrated lower seed set, probably resulting from post-zygotic abortion. Thus, the selfing rate found in this study may be an underestimate of self-fertilization in the natural population.

Self-fertilization in a natural population requires overlap of the male (or pollen remaining viable) and the female stages (or stigmas remaining receptive) within individuals. Therefore, it is considered that the degree of temporal overlap between male and female functions within individuals may be an important factor contributing to the variable selfing rates among maternal trees (0.01-16.2%). Specifically, the maternal tree *PP4762* with 9.6% of seeds self-fertilized showed a cosexual stage, in which female flowers remained in bloom in the upper layer of the tree while male flowers occurred in the lower layer. Although our observations in this study detected cosexual stages only in a few protogynous individuals, Sato (2002) described cosexual stages in protandrous individuals of *A. japonicum* between the male phase and the second male phase, suggesting a probability of self-fertilization in protandrous individuals. We conclude that the apparent but imperfect segregation of male and female flowering periods ensures high outcrossing in *A. mono*.

The hypothesis of between-type mating was not supported for all of the maternal trees (Fig. 6). Otherwise, a higher contribution of pollen donors just requires synchronicity between male flowering of pollen donors and female flowering of maternal trees (Fig. 7). Specifically, in the maternal tree PP5249, the female flowering phase lasted until the male flowering periods of many of the protogynous individuals in the plot, resulting in high pollen contribution from the same flowering type. Subsequently, the ratio of between-type mating to within-type mating was 2.94, which exceeded the expected value of potential mating probability (2.44).

Other than flowering synchronicity, flower production of pollen donors was considered a factor that increases their pollen contribution (Fig. 8). Interaction of these factors may well explain mating patterns of *A. mono* within this plot. We did not detect a significant negative relationship between distance and effective pollen dispersal. Effective pollination occurred over distances greater than 150 m (Fig. 8). Moreover, although the number of mating events dropped at distances greater than 180 m, more than 30% of the seeds were still sired by individuals not found within the plot (Fig. 5). Extending the spatial scale of paternity testing will be required to capture the negative effect of distance on pollen dispersal.

Analysis of spatial genetic structure provides an indirect estimate of the levels of gene flow via pollen and seeds. Spatial autocorrelation analysis in this study clarified significant genetic structure both within the 6-ha plot in the conserved site and within the fragmented site. The x-axis intercepts, where the relationship coefficient r first crossed the x-axis, suggest that gene flow of *A. mono* becomes restricted at the geographical scale of about 100-300 m. In the fragmented site, high r-values at distance classes up to 100 m represent spatial clustering of genetically related individuals in two younger forest stands with high density of this maple (Fig. 1). Moreover, the inbreeding coefficient F_{IS} was significantly positive in the fragmented site, whereas it did not depart from the null hypothesis in the conserved site. This evidence suggests reduced gene flow of *A. mono* throughout the fragmented forest.

Effective pollination should occur over hundreds of meters; however, isolation of reproductive individuals of *A. mono* by forest fragmentation may reduce the availability of suitable pollen donors with reciprocal flowering synchronicity and flower abundance. This study suggests two possible scenarios: increased selfing, if female and male functions temporarily overlap within individuals, and reduced seed production, if such overlap does not occur. Further analysis of the exact mating patterns within fragmented sites should be conducted.

References

Asai T (2000) Dichogamy in fullmoon maple (*Acer japonicum* THUNB.). *Bulletin of the Hokkaido Forestry Research Institute* **37**: 27-40 (in Japanese).

Bai W, Zeng Y, Liao W, Zhang D (2006) Flowering phenology and wind-pollination efficacy of heterodichogamous *Juglans mandshurica* (Juglandaceae). *Annals of Botany* **98**: 397-402.

Bragg DC (2001) A local basal area adjustment for crown width prediction. *Northern Journal of Applied Forestry* **18**: 22-28.

de Jong PC (1994) Taxonomy and reproductive biology of maples. In: *Maples of the World* (eds. Van Gelderen DM, de Jong PC, Oterdoom HJ), pp. 69-103. Timber Press, Portland, OR, USA.

Forestry and Forest Products Research Institute (2003) Forest Dynamics Database. http://fddb.ffpri-108.affrc.go.jp/ Viewed 15 August 2007.

Gabriel WJ (1966) Reproductive behavior in sugar maple: self-incompatibility, cross-compatibility, agamospermy, and agamocarpy. *Silvae Genetica* **16**: 165-168.

Gleeson SK (1982) Heterodichogamy in walnuts: inheritance and stable ratios. *Evolution* **36**: 892-902.

Gleiser G, Verdú M (2005) Repeated evolution of dioecy from androdioecy in *Acer*. *New Phytologist* **165**: 633-640.

Gouldet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). http://www.unil.ch/izea/softwares/fstat.html.

Hardy OJ, Vekemans X (2002). SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* **2**: 618-620.

Kalinowski ST, Taper ML & Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**: 1099-1006.

Kikuchi S, Shibata M (2007) Development of polymorphic microsatellite markers in *Acer mono* Maxim. *Molecular Ecology Notes* (in press).

Kimura M, Seiwa K, Suyama Y, Ueno N (2003) Flowering system of heterodichogamous *Juglans ailanthifolia*. *Plant Species Biology* **18**: 75-84.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**: 639-655.

Mitigami Y, Mizui N, Kikuzawa K (1989) Flowering patterns and fruit characteristics of *Acer mono. Transactions of the Meeting in Hokkaido Branch of the Japanese Forestry Society 37: 30-32 (in Japanese).*

Mukai Y, Yamamoto N (1997) DNA and RNA isolation method of woody plants. In: *PCR Experimental Protocols* *for Plants* (eds. Shimamoto K, Sasaki T), pp. 57-62. Shujunsha, Tokyo (in Japanese).

Murray MG, Thompson WF (1980) Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* **8**: 4321-4325.

Pandey M, Gailing O, Fischer D, Hattemer HH, Finkeldey R (2004) Characterization of microsatellite markers in sycamore (*Acer pseudoplatanus* L.). *Molecular Ecology Notes* **4**: 253-255.

Peakall, R, Smouse PE (2006) GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6**, 288-295.

Renner SS (2001) How common is heterodichogamy? *Trends in Ecology and Evolution* **16**: 595-597.

Sato T (2002) Phenology of sex expression and gender variation in a heterodichogamous maple, *Acer japonicum*. Ecology **83**: 1226-1238.

Terui H, Lian CL, Saito Y, Ide Y (2006) Development of microsatellite markers in *Acer capillipes*. *Molecular Ecology Notes* **6**: 77-79.

Wang J. 2002. An estimator for pairwise relatedness using molecular markers. *Genetics* **160**: 1203-1215.

Weir BS, Cockerham CC 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* **38**: 1358-1370.

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Effects of Human Disturbance of Forest on Reproduction of a Heterodichogamous Maple, *Acer mono*

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Introduction

There is concern about the effect of human disturbance of forests on trees' reproductive success, which underpins forest ecosystems. To predict that effect, it is necessary to investigate and analyze factors affecting plant reproduction. One of the factors, local population density, which is generally altered by anthropogenic forest use, is particularly important. Many studies report low population density causing low pollination success due to there being less visitation of pollinators to flowering plants (Kunin 1997, Ghazoul and McLeish 2001, Wagenius 2006), fewer mating individuals, and inbreeding depression due to the receipt of low-quality pollen (Bosch and Waser 1999). These negative effects on pollination efficiency reduce seed set (House 1992, Aizen and Feinsinger 1994, , Cascante et al. 2002). However, several studies have showed positive effects of low population density on other reproductive stages, such as low seed predation or fungal attack (Cascante et al. 2002, Fujimori et al. 2006).

In addition to population density, other factors such as tree size may have large effect on reproduction. Size-dependent resource allocation, whereby larger plants can invest more resources in fruits and seeds, has been observed in several plant species (Ohlson 1988, de Jong and Klinkhamer 1989). Such seeds may have higher levels of soundness. Since larger plants generally have larger floral displays, they will attract more pollinator insects (Klinkhamer et al. 1989), and may have better pollination efficiency.

Many plant species of a wide variety of taxa have dichogamous flowering systems. Sex expression is also an important reproductive factor for these species. For instance, in heterodichogamous species, which have a mixture of protogynous (stigmas are receptive before pollen is shed) and protandrous (pollen is shed before stigmas are receptive) mating types in a population (Renner 2001), resource investment to fruit maturation was higher in protogynous types than protandrous types (Asai 2000, Sato 2002). It is thought that heterodichogamous plants have reciprocal mating among different sex morph types (Gleeson 1982, Dommee et al. 1990, Kimura et al. 2003) to avoid self-pollination (Cruden and Hermann-Parker 1977) and reduce self-interference (Lloyd and Webb 1986). If such pollination systems are common, individuals are limited to mating with others of reciprocal sex morph, and their pollination efficiency will be more affected by spatial distribution of the reciprocal sex morph type rather than by the overall population density.

Thus, when we consider effect of human disturbance of forest on reproduction of trees, we should assess the effect of gradient of local population on reproductive success of trees together with the effect of other factors mentioned above. However, reproductive consequences of negative or positive impact of those factors are not yet well known, especially for trees of temperate forests. Therefore, we investigate the whole fruiting processes of *A. mono* Maxim. var. marmoratum (Nichols.) Hara f. dissectum (Wesmael) Rehder, which is a temperate forest component. This species is known to have an insect pollination system and heterodichogamous flowers as other *Acer* species. Our objective of this study is to clarify which stages of the fruiting process are affected by local population density, sex morph or individual tree size.

Species

Acer mono Maxim. var. marmoratum (Nichols.) Hara f. dissectum (Wesmael) Rehder (hereafter *A. mono*) is one of main canopy component trees in cool temperate deciduous forests in Japan. Inflorescences commonly form a compound umbel with two types of small flowers. One is a male flower with dehisced anthers and no pistil or an atrophied (sterile) pistil. The other is a female flower with indehiscent anthers and a healthy (fertile) pistil. In natural populations, a few trees have only inflorescences with male flowers and most trees have one of three types of inflorescence: (1) female flowers bloom before male flowers (female-male), (2) male flowers bloom before female flowers (male-female), or (3) male flowers bloom before and after female flowers (male-female-male). In this paper, we term (1) the protogynous (PG) type, and (2) and (3) the protandrous (PA) type. In most trees, the blooming period of each type of flower is synchronized at the individual tree level (Shibata M. personal observation). Thus, each tree has generally a male phase and a female phase in a flowering season. Various types of insects, such as flies, hoverflies and small solitary bees (Halictidae, Andrenidae) visit the flowers of this species (Matsui 1991). Thus, this species is a generalist plant; i.e. pollinated by several or many species from different taxa.

Study site

The study was carried out at Ogawa Forest Reserve (OFR) and neighboring fragmented forest, located in the southern part of the Abukuma Mountains, central Japan. The core area of OFR (ca. 100 ha) is an old-growth temperate deciduous forest. It is known that the land surrounding OFR has suffered human disturbance such as forest burning in the past (Suzuki 2002). Although OFR has been protected for at least 80 years, most of the edge area of this forest reserve is secondary forest likely to have been affected by human disturbance. Species composition and structure in the fragmented forest areas are similar to OFR (Masaki T. unpublished). The fragmented forest areas also have both old-growth and secondary forest stands. Information about the spatial location of OFR and the neighboring fragmented forest areas is shown in Isagi et al. (2007) and Fujimori et al. (2006)

Methods

Mapping of reproductive adult trees

We marked all flowering trees of *A. mono* as adult trees in a 6 ha plot of OFR and the fragmented forest areas in 2002. Canopy condition (canopy, suppressed, in gap, or gap edge), sex morph, and DBH of each tree were recorded. In order to determine the sex morph (PA or PG) of each tree, several inflorescences were collected in mid flowering season, and the condition of male and female flowers (bud, flowering, wilted, or dead) in the inflorescences was observed to determine the sexual sequence of flowering.

Since forest management differed between OFR and the fragmented forest, there was a certain degree of gradient of local population density. The geographical position of each tree was recorded on a map of the area. Based on this map, sample trees from sites of different local population densities were selected. For each sample tree, the average distance from the nearest five adults was measured as an index of local population density. The average distance from the nearest five adults was measured in two ways: DIS-N, distance from the nearest adults irrespective of sex morph, and DIS-RS, distance from the nearest adults that have the reciprocal sex morph (for instance, the distance from the nearest five PG trees was measured for PA trees).

Comparing seed demography

In order to compare reproductive performance between canopy trees with different local population density, individual tree size, and sex morph, we sampled seeds from 17 trees in 2002, 23 trees in 2003, and 40 trees in 2005. Most seeds were collected directly from branches just before the seed fall season (late October). The number of sampled seeds was from 100 to 500 for each tree. All seeds were cut and their kernel condition was examined, categorizing them according to condition as empty, subjected to predation by insects, decayed, or sound. Percentages of these seed conditions were calculated for each tree. Other than these parameters, seed size and percentage of immature seed fall were measured in 2003 and 2005, respectively. Average kernel weight of a sound seed as an index of seed size was measured for 12 of 23 sample trees in 2003. Percentage of immature seed fall was estimated for 30 of 40 trees in 2005.

Factors affecting seed production were analyzed by multiple regression analysis. The explaining variables were 3 factors: DIS-N or DIS-RS as an index of local population density, DBH as individual tree size, and type of sex morph. DIS-N and DIS-RS were transformed to log scales. The dependent variables were 6 demographic parameters: percentage of immature seed fall, empty seeds, seeds subjected to predation by insects, decayed seeds, sound seeds, and seed kernel weight. For the percentage of empty seeds, seeds subjected to predation by insects, decayed seeds, and sound seeds, data were pooled among the 3 observation years to enlarge sample size and reveal overall trends including annual variation of seed crop.

Results

We constructed two multiple regression models, one had DIS-N, DBH, and sex morph for the explaining variables, and the other had DIS-RS, DBH, and sex morph. The latter had a lower value of AIC (Akaike's Information Criterion) than the former for all the 6 dependent variables, suggesting that DIS-RS was a clearer index than DIS-N for the effect of local population density.

Distance from conspecific adults had a significant positive correlation with the percentage of immature seed fall and empty seeds (Tab. 1), but a negative correlation with the percentage of seeds subjected to predation and decayed seeds. Distance from conspecific adults did not have significant correlation with the percentage of seed soundness. However, its positive effect on seed kernel weight was marginally significant. Sex morph was only related to immature seed fall. Trees of PG type had a significantly lower percentage of immature seed fall than trees of PA type (Tab. 1). No effect was detected for size of individual trees (Tab. 1). These trends in the explaining variables were the same for the two models.

Discussion

Factors affecting pollination efficiency

The positive effect of the distance of conspecific adults on the percentage of immature seed fall and empty seeds (Tab. 1) suggested pollination efficiency increasing with higher local population density. We expected that a larger plant would have higher pollination efficiency because of the larger number of flowers to attract more pollinator insects (Klinkhamer et al. 1989). However, the percentages of immature seed fall and empty seeds were not affected by tree sizes but were instead influenced by local population density (Tab. 1). This indicates that the number of flowers at the local population level (several hundred square meter scale) was more important for pollination success than that at the individual level (several dozen square meter scale) for *A. mono*.

In contrast to *A. mono*, pollination efficiency of *Kalopanax pictus,* which is also a main component tree species in this forest, was not affected by local population density (Fujimori et al. 2006). We presume that such different responses between tree species reflect differences in pollinator foraging range and abundance. The most frequent flower visitors of *K. pictus* is the honeybee, which has a large foraging range (Fujimori et al. 2006); its foraging distance can range 1-10 km (Visscher and Seeley 1982; Sasaki 1999). Honeybees contributed to effective pollination in sparsely-distributed *Dinizia excelsa* trees (distance between trees was ca. 1500 m) in fragmented forests in Brazil (Dick et al. 2003). Honeybees in this forest may also contribute to effective pollination for *K. pictus*. The most frequent flower visitors of *A. mono* were small solitary bees, hoverflies, and flies. Such insects probably work as pollinators. They showed large variations in abundance and species composition with landscape change even over small distance (Steffan-Dewenter et al. 2002, Sueyoshi et al. 2003), indicating that small solitary bees and flies have a narrower foraging area and are sensitive to changes in stand conditions. We presume that pollination efficiency of *A. mono* varies with local population density due to changes in pollinator abundance and behavior in responding to the local flowering tree density.

We expected that local population density of the reciprocal sex morph rather than that of both types may have a stronger effect on pollination for *A.mono*. However, the difference between them was not so large; AIC of the multiple regression models constructed with DIS-RS had a slightly lower value than that with DIS-N. This is probably caused by mixed spatial distribution of both sex morphs. Local population density was similar in both the models, and DIS-RS had a high correlation with DIS-N (r=0.94). It will depend on the degree of deflection of spatial distribution of each sex morphs whether local density of the reciprocal sex morph is more important or not.

Heterodichogamous trait was important as an individual level factor. Trees of PG type had significant lower immature seed fall than PA (Tab. 1). This result suggests that the former had higher efficiency of pollen acceptance (bias to female function) than the latter. Therefore, heterodichogamy relates not only to the reciprocal pollination system but also to the difference of gender specialization linked with sex morph. Several reports said that heterodichogamy was one of evolutional pathway from monoecy to dioecy (Pendleton et al. 2000, Sato 2002). The bias of female function in PG in this study may reflect such evolutional background. In contrast to PG, PA, which has higher immature seed fall, may expend effort to pollen supply like *Juglans ailanthifolia* (Kimura et al. 2003).

Density dependent seed mortality

Density dependent mortality has been well reported at the post-dispersal seed stage and seedling stage for many species (Shibata and Nakashizuka 1995, Hille Ris Lambers and Clark 2003, Wright et al. 2005). Our results showed density dependent mortality is also occurring at the pre-dispersal seed stage (Tab. 1) similar to other tree species that have been studied recently: *Samanea saman* in a tropical forest (Cascante et al. 2002), and *K. pictus* (Fujimori et al. 2006) and *Magnolia obovata* in a temperate forest (Isagi et al. 2007). We think that density dependent mortality is also a common phenomenon in the fruiting process.

Steffan-Dewenter et al. (2001) pointed out that decreasing predation at a low population density site counterbalances the disadvantage of the low pollination success. Our study also detected a similar situation. As a consequence of seed set, population density did not affect soundness of seeds in the spatial scale of this study (Tab. 1). However, we have to be careful not to give a simple explanation that local population density does not influence reproduction, because different functional groups, namely pollinators and seed predators, counterbalance their effects with respect to local population density. Unfortunately, we do not currently know the critical spatial scale of the habitats for these functional groups in detail. This study shows that the effect of local population density on plant reproduction was very complicated. We have to examine further the counterbalance between pollination and seed mortality and this will be part of an investigation including a wider range of the population densities of host plants.

Factors affecting seed maturation

Contrary to our expectations, individual tree size did not have a clear relationship with either seed soundness or seed size (Tab. 1). On the other hand, growth of the seed was affected by local population density. These results suggest that seed development of this species is regulated more by pollination than by individual resource conditions. However, seed size tends to be rather smaller at high local population density sites (Tab. 1). If neighboring individuals at the high local population density site are closely related to each other, and pollinators remain within the site, inbreeding depression among neighboring trees will occur. We presume that downsizing of seed results from such inbreeding depression. This means that high local population density has a negative effect on the quality of pollination like biparental inbreeding (Ritland and Jain 1981). To examine this suggestion, it is important to investigate mechanisms of the reproductive consequence related to local population by revealing the actual pollen flow by genetic approaches as a part of future study.

Conclusion

This study showed that local population density and sex morph had effects on various stages of the fruiting process. Impacts operated both negatively and positively. This complicated interaction may lead to autonomous control of abundance of this species, as with *Magnolia obovata* (Isagi et al. 2007). However, the response of each species depends on the variety of pollinators and seed predators as mentioned above. The response of local population density may also change with annual fluctuation of seed production and insect population dynamics. To consider effects of human disturbance of forest on tree reproduction, it is important to clarify plant-animal interaction in reproduction and in the long-term dynamics of target species.

References

Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. Ecology 75(2):330-351.

Asai T (2000) Dichogamy in fullmoon maple. (In Japanese with English summary) Bulletin of the Hokkaido Forestry Research Institute 37:27-40.

Bosch M, Waser NM (1999) Effects of local density on pollination and reproduction in *Delphinium nuttallianum* and *Aconitum columbianum*. American Journal of Botany 86(6):871-879.

Cascante A, Quesada M, Lobo JJ, Fuchs EA (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. Conservation Biology 16:137-147.

Cruden RW, Hermann-Parker SM (1977) Temporal dioecism: an alternative to dioesism? Evolution 31(4):863-866.

Dick CW, Etchelecu G, Austerlitz F (2003) Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and african honeybees in pristine and fragmented Amazonian rainforest. Molecular Ecology 12:753-764.

Dommee B, Bompar JL, Denelle N (1990) Sexual tetramorphism in *Thymelaea hirsuta* (thymelaeaceae): evidence of the pathway from heterodichogamy to dioecy at the infraspecific level. American Journal of Botany 77(11):1449-1462.

Fujimori N, Samejima H, Kenta T, Ichie T, Shibata M, Iida S, Nakashizuka T (2006) Reproductive success and distance to conspecific adults in the sparsely distributed tree *Kalopanax pictus*. Journal of Plant Research 119(3):195-204.

Ghazoul J, McLeish M (2001) Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. Plant Ecology 153 (1-2): 335-345.

Gleeson SK (1982) Heterodichogamy in walnuts: inheritance and stable ratios. Evolution 36:892-902.

Hille Ris Lambers J, Clark JS (2003) Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. Canadian Journal of Forest Research 33:783-795.

House SM (1992) Population density and fruit set in three dioecious tree species in Australian tropical rain forest. Journal of Ecology 80:57-69.

Isagi Y. Tateno R, Matsuki Y, Hirao A, Watanabe S, Shibata M (2007) Genetic and reproductive consequences of forest fragmentation for populations of *Magnolia obovata*. Ecological Research 22:382-389.

Jong TJ de, Klinkhamer PGL (1989) Size-dependency of sex-allocation in hermaphroditic, monocarpic plants. Functional Ecology 3:201-206.

Kimura M, Seiwa K, Suyama Y, Ueno N (2003) Flowering system of heterodichogamous *Juglans ailanthifolia*. Plant Species Biology 18:75-84.

Klinkhamer PGL, Jong TJ de, Bruyn GJ de (1989) Plant size and pollinator visitation in *Cynoglossum officinale*. Oikos 54:201-204.

Kunin WE (1997) Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology 85 (2): 225-234.

Lloyd DG, Webb CJ (1986) The avoidance of interference between the presentation of pollen and stigmas in anginosperms. I. Dichogamy. New Zealand Journal of Botany 24:135-162.

Matsui K (1991) Pollination ecology of four *Acer* species in Japan with special reference to bee pollinators. Plant Species Biology 6:117-120.

Ohlson M (1988) Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. Journal of Ecology 76(4):1007-1016.

Pendleton RL, Freeman DC, McArther ED, Sanderson SC (2000) Gender specialization in heterodichogamous *Grayia brandegei* (Chenopodiaceae): evidence for an alternative pathway to dioecy. American Journal of Botany 87(4):508-516.

Renner SS (2001) How common is heterodichogamy? Trends in Ecology and Evolution. 16(11):595-597.

Ritland K, Jain SK (1981) A model for the estimation of outcrossing rate and gene frequencies using *n* independent loci. Heredity, 47, 35-52.

Sasaki M (1999) Wonders of the Japanese Honeybee, Biology of Northernmost *Apis cerana*. (In Japanese) Kaiyusha Publishers, Tokyo pp10-11.

Sato T (2002) Phenology of sex expression and gender variation in a heterodichogamous maple, *Acer japonicum*. Ecology 83(5):1226-1238.

Shibata M, Nakashizuka T (1995) Seed and seedling demography of four co-occurring *Carpinus* species in a temperate deciduous forest. Ecology 76(4): 1099-1108.

Steffan-Dewenter I, Munzenberg U, and Tscharntke T (2001) Pollination, seed set and seed predation on a landscape scale. P. Roy. Soc. of Lond. B Bio. 268(1477):1685-90.

Steffan-Dewenter I, Munzenberg U, Burger C (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83(5):1421-1432.

Sueyoshi M, Maeto K, Makihara H, Makino S, Iwai T (2003) Changes in dipteran assemblages with secondary succession of temperate deciduous forests following clear-cutting. (In Japanese with English summary) Bulletin of FFPRI 2(3):171-191.

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. In: Nakashizuka T and Matsumoto Y (eds), Ecological studies 158, Springer-Verlag,Tokyo pp. 27-40.

Visscher PK, Seeley DK (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63: 1790-1801.

Wagenius S (2006) Scale dependence of reproductive failure in fragmented *Echinacea* populations. Ecology 87(4): 931-941.

Wright SJ, Muller-Landau HC, Calderon O, Hernandes A (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology 86(4):848-860.

Table 1. Multiple regression analyses of factors affecting the fruiting process.

Demographic parameters	Factors						Regression model's	
	Distance from eighboring adults		Tree size		Sex morph			
	effect	Prob.	effect	Prob.	effect	Prob.	R^2	AIC
Seed mortality								
Pollination failure								
Immature seed fall	＋	0.014	ns	---	PG<PA	0.005	0.41	151.8
Empty seeds	＋	<.0001	ns	---	ns	---	0.26	437.4
Suffering predation	-	0.041	ns	---	ns	---	0.07	423.9
Decay	-	0.003	ns	---	ns	---	0.13	439.9
Seed maturation								
Soundness	ns	---	ns	---	ns	---	<.00	467.2
Seed kernel weight	(＋)	0.071	ns	---			0.56	91.8

DIS-RS and DBH are shown as an indicator of distance from conspecific adults and tree size, respectively.

Symbols of effect are as follows; ＋: a positive effect, -: a negative effect, (+): marginally significant positive effect, ns: no significant effect.

Fruit Utilization by Five Types of Understory Bird Assemblages in Sarawak, Malaysia

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Introduction

In the Oriental Region, highly frugivorous bird species occur in 17 families (of 82), and some degree of frugivory has been reported for 50% of bird families (Corlett 1998). Many frugivorous birds feed on only a portion of the diversity of fleshy fruits produced in any habitat. Fruit selection presumably depends on the behavior, morphology, and nutritional requirements of birds, the abundance of alternative food resources, and fruits characteristics such as temporal availability, habitat, color, abundance, pulp-to-seed ratio and nutrient composition (Corlett 1998, Herrera 1998, Witmer 2001, Alcántara and Rey 2003).

Fruit size may be critical to selection. Sekercioglu (2006) argued that large-seeded plants depend on large frugivores (e.g., hornbills), which account for a relatively small part of the avian fauna, for seed dispersal. Since larger birds have larger gapes, they could potentially eat fruits with a wider range of seed size and a larger number of fruit species. However, it is unlikely that large birds eat small fruits in open spaces and the understory. Therefore, understory birds with gapes of different size should also play some roles in seed dispersal in open spaces and the understory.

The relative abundance of bird groups, based on gape width and frugivory level, was clearly different among forest types (Moran et al. 2004). Also, they discussed potential fruit utilization; however, it is essential to connect gape size with plant species that frugivorous birds actually eat for approach to ecological and conservational subjects. Also, previous studies have investigated how the distribution of understory frugivorous birds changed within a forest (Restrero et al. 1999; Pearman 2002). However, there has been little research that birds actually feed on how fruits of different plant life forms. By investigating it, the characteristic of fruits utilization of birds within a forest can be expressed.

The purpose of our study was to examine the relationship between smaller birds living in the understory and their fruit utilization in Sarawak, Malaysia. More specifically, we asked three questions: (1) How fruits do understory birds eat on plant life forms? (2) Do understory birds with larger gapes utilize a larger number of fruit species? (3) Do birds with similar gape size overlap about the fruit species they consume?

Methods

Study site

This study was conducted in Lambir Hills National Park (4˚12'N, 114˚02'E), Sarawak, Malaysia. The rain forest in this park is composed of primary mixed dipterocarp (Dipterocarpaceae) forest.

The relationships between birds and fruits

To clarify the fruit species eaten by understory birds, we conducted three investigations. We referred to

Robson (2000) for the identification of bird species in the field. If the captured bird did not appear in Robson, we referred to MacKinnon and Phillipps (1993).

Indirect observation We set sensor cameras near fruiting trees in the canopy and understory for one or more weeks from April 2005 to June 2006, except in November 2005 and from February to April 2006. The camera lens was pointed toward the fruits. Photographed birds were then identified.

Direct observation The birds visiting fruiting trees were observed using a field scope and binoculars from April 2005 to January 2006, except in August and November 2005. We recorded the species of birds that ate fruits. We intensively observed trees bearing many fruits or those growing in open spaces where the sensor cameras could not be set.

Captured birds and excreted seeds We caught birds with mist nets from March 2005 to June 2006, except in August and November 2005 and from February to April 2006. Two mist nets per day per site were set at a total of five points at the forest edge or in the understory of the forest interior from 07:00 to 17:00. We used four shelf-mist nets that were 6 or 12 m long and 2.5 m high and had a 24- or 36-mm mesh size. The captured birds were carefully removed from the nets and kept for 1 hour in cotton bags where they could not hurt themselves. After the hour, we measured their body mass, wing length, tail length, gape length, and gape width, and released all birds uninjured. We then recorded the number, weight, and size of seeds contained in the excrement found in the cotton bag. The seeds were identified by comparing them with seeds of fruiting plants that had been collected during the field study.

Analysis When excreted seeds could not be identified, the data were not included in the analysis. Birds seen feeding on fruits during direct and indirect observations were included in the analysis along with data from the captured birds.

We showed fruit utilization by the five bird assemblages based on taxonomy and gape width, which were observed feeding on fruits of 28 plant species. The plant species were classified into three groups in terms of life forms: pioneer plants (forest edge and gaps), understory plants (understory of the forest interior), and canopy plants (canopy). Climbing and epiphytic *Ficus* species were categorized as canopy plants.

Results

Of the 56 species (15 families) that we captured, 19 species (four families) excreted feces containing seeds (Table 1). Captured frugivorous species recorded were divided into five types based on taxonomy and gape width (Table 2).Of seven emerald doves (*Chalcophaps indica*), one excreted intact seeds of *Macaranga bancana* (Euphorbiaceae); however, three doves excreted destroyed seeds. For this reason, we considered that *C. indica* was a seed predator rather than a seed disperser, and *C. indica* was not included in further analysis. Also, a little spiderhunter (*Arachnothera longirostra*) excreted intact seeds, however; *A. longirostra* was not included in further analysis because the seeds were not identified. In contrast, yellow-vented bulbuls (*Pycnonotus goiavier*) and Cream-vented bulbuls (*Pycnonotus simplex*) did not excrete seeds. However, these two bulbuls were included in further analysis because it was recorded that they fed on some fruits in direct observation.

All five types of frugivorous species utilized pioneer plants (Fig. 1). Medium-gaped bulbuls fed on various fruit species (25 of the 28 available species). Moreover, bulbuls with small and medium gapes utilized all three types of habitat for feeding on fruits. Barbets and flowerpeckers did not feed on understory fruits, and sunbirds did not feed on canopy fruits.

Diets of bird types have no overlap in understory plants, except for the overlap between small-gaped and medium-gaped bulbuls (Fig. 2). Barbets fed on fruits of pioneer and canopy plants but did not utilize understory plants. Fruits of *Ficus* accounted for three of seven plants. Fruit diets of flowerpeckers were composed of pioneer plants and *Ficus*. The fruit diet of small-gaped bulbuls was completely included in that of medium-gaped bulbuls. The fruit consumed by sunbirds did not overlap with that of barbets or flowerpeckers. Sunbirds fed only on four fruit species, three of which were pioneer *Macaranga* trees.

Discussion

Many pioneer trees produce fruits frequently (Davies and Ashton 1999; Sakai et al. 1999; our observations) and attract avian dispersers. At our study site, all understory birds fed on fruits of pioneer plants. Pioneer plants might constantly support understory frugivorous birds. Also, bulbuls fed on a wide range of fruits (Figs. 1, 2). In particular, they fed on a larger number of understory fruit species than the other bird groups. Hence, bulbuls seem to be essential for the seed dispersal of understory trees.

Of the five bird types, it was expected that barbets, which have the largest gapes, could potentially eat the largest number of fruit species. However, medium-gaped bulbuls utilized a greater number of different types of fruit than barbets (Fig. 1). In the same family (Pycnonotidae), small-gaped bulbuls fed on fewer fruit species than medium-gaped bulbuls. There are two possible reasons why medium-gaped bulbuls utilized all kinds of fruits. First, Pycnonotidae birds may not be very selective in feeding on fruits and can therefore utilize a wide variety of fruits. Second, a medium-sized gape might enable them to feed on fruits having a wider range of seed size, making them the most adaptable frugivorous birds in the forest understory.

Both the taxonomy and gape width of sunbirds were similar to those of flowerpeckers (Table 2); however, the fruit species eaten by sunbirds did not completely overlap with those eaten by flowerpeckers (Fig. 2). In general, frugivores select fruits in terms of fruit color, fruit size, seed size, and nutrient composition of the fresh pulp (Stiles 1993; Bollen et al. 2004). Both sunbirds and flowerpeckers utilize fruits; however, sunbirds mainly feed on nectar and insects and flowerpeckers mainly feed on the fruits (Corlett 1998). Sugar preferences also differ between nectar- and fruit-eating birds (Lotz 2006), and fruits eaten by these two bird types might be distinguished by the nutrient composition of the pulp.

All understory birds fed on fruits of pioneer plants. Pioneer plants might constantly support understory frugivorous birds. Also, Taxonomy rather than gape size might explain fruit utilization of understory birds.

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References

Alcántara JM, Rey PJ (2003) Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. J. Evol. Biol. 16:1168–1176.

Bollen A, Van Elsacker L, Ganzhorn JU (2004) Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. J. Trop. Ecol. 20:599–612.

Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indmalayan) Region. Biol. Rev. 73:413–448.

Davies SJ, Ashton PS (1999) Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiacea) in Borneo. Am. J. Bot. 86:1786–1795.

Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. Ecol. Monogr. 68:511–538.

Lotz CN (2006) Sugar preferences in nectar- and fruit-eating birds: behavioral patterns and physiological causes. BIOTROPICA 38:3–15.

MacKinnon J, Phillipps K (1993) A Field Guide to The Birds of Borneo, Sumatra, Java and Bali. Oxford University Press.

Moran C, Catterall CP, Green RJ, Olsen MF (2004) Functional variation among fruigivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. Oecologia 141:584–595.

Pearman PB (2002) The scale of community structure: habitat variation and avian guilds in tropical forest understory. Ecol. Monogr. 72:19–39.

Restrero C, Gomez N, Heredia S (1999) Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. Ecology 80:668–685.

Robson C (2000) A Field Guide To The Birds of South-East Asia. New Holland Publishers (UK).

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T, Inoue T (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am. J. Bot. 86:1414–1436.

Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends Ecol. Evol. 21:464–471.

Stiles EW (1993) The influence of pulp lipids on fruit preference by birds. Vegetatio 107/108:227–235.

Witmer MC (2001) Nutritional interactions and fruit removal: Cedar Waxwing consumption of *Viburnum opulus* fruits in spring. Ecology 82:3120–3130.

Table 1. List of captured birds, the number and the proportion of the bird excreting seeds.

Faimly	Species	Common name	The number of captured birds	The number of the bird excreting seeds	The proportion of the bird excreting seeds
Apodidae	*Collocalia esculenta*	Glossy Swiftlet	2	0	0.00
Columbidae	*Chalcophaps indica*	Emerald Dove	7	1	0.14
Alcedinidae	*Alcedo meninting*	Blue-eared Kingfisher	9	0	0.00
	Ceyx rufidorsa	Rufous-backed Kingfisher	3	0	0.00
Halcyonidae	*Lacedo pulchella*	Banded Kingfisher	1	0	0.00
Cuculidae	*Cuculus micropterus*	Indian Cuckoo	2	0	0.00
	Surniculus lugubris	Drongo Cuckoo	1	0	0.00
Megalaimidae	*Megalaima mystacophanos*	Red-throated Barbet	3	3	1.00
Picidae	*Blythipicus rubiginosus*	Maroon Woodpecker	1	0	0.00
	Meiglyptes tukki	Buff-necked Woodpecker	7	0	0.00
	Sasia abnormis	Rufous Piculet	6	0	0.00
Cisticolidae	*Prinia flaviventris*	Yellow-bellied Prinia	2	0	0.00
Corvidae	*Hypothymis azurea*	Black-naped Monarch	7	0	0.00
	Rhipidura javanica	Pied Fantail	1	0	0.00
	Rhipidura perlata	Spotted Fantail	1	0	0.00
	Philentoma pyrhopterum	Rufous-winged Philentoma	2	0	0.00
Eurylaimidae	*Cymbirhynchus macrorhyncho*	Black-and-red Broadbill	1	0	0.00
Muscicapidae	*Copsychus malabaricus*	White-rumped Shama	14	0	0.00
	Cyornis caerulatus	Large-billed Blue-Flycatcher	1	0	0.00
	Cyornis turcosus	Malaysian Blue-Flycatcher	2	0	0.00
	Cyornis spp.	Blue-Flycatcher	3	0	0.00
	Rhinomyias umbratilis	Grey-chested Jungle-Flycatche	2	0	0.00
Nectariniidae	*Dicaeum trigonostigma*	Orange-bellied Flowerpecker	1	0	0.00
	Prionochilus maculatus	Yellow-breasted Flowerpecker	11	9	0.82
	Prionochilus xanthopygius	Yellow-rumped Flowerpecker	5	3	0.60
	Aethopyga siparaja	Crimson Sunbird	3	0	0.00
	Anthreptes malacensis	Plain-throated Sunbird	2	1	0.50
	Anthreptes rhodolaem	Red-throated Sunbird	1	1	1.00
	Anthreptes simplex	Plain Sunbird	7	5	0.71
	Anthreptes spp.	Sunbird	8	4	0.50
	Anthreptes singalensis	Ruby-cheeked Sunbird	3	0	0.00
	Arachnothera longirostra	Little Spiderhunter	96	1	0.01
	Hypogramma hypogrammicum	Purple-naped Sunbird	13	7	0.54
	unidentified	Sunbird	1	0	0.00
Passeridae	*Lonchura fuscans*	Dusky Munia	36	0	0.00
Pycnonotidae	*Alophoixus bres*	Grey-cheeked Bulbul	6	5	0.83
	Alophoixus phaeocephalus	Yellow-bellied Bulbul	15	8	0.53
	Iole olivacea	Buff-vented Bulbul	1	1	1.00
	Pycnonotus atriceps	Black-headed Bulbul	24	19	0.79
	Pycnonotus brunneus	Red-eyed Bulbul	12	11	0.92
	Pycnonotus erythropthalmos	Spectacled Bulbul	25	22	0.88
	Pycnonotus eutilotus	Puff-backed Bulbul	13	11	0.85
	Pycnonotus goiavier	Yellow-vented Bulbul	1	0	0.00
	Pycnonotus plumosus	Olive-winged Bulbul	10	6	0.60
	Pycnonotus simplex	Cream-vented Bulbul	1	0	0.00
	Tricholestes criniger	Hairy-backed Bulbul	3	2	0.67
Sylviidae	*Orthotomus atrogularis*	Dark-necked Tailorbird	4	0	0.00
	Orthotomus sericeus	Rufous-tailed Tailorbird	10	0	0.00
	Alcippe brunneicauda	Brown Fulvetta	1	0	0.00
	Macronous ptilosus	Fluffy-backed Tit-Babbler	3	0	0.00
	Malacocincla malaccensis	Short-tailed Babbler	3	0	0.00
	Malacocincla sepiarium	Horsfield's Babbler	1	0	0.00
	Malacopteron affine	Sooty-capped Babbler	1	0	0.00
	Malacopteron cinereum	Scaly-crowned Babbler	2	0	0.00
	Pellorneum capistratum	Black-capped Babbler	1	0	0.00
	Stachyris erythroptera	Chestnut-winged Babbler	8	0	0.00
	Stachyris maculata	Chestnut-rumped Babbler	6	0	0.00
	Stachyris nigricollis	Black-throated Babbler	2	0	0.00
	Trichastoma rostratum	White-chested Babbler	1	0	0.00
Total			419	120	0.29

Table 2. List of the analyzed 19 bird species and thier body mass and gape width.

Bird type	Faimly	Tribe	Species	Body mass (g)	Gape width (mm)	Gape size class
Barbets	Megalaimidae		*Megalaima mystacophanos*	75.2	21.59	l
Flowerpeckers	Nectariniidae	Dicaeini	*Dicaeum trigonostigma*	6.4	5.99	s
			Prionochilus maculatus	8.6	6.74	s
			Prionochilus xanthopygius	7.7	6.37	s
Sunbirds	Nectariniidae	Nectariniini	*Anthreptes malacensis*	11.4	7.08	s
			Anthreptes rhodolaem	NA	7.28	s
			Anthreptes simplex	8.4	6.73	s
			Hypogramma hypogrammicum	11.9	8.67	s
Medium-gaped bulbuls	Pycnonotidae		*Alophoixus bres*	42.0	14.16	m
			Alophoixus phaeocephalus	31.4	12.58	m
			Iole olivacea	24.4	10.74	m
			Pycnonotus brunneus	25.6	10.66	m
			Pycnonotus eutilotus	35.8	12.50	m
			Pycnonotus goiavier	28.0	12.79	m
			Pycnonotus plumosus	30.3	11.75	m
Small-gaped bulbuls	Pycnonotidae		*Pycnonotus atriceps*	22.0	9.88	s
			Pycnonotus erythropthalmos	17.7	9.61	s
			Pycnonotus simplex	23.0	9.27	s
			Tricholestes criniger	16.2	9.37	s

NA: not available, s: small-gaped (<10 mm), m: medium-gaped (10-15 mm), l: large-gaped (>15 mm).

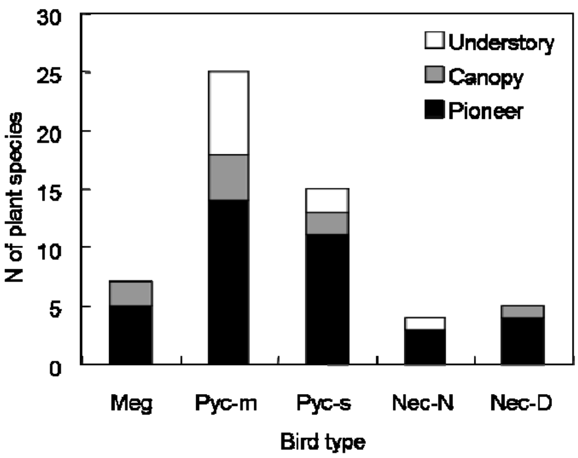
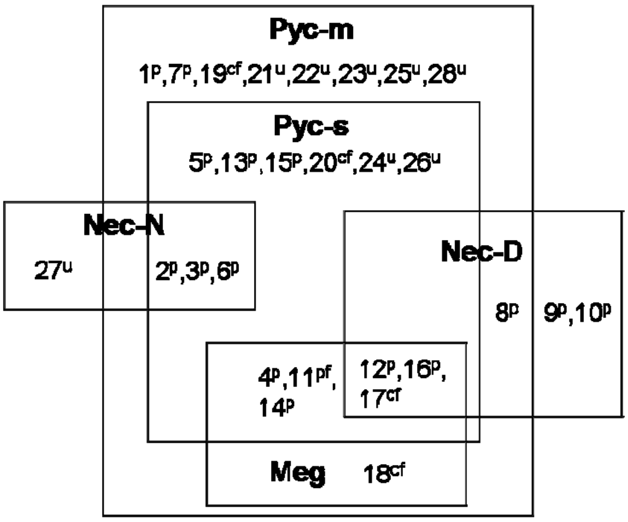


Fig. 1. The fruit utilization by five bird types: barbets (Meg), medium-gaped bulbuls (Pyc-m), small-gaped bulbuls (Pyc-s), sunbirds (Nec-N) and flowerpeckers (Nec-D).



1^{p}	*Dillenia suffruticosa*	(Dilleniaceae)
2^{p}	*Macaranga bancana*	(Euphorbiaceae)
3^{p}	*Macaranga beccariana*	(Euphorbiaceae)
4^{p}	*Macaranga gigantea*	(Euphorbiaceae)
5^{p}	*Macaranga hosei*	(Euphorbiaceae)
6^{p}	*Macaranga winkleri*	(Euphorbiaceae)
7^{p}	*Leea indica*	(Leeaceae)
8^{p}	*Melastoma malabathricum*	(Melastomatacea)
9^{p}	*Pternadra multiflora*	(Melastomatacea)
10^{p}	Melastomatacea sp.	(Melastomatacea)
11^{pf}	*Ficus fulva*	(Moraceae)
12^{p}	*Callicarpa pentandra*	(Verbenaceae)
13^{p}	*Callicarpa havilandii*	(Verbenaceae)
14^{p}	*Vitex pinnata*	(Verbenaceae)
15^{p}	Specimen NO.73	
16^{p}	Specimen NO.77	
17^{cf}	*Ficus acamptophylla*	(Moraceae)
18^{cf}	*Ficus stricta*	(Moraceae)
19^{cf}	*Ficus subgelderi*	(Moraceae)
20^{cf}	*Ficus sp1*	(Moraceae)
21^{u}	*Gomiphia serrata*	(Ochnaceae)
22^{u}	*Ixora woodii*	(Rubiaceae)
23^{u}	*Ixora sp2.*	(Rubiaceae)
24^{u}	*Lasianthus pilosus*	(Rubiaceae)
25^{u}	Specimen NO.38	
26^{u}	Specimen NO.44	
27^{u}	Specimen NO.76	
28^{u}	Specimen NO.88	

Fig. 2. The fruit diet information was classified into five bird types: barbets (Meg), medium-gaped bulbuls (Pyc-m), small-gaped bulbuls (Pyc-s), sunbirds (Nec-N) and flowerpeckers (Nec-D). In addition, the fruit species was classified into three groups: pioneer plants (p), understory plants (u), canopy plants (c). Climber/epiphyte plants of genus *Ficus* (f) were included in canopy plants.

Seed Dispersal by Mammals in Different Harvesting Intensities with Reduced-Impact and Conventional Logging in Sabah, Malaysia

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Introduction

Large mammals and birds are highly vulnerable to human disturbance such as hunting, habitat fragmentation and forest logging (Peres 2000), and their populations have rapidly diminished especially in Southeast Asia (Corlett 2002). Recent studies of fruit–frugivore interactions showed that large-seeded plants depend on large frugivores for seed dispersal (Corlett 1998; Kitamura et al. 2002). Large-seeded plants may thus be negatively affected by the decline of such animal populations. Urgent research is required into interactions between large-seeded fruits and frugivores where the latter still occur (Kitamura et al. 2002).

Reduced-impact logging is a set of guidelines to reduce the physical impacts on the ground, remaining standing trees, streams and ecosystem as a whole with the combination of a pre-harvest census, carefully controlled felling and skidding, lowered allowable cut and regulated machinery use (Putz and Pinard 1993). Previous studies showed that relative densities of frugivorous mammals such as orangutan and civets (Viverridae) were higher in reduced-impact logged forest than in conventional logged forest in Sabah, Malaysia (Ancrenaz et al. 2005; Onoguchi 2007). As a next research question, we need to know if and how the difference in the density of frugivorous mammals translates to seed dispersal.

To understand the fruit-frugivore interaction in different harvesting intensities between reduced-impact and conventional logging, we investigated the seed dispersal by mammals in both forests. We conducted (1) the identification of seed dispersers of genus *Durio* that is one of the largest-seeded groups in Southeast Asia, with direct observation and camera trap, and (2) the comparative study on seed dispersal by civets that is one of the most important seed dispersers in Southeast Asia with route census in reduced-impact logged forest and conventional logged forest.

Materials & Methods

Study site

Our study was conducted in Deramakot Forest Reserve (55,083ha), a reduced-impact logged forest and adjacent Tangkulap Forest Reserve (27,550ha), a conventionally logged forest, in Sabah, Malaysia. The climate is humid equatorial with a mean annual temperature of about 26℃. Mean annual rainfall is about 3,500 mm (Huth and Ditzer 2001). The major vegetation of Deramakot is a mixed dipterocarp forest dominated by the family Dipterocarpaceae, while that of Tangkulap is a forest dominated by pioneer species such as the genus *Macaranga* (Euphorbiaceae) (Seino et al. 2006). All of the large mammal species of

Sabah, including Asia elephants *Elephas maximus* (Linnaeus, 1758), orangutans *Pongo pygmaeus* (Hoppius, 1763) and sun bears *Helarctos malayanus* (Raffles, 1821), with the exception of the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814), inhabit these forests (Matsubayashi et al. 2006; Onoguchi 2007; Matsubayashi et al. in press).

Focal Durio species

The studied durian species were *Durio graveolens* Becc. and *D. zibethinus* Murray. Both species have the typical fruit structure of *Durio*, with large, tough husks and acute spines, containing arillate seeds, but the species vary in aril color, and the timing of dehiscence. *Durio graveolens* has a pale orange globose husk, 10.1 ± 1.4 cm long and 9.1 ± 1.2 cm wide (mean ± SD, n = 20), which completely splits into five valves on the tree (before the fruits fall). The seeds, 3.8 ± 0.5 cm long and 2.0 ± 0.1 cm wide (n = 30), are surrounded by red aril which is not sweet and has no odor. The number of seeds per fruit is 7.6 ± 2.2 (n = 20). In contrast, *D. zibethinus* has an ellipsoid green husk, 13.2 ± 3.1 cm long and 10.0 ± 3.3 cm wide (n = 20), which opens after the fruits have fallen. The seeds, 3.9 ± 0.3 cm long and 2.6 ± 0.2 cm wide (n = 30), are surrounded by white aril which is sweet in taste with a strong odor. The number of seeds per fruit is 5.5 ± 3.2 (n = 20).

Study sites are *ca* 30 km from the nearest village, and no fruits were removed by humans. In 2005, *Durio* bore many fruits from July to September in Deramakot. Observations were conducted at three *D. graveolens* trees (tree code: ET1, ET2, and ST3) and one *D. zibethinus* (K5). The *D. graveolens* trees were 223 ± 46 cm dbh, while the *D. zibethinus* was 345 cm. Our observations started before fruits were fully matured (developed full in fruit size with incomplete arillate seeds).

Camera trap and direct observation

When fruits were still immature (*i.e.*, intact on the trees for both species), both durian species were watched from a concealed position on the ground *ca* 20 m from the tree from 0530 h to 1830 h in almost all weather conditions except heavy rain (ET1: 28 July–7 August, ET2: 11–17 August, ST3: 5–12 September, K5: 3–16 August). When fruits matured (*i.e.*, those of *D. graveolens* retained on the tree, but those of *D. zibethinus* fallen), *D. graveolens* trees were observed directly from 0530 h to 0030 h (ET1: 8–10 August, ET2: 18–20 August, ST3: 13–19 September), and *D. zibethinus* was monitored with an automatic digital camera system (CAMEDIA digital camera X-350, OLYMPUS, and Magical Finger HAS-NF1, HOGA, Japan) on a 24-h basis (K5: 15–31 August). For the latter, we relocated all dropped fruits of *D. zibethinus* to the front of the automatic camera system.

In direct observation, we recorded the following: (1) visiting animal species; (2) length of time on tree; (3) the number of fruits consumed; and (4) the method of handling the seeds. We were unable to precisely count the number of fruits consumed, since fruits were concealed by leaves. Thus, the number of fruits consumed by each individual was estimated based on the number consumed during direct sightings divided by the proportion of the duration of direct sighting to the total duration of the visit. These points could be materialized for both species in most cases. Even when using an automatic camera, (3) and (4) were recorded by applying no photographic delay interval, which enabled us to use the camera like a video camera. Total fruit number was estimated from the total number of fallen husks with intact stalks during one season. This is likely to be an underestimate, because we may have overlooked fallen husks with intact stalks, and we observed that some animals consumed fruits after removal beyond the crown of a mother tree, so total fruit number here is approximate one. These observations were continued daily until all fruits which could be seen from the ground had been consumed. In total, we conducted 288 h direct observation on *D. graveolens* (ET1: 93 h, ET2: 65 h, ST3: 130 h), and 96 h direct observation and 384 h observation with the automatic camera on *D. zibethinus* (K5: 504 h).

Route census of seed dispersal

We conducted route census with a total of 30 km logging road, 17km in the reduced-impact logged forest for 52 days and 13km in the conventional logged forest for 23 days in 2004 and 2005 on foot and by motorbike during day. Dispersed seeds with feces of civets were photographed (Fig. 1), and the seeds were classified by aril color and shape. To identify seeds, we relied on Jaiwit P. and Gubilil M. who are the staff of Forest Research Centre, Sabah Forestry Department. We compared the frequency of the detection of the feces and number of the seeds species recorded in both of the forests.

Results

Seed dispersers of the Durio

Total fruit number was 99, 27, 252 and 58 at ET1, ET2, ST3 and K5, respectively. The results of our observations are shown in Table 1. We defined dispersal (D) as transporting seeds 20 m or more from the parent tree, neutral consumption (NC) as dropping intact seeds under the parent tree crown and predation (P) as destroying seeds.

During our observations of both species, orangutans consumed more fruits than any other consumers (ET1: $\chi^2 = 46.1$, df = 1, $P < 0.001$; ET2: $\chi^2 = 21.2$, df = 1, $P < 0.001$; ST3: $\chi^2 = 162$, df = 1, $P < 0.001$; K5: $\chi^2 = 29$, df = 1, $P < 0.001$; Table 1). When orangutans visited the trees, arillate seeds were still immature. They plucked fruits with hands and/or teeth, and easily tore apart husks with their hands and incisors. They picked up the arillate seeds, sucked aril, chewed the seed and spat out only the seed coats. At times, they made longer visits, making a bed on or near a fruiting tree and consuming fruits on two consecutive days. One male consumed 119 fruits during two days in one visit. In terms of function, they therefore appear to be the most important predators.

When *D. graveolens* matured, fruits dehisced on the trees, and they were consumed mainly by arboreal animals; Prevost's squirrels *Callosciurus prevostii* (Desmarest, 1822), black hornbills *Anthracoceros malayanus* (Raffles, 1822), civets (Viverridae) and long-tailed macaques *Macaca fascicularis* (Raffles, 1821)(Table1). Black hornbills visited two trees (ET1, ST3), swallowed arillate seeds and did not regurgitate before leaving the tree, so they clearly dispersed seeds. The number of seeds handled by them (Table 1) was probably overestimated, especially at ST3, because they did not appear to eat fruits when perched in places that we were unable to observe. We directly observed hornbills eating only 7 seeds in 4 fruits. A civet visited one tree (ET1) during the night. The animal was concealed by leaves, so we were unable to identify it to species or how it handled the seeds. However, when we fed three captive common palm civets *Paradoxurus hermaphroditus* (Pallas, 1777) with *D. graveolens* fruits, they chewed and destroyed the seeds, and swallowed them (Y. Nakashima pers. obs.). In summary, *D. graveolens* seeds were predated mainly by orangutans and dispersed by black hornbills.

In contrast, *D. zibethinus* fruits were consumed once fallen to the ground, mainly by terrestrial animals (Table 1). Fruits remained unopened on the ground for some time. Before the fruits opened naturally, sun bears *Helarctos malayanus* visited and opened them with their clacks or teeth. The bears ate only arils and spat out intact seeds, so they are neutral consumers in our observations. Long-tailed giant rat *Leopoldamys sabanus* (Thomas, 1887), large tree shrew *Tupaia tana* (Raffles, 1821), horse-tailed squirrel *Sundasciurus hippurus* (Geoffroy, 1831), Malayan porcupine *Hystrix brachyura* (Linnaeus, 1758) and long-tailed porcupine *Trichys fasciculata* (Shaw, 1801) were observed to visit the seeds left by the sun bears. Long-tailed giant rats sometimes carried seeds in their mouths and these seeds were probably quickly predated. When we traced 200 seeds of *D. zibethinus* (and 100 *D. graveolens*) with a thread-marking method (Yasuda et al. 2000), most seeds were predated within 1 day, and we have no evidence that scatter-hoarded seeds grew to seedlings (Y. Nakashima, unpublished data). Long-tailed macaques visited when the fruits were already dehisced on the ground. They cleaned arils in front of the mouth and then dropped the seeds. They sometimes carried the fruits > 10 m by hand. We found seed and husk discarded 23 m from the mother tree (transporting the fruit the first 18 m). Thus, these macaques do transport seeds beyond the crown of a mother tree although this behavior may be rare. The *D. zibethinus* seeds were mainly predated by orangutans and dispersed by long-tailed macaques.

Seed dispersal by civets

Frequency of detection of the feces was greater in the reduced-impact logged forest (1.13feces/day; the total number of feces is 59; total census day is 52 days) than that of in the conventionally-logged forest (0.61feces/day; 14 feces and 23days). Table 2 shows the family of seeds and the probably number of species in each family. In total, 28 species of seeds were detected in two forests. Twenty-seven species were in reduced-impact logged forest, and nine species were in conventionally-logged forest. Eight of the nine species found in the conventionally-logged forest were also detected in the reduced-impact logged forest.

Discussion

Our results show that many fruits of the two durian (*Durio*) species are predated, especially by orangutans. The majority of seeds did not germinate due to high predation pressure by orangutans, despite high investment into extremely large fruits. Some studies reported that orangutans especially preferred the fruits of *Durio* (Rijksen 1978; Galdikas 1982, 1988; Leighton 1993). In areas inhabited by orangutans, *Durio* dispersal success is probably lower than that in uninhabited areas. Although we report a predominant role of orangutans as predators, we also observed them to discard > 1000 mature intact seeds under one *D. graveolens* tree (TL1). This suggests that seed handling strategy varies among individuals, or even between trees by the same individuals. Galdikas (1982) highlighted their role as dispersal agents after observing orangutans discard *D. oxleyanus* seeds up to 50 m away from a mother tree. However, at least in

Deramakot, this is unlikely to occur. We also found many discarded seed coats under the other 8 fruiting trees, suggesting that they usually destroy and eat seeds. We always found their beds on or near fruiting trees, indicating that they stayed for up to several days to consume fruits and did not transport the seeds beyond the crown of mother tree even when they spat out the seeds.

Ridley (1984) suggested that *Durio* species with small red arils are probably dispersed by hornbills, and *D. zibethinus* is dispersed by bears. Our observations support the former, but not the latter. When we fed two captive bears with *D. zibethinus* fruits at the Sepilok Orangutan Rehabilitation Centre in Sabah, they did not swallow seeds. However, one individual at Sandakan Crocodile Farm in Sabah swallowed and excreted the intact *D. zibethinus* seeds. These results suggest that seed handling strategies differ among and/or within individuals of bear. In the wild, the Asian elephant *E. maximus* can probably also disperse seeds of *D. zibethinus*. The intact seeds were observed in their feces in the natural habitat. (A. Ahmad who is a staff of Sabah Forestry Department, pers. comm.). In addition, Prevost's squirrel may carry the seeds of the two species at least as far as to the adjacent tree crowns, as was reported in Peninsular Malaysia (Becker et al. 1985), although we did not observe such a behavior.

Our results suggest that both *Durio* species studied face difficulties with seed dispersal due to high predation pressure, especially by orangutans, and limited occurrence of alternative dispersal agents. The low density of wild *Durio* may be in part caused by high predation pressure. Our study did not reveal the main seed dispersers of *D. zibethinus*, but it is clear that the two *Durio* species are dispersed by different animals; *D. graveolens* by hornbills and *D. zibethinus* by large terrestrial mammals such as elephant and bear. These animals have been reported to be negatively affected by habitat degradation including fragmentation and logging (Corlett 2002). Therefore, our results suggest that the loss of large animals due to habitat degradation affects the regeneration of both species of *Durio*.

The frequency of the occurrence of civet feces and the number of dispersed seeds tended to diminish in the conventionally logged forest than in the reduced-impact logged forest. The former may reflects the reduction of the density of civets in the conventionally-logged forest. Seven species of civets were recorded in Deramakot (Matsubayashi et al. 2006; Onoguchi 2007; Matsubayashi et al. in press). Although we could not identify the species of civet for each dispersed seed, much of the seeds might have been dispersed by common palm civet *P. hermaphroditus* and/or Malay civet *Viverra tangalunga* (Gray, 1832) because these two species were often observed on the road at night and the density (indexed by camera trap) of those species tended to decrease in the conventionally-logged forest (Onoguchi 2007). The latter may reflect the decrease of the food resources for civets in the conventionally-logged forest. For example, seeds of Sapotaceae (Fig.1; vernacular name, Nyatoh), a group of climax trees that are commercially harvested, were detected in the reduced-impact logged forest only. The seeds of Sapotaceae could not be detected in the conventionally-logged forest probably because Sapotaceae tree were heavily harvested.

Our results correspond with the previous comparative study on vegetation and mammal fauna in the two forests (Seino et al. 2006; Onoguchi 2007), and imply that heavier logging intensities cause the degradation of the ecological function of civets, which in turn may feed-back to the forest regeneration through reduced seed dispersal.

References

Ancrenaz M, Gimenez O, Ambu L, Ancrenaz K, Andau P, Goossens B, Payne J, Sawang A, Tuuga A, Lackman-Ancrenaz I (2005) Aerial surveys give new estimates for orangutans in Sabah, Malaysia. PLoS Biology, 3, 1-8.

Becker P, Leighton M, and Payne JB (1985) Why tropical squirrels carry seeds out of source crowns? Journal of Tropical Ecology 1: 183-186.

Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. Biological Review 73: 413-448.

Corlett RT (2002) Frugivory and seed dispersal in degraded tropical East Asian landscapes. In D. Levey, W. Silva and M. Galetti. (Eds). Seed dispersal and frugivory: ecology, evolution and conservation. pp 451-465. CABI Publishing, New York, New York.

Galdikas BMF (1982) Orangutans as seed dispersers at Tanjung Puting, Central Kalimantan: Implications for conservation. In L. E. M. Boer (Ed.). The Orangutan. Its Biology and Conservation. pp 285-298. Boston Hingham, The Hague, The Netherlands.

Galdikas BMF (1988) Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. International Journal of Primatology 9: 1-35.

Huth A and Ditzer T (2004) Long-term impacts of logging in a tropical rain forest – a simulation study. Forest Ecology and Management 142: 33-51.

Kitamura S, Yumoto T, Poonswad P, Chuailua P, Plongmai K, Maruhashi T, and Noma N (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. Oecologia 133: 559-572.

Leighton M (1993) Modeling dietary selectively by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. International Journal of Primatology 14: 257-313.

Matsubayashi H, Lagan P, Majalap N, Tangah J, Sukor JRA, and Kitayama K (2006) Diversity of mammalian species at natural licks in rain forest of Deramakot and their conservation. In: Lee YF et al. (eds.) Synergy between carbon management and biodiversity conservation in tropical rain forests, the proceedings of the 2nd workshop, 30 Nov.-1 Dec. 2005, Sandakan, Malaysia. DIWPA, Shiga, Japan.

Matsubayashi H, Lagan P, Majalap N, Tangah J, Sukor JRA, and Kitayama K (in press) Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecological Research. (DOI: 10.1007/s11284-006-0313-4)

Onoguchi G (2007) Can reduced-impact logging preserve mammals in tropical rainforests? -A comparative survey on mammalian fauna by camera-trapping in Sabah, Borneo- Graduation thesis, Kyoto University.

Peres CA (2000) Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology 14: 240-253.

Ridley HN (1894) On the dispersal of seeds by mammals. Journal of the straits branch of the royal Asiatic society 25: 11-32.

Rijksen HD (1978) A Field Study on Sumatran Orangutans (*Pongo pygmaeus abelii* Lesson 1827): Ecology, Behavior and Conservation. pp 420. H. Veenman & Zonen B. V. Wageningen, The Netherlands.

Seino T, Takyu M, Aiba S, Kitayama K, and Ong RC (2006) Floristic composition, stand structure, and above-ground biomass of the tropical rain forests of Deramakot and Tangkulap Forest Reserve in Malaysia under different forest managements. In: Lee YF et al. (eds.) Synergy between carbon management and biodiversity conservation in tropical rain forests, the proceedings of the 2nd workshop, 30 Nov.-1 Dec. 2005, Sandakan, Malaysia. DIWPA, Shiga, Japan.

Yasuda M, Miura S, and Hussein NA (2000) Evidence for food hoarding behaviour in terrestrial rodents in Pasoh Forest Reserve, a Malaysian lowland rain forest. Journal of Tropical Forest Science 12: 164-173.

Table 1. The estimated numbers of the durian fruits consumed by each of visiting animals.

				Unripe fruit		Ripe fruit	
Tree species	Tree code	Animal species	Seed handling[1]	Visits (*N*)	Fruit consumed (*N*)	Visits (*N*)	Fruit consumed (*N*)
D. graveolens	ET1	*Pongo pygmaeus* (♀)	P	1	62	0	0
		Callosciurus prevostii	NC/P	3	0	4	3
		Macaca fascicularis (♂)	NC	0	0	1	3
		Viverridae sp.	-	0	0	1	?
	ET2	*P. pygmaeus* (♀)	P	1	24	0	0
		C. prevostii	NC/P	2	0	1	1
		Anthracoceros malayanus (♂)	D	0	0	1	0
	ST3	*P. pygmaeus* (♂)	P	2	206	0	0
		C. prevostii	NC/P	0	0	1	4
		A. malayanus (♂)	D	0	0	3	12
D. zibethinus	K5	*P. pygmaeus* (♀)	P	1	52	0	0
		C. prevostii	NC/P	2	1	0	0
		Helarctos malayanus	NC	0	0	7	16
		M. fascicularis (♂, ♀)	NC/D	0	0	1	9
		Leopoldamys sabanus	P	0	0	1	1

Tree codes correspond to main text.

[1] P = predation, NC = neutral consumption, D = dispersal

Table 2. Family of the seeds found in civet feces and the estimated number of species in each family in the reduced-impact logged forest and the conventionally-logged forest.

Census sites	Family	Detected no. of species (total)
Reduced-impact logged forest	Annonaceae	2
	Cucurbitaceae	1
	Leeaceae	1
	Meliaceae	3
	Passifloraceae	1
	Sapotaceae	1
	Solanaceae	1
	Theaceae	1
	Unidentified	16
		(27)
Conventionally-logged forest	Meliaceae	1
	Passifloraceae	1
	Rubiaceae	1
	Unidentified	6
		(9)

Figure 1. Dispersed seeds (Sapotaceae) in the feces of civets in the reduced-impact logged forest.

Effects of Past Forest Use on *Ficus* Fruiting Behavior in the Western Lowlands of Yakushima Island

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Introduction

Strangling *Ficus* trees develop a huge crown and produce large amounts of fruit throughout the year. Thus, they can act as "keystone" species in tropical and subtropical forests (Lambert & Marshall 1991; Richards 1996). In the lowlands of Yakushima Island, Japan, located at the southern end of the warm temperate zone, *Ficus superba* var. *japonica* provides fruits for Japanese macaque and various bird species throughout the year (e.g., Hanya et al. 2003), indicating the importance of this species in plant–animal interactions and forest ecosystems. However, it seems that year-round fruiting is more vulnerable in the temperate zone, in which environmental conditions fluctuate seasonally, than in the tropical zone, which has constant high temperatures.

In addition to seasonal changes in environmental conditions, the warm-temperate forest of the western lowlands of Yakushima Island, which is a World Natural Heritage area, experienced human disturbances such as clear-cut logging in the early 1940s (see section 2.1.3.3. for details). Past human impacts can affect the current landscape and tree distribution over a time span of 100 years (Ohtani & Koike 2005). Intensive logging in western Yakushima Island may have also affected ecological functions such as fruit production and the spatial distribution of a keystone *Ficus* species within the forest. Thus, we examined the effects of past logging on *Ficus* fruiting behavior in relation to its distribution and genetic characteristics.

Materials & Methods

The study site of Kawahara was located in the western coastal area of Yakushima Island, southwestern Japan (30°20' N, 130°30' E). The annual mean temperature was 19.8°C, and the monthly mean temperature ranged from 10.6°C in January to 26.2°C in August. This site was covered by secondary warm-temperate broad-leaved forest with dominant species such as *Quercus salicina* (Fagaceae), *Castanopsis sieboldii* (Fagaceae), *Litsea acuminata* (Lauraceae), *Ardisia sieboldii* (Myrsinaceae), and *Distylium racemosum* (Hamamelidaceae). Six *Ficus* species occurred at the study site: two stranglers, *F. superba* var. *japonica* and *F. microcarpa*; a shrub, *F. erecta*; and three vines, *F. nipponica*, *F. thunbergii*, and *F. pumila*. The strangler *F. superba* var. *japonica* occurred frequently in the lowlands of Yakushima Island. The density of the strangler *F. microcarpa* was much lower than that of *F. superba* var. *japonica* at the study site; the island is the northern limit of *F. microcarpa* habitat. Thus, we examined the fruiting phenology of *F. superba* var. *japonica*. Hereafter, "*Ficus* tree" refers to *F. superba* var. *japonica*.

In the Kawahara area, *Ficus* trees inhabited two types of site: sites that were subjected to intensive or clear-cut logging in the early 1940s; and sites that experienced relatively light logging mainly for charcoal production in the 1940s–1950s. Some huge strangler *Ficus* trees were found in the sites used for charcoal production. In contrast, most *Ficus* trees in the clear-cut sites had relatively small crowns and grew on rocks; these trees seemed to have established after the clear-cut logging.

In total, 74 *Ficus* trees were surveyed using a GPS receiver (Pathfinder Pro XRS, Trimble, Tokyo) and their crown projection area was determined as an index of tree size. Fruiting behavior has been monitored at 3- to 4-week intervals (on average, 26.4 days per interval) since June 2003, and the amount and maturity of fruit is recorded at each census. The amount of fruit was ranked from 0 = no fruit to 8 = vast amount of fruit, indicating the relative fruit abundance within an individual tree. Here, we analyzed data from June 2003 to December 2006.

To examine the relationship between genetic characteristics and fruiting patterns of individual trees, we conducted microsatellite genotyping of the 74 *Ficus* trees monitored. Fresh leaf samples were obtained from each tree between June and August 2004, and DNA was extracted using a DNeasy Plant Mini Kit (QIAGEN). We used six microsatellite primers that were developed for other *Ficus* species: FinsA1, FinsH5, FinsJ10, FinsM5, FM4-70, and FS3-31 (Vignes et al., 2006; Zavodna et al., 2005). The loci were amplified in two multiplex polymerase chain reactions (PCRs), with each containing four and two primer pairs (FinsH5 / FinsM5 / FM4-70 / FS3-31 and FinsA1 / FinsJ10) and 10 ng of template DNA. PCR amplifications were performed using a GeneAmp PCR System 9700 (Applied Biosystems) with: initial denaturation at 95°C for 15 min; 25 cycles of denaturation at 94°C for 30 s, annealing at 57°C for 90 s, and extension at 72°C for 60 s; and a final incubation at 60°C for 30 min and holding at 4°C. PCR products were denatured at 95°C for 3 min and electrophoresed along with the GENESCAN 400-HD ROX size standard on a 3100 Genetic Analyzer using GENESCAN analysis software and GENOTYPER software (Applied Biosystems).

Results & Discussion

Of the 74 *Ficus* trees monitored, four were of relatively small size did not produce any fruits during the study period and so were excluded from the analyses. K-means clustering classified the 70 *Ficus* trees into two groups according to the amount of fruit at each census. The mean amount of fruit for the first group (20 trees) increased periodically in winter (Fig. 1). In contrast the mean amount of fruit for the second group (50 trees) was consistently low, with no apparent seasonal changes. The 20 trees that bore abundant fruit in winter had larger crown projection areas than the remaining 50 trees (U-test, $z = 3.18$, $p = 0.001$; Fig.2). The crown projection area was positively correlated with the fruiting frequency per year ($n = 70$, $r = 0.52$, $p < 0.001$; Fig. 2). This suggests that larger trees have the potential for frequent fruiting within a year and heavy fruiting in winter, which increases their relative contribution to the year-round fruiting and the plant–animal interactions.

The *Ficus* trees in Kawahara were distributed mainly in areas that were not clear-cut logged in the early 1940s, although some relatively small trees inhabited prior intensively logged sites (e.g., Fig. 3, southwestern corner). *Ficus* trees with the two types of fruiting pattern, i.e., heavy winter fruiting or no apparent trend, were randomly dispersed (Fig. 3), indicating no spatial bias in the tree distribution corresponding to the type of fruiting pattern. However, some large *Ficus* trees with heavy winter fruiting were located exclusively in sites that had not been clear-cut in the early 1940s (Fig. 3).

Six microsatellite loci were consistently resolved in the *Ficus* trees. A total of 23 alleles were detected: two for each of FinsJ10, FinsM5, and FS3-31; five for FinsH5; and six for each of FinsA1 and FM4-70. Based on the allele types for these six microsatellite loci, we performed a principal components analysis with respect to fruiting pattern (Fig. 4). The eigenvalues of axes 1 and 2 were 5.27 and 3.82, respectively. *Ficus* trees classified into the two fruiting patterns were scattered randomly in the analysis (Fig. 4), suggesting that the genotypes determined using the six microsatellite loci had no relation to the fruiting behavior and that the fruiting pattern of individual trees was governed by other factors such as variation in solar insolation.

The lack of large *Ficus* trees in the prior clear-cut sites indicated that the sizes and populations of *Ficus* trees are still developing and recovering from human disturbances that occurred approximately 60 years ago. Given their potential for heavy fruiting in winter, large *Ficus* trees can play a much more important role than small trees. However, some large *Ficus* trees growing on rocks or steep slopes fell over, probably as a result of strong wind and their own weight, implying a tree size limitation for *Ficus* tree growing on rocks. Large-sized host trees such as *Persea thunbergii* and *D. racemosum* appear to be required for the development of large strangling *Ficus* trees. Thus, it may take strangling *Ficus* species longer to recover than the general forest structure.

In the lowlands of Yakushima Island, as well as in the coastal areas of southwestern Japan, forests have been exposed to various human disturbances, including conversion to other land uses. Protected areas in lowlands and coastal sites are required to conserve rich ecosystems, including *Ficus*–animal interactions, in the warm temperate zone.

References

Hanya, G., Noma, N. and Agetsuma, N. (2003) Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. Primates 44: 51-59.

Lambert, F. R. and Marshall, A. G. (1991) Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. Journal of Ecology 79: 793-809.

Ohtani, S. and Koike, F. (2005) Implications of 19th century landscape patterns for the recovery of *Fagus crenata* forests. Applied Vegetation Science 8: 125-132.

Richards, P. W. (1996) The tropical rain forest—an ecological study. Second edition. Cambridge University Press.

Vignes, H., Hossaert-Mckey, M., Beaune, D., Anstett, A. C., Borges, M., Kjellberg, F. and Chevallier, H. (2006) Development and characterization of microsatellite markers for a monoecious *Ficus* species, *Ficus insipida* and cross-species amplification among different sections of *Ficus*. Molecular Ecology Notes 6: 792-795.

Zavodna, M., Arens, P., Van Dijk, P. J. and Vosman, B. (2005) Development and characterization of microsatellite markers for two dioecious *Ficus* species. Molecular Ecology Notes 5: 355-357.

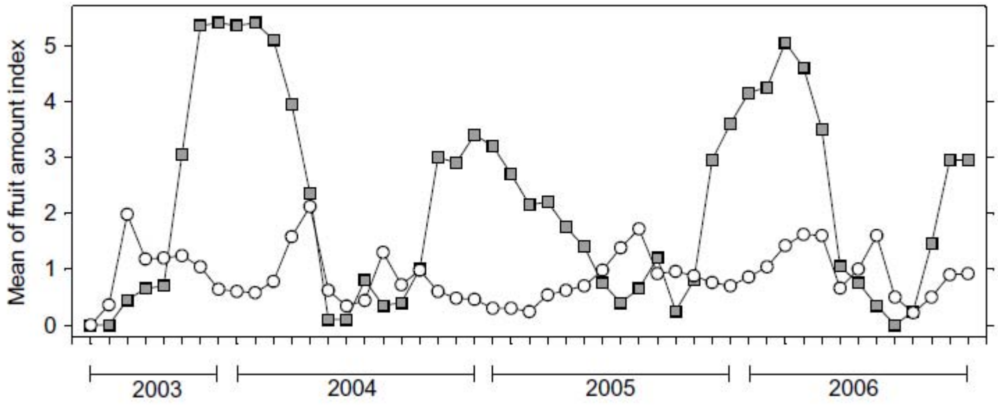

Fig. 1. Time series of the mean amount of fruit for two groups of *Ficus* classified using K-means clustering. One group (gray squares) tended to produce large amounts of fruit in winter; the other group (white circles) had no conspicuous seasonal trend.

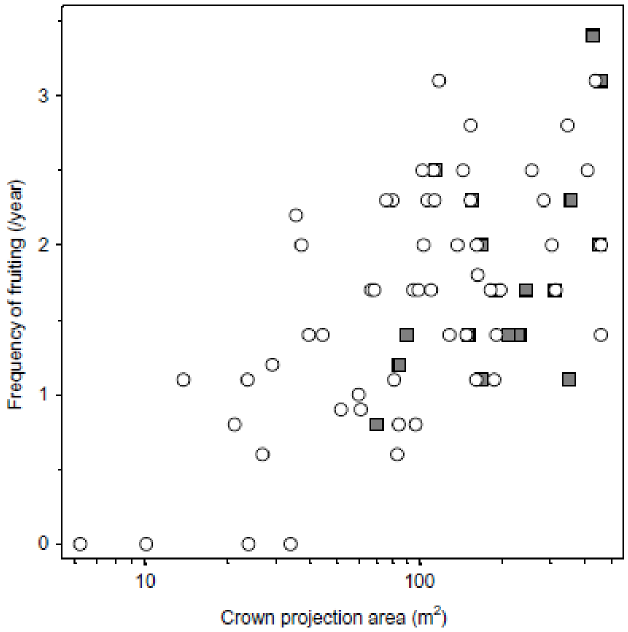

Fig. 2. The relationship between crown projection area and fruiting frequency per year of *Ficus superba* var. *japonica*. A significant positive correlation was detected ($n = 70$, $r = 0.52$, $p < 0.001$); four trees that did not produce fruit during the study period were excluded from the analysis.
See Fig. 1 legend for symbols.

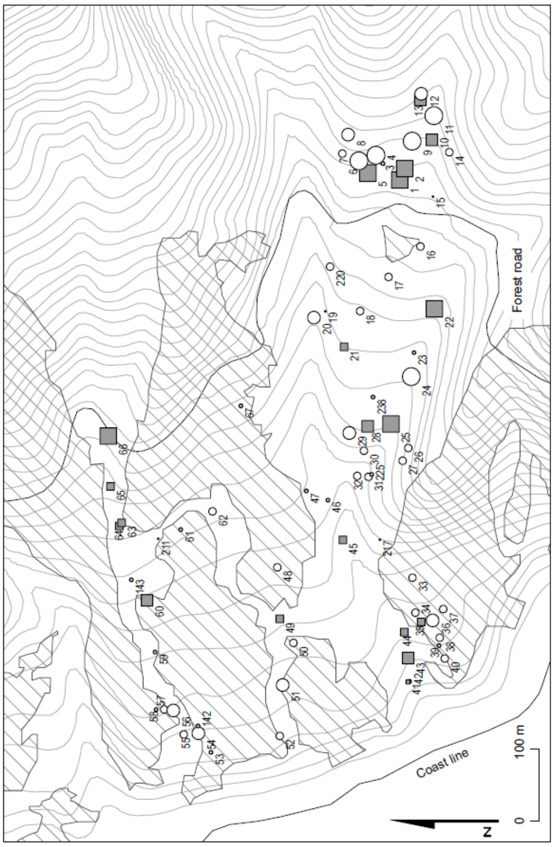

Fig. 3. The locations of *Ficus* trees classified into two groups based on fruiting pattern. See Fig. 1 legend for symbols. Symbol size represents relative tree size in four ranks. Shaded polygons indicate areas that were clear-cut in the early 1940s, derived from aerial photographs taken in 1947.

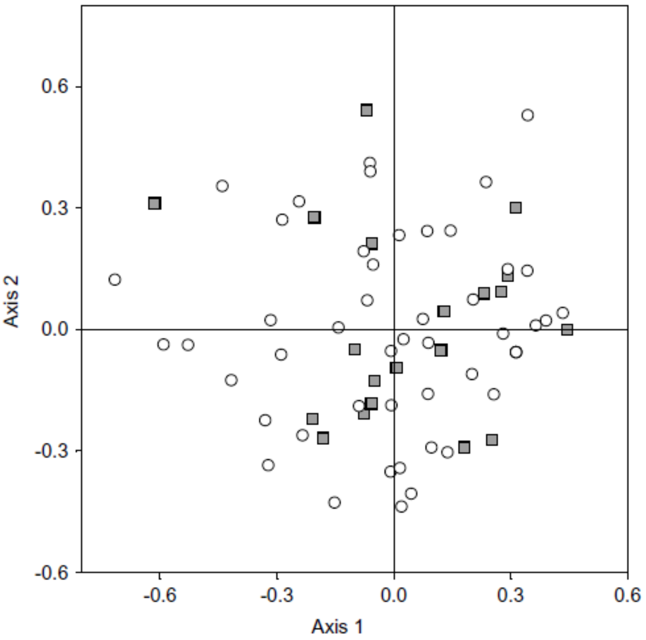

Fig. 4. Principal components analysis of the genotypes of 70 *Ficus* trees characterized using six microsatellite loci. See Fig. 1 legend for symbols.

Reduced Seed Dispersal Effectiveness of the Large-Seeded Tree *Myrica rubra* in the Absence of Japanese Macaque

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Introduction

Seed dispersal is a critical stage in a plant's reproductive cycle for the purpose of establishing new populations. The process of seed dispersal not only enhances the fitness of the maternal plant (reviewed by Howe and Smallwood 1982; Willson and Traveset 2000), but also has a direct effect on the genetic structure of plant populations (Hamrick et al. 1993). Diaspores have many adaptations that enhance long-distance seed dispersal by using vectors such as wind, water, and animals. However, a large proportion of plants in most communities are dispersed by animals (Howe and Smallwood 1982). Therefore, seed dispersal by animals is considered to play an important role in the genetic structure of plant populations and the maintenance of biodiversity within forests.

Large frugivores are effective seed dispersers quantitatively, but they are extremely sensitive to habitat modifications caused by human activity. If plant species depend only on large frugivorous animals for seed dispersal, the disappearance of these animals because of human activity could lead to a failure in seed dispersal. A two-step approach may be used to assess the effect of human activity on seed dispersal: compare seed dispersal with and without the aid of large frugivores and determine what type of effect the extinction of these frugivores would have on the dispersal of plant populations.

We examined Japanese macaque (*Macaca fuscata*) as a large seed disperser of *Myrica rubra*, a large-seeded tree species. Potential seed dispersers of *M. rubra* may be limited because the fruit and seed sizes of *M. rubra* are large (fruit: 13.2 mm in diameter, seed: 7.7 mm in diameter) and small frugivores cannot swallow these seeds. To evaluate the effectiveness of seed dispersal by Japanese macaque, we compared the seed dispersal of *Myrica rubra* in two forests, one with and one without Japanese macaque. We also examined the seed dispersal of *M. rubra* using genetic analysis of seeds found in the feces of macaques.

Materials & Methods

Study site

The study sites were located in warm temperate evergreen forests on Yakushima Island (30°20' N, 130°30' E) and Tanegashima Island (30°43' N, 130°58' E), located in southwest Japan. Both islands shared similar low-altitude broad-leaved evergreen forests. On the western part of Yakushima Island, a subspecies of Japanese macaque (*Macaca fuscata yakui*) lived in social groups of 20–30 individuals in the wild, without provisioning, in a protected National Park. Furthermore, these macaques had been habituated to observers and their social and feeding ecology had been studied continuously since 1976 (Maruhashi 1980; Yumoto et al. 1998; Hanya 2003). In contrast, Japanese macaque is thought to have been extirpated from Tanegashima Island for approximately 80 years as a result of human activity.

Study species

Myrica rubra (Myricaceae) was a common dioecious evergreen tree on both islands. It produces a large amount of fleshy fruit from late May to late June, and the fruits are an important food source for frugivores, especially for Japanese macaque on Yakushima Island. Japanese macaque is a local seed disperser of *M. rubra*, along with some bird species. Because the Japanese macaque has cheek pouches (i.e., a pocket in the cheek that opens into the mouth), it can store various fruits and seeds and travel long distances before choosing to either spit out or swallow the seeds (Yumoto et al. 1998).

Comparison of fruit consumption with and without macaques

To collect information on frugivorous tree visitors, observations were carried out on one tree by a single observer on Yakushima Island (with macaques) and on Tanegashima Island (without macaques; total observation times: Yakushima Island 73 h 46 min, Tanegashima Island 63 h 44 min). Observations were conducted from 600 to 1800, except during rainy periods. All visitors to the focal trees and all species observed around the focal trees were recorded. The visiting and feeding times of each visitor were also noted. If direct observation was possible, the number of fruits consumed per minute was recorded. We calculated the number of fruits consumed by each visitor species per visit using data on the feeding period per visit and the number of fruits consumed per minute by each visitor species. Finally, we estimated the total number of consumed fruits on each tree per day using the average data of the number of fruits consumed by each visitor species per visit and the number of visitors per day.

Development of microsatellite markers for maternal analysis

To conduct a maternal analysis of seeds dispersed by macaques under natural conditions, we developed 13 microsatellite markers from a genomic library enriched for dinucleotide (CT) repeats in the dioecious evergreen tree *M. rubra* and screened loci from 32 adult trees (Terakawa et al. 2006).

Maternal analysis of seeds dispersed by macaques using microsatellite markers

To collect macaque feces, we followed a single habituated troop of Japanese macaque living in the evergreen forest on the western part of Yakushima Island from 600 to 1800 during three sessions in 2005: 25–30 May (late May), 4–6 June (early June), and 17–20 June (late June). This troop comprised 26 individuals: seven adult males, seven adult females, and 12 young individuals (E troop; Nishikawa, unpublished data).

We identified the maternal origins of dispersed seeds using the multilocus genotypes of 10 microsatellite loci of the seed endocarp. The genotype of endocarp tissue is identical to the genotype of the maternal tree because the endocarp is derived from the mother (Godoy and Jordano 2001). We determined the variation in maternal origin of dispersed seeds of *M. rubra* in feces of Japanese macaque during the fruiting period of *M. rubra* using the diversity and overlap index proposed by Grivet et al. (2005) as an index of the probability of maternal identity within and between gene pools. The diversity index of the maternal origin of dispersed seed ranges from 0 = highest diversity to 1 = lowest diversity. The overlap index of the maternal origin of dispersed seed ranges from 0 = lowest degree of overlap to 1 = highest degree of overlap. The inverse of the diversity index indicated the effective number of seed maternal origins; we calculated this for each period.

Results

Comparison of fruit consumption with and without macaques

We observed 25 species around the focal trees of *M. rubra* (Yakushima Island: Japanese macaque and 13 bird species; Tanegashima Island: 21 bird species). Six of the observed species were frugivores and five species were common to both islands. On Yakushima Island, the principal visitors of *M. rubra* were Japanese macaque and bulbul (*Hypsipetes amaurotis*; mean ± standard error number of visitors per day: macaque, 4.7 ± 1.4; bulbul, 3.2 ± 0.9; other birds, 0.3 ± 0.2). On Tanegashima Island, the principal visitor was bulbul (number of visitors per day: bulbul, 3.8 ± 0.9; other birds, 0.2 ± 0.1). There was no difference in the number of visits by bulbul between the two islands (*U*-test, $P > 0.05$).

The feeding time per visit of each visitor species differed significantly on Yakushima Island (mean ± standard error minutes per visit: macaque, 10.8 ± 1.0; bulbul, 0.8 ± 0.1; *U*-test, $P < 0.001$). However, there was no difference in the feeding time per visit for bulbul between the two islands (0.5 ± 0.1 min per visit; *U*-test, $P > 0.05$). The number of fruits consumed per minute by the macaques (14.0 ± 2.4) was greater than that by bulbul (5.5 ± 1.3). The number of fruits consumed per visit by the macaques was more than 30 times that by bulbul (Yakushima Island: macaque, 151.9 ± 13.8; bulbul, 4.3 ± 0.6; Tanegashima Island: bulbul, 3.0 ± 0.6). In summary, the number of fruits consumed per day per tree on Yakushima Island (all, 730.7; macaque, 716.9; bulbul, 13.8) was greater than on Tanegashima Island (all, 11.4; bulbul, 11.4).

Development of microsatellite markers for maternal analysis

The number of alleles of the microsatellite markers ranged from 2 to 14, and the expected heterozygosity ranged from 0.324 to 0.884 (Table 1). The total paternity exclusionary power when the mother was known was 0.99965. We tested linkage disequilibrium (LD) using Genepop version 3.4 software (Raymond and Rousset 1995). Three pairs of loci (my0043 and my0186, my0472 and my0792, and my0472 and my0793) showed significant LD in 78 pairwise tests with 13 loci ($P < 0.05$). These loci allow mating system and parentage analyses to be carried out for *M. rubra*, thereby supporting studies of *M. rubra* seed dispersal by macaques.

Genetic analysis of seed dispersal by macaques

We collected 89 feces in total: 19 in late May, 20 in early June, and 50 in late June. For all periods, the average number of seeds per feces was 8.56 (± 1.11 SE) with a range of 0 to 48. This number increased slightly between late May (9.26 ± 2.22 SE) and early June (15.95 ± 3.25 SE) and decreased significantly from early June to late June (5.34 ± 0.96). These changes in the number of seeds per feces in relation to the study period were statistically significant (Kruskall Wallis test: $H = 12.248$, $P = 0.002$), with a significant difference between early June and late June (Steel-Dwass test: t = 3.251, $P = 0.003$).

After genotyping, we identified 111 different maternal genotypes from 360 seeds in 41 feces (late May: 28 mothers from 106 seeds in 13 feces; early June: 52 mothers from 168 seeds in 11 feces; late June: 44 mothers from 86 seeds in 17 feces). The average number of different maternal genotypes per feces was 3.85 (± 0.40 SE), with a range of 2 to 11. Thus, macaques can disperse seeds from several different mother trees at a time (Fig. 1).

The average diversity of seed maternal origin per feces was very high (0.298) throughout the study period and increased from late May (0.425) to late June (0.239; 0.249 for early June). The total effective number of seed maternal origins in each period increased from late May (8.083) to late June (28.667).

Twenty-four maternal genotypes were shared between 92 pairs of feces of the 820 possible pairs (Fig. 1). Therefore, the seed maternal origin overlap among feces was very low (0.017). The seed maternal origin overlap among feces in each period decreased from late May (0.080) to late June (0.008).

Discussion

Comparison of fruit consumption with and without macaques

M. rubra seeds were dispersed by macaques and bulbul, and the disappearance of macaques could lead to a decrease in the number of seeds dispersed from mother trees. We observed a white-eye (*Zosterops japonicus*, gape size: 6.1 mm; Noma and Yumoto 1997) swallowing one red fruit of *M. rubra*. Bulbul and white-eye typically eat fruits, but capture insects to feed their offspring in the breading season. It is difficult for frugivorous birds on Tanegashima Island to fill the role in seed dispersal that macaques fill on Yakushima Island. This suggests that the loss of macaques may significantly affect seed dispersal, producing a gap that other frugivores may not be able to fill. Furthermore, the loss of seed dispersers as a result of human activity may affect tree species that produce sap fruits.

Seed dispersal of M. rubra by macaques on Yakushima Island

Macaques could disperse seeds from several maternal origins at the same time. Considering that the diversity of the maternal origin of *M. rubra* seed within feces was very high, macaques might efficiently enhance gene flow among local patches and populations of *M. rubra* and favor the settlement and growth populations with high genetic diversity. Seed dispersal is a critical process affecting genetic structure in plant populations (Hamrick et al. 1993). However, the seed dispersal range would still be limited by the macaque's home range; seed dispersal by macaques may play an important role the population genetic diversity of *M. rubra*.

Our results suggest that the feeding behavior of macaques determines the seed dispersal pattern of *M. rubra* on Yakushima Island. The number of seeds and maternal diversity of seeds within feces, and the maternal overlap of seeds among feces were different in each sampling period. Macaques changed their feeding behavior during the fruiting of *M. rubra* to conform to food availability (Agetsuma and Noma 1995).

References

Agetsuma N, Noma N (1995) Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) as a reaction to heavy fruiting of *Myrica rubra*. Int J Primatol 16: 247–260.

Godoy JA, Jordano P (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Mol Ecol 10: 2275–2283.

Grivet D, Smouse PE, Sork VL (2005) A novel approach to an old problem: tracking dispersed seeds. Mol Ecol 14: 3585–3595.

Hamrick JL, Murawski DA, Nason JD (1993) The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. Vegetatio 107/108: 281-297.

Hanya G (2003) Age differences in food intake and dietary selection of wild male Japanese macaques. Primates 44: 333–339.

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Ann Rev Ecol Syst 13: 201–228.

Maruhashi T (1980) Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 21: 141–160.

Noma N, Yumoto T (1997) Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. Ecol Res 12: 119–129.

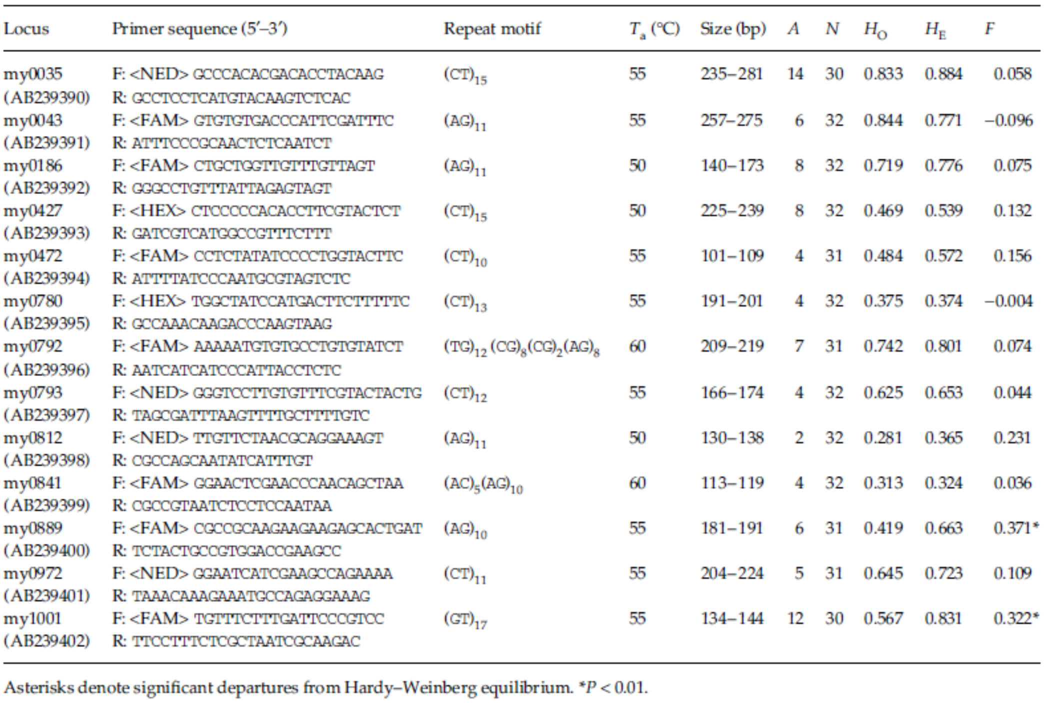
Raymond M, Rousset F (1995) Genepop (version 1.2): population genetics software for exact tests and ecumenicism. J Heredity 86: 248–249.

Terakawa M, Kikuchi S, Kanetani S, Matsui K, Yumoto T, Yoshimaru H (2006) Characterization of 13 polymorphic microsatellite loci for an evergreen tree, *Myrica rubra*. Mol Ecol Notes 6: 709–711.

Willson MF, Traveset A (2000) The ecology of seed dispersal. pp. 85–110. In: Seeds: The ecology of regeneration in plant communities. 2nd. Edition. M Fenner (ed.). CAB International, Wallingford, UK. [Reprint]

Yumoto T, Noma N, Maruhashi T (1998) Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 39: 325–338.

Table 1. Microsatellite loci for *Myrica rubra*, including primer sequences, repeat motifs, annealing temperatures (*T*a), size ranges (bp), number of alleles detected (*A*), number of genotyped individuals (*N*), observed heterozygosity (*H*O), expected heterozygosity (*H*E) and fixation index (*F*). DNA Database of Japan accession numbers are listed in parentheses under each locus.



Locus	Primer sequence (5′–3′)	Repeat motif	T_a (°C)	Size (bp)	*A*	*N*	H_O	H_E	*F*
my0035 (AB239390)	F: <NED> GCCCACACGACACCTACAAG R: GCCTCCTCATGTACAAGTCTCAC	$(CT)_{15}$	55	235–281	14	30	0.833	0.884	0.058
my0043 (AB239391)	F: <FAM> GTGTGTGACCCATTCGATTTC R: ATTTCCCGCAACTCTCAATCT	$(AG)_{11}$	55	257–275	6	32	0.844	0.771	−0.096
my0186 (AB239392)	F: <FAM> CTGCTGGTTGTTTGTTAGT R: GGGCCTGTTTATTAGAGTAGT	$(AG)_{11}$	50	140–173	8	32	0.719	0.776	0.075
my0427 (AB239393)	F: <HEX> CTCCCCCACACCTTCGTACTCT R: GATCGTCATGGCCGTTTCTTT	$(CT)_{15}$	50	225–239	8	32	0.469	0.539	0.132
my0472 (AB239394)	F: <FAM> CCTCTATATCCCCTGGTACTTC R: ATTTTATCCCAATGCGTAGTCTC	$(CT)_{10}$	55	101–109	4	31	0.484	0.572	0.156
my0780 (AB239395)	F: <HEX> TGGCTATCCATGACTTCTTTTTC R: GCCAAACAAGACCCAAGTAAG	$(CT)_{13}$	55	191–201	4	32	0.375	0.374	−0.004
my0792 (AB239396)	F: <FAM> AAAAATGTGTGCCTGTGTATCT R: AATCATCATCCCATTACCTCTC	$(TG)_{12}\,(CG)_8(CG)_2(AG)_8$	60	209–219	7	31	0.742	0.801	0.074
my0793 (AB239397)	F: <NED> GGGTCCTTGTGTTTCGTACTACTG R: TAGCGATTTAAGTTTTGCTTTTGTC	$(CT)_{12}$	55	166–174	4	32	0.625	0.653	0.044
my0812 (AB239398)	F: <NED> TTGTTCTAACGCAGGAAAGT R: CGCCAGCAATATCATTTGT	$(AG)_{11}$	50	130–138	2	32	0.281	0.365	0.231
my0841 (AB239399)	F: <FAM> GGAACTCGAACCCAACAGCTAA R: CGCCGTAATCTCCTCCAATAA	$(AC)_5(AG)_{10}$	60	113–119	4	32	0.313	0.324	0.036
my0889 (AB239400)	F: <FAM> CGCCGCAAGAAGAAGAGCACTGAT R: TCTACTGCCGTGGACCGAAGCC	$(AG)_{10}$	55	181–191	6	31	0.419	0.663	0.371*
my0972 (AB239401)	F: <NED> GGAATCATCGAAGCCAGAAAA R: TAAACAAAGAAATGCCAGAGGAAAG	$(CT)_{11}$	55	204–224	5	31	0.645	0.723	0.109
my1001 (AB239402)	F: <FAM> TGTTTCTTTGATTCCCGTCC R: TTCCTTTCTCGCTAATCGCAAGAC	$(GT)_{17}$	55	134–144	12	30	0.567	0.831	0.322*

Asterisks denote significant departures from Hardy–Weinberg equilibrium. $^*P < 0.01$.

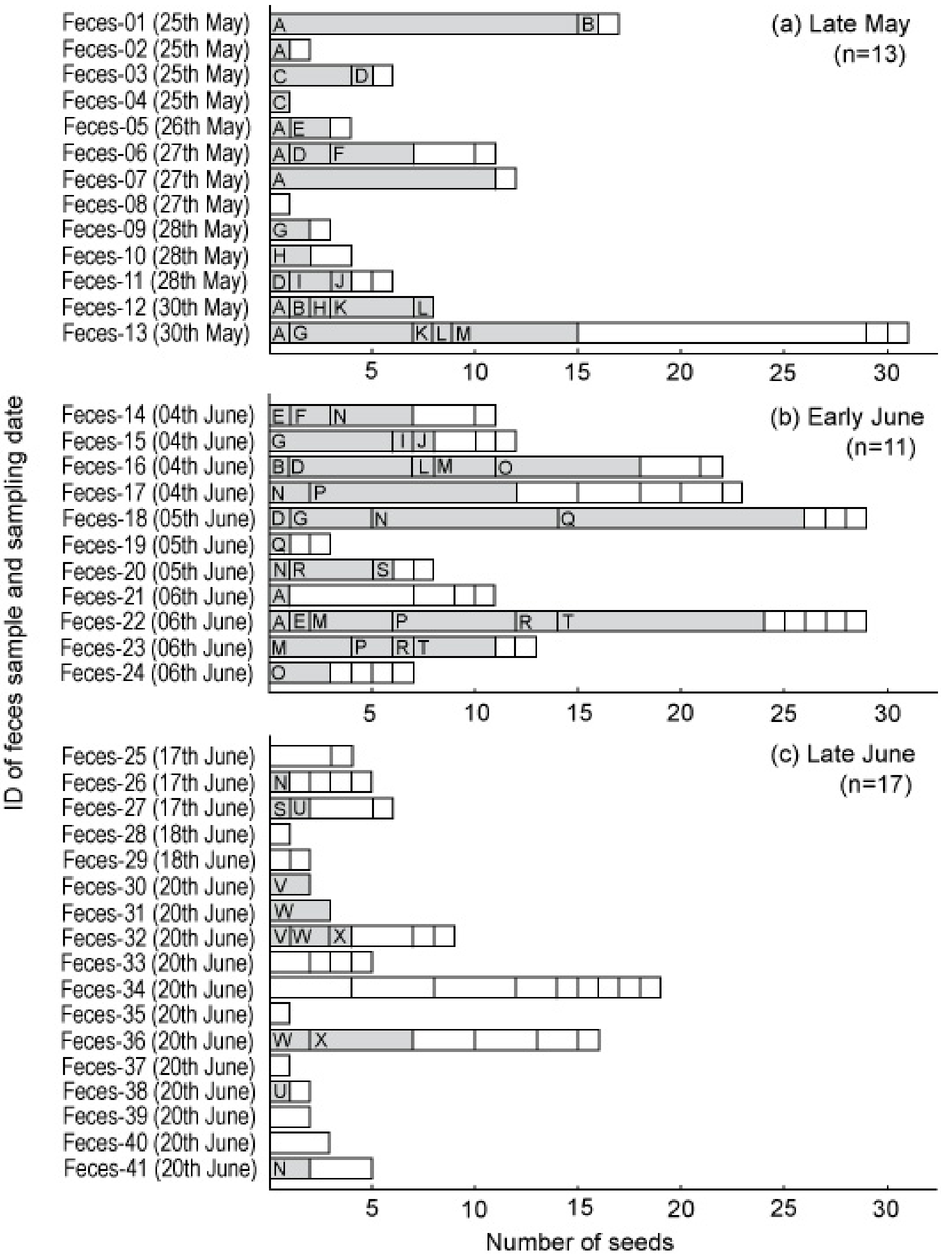


Figure 1. Number and maternal origin of seeds within feces sampled in (a) late May, (b) early June, and (c) late June. The same maternal origin of seeds found in two or more feces samples are indicated by a letter (A to X) and gray shading; n indicates the number of feces samples.

Pre-Dispersal Seed Predation of *Myrica rubra* on Yakushima Island

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Introduction

Myrica rubra Sieb. et Zucc. (Myricaceae) is a common evergreen tree on Yakushima Island and produces a large amount of fleshy fruit. The fruit is an important food source for frugivores, especially for Yakushima macaques (*Macaca fuscata yakui*). However, *M. rubra* fruit production fluctuates greatly from year to year, and this annual change in crop size can affect the behavior of frugivores.

The predator satiation hypothesis was proposed by Janzen (1971) as one of ultimate causes of mast fruiting. Pre-dispersal seed predation has substantial negative effects on the relative reproductive success of individuals by limiting the number of viable seeds (Ida et al. 2004; Nakagawa et al. 2005; Sun et al. 2004). According to this hypothesis, many plants escape seed predators in mast years by controlling the number of predators in poor fruiting years via predator starvation. However, it is not known whether *M. rubra* suffers from seed predation and whether predator satiation reduces the proportion of seeds attacked.

We collected living and aborted fruit to identify major seed predators and to determine the proportion of fruit that was attacked by insects. In addition, we described the pre-dispersal survivorship patterns of fruit in 2006. We addressed the following questions. Who is the major seed predator of *M. rubra*? When does seed predation occur most heavily? Are there differences between the proportions of attacked living and attacked aborted fruit?

Materials & Methods

Study species

M. rubra is a dioecious evergreen tree that grows to approximately 15 m in height. On Yakushima Island, flowering starts from mid-March to early-April, and fleshy fruit is produced from late May to June. Each fruit has one seed. The fruit are an important food source for Japanese macaques as well as some bird species such as Japanese bulbuls.

Study site

The study site was located in a warm-temperate, evergreen, broad-leaved forest on Yakushima Island, which is located 70 km south of Kyushu, Japan. The canopy mainly consisted of Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae (Agetsuma 1995). The mean annual temperature was 21°C, and the annual rainfall was 2600 mm (Tagawa 1980).

In a 4-ha plot of a secondary stand (30°22’ 01.26” N, 130°23’ 08.23” E; 120 m above sea level), we deployed three seed traps (each covered a 0.5 m^2 area) below each of five female trees (one was added in 2006 for six trees) during the fruiting period. The seed traps were made of nylon cloth and were placed 1 m above the ground. To observe patterns of fruiting phenology and fruit predation, we placed a ladder at three of the six female trees in 2006 to access the crown.

Patterns of seed survivorship

To describe the pre-dispersal survivorship patterns of fruit, we marked 30 branches of each of three *M. rubra* trees and counted the numbers of surviving fruit > 1 mm in diameter on 8 April, 15 May, 4 June, and 15 June in 2006. Two of the three female trees were still flowering on 8 April; therefore, we estimated the numbers of fruit by multiplying the number of infructescences by the number of fruit per infructescence determined from observations of the other individual.

Seed predators and patterns of seed predation

Aborted fruit

To monitor the patterns of seed fate and predation, all of the fruit that fell into seed traps was collected weekly from the end of April to the end of June. We extracted and counted the number of fruit > 1 mm in diameter. Some of the fruit was measured: 10 fruit from each individual in 2005; 90 fruit from each individual in 2006. We ignored dropped flowers.

For each collection, we stored a maximum of 300 fruit per tree in 2005 and 30 fruit per tree in 2006 in plastic containers (280 cm^3) and allowed any insect larvae within the fruit to emerge. We placed up to 10 fruit in each container, along with a piece of moist cotton to prevent desiccation, and observed them for 3 months. The containers were checked every two days; if insects had emerged, they were collected, killed by freezing, and mounted on pins for later identification.

After 3 months, we dissected all of the fruit stored in the containers and classified each fruit as attacked or non-attacked. Fruit that was attacked by insects had larvae, feces, and/or a hole through which the insects had escaped from inside the fruit. We considered fruit that had these marks as attacked and that without these marks as non-attacked. In 2006, we also dissected 60 fruit from each female tree soon after collection from the seed traps for comparison with the proportion of surviving fruit that was also attacked by insects.

Living fruit

Throughout the fruiting period, 50 fruit per female tree were sampled from the canopy of three female trees using a ladder on 8 April, 15 May, 4 June, and 15 June in 2006. Upon collection, the diameter of each fruit was measured, and 10 fruit from each female tree were stored in containers in the same way as for aborted fruit. The remaining fruit was dissected and classified as attacked or non-attacked.

Data analysis

The proportion of attacked fruit was calculated by pooling the data for all female trees. For aborted fruit, the difference in the proportion of attacked fruit between 2005 and 2006 was examined using a chi-square test. To compare living and aborted fruit in 2006, we calculated the proportions of attacked fruit based on data from the fruit that was dissected upon collection, and the difference was examined using a chi-square test.

Results

Patterns of seed survivorship

Fruit mortality was highest during the first month after flowering. In all individuals, the numbers of living fruit on branches decreased rapidly from mid-April to mid-May and moderately from late May to mid-June (Fig. 1). By late July, no fruit remained on the branches.

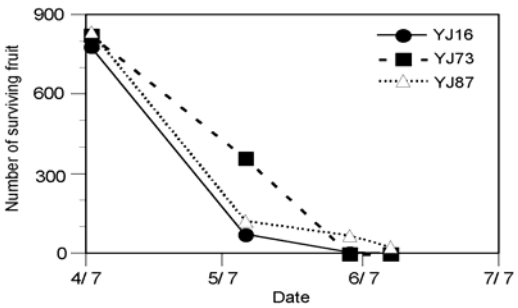

Fig. 1. Survivorship curves of fruit remaining on the branches of three female *Myrica rubra* trees. Symbols (●, ■ and △) indicate the total numbers of surviving fruit on 30 branches of each female tree.

Seed predators

In 2005, 598 individuals of *Thiotricha pancratiastis* Meyrick (Gelechiidae), two individuals of *Neoblastobasis spiniharpella* Kuznetzov & Sinev (Gelechiidae), and 109 individuals of parasitic wasp comprising seven species of Braconidae, two species of Ichneumonidae, and one species of Elasmidae emerged from 6188 stored fruit that were collected from seed traps. In 2006, 143 individuals of *T. pancratiastis* and 10 individuals of parasitic wasp emerged from 1090 stored fruit that were collected from seed traps. One individual of *T. pancratiastis* emerged from the stored fruit that was sampled directly from the branches (Fig. 2, Table 1).

Table 1. The number of insects that emerged from 6188 and 1090 aborted fruit in 2005 and 2006, respectively.

	Thiotricha pancratiastis	*Neoblastobasis spiniharpella*
2005	598	2
2006	143	0

Fate of fruit and predation

The total number of aborted fruit varied annually, at 10584 in 2005 and 6122 in 2006, and peaked at the early phase of development before fruit maturation (Fig. 3). In 2005, the peak was very clear; approximately 40% of aborted fruit fell during a single week

from 30 April to 7 May. The mean ± standard deviation fruit size during this term was 7.7 ± 2.8 mm. Ripe fruit typically reached between 15 and 20 mm in diameter. It was clear that many immature fruit were aborted during this period. In 2006, 64% of aborted fruit dropped during the first month after flowering (Fig. 3). Insects attacked fruit intensively during the primary stage of fruit development. The proportion fruit attacked by insects reached as high as 64.9% between 7 and 14 May (Fig. 4). At other times, the attack rate was relatively low.

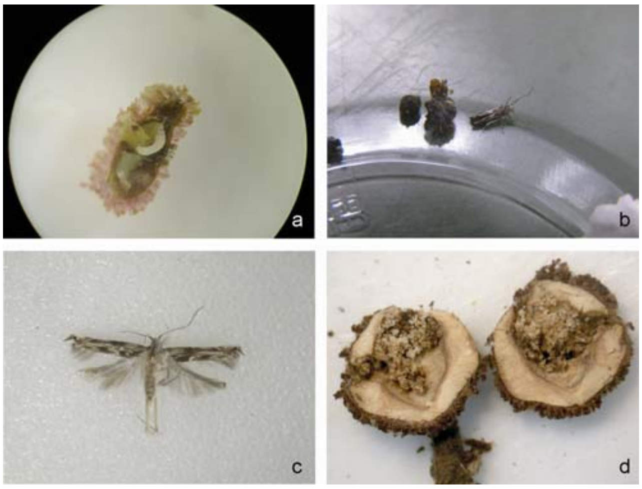

Fig. 2. Photographs of *Thiotricha pancratiastis* Meyrick (Gelechiidae) and attacked fruit. (a) Fruit infested by a larva. (b) *T. pancratiastis* adult just after emergence. (c) *T. pancratiastis* adult. (d) Attacked fruit containing insect feces.

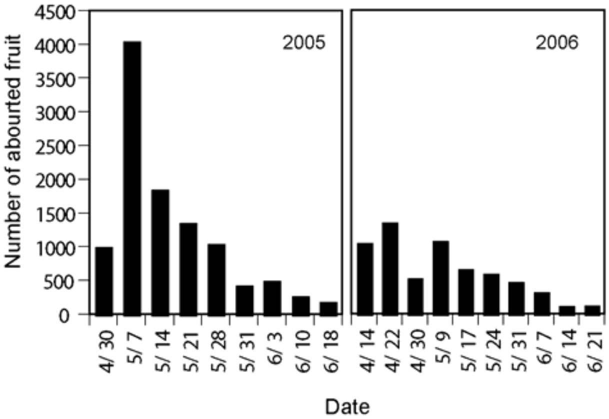

Fig. 3. Patterns of seed abortion throughout the fruiting period in 2005 and 2006.Data from all individuals were

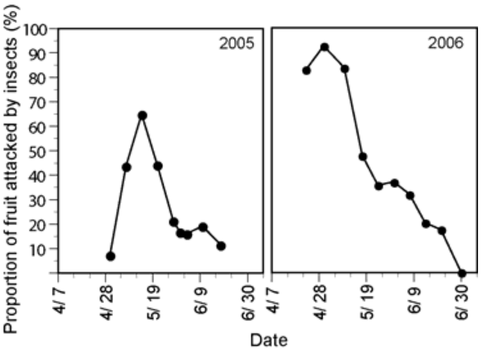

Fig. 4. Proportions of fruit that suffered predation by insects in 2005 and 2006.

Thus, predation by insects occurred only during the early phase of fruit development in 2005. In contrast, in 2006, insects attacked fruit continuously and at a higher intensity than in 2005 from just after flowering onward. From mid-April to mid-May, most of the aborted fruit was infested by insects, with the highest percentage of 92.6% occurring during the week of 23–30 April (Fig. 4). The overall proportion of fruit attacked throughout the fruiting period of 2006 was 50.5%, which was approximately 20% higher than in the previous year. A greater proportion of fruit was attacked in 2006 than in 2005 ($\chi^2 = 175.51$, $p < 0.001$; Table 2).

Table 2. Comparison of the annual percentage of attacked fruits between 2005 and 2006. *** p<0.001.

	Number of fruits		χ^2
	Attacked	Non-attacked	
2005	2121	4067	175.51***
2006	540	415	

For the surviving fruit, the proportion of fruit attacked was consistently low throughout the fruiting period, with the highest proportion of 19.6% measured on 8 April. The proportion of attacked fruit differed significantly between surviving and aborted fruit; from early April to early June, the insect predation rate was significantly lower in surviving than in aborted fruit (8–14 April, $\chi^2 = 64.4$, $p < 0.001$; 14–17 May, $\chi^2 = 83.19$, $p < 0.001$; 4–7 June, $\chi^2 = 11.6$, $p < 0.001$; Fig. 5). However, there was no difference after mid-June (15–21 June; $\chi^2 = 0.58$, $p = 0.448$; Fig. 5).

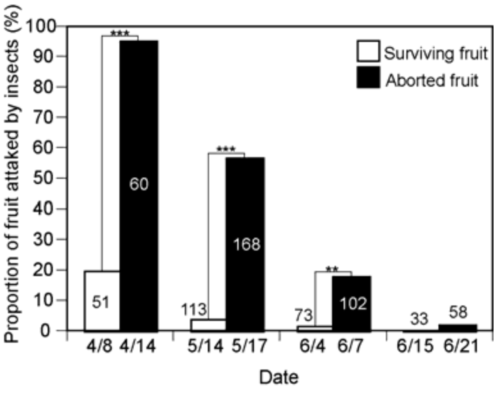

Fig. 5. Comparison of insect attack between living and aborted fruit in 2006. Bars indicate the proportions of aborted attacked (■) and surviving attacked (□) fruit pooled for all six female trees sampled. The numbers in the bars indicate the numbers of dissected fruit. The numbers under the bars indicate the dates on which fruit was collected; living fruit was collected that day and aborted fruit was collected 1 week from that day. *p ＜ 0. 05, **p ＜ 0. 01, ***p ＜ 0. 001.

Discussion

Throughout the 2 years of the study, we identified two lepidopteran species that may be major seed predators of *M. rubra*. The emergence of large numbers of *T. pancratiastis* individuals in both years indicates that it is a major seed predator and may play an important role in the pre-dispersal seed predation of *M. rubra* on Yakushima Island. We confirmed that pre-dispersal seed predation by insects occurred mainly during the early phase of fruit development and that predation by *T. pancratiastis* possibly had a significant effect on the survivorship of young fruit. We observed that some individuals of *T. pancratiastis* emerged from one fruit and entered into another one. Therefore, individual larvae may have attacked more than one fruit.

The pattern of fruit survivorship was similar among the three female trees sampled: a dramatic decrease occurred just after flowering, followed by a moderate decrease. Predation by *T. pancratiastis* may partly explain this pattern.

The proportion of living fruit attacked by insects was very low throughout the fruiting period, suggesting that some sound fruit remained on the trees. In contrast, much of the aborted fruit suffered from predation. If fruit abortion occurs at random, there should be no difference in the proportions of living and aborted fruit that are attacked. Mother plants may selectively abort attacked fruit. The Yakushima macaque, which is a major seed disperser of *M. rubra* on Yakushima Island, eats and disperses mature fruit from mid-June to early July. Thus, many non-attacked fruit would be dispersed by Yakushima macaque.

M. rubra exhibits mast fruiting. According to the predator satiation hypothesis, the population density of seed predators becomes small in poor harvest years because of starvation, and in a mast year, plants produce many sound seeds that escape predation because the increase in the predator population density can not catch up with the increase in resource abundance. The crop size of five female *M. rubra* was approximately twice as large in 2005 than in 2006, and seed predation on *M. rubra* was 1.5 times higher in 2006 than in 2005. Thus, mast fruiting may have reduced the predation rate.

However, *T. pancratiastis* attacks not only fruit, but also new leaves. *T. pancratiastis* stays in the leaf veins and eats the new leaf tissue. Before pupating, it severs the new leaf in which it occurs and falls to the ground with the leaf tip. On the ground, it makes a nest out of the leaf tip and pupates inside the nest (personal observations). From early June to late June, we collected these nests from the seed traps and reared 283 adult *T. pancratiastis* from 554 pupae. Thus, *T. pancratiastis* may maintain its population density by using new leaves in years of limited fruiting. To evaluate the effect of pre-dispersal seed predation on *M. rubra*, it is important to understand the life history of seed predators and their resource use.

References

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. International Journal of Primatology 16: 611–627.

Ida H, Hotta M, Ezaki Y (2004) Predispersal seed predation by rodents to beechnuts (*Fagus crenata* Blume). Ecological Research 19: 503–509.

Janzen DH (1971) Seed predation by animals. Annual Review of Ecology and Systematics 2: 465–492.

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. Biotropica 37(3): 389–396.

Sun S, Gao X, Chen L (2004) High acorn predation prevents regeneration of *Quercus liaotungensis* in the Dongling Mountain region of North China. Restoration Ecology 12 (3): 335–342.

Tagawa H (1980) Vegetation on the western slope of Mt. Kuniwaridake, Yakushima Island. Science Reports of Kagoshima University 29: 121–137. (in Japanese)

Effects of Forest Fragmentation on Tree Regeneration from Bird-Dispersed Seeds in a Temperate Forest in Japan

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Introduction

The loss and fragmentation of natural habitats caused by human activities are pervasive phenomena in terrestrial ecosystems and are considered to be major threats to biodiversity (Fisher & Lindenmayer 2007). Today, habitat fragmentation has become one of the most important research themes in conservation biology. With increased levels of research, our understanding of the processes involved in fragmentation and the effects of fragmentation on habitats has developed considerably over recent decades (Hobbs & Yates 2003). Important research advances include results from long-term fragmentation experiments (e.g., Bierregaard et al. 2001), the elucidation of the variety of effects caused by the creation of edges between fragments and surrounding altered land (e.g., Laurence 2000), and detailed considerations of the genetic and demographic consequences of fragmentation (e.g., Young & Clarke 2000; Isagi et al. 2007) and the alteration of plant–animal interactions, especially in plant reproductive processes (e.g., Aguilar et al. 2006).

Despite these advances, we are still a long way from developing a comprehensive conceptual framework for how forest fragmentation influences community composition, species diversity, and the dynamics of individual species (Hobbs & Yates 2003) for several reasons. First, the effects of fragmentation strongly depend on the characteristics of the focal ecosystem and the type of fragmentation (area, surrounding conditions, etc.). We cannot apply results for a tropical forest to a temperate forest, or those from a primary forest to a secondary forest. Fragmentation caused by land-use changes from forest to tree plantation may be entirely different from that caused by the expansion of agricultural lands. Second, many observations and experiments report changes after fragmentation or differences between continuous and fragmented forests, but it is difficult to provide clear insights into the ecological mechanisms of the changes or differences. Third, many studies examine only one or a few aspects of effects of the fragmentation. For the consideration of the long-term and total effects of forest fragmentation on biodiversity and ecosystem functions, pervasive studies of all biological processes of a species or forest are essential. In the case of plants, studies of the effects on reproductive processes such as pollination are abundant, whereas few studies have examined the effects on seedling survival and growth (Hobbs & Yates 2003).

Therefore, we investigated the effects of habitat fragmentation in a community of trees that use birds for seed dispersal in temperate forests in Japan. Although most dominant tree species in temperate forests are wind-pollinated and wind-dispersed, bird-dispersed tree species (which are mainly pollinated by insects) are important because they provide food for birds and mammals, play important roles in forest regeneration and forest succession, and maintain high species diversity. We monitored several biological processes using various methods in these forests: species composition in permanent plots; fruiting and dispersal using seed traps; the activities of seed dispersers by observing birds; and seedling germination and demography in permanent plots. Here, we report preliminary results.

Methods

Study site

The study was conducted in a mixed deciduous forest, the Ogawa Forest Reserve, at the southern edge of the Abukuma mountain region, central Japan (36º56’ N, 140º35’ E; 600–660 m above sea level). The reserve consists of a mixed deciduous old-growth forest of 98 ha (conserved forest) and remaining strips of old-growth forest approximately 50 m wide (fragments), surrounded by evergreen conifer plantations, secondary forests, and agricultural lands (pastures and vegetable or paddy fields; Fig. 1). The annual precipitation is approximately 1750 mm, and the mean annual temperature is 9.0°C, with an average monthly temperature range of –1.6°C in February to 20.5°C in August.

In the conserved forest, the total basal area and density of trees > 5 cm in diameter at breast height (DBH) were 33 m^2 ha^{-1} and 850 stems ha^{-1}, respectively (Masaki et al. 1992). The dominant tree species in terms of total basal area were *Quercus serrata* (27%), *Fagus japonica* (20%), and *F. crenata* (9%). Dwarf bamboos (*Sasa*, *Sasaela*, and *Sasamorpha* spp.) covered parts of the forest floor. Disturbances related to human activity, grazing, and fire, affected the forest until the 1930s, especially at the margins of the forest reserve (Suzuki 2002). The fragments are similar in composition and structure to the old-growth forest; however, they are small in area because large parts of the old-growth forest were cut during the 1970s and were converted into conifer plantations. The plantations are pure stands of *Cryptomeria japonica* or *Chamaecyparis obtusa*. The remaining area is covered by secondary forests and agricultural fields. The secondary forests have been managed for the production of firewood and charcoal for several decades. The dominant secondary forest species are *Q. serrata*, *Pinus densiflora*, and *Carpinus turczaninovii*.

Monitoring of plants

A 6-ha permanent plot (200 x 300 m) was established in 1987 in the central part of the Ogawa Forest Reserve (Fig. 1). The plot has been censused regularly for factors such as light, topography, and tree demography and growth within the plot (Tanaka & Nakashizuka 2002). In addition, we established two 1-ha plots in the fragmented forest area in 2006 (Fig. 1). All trees with DBH > 5 cm were measured, identified, and tagged. The plots in the conserved forest and the fragment have 1 x 1 m quadrats located at every 10 x 10 m grid point (total: 651 quadrats in the conserved forest and 132 in the fragment). In July 2006 and July 2007, we marked and monitored all current-year seedlings of bird-dispersed species in the quadrats. Seedling survival in 2006 was censused in October. To monitor seed rain and seed dispersal, we placed 329 and 67 seed traps at regular spacing in the plots of the conserved forest and the fragment, respectively. Seeds of bird-dispersed species were collected from the seed traps twice a month from July to December 2006 and identified to species. Seeds that were still covered with fleshy parts such as the mesocarp or aril probably dropped without being dispersed by birds; therefore, seeds that had lost the fleshy parts after being eaten and excreted by birds were distinguished and counted separately.

Monitoring of birds

To assess numbers and composition of bird dispersers, we conducted bird censuses within the plots and in an additional census site in the fragment from July to December 2006. We counted and identified birds passing through a 40 x 100 m area within a 15-min period. Each census was conducted early in the morning (first 3 h after dawn) and repeated three times at different points in the conserved forest and the fragment to obtain data for each census, except for three of the censuses in the fragment, which were only conducted twice. The censuses were done two to ten times a month, and more censuses were done in the bird migration season. In total, 33 censuses were completed in 2006. Frugivorous birds, which were the potential dispersers, were identified based on the literature (e.g., Kiyosu 1966; Kanouchi 2006). Differences in the densities of bird dispersers between the conserved forest and the fragment were examined using analysis of variance (ANOVA), with month and site as dependent variables.

Results

We compared the basal area of bird-dispersed woody species between the conserved forest and the forest fragment. For the bird-dispersed species *Prunus grayana, Ilex macropoda,* and *Eleutherococcus sciadphylloides*, the basal area in the fragment was more than twice that in the conserved forest (Table 1). The difference was especially large in *E. sciadphylloides*, at 9.3 times.

We compared the relative seed production per unit tree basal area for the three bird-dispersed species *Prunus verecunda, I. macropoda,* and *E. sciadphylloides,* for which > 30 seeds were trapped (Table 2). In all three species, the relative seed production was greater in the fragment than in the conserved forest, and the differences were significant. In contrast, the proportion of seeds dispersed by birds tended to be lower in the fragment than in the conserved forest, except for the liana *Rhus ambigua* (Table 3). The difference was significant for two tree species: *I. macropoda* and *E. sciadphylloides*.

We found 10 or more seedlings of at least 1 year old for six species in the two plots. The seedling densities of *E. sciadphylloides* and *Rhus ambigua* were considerably higher in the fragment than in the conserved forest in both study years. There was a significant difference in the survival of current-year seedlings only for *Cornus controversa*, for which the numbers were higher in the fragment than in the conserved forest (Table 4).

The number of bird species, frugivorous species, and bird diversity measured by the Shannon diversity index (H') did not differ significantly between the conserved forest and the fragment (Table 5). The number of frugivorous individuals was slightly greater in the fragment than in the conserved forest.

Discussion

Although these preliminary analyses were mostly based on data obtained in a single year, and 2006 was a poor year in terms of seed production (T. Masaki, unpublished data), we did detect some potential effects of fragmentation on seed production, seed dispersal, and seedling survival. Considering the relatively large differences in the basal area of some of the tree species, these effects may have already caused differences in the species composition of mature trees in the 30 years since forest fragmentation. Laurence et al. (2006) similarly reported a significant increase in trees with a DBH of 10–20 cm along forest edges 22 years after fragmentation. These effects may be positive or negative, depending on the processes and species involved. Positive effects of forest fragmentation were observed in seed production per unit tree basal area (Table 2) and in seedling survival for some species (Table 4). In terms of plant species reproduction, Aguilar et al. (2006) found an overall large negative effect of forest fragmentation on pollination and plant reproduction that was probably caused by pollination limitation. Positive effects have rarely been reported (e.g., Aizen & Feinsinger 1994). Our contradictory results may have occurred partly because our fragment has relatively large forests in close proximity, and the pollinator fauna may thus be little affected. In addition, the edge effect may have improved light conditions within the fragment, resulting in greater resources available for reproduction. The location of the fragment, i.e., on ridges or close to roads and rivers, could also be responsible for the better light conditions.

Unlike pollination, few studies have investigated the effect of fragmentation on seed dispersal and seedling density. Farwig et al. (2006) reported a marginally lower density of frugivorous birds, but significantly higher seed removal in forest fragments than in continuous forests, probably because of the paucity of other available fruit resources. Some studies have measured declines in the density of birds or frugivores with fragmentation (e.g., Andrén 1994; Cordeiro & Howe 2003; Luck & Daily 2003). Others have reported that forest fragmentation results in edge effects, namely high rates of nest predation and parasitism near forest edges, that can threaten bird populations by reducing nesting success in the remnant forest habitats (Batáry & Báldi 2004; Hoover et al. 2006). Our bird censuses indicate that bird densities or activities were slightly higher in the forest fragment. However, considering the difference in the amount of fruit, which was higher in the fragment, the difference is relatively small and may explain the lower proportion of dispersed seeds in the fragments than in the conserved forest. One further important consideration is that it may be more useful to examine actual dispersal patterns, rather than simply comparing the proportion of dispersed seeds (Schupp 1993). Further analyses, by combining examinations of seed dispersal, germination, and seedling survival over more than 1 year, will be important.

Our preliminary results reveal the importance of edge effects on the regeneration of bird-dispersed tree species such as an increase in fruit resources associated with an increase in frugivorous birds leading to an improvement in the survivorship of seedlings. It is essential to have a complete life history of the area and its species to understand the total effects and long-term results of forest fragmentation. The susceptibility to the effects of fragmentation may vary among tree species. Contrary to tropical forests, which are dominated by animal-dispersed trees, many bird-dispersed tree species that occur in temperate forests are mid-successional species. These species may be more robust than tropical species in their responses to forest fragmentation.

References

Aguilar R, Ashworth L, Galetto L, Aizen MA. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Letters 9:968-980

Aizen NA, Feinsinger P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75:330-351

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat – a review. Oikos 80:193-196

Batáry P, Báldi A. 2004. Evidence of an edge effect on avian nest success. Conserv Biol 18:389-400

Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (eds). 2001. Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven, CT

Cordeiro NJ, Howe HF. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proc Nat Acad Sci 100:14052-14056

Farwig N, Böhning-Gaese K, Bleher B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests. Oecologia 147:238-252

Fisher J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeog 16:265-280

Hobbs RJ, Yates CJ. 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. Aust J Bot 51:471-488

Hoover JP, Tear TH, Baltz ME. 2006. Edge effects reduce the nesting success of Acadian Flycatchers in a moderately fragmented forest. J Field Ornithology 77:425-436

Isagi Y, Tateno R, Matsuki Y, Hirao A, Watanabe S, Shibata M. 2007. Genetic and reproductive consequences of forest fragmentation for populations of *Magnolia obovata*. Ecol Res 22:382-389

Kanouchi T. 2006. The handbook of birds and fruits. (in Japanese). Bunichi-sougou-shuppan, Tokyo

Kiyosu Y. 1966. Encyclopedia of wild birds. (in Japanese). Tokyodo-shuppan, Tokyo

Laurence WF. 2000. Do edge effects occur over large spatial scales? Trends Ecol Evol 15:134-135

Laurence WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, Giraldo JP, Lovejoy TE, Condit R, Chave J, Harms KE, D'Angelo S. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. Proc Nat Acad Sci 103: 19010-19014

Luck GW, Daily GC. 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. Ecol Appl 13:235-247

Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashhizuka T. 1992. Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98:97-111

Schupp EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107:15-29

Suzuki W. 2002. Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. In: Nakashizuka T, Matsumoto Y (eds), Diversity and interaction in a temperate forest community. Ecological Studies 158, 27-40. Springer-Verlag, Tokyo

Tanaka H, Nakashizuka T. 2002. Ground design of the research site. In: Nakashizuka T, Matsumoto Y (eds), Diversity and interaction in a temperate forest community. Ecological Studies 158, 43-49. Springer-Verlag, Tokyo

Young AG, Clarke GM (eds). 2000. Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge, UK

TABLE 1. Basal area of major tree species in plots in the conserved forest (6-ha plot) and forest fragment (two 1-ha plots).

	Basal area (cm^2/ha)	
Species	Conserved forest	Fragment
Bird-dispersed plants		
Prunus verecunda	9249	4266
Prunus grayana	508	1632
Ilex macropoda	1020	2419
Cornus controversa	13411	9737
Eleutherococcus sciadphylloides	805	7512
Kalopanax septemlobus	7989	4027
Other plants		
Fagus crenata	29102	20904
Fagus japonica	63330	11615
Quercus serrata	93457	76164
Quercus crispula	11005	51239
Castanea crenata	15022	63890
Styrax obassia	8653	5421
Acer amoenum	12209	14411
Acer mono	11350	3708
Carpinus laxiflora	15108	19493

TABLE 2. Relative seed production per unit basal area in the conserved forest and the forest fragment in 2006. Tree species with 30 > seeds for both forests are included.

	Relative seed production (no./cm^2)	
Species	Conserved forest	Fragment
Prunus verecunda	0.016	0.020**
Ilex macropoda	0.067	0.094**
Eleutherococcus sciadphylloides	0.011	0.020**

***p* < 0.01, chi-square test for independence.

TABLE 3. Comparison of seed removal rates between the conserved forest and forest fragment in 2006. Species with 30 > seeds for both forests are included.

Species	Conserved forest	Fragment
Prunus verecunda	0.17	0.15
Ilex macropoda	0.59**	0.44
Eleutherococcus sciadphylloides	0.53**	0.25
Rhus ambigua	0.52	0.66

***p* < 0.01, chi-square test for independence.

TABLE 4. Density of current-year seedlings in July 2006 and 2007 in the conserved forest and forest fragment, and survival rates of the seedlings from July to October 2006.
Species with 10 > seedlings in either year are included.

	Seedling emergence (no./m^2)				Survival rate (Jul-Oct 2006)	
	2006		2007			
Species	Conserved forest	Fragment	Conserved forest	Fragment	Conserved forest	Fragment
Ilex macropoda	-	-	0.03	0.08	-	-
Cornus controversa	0.31	0.40	0.85	0.65	0.08	0.25**
E. sciadphylloides	0.07	1.09	0.07	0.89	0.57	0.41
Kalopanax septemlobus	-	-	0.57	0.19	-	-
Rhus ambigua	0.04	0.08	0.36	1.11	0.19	0.10
Euonymus oxiphyllus	0.26	0.13	0.40	0.05	0.4	0.29

**$p < 0.01$, chi-square test for independence.

TABLE 5. Comparison of the number and diversity of birds between the conserved forest and the forest fragment observed from July to December 2006.

	Conserved forest	Fragment
Number of bird species	26	27
Shannon diversity index (H')	2.64	2.58
Number of frugivorous species	22	22
Number of frugivorous individuals	283	344*

*$p < 0.05$, one-way ANOVA.

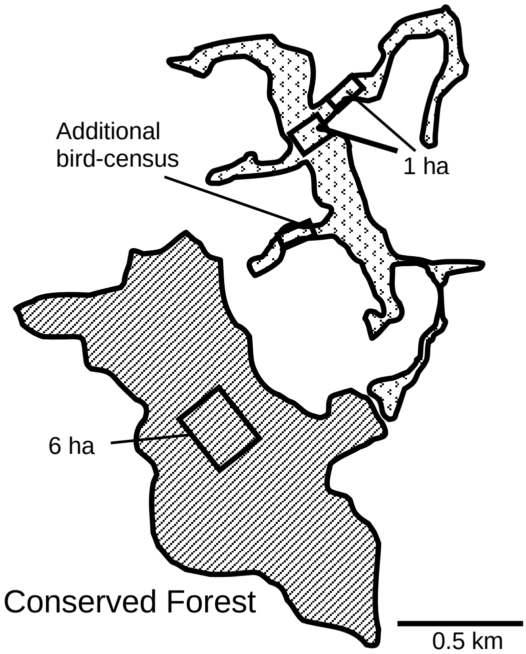

FIGURE 1. Location of plots and bird census sites in the conserved forest and the forest fragment in Ogawa Forest Reserve.

Effects of Deforestation on Mutualistic Interactions of Ants with Plants and Hemipterans in a Tropical Rain Forest of Borneo

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Introduction

In Southeast Asia, the area of lowland tropical rain forests has decreased rapidly as a result of deforestation by humans, resulting in the creation of several types of secondary forest (Sodhi et al. 2004). This decrease has been accompanied by a dramatic loss of species richness. So far, deforestation-related effects of humans on tropical rain forest biodiversity have been evaluated only by determining the species losses caused by deforestation (e.g., Levings and Windsor 1985; Lawton et al. 1998; Dunn 2004). To better understand the effects of deforestation on biodiversity, however, we must explore not only the effects on species richness, but also those on interspecific interactions within a biological community; interspecific interactions are likely to be involved in the processes and mechanisms that allow species to coexist in the community. Therefore, it is important to clarify differences in the properties of interspecific interactions, as well as differences in species richness, in relation to the degree of deforestation.

Ants have often been used as indicators of the effects of forest disturbance on biodiversity (e.g., Belshaw and Bolton 1993; Brühl et al. 2003; Bickel et al. 2006) because they dominate the terrestrial and arboreal arthropod fauna of tropical forests (Stork 1988; Belshaw and Bolton 1993; Floren and Linsenmair 1997) and are considered to contribute to local species richness through their involvement in various types of interactions, including mutualistic interactions with a wide taxonomic range of organisms. Ant plants (myrmecophytes), plants with extrafloral nectaries (EFNs), and honeydew-producing hemipterans commonly enter into mutualistic relationships with ants in the tropics (Buckley 1982; Hölldobler and Wilson 1990; Oliveira and Oliveira-Filho 1991; Koptur 1992; Davidson and McKey 1993; Davidson 1998).

What effect does deforestation have on such mutualistic interactions? To date, few studies have addressed this question by focusing on changes in the properties of ant-associated mutualistic interactions caused by deforestation (e.g., Bruna et al. 2005), although some studies have attempted to estimate the effects of deforestation on biodiversity by measuring the loss of ant species (e.g., Belshaw and Bolton 1993; Brühl et al. 2003). The main purpose of the present study was thus to describe how the properties of ant-associated mutualistic interactions differ among forests of different stand ages (i.e., different elapsed time since the last slash-and-burn event) in a given locality. For this purpose, we measured the frequency of occurrence and the species composition involved in mutualistic interactions between ants and plants or hemipterans in primary and secondary forest plots differing in stand age. By comparing these parameters among forest plots, we attempted to examine the effects of deforestation on the interactions of ants with plants and hemipterans in tropical rain forests.

Methods

The study was conducted from August to September 2003 in a primary forest of the Lambir Hills National Park, Sarawak, Malaysia and in secondary forest of differing stand age around the outside of the park. We chose 15 secondary forest plots of three stand types for our survey: four plots of 1-year-old secondary forest stands (abbreviated as 1SF), five of 5-year-old secondary forest (5SF), and six of old secondary forest (>19 years old; OSF). We established one 100×10 m study plot at or near the center of each of the 15 secondary forest stands. In the park's primary mixed dipterocarp forest, we established four shaded primary forest study plots (SPF) in the same way as in the secondary forest stands. Most of the forest floor inside the four plots was relatively shady, with a thick canopy layer, and no obvious forest gaps were included in the plots. We also selected two gaps approximately 10 m in diameter near the four shaded plots. Then, the 2 m-wide fringes of the gaps were set in the additional study plots (GPF) for gaps in the primary forest.

We conducted a field census of ants found attending EFNs, hemipterans, and myrmecophytes in each study plot. Except for the GPF plots, each 100×10 m plot was divided into 40 subplots of 25 m^2 each. In each subplot, we randomly selected 10 tree saplings or young trees that were 0.5 to 2.0 m in height. In each GPF plot, we randomly selected 400 tree saplings or shrubs 0.5 to 2.0 m in height. In several plots, the total number of census trees ranged between 400 and 410 because of miscounts.

During each census, we checked whether ants were present attending EFN glands or hemipterans on the selected trees. Lianas were omitted from the census because it was difficult to identify them. EFNs and hemipterans that were not attended by ants were omitted from our census. We also checked whether the selected trees were myrmecophytes by searching for domatium-like structures that ants could inhabit and for the presence of any entrance and exit holes for ants; in addition, we tested whether ant symbionts had been recruited by manually shaking the trees. We also checked whether the weaver ant *Oecophylla smaragdina* (Fabricius) (Formicinae) was present on the selected trees because this species maintains large territories around arboreal nests located on multiple trees in which it excludes other ants from any EFNs and hemipterans present in the territory (Hölldobler and Wilson 1990; Blüthgen and Fiedler 2002).

We calculated the frequency of each association as the percentage of all sampled trees (ca. 400) in a plot on which a given association was recorded. We compared the frequencies of EFN-bearing trees on which the EFNs were attended by ants, of trees with hemipteran-attending ants, of myrmecophytes, and of trees with *O. smaragdina*, among the five types of forest stand (1SF, 5SF, OSF, SPF, and GPF) using a *G*-test. We also calculated the average numbers of species of EFN-attending ants, hemipteran-attending ants, trees that harbored such interactions, and myrmecophytes in each forest type.

In addition to comparisons among forest stands of different ages, we assessed the inferred effect of deforestation on ant-associated interactions by calculating the above-mentioned variables for primary and secondary forest vegetation as separate categories. To estimate the properties of ant-associated interactions for primary forest as a whole (PF), we combined the data from the GPF and SPF forest types. To estimate the properties for the secondary forest as a whole (SF), we combined the data from the three secondary-forest types (1SF, 5SF, and OSF).

Results

The frequency of trees on which EFNs were attended by ants differed significantly among forest stand types (*G* = 180.05, *P* < 0.001). The mean frequencies of EFN-bearing trees attended by ants (3.2 to 5.6%, respectively) were conspicuously higher in GPF and 1SF than in 5SF, OSF, and SPF (<0.5% in each). However, the mean frequency of EFN-bearing trees attended by ants did not differ between PF and SF (*G* = 1.02, *P* = 0.30).

The average number of ant species per plot found attending EFNs in PF (3.7± 2.0 species per plot) was higher than that in SF (1.3 ± 0.7). The average number of ant species was highest in GPF (10.0 ± 1.0) and second-highest in 1SF (4.3 ± 2.1). For 5SF, OSF, and SPF, an average of only 0.2 to 0.5 species of ants were observed attending EFNs. No ant species attended EFNs in both PF and SF.

The average number of species of EFN-bearing trees per plot in PF (2.7 ± 2.0) was higher than that in SF (0.4 ± 0.2). The average number of species of EFN-bearing trees was highest in GPF (7.0). In the other forest stand types, only 0.2 to 1.0 species of EFN-bearing trees per plot were found. Of all the species of EFN-bearing trees that were observed in PF, only 13% were also observed in SF. In 1SF, 96% of all 52 EFN-bearing trees that we observed belonged to one species (*Homalanthus populneus* (Geiseler), Euphorbiaceae), and most trees were attended by one of two ant species: *Crematogaster* sp. 85 (Myrmicinae) and *Tapinoma* sp. 1 (Dolichoderinae).

The frequency of trees on which hemipterans were attended by ants differed significantly among forest stand types (*G* = 48.01, *P* < 0.001). The mean frequencies in 5SF, GPF, and SPF ranged from 1.5 to 2.6%, whereas those in OSF and 1SF were <0.65%. The mean frequency did not differ between PF and SF (*G* = 1.59, *P* = 0.20).

The average number of ant species per plot attending hemipterans in PF (3.5 ± 0.7) was higher than that in SF (0.9 ± 0.3). The average number of ant species was highest in GPF (4.0 ± 1.0) and second-highest in SPF (3.3 ± 1.0). In 1SF, 5SF, and OSF, an average of 0.8 to 1.2 species of ants were observed attending hemipterans. Of all the species of ant that were observed in PF, only 19% were also observed in SF.

The average number of tree species per plot on which hemipterans were attended by ants in PF (2.8 ± 0.5) was higher than that in SF (0.6 ± 0.2). The average number of tree species was highest in GPF (3.0 ± 1.0) and second-highest in SPF (2.8 ± 0.8). In each of the three types of secondary forest stand, fewer tree species were found per plot than in any type of primary forest stand. No tree species on which hemipterans were attended by ants was observed in both PF and SF. In 5SF, *Melastoma malabathricum* (Melastomataceae) accounted for about 89% of the 53 trees with hemipterans that were attended by ants of one species, *Dolichoderus affinis* (Dolichoderinae), which was also observed on other trees.

All 10 species of myrmecophytic trees belonged to the genus *Macaranga* (Euphorbiaceae). The frequency of myrmecophytes differed significantly among forest stand types (*G* = 248.55, *P* < 0.001). The frequency was higher in GPF than in any other forest stand type, and was about seven times the value in 5SF, which had the second-highest frequency. The frequencies in OSF, 1SF, and SPF were less than 7%, 4%, and 2% of the frequency in GPF, respectively. The total frequency of *Macaranga* myrmecophytes in PF was significantly higher (6.2 versus 1.5%) than that in SF (*G* = 23.80, *P* < 0.001).

The average number of myrmecophytic *Macaranga* species per plot in PF (3.2 ± 1.6) was higher than that in SF (1.1 ± 0.3). The average number of species of myrmecophytic *Macaranga* was highest in GPF (8.0). In the other forest stand types, only 0.8 to 1.6 species of myrmecophytic *Macaranga* per plot were found. All *Macaranga* myrmecophytes observed in SF were also found in PF. In 5SF, *Macaranga bancana* accounted for 89% of the 56 *Macaranga* individuals. The occurrence of this species was higher in SF (82 individuals) than in PF (24 individuals).

The frequency of trees occupied by *O. smaragdina* differed significantly among forest stand types (G = 126.06, $P < 0.001$). The frequency was notably higher in 1SF (3.5% ± 2.1%) than in the other forest stand types (0.7% ± 0.6% for 5SF, 0.3% ± 0.3% for OSF, 0% for SPF, and <0.01% for GPF) and tended to decrease as stand age increased. The total frequency of trees occupied by *O. smaragdina* in SF was significantly higher than that in PF (1.3 vs. <0.01%; G = 36.97, $P < 0.001$).

Discussion

Our results demonstrate that slash-and-burn deforestation affects the properties of ant-associated mutualistic interactions. For ants attending both EFNs and hemipterans, for trees bearing EFNs, and for trees with hemipteran-attending ants, the number of species was higher in primary than in secondary forest, and fewer than 20% of the species observed in the primary forest plots were also recorded in the secondary forest plots. For *Macaranga* myrmecophytes, both the number of species and the frequency of occurrence were higher in primary than in secondary forest, and the species observed in secondary forest comprised approximately one-third of the species occurring in primary forest. In contrast, the weaver ant *O. smaragdina*, which tended to exclude other arboreal ant species, was significantly more abundant in secondary than in primary forest. These results suggest that slash-and-burn deforestation drastically decreases the diversity of species involved in ant-associated mutualistic interactions and simplifies the composition of the involved species. We also found that these effects of deforestation lasted for 19 years.

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References

Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf litter ant fauna in Ghana. Biodiversity Conserv 2(6):656-666

Bickel TO, Brühl CA, Gadau JR, Hölldobler B, Linsenmair KE (2006) Influence of habitat fragmentation on the genetic variability in leaf litter ant populations in tropical rainforests of Sabah, Borneo. Biodiversity Conserv 15(1):157-175

Blüthgen N, Fiedler K (2002) Interactions between weaver ants *Oecophylla smaragdina*, homopterans, trees and lianas in an Australian rain forest canopy. J Anim Ecol 71(5):793-801

Brühl CA, Eltz T, Linsenmair KE (2003) Size does matter – effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity Conserv 12(7):1371-1389

Bruna EM, Vasconcelos HL, Heredia S (2005) The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants. Biol Conserv 124(2):209-216

Buckley RC (1982) Ant-plant Interactions in Australia. Dr. W. Junk Publishers, The Hague

Davidson DW (1998) Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecol Ent 23(4):484-490

Davidson DW, McKey D (1993) The evolutionary ecology of symbiotic ant-plant relationships. J Hymenop Res 2(1):13-83

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conserv Biol 18(2):302-309

Floren A, Linsenmair KE (1997) Diversity and recolonisation dynamics of selected arthropod groups on different tree species in a lowland rain forest in Sabah, Malaysia. In: Stork NE, Adis J, Didham RK (eds). Canopy arthropods. Chapman & Hall, London, pp 344-381

Hölldobler B, Wilson EO (1990) The ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts

Koptur S (1992) Extrafloral nectary-mediated interactions between insects and plants. In: Bernays E (ed). Insect-plant interactions. CRC Press, Florida, pp 81-129

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391(6662):72-76

Levings SC, Windsor DM (1985) Litter arthropod populations in a tropical deciduous forest: relationships between years and arthropod groups. J Anim Ecol 54(1):61-69

Oliveira PS, Oliveira-Filho AT (1991) Distribution of extrafloral nectaries in the woody flora of tropical communities in Western Brazil. In: Price PW, Lewinsohn TM, Fernandes WG, Benson WW (eds). Plant-animal interactions. John Wiley & Sons, New York, pp 163-175

Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19(12):654-660

Stork NE (1988) Insect diversity: facts, fiction, and speculation. Biol J. Linn Soc 35(4):321-338

Effects of Canopy Gaps on Ant–Hemiptera–Plant Interactions in Lambir Hills National Park, Sarawak

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Introduction

When a tree dies in a closed-canopy forest, it creates a "canopy gap", which is the initial stage of a mini-successional sequence called gap-phase regeneration, culminating in the replacement of the original canopy tree by one or more new trees (Hubbell et al. 1999). Over the past few decades, a considerable number of studies have been done on tree species in canopy gaps (Lawton and Putz 1988; Denslow 1995; Hubbell et al. 1999). Canopy gaps are considered to provide seedlings of many tree species with micro-environmental conditions suitable for their growth (Denslow 1995). Since light is relatively intense in canopy gaps compared with that in the area surrounding gaps, the growth performance of seedlings of most tree species, including pioneer trees that can hardly survive and grow under the forest canopy, is high. Canopy gaps give r-type individuals, which invest little in survivorship or consume resources heavily, a chance to reproduce. Hence gap formation is considered to contribute to the maintenance of tree species diversity and substantially affect the ecological and evolutionary dynamics of many tropical forests (Denslow 1995).

Taking into account that secondary production depends on primary production (Brylinski and Mann 1973; Cole et al. 1988), gap formation is expected to influence organisms that interact with trees. Because areas under canopy gaps have continuously higher resource availability as compared with those under a closed canopy, Levey (1990) categorized canopy gaps as "keystone habitats" for frugivores. However, little is understood about the effects of canopy gaps on the diversity and dynamics of a community of organisms other than the trees. A few studies have evaluated the effects of canopy gaps on fauna or interactions between trees and other organisms, including work on plant–frugivore interactions (Levey 1988, 1990; Beck et al. 2004) and on plant–herbivore interactions (Coley 1983). Thus, the effects of canopy gaps and their role as "keystone habitats" for organisms other than trees have not been adequately studied.

Ants (Hymenoptera: Formicidae) comprise up to 94% of arthropods in insecticidal fogging samples from tropical rain forest canopies and 86% of the biomass of those samples (Tobin 1995; Davidson 1997). Ants often interact with plants both directly over extrafloral nectaries (EFNs) and indirectly over honeydew excreted by myrmecophilous insects such as hemipterans or lepidopteran caterpillars. Ants attend such myrmecophilous insects or EFNs to collect honeydew or nectar, and they protect the myrmecophilous insects or EFN-bearing plants from natural enemies (Hölldobler and Wilson 1990). Thus, ant–hemipteran and ant–plant interactions are sometimes known as mutualisms. Since ants or hemipterans have a close relationship to plants, they would be affected by canopy gaps possessing high plant productivity. However, there is little understanding of the effects of canopy gaps upon ants through their strong relationship with plants or hemipterans. In this study, we were concerned with the effect of canopy gaps on ant–hemipteran–plant interactions.

Materials and Methods

Study site

The data were collected around the Canopy Biology Plot (8 ha) and the Crane Plot (4 ha) in Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E; 50–200 m a.s.l.). The park is located about 10 km inland from the coast in the northern part of Sarawak, and the climate is humid tropical, with a constant high temperature and a weak seasonal change in rainfall (Kato et al. 1995). Most of the park is covered with primary evergreen forests, much of which is classified as lowland mixed dipterocarp forest, thought to be one of the richest forests in the world in terms of the diversity of tree species. The canopy of this multi-layered forest, which has developed on nutrient-poor sandy or clayey soil, is about 35 to 40 m high, with emergent trees penetrating the canopy layer attaining heights of more than 70 m (Kato et al. 1995).

In Lambir Hills National Park, 119 families, 437 genera, and 1153 species of vascular plants were identified by Nagamasu and Momose (1997), and more than 257 ant species have been recorded by Yamane and Nona (1994). Yamane and Nona (1994) also showed that the ant fauna on the ground is different from that on tree trunks (ca. 1 to 1.5 m above the ground).

Ant–hemiptera–plant interactions

There were some open canopy areas in the primary forest, most of which were less than about 100 m^2 in area. In order to clearly distinguish canopy gaps from closed-canopy areas, we defined canopy gaps as open canopy areas around which we could find a fallen tree. We set up 20 quadrats in canopy gaps at the forest floor (the gap sites); each quadrat was 5 m × 5 m. We also placed a quadrat of the same size about 10 m away from each gap quadrat in a closed-canopy area (the non-gap sites). At each quadrat (a total of 40), all plants taller than 50 cm and with leaves below a height of 2 m above the ground were examined up to a height of 2 m above the ground. We recorded when ants attended EFNs or hemipterans, and collected samples from these plants. All of the collected specimens of ants, plants, and hemipterans (except for a very small number of lost samples) were sorted and identified to species, morphospecies, or higher taxonomic level (genus or family).

We checked the ant-attended parts of the plants for the presence of “shelters” that had been constructed by ants. The ant-attended leaves or shoots were also categorized by color, size, and freshness (hard or soft tissue).

We defined “the frequency of ant–hemiptera interaction” and “the frequency of ant–EFN interaction” as the proportion of plants in which we found ant–hemiptera or ant–EFN interactions (i.e., the number of plants exhibiting such interactions divided by the total number of investigated plants for each quadrat).

We also found some myrmecophytes in the study area. Myrmecophytes prepare special nesting space (domatia) for their obligate ant partners and often provide the ants with food. Most of the obligate mutualisms between ants and myrmecophytes involve scale insects (Hemiptera: Sternorrhyncha: Coccoidea), and ants live only on the plants and feed exclusively on plant food bodies and honeydew excreted by sap-sucking homopterans in the domatia. The ants, in return, protect the plant from herbivores and vines

(Itioka et al. 2000; Fiala and Maschwitz 1990). There is thus a strong relationship between ants, hemipterans, and plants. In this study, we treated the myrmecophytes separately as an independent symbiotic system.

The plants were categorized into three phases of leaf opening, (1) leaves not yet opened, (2) leaves just after opening, (3) plants having both previous categories present. Plants in the third category are defined as having a continuous succession of new leaves available.

Evaluation of light intensity

To assess light intensity, hemispherical photographs were taken with a Nikon camera (Nikon Co., Tokyo, Japan) equipped with an 8-mm fisheye lens at each quadrat. These digital photographs were analyzed using Gap Light Analyzer Version 2.0 (GLA; Frazer et al. 1999). We estimated the amount of direct solar radiation intensity per day (MJ m^{-2} d^{-1}) at the floor.

Results

Hemipterans and EFN attended by ants

As expected, the frequencies of both ant–hemipteran and ant–EFN interactions were significantly higher at gap sites than at non-gap sites (Wilcoxon signed-rank test, $P = 0.0021$; 0.0026, respectively). In addition, the species richness of ants, hemipterans, and plants were also higher at canopy gap sites than at non-gap sites. The frequency of myrmecophytes was also higher at gap sites (Wilcoxon signed-rank test, $P = 0.0067$).

Compared with non-gap sites, hemipterans being attended by ants tended to use younger parts of the plants in canopy gaps (Fisher's exact test, $P = 0.017$). Conversely, the proportion of hemipterans around which ants formed a shelter was significantly higher at non-gap sites than at gap sites (Fisher's exact test, $P < 0.001$).

When we classified hemipterans by their movement ability, the groups with relatively good flying ability (e.g., Membracidae and Cicadellidae) tended to appear in gap sites, and other groups with poor flying ability (e.g., Coccoidea and Aphididae) used non-gap sites (Fisher's exact test, $P = 0.016$).

We detected ant–EFN interactions at the young part of plants (e.g., new leaves) (binomial test, $P < 0.001$; young parts = 26, older parts = 4).

Ant–hemipteran–plant interactions

We detected no pattern of specific ants using specific plants or hemipterans, or vice versa. Of 17 ant species found in at least two trophobioses, none was restricted to a single plant family.

Light intensity and new leaf availability of plants

Gap quadrats have a significantly higher ratio of plants with a continuous availability of new leaves compared with non-gap quadrats (Wilcoxon signed-rank test, $P = 0.0018$). Furthermore, this proportion was significantly correlated with the light intensity at the sampling location (Spearman’s rank correlation coefficient = 0.41, $R^2 = 0.12$, $P = 0.0093$). The numbers of ant–hemipteran and ant–EFN interactions per quadrat both increased significantly with the number of plants that have a continuous availability of new leaves.

Discussion

The effect of canopy gaps on plants has been emphasized for a long time (Lawton and Putz 1988; Denslow

1995; Hubbell et al. 1999; Galhidy et al. 2006). In this study, we revealed that there is a higher proportion of ant-attended plants in canopy gaps, as well as a higher number of ants species in canopy gaps, compared with in closed-canopy areas. Since numerous arboreal ants in tropical rain forests feed mainly as herbivores or on insect exudates (e.g., from hemipterans; Davidson et al. 2003), canopy gaps may be an important factor in sustaining the biomass and diversity of ants in tropical rain forests. Moreover, plants and hemipterans that offer liquid food to ants were also diverse in canopy gaps. These results indicate that the canopy gap environment influences not only plants but also ant–hemipteran–plant interactions.

In addition, these effects are varied and not limited to certain species or interactions because no patterns of specificity were found. Furthermore, certain ant species used EFNs and hemipterans simultaneously on the same plants. This plasticity will enable ants to use nearby plants both directly and indirectly. It is likely that the complex web containing potential species replacements leads to the maintenance of species diversity in canopy gaps. Plants in canopy gaps act as a food supply not only for ants that live in the gaps but also for those in the surrounding closed-canopy areas because most of the ant species found in the non-gap areas were also found at the canopy gaps. Levey (1990) described canopy gaps as keystone habitats for frugivores because of the availability of abundant food resources. Similarly, we can say that canopy gaps also work as essential space—as Levey put it, “keystone habitats”—for ants and ant–hemipteran–plant interactions.

Judging from our results, we speculate that canopy gaps have a more multifarious influence than previously thought. They may contribute to increasing and maintaining diversity for various groups, especially in the tropical forest. We expect that future studies of insects (besides ants and hemipterans), other arthropods, and mammals and of other ecosystems will demonstrate the great effect of canopy gaps.

Ant-attended hemipterans and EFNs tended to be present on the younger parts of plants. It is likely that the increased amount of sunlight reaching the forest floor in canopy gaps causes the increased number of new leaves and brought about the increase in ant–hemipteran–plant interactions.

The occurrence of canopy gaps is unpredictable, and they do not last long. The fact that hemipterans with relatively good flying ability appeared in canopy gaps shows that the ability to move enables hemipterans to become established on the productive plants in canopy gaps. Conversely, closed-canopy areas are stable compared with canopy gaps. Therefore, hemipterans with limited migration ability found in the shaded understory might put a greater value on a stable relationship with ants rather than on the increased resource availability in gaps. The flight ability of hemipterans may thus represent an adaptation to their preferred environment (i.e., gap vs. non-gap). Our results show that the variations of plants caused by canopy gaps can affect fauna or mutualisms through the process of a nutritional cascade. A slight environmental difference might produce variation in the quantity and quality of interactions. MacArthur et al. (1966) suggested that, because of the higher structural heterogeneity in tropical forests than in the temperate areas, tropical individuals should have higher habitat specificity than individuals in the temperate zone. It was observed in our study that canopy gaps work as keystone habitats for ants and ant–hemipteran–plant interactions, and adaptations to different environments (i.e., gap vs. non-gap) are also important for maintenance of species diversity. Our results should provide insights into the maintenance of species diversity in the tropical rain forest.

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References

Beck H, Gaines MS, Hines JE, Nichols JD (2004) Comparative dynamics of small mammal populations in treefall gaps and surrounding understorey within Amazonian rainforest. Oikos 106:27–38

Brylinski M, Mann KH (1973) An analysis of factors governing productivity in lakes and reservoirs. Limn. Ocean. 18:1–14

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross systems overview. Mar. Ecol. Prog. Ser. 43:1–10

Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Mon. 53:209–233

Davidson DW (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol. J. Linn. Soc. 61:153–181

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300:969–972

Denslow JS (1995) Disturbance and diversity in tropical rain forests - the density effect. Ecol. Appl. 5:962–968

Fiala B, Maschwitz U (1990) Studies On the South East-Asian ant-plant association Crematogaster-Borneensis Macaranga - adaptations of the ant partner. Insect. Soc. 37:212–231

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyzer (GLA), Version 2.0:Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation. Simon Fraser University, Burnaby, British Columbia and Institute of Ecosystem Studies, NY

Galhidy L, Mihok B, Hagyo A, Rajkai K, Standovar T (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. Plant Ecol. 183:133–145

Hölldobler B, Wilson EO (1990) The Ants. Harvard University Press, Cambridge

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, Lao SL (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557

Itioka T, Nomura M, Inui Y, Itino T, Inoue T (2000) Difference in intensity of ant defense among three species of Macaranga myrmecophytes in a southeast Asian dipterocarp forest. Biotropica 32:318–326

Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T (1995) Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. Res. Pop. Ecol. 37:59–79

Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69:764–777

Levey DJ (1988) Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69:1076–1089

Levey DJ (1990) Habitat-dependent fruiting behavior of an understorey tree, Miconia-Centrodesma, and tropical treefall gaps as keystone habitats for frugivores in Costa-Rica. J. Trop. Ecol. 6:409–420

MacArthur RH, Recher H, Cody M (1966) On the relationship between habitat selection and species diversity. Am. Nat. 100:319–332

Nagamasu H, Momose K (1997) Flora of Lambir Hills National Park, Sarawak, with special reference to the Canopy Biology Plot. In: Canopy biology program in Sarawak. II. General flowering of tropical forests in Sarawak (eds. Inoue T and Hamid AA) pp. 20–67. Center for Ecological Research, Kyoto University, Otsu

Tobin JE (1995) Ecology and diversity of tropical forest canopy ants. In: Forest canopies (eds. Lowman MD and Nadkarni N) pp. 129–147. Academic Press, New York

Yamane S, Nona AR (1994) Ants from Lambir Hills National Park. In: Canopy biology program in Sarawak. I. Plant reproductive systems and animal seasonal dynamics (eds. Inoue T and Hamid AA) pp. 223–226, Kyoto

Predator Avoidance Effects of Southeast Asian Danaid Butterflies in the Wild

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Chemical defenses, a typical butterfly defense strategy, have been well studied (Turner 1984), especially for danaid butterflies. The monarch butterfly, *Danaus plexippus* (Danaidae), which ranges mainly in North and Central America, is the best studied species in this family. Monarchs become unpalatable to birds, the major predators of adult butterflies (Edmunds 1974), when their larvae feed on poisonous milkweed (*Asclepias* spp., Asclepiadaceae) or other plants that contain cardiac glycosides (cardenolides). Birds learn to reject monarch butterflies after they have eaten one and vomited (Brower 1958; Brower 1969). Not all of the monarch butterfly's food plants contain cardenolides, however, and birds repeatedly ate monarchs reared on plants that lacked cardenolides (e.g., *Asclepias syriaca*, *A. tuberosa*, and *A. incarnata*). These studies indicate that the palatability of monarch butterflies was directly related to the species of plant ingested by the larvae (Brower 1969).

Other studies have raised doubts about predator avoidance of danaid butterflies in Southeast Asia. Several species of the danaid butterflies in this area are polyphagous and have been observed feeding on a wide range of seven plant families (Robinson et al. 2001), and there is no evidence of cardenolides in these plants. Furthermore, chemical analyses have shown that *Euploea core* (Danaidae), which is one of the most common species of danaid butterfly in this area, stores emetic cardenolides only as larvae and not as pupae and adults when reared on *Nerium oleander* (Apocynaceae) (Malcolm and Rothschild 1983).

We found no field studies of predator avoidance of danaid butterflies in Southeast Asia except for Ohsaki (1995)'s examination of predator avoidance of danaid butterflies. He used "beak marks" (certain types of wing damage that represent an unsuccessful attack by birds; Johki 1985) on butterfly wings as an indicator of predation pressure by birds. A high frequency of beak-marked species should reflect a high attack rate by birds (Edmund 1974). Ohsaki showed that the proportion of individuals with beak marks in the Danaidae family was significantly lower than it was for other nonpoisonous families of butterflies. However, beak-mark frequency is only indirect evidence of bird predation pressure (Edmunds 1974). Thus, we need to evaluate avoidance effects with a more direct method.

Our objective was to investigate the avoidance effects of Southeast Asian danaid butterflies in the wild. We evaluated how much these butterflies were avoided by predators compared with putative nonpoisonous butterflies (mostly Nymphalidae, Satyridae, Pieridae, and Papilionidae) in a tropical rainforest in Lambir National Park (4°20'N, 113°50'E), Sarawak, Malaysia. First, we regularly collected the butterflies and scored them for the presence of beak marks on their wings. Then, as a more direct method of observation, we conducted field presentation experiments employing the butterfly specimens.

Materials and Methods

Beak-mark rate

To determine the proportion of individuals with beak marks (the beak-mark rate), we collected butterflies on an approximate 3-km transect across the inside and outside of a primeval forest in Lambir National Park from 2004 to 2006. We walked the transect in both directions twice a week and captured butterflies that were within 3 m on either side and 5 m in the front with a net (for details on the method, see Pollard 1975). We then recorded the presence or absence of beak marks on the butterfly's wings (for details on the method, see Johki 1985).

We compared the beak-mark rate of danaid butterflies with those of butterflies from four nonpoisonous families (Nymphalidae, Satyridae, Pieridae, and Papilionidae). We omitted some genera (e.g., *Delias, Cethosia, Elymnias,* and *Chilasa*) from this analysis because most of them are thought to be poisonous or to mimic other unpalatable butterflies.

Field presentation experiment

For the field presentation experiment, we selected four abundant species of danaid butterfly (*Euploea diocletianus*, *E. mulciber*, *E. crameri,* and *Parantica aspasia*) and two species of nymphalid butterfly (*Lexias pardalis* and *Tanaecia munda*), which had roughly the same wing size (Otsuka 1998) and sometimes shared the same habitat (personal observation). Food plants of these butterflies at this study site are unknown, but there are several reports that *Euploea* and *Parantica* in Southest Asia feed mainly on Asclepiadaceae, Apocynaceae, and Moraceae (many species in these families are inferred to be poisonous), whereas *Tanaecia* and *Lexias* probably feed on plants that are not poisonous (e.g., Lecythidaceae and Hypericaceae, respectively) (Robinson et al. 2006).

We carried out a field presentation experiment during the day in March, May-June, and August-October 2003 and April 2004. We caught the butterflies with a net and stored them in a freezer. One day before the experiments, we took them out of the freezer and then unfolded the specimen's wings at about a 90° angle and fixed them in order to make the specimens imitate the natural state of a butterfly's wings.

We paired one specimen from each of the four Danaidae species with one from each of the two Nymphalidae species to make eight different types of butterfly pairs. We selected a pair from among the eight and tied the thorax of each butterfly specimen with a fishing line. The line was attached to a fishing rod, and two rods were used for the presentation of one pair.

We simultaneously passed the ends of lines holding the specimen pair from the canopy walkway to the subcanopy layer (roughly 10 m below). We defined a wild bird's response as an "approach" when a bird came within 2 m of either specimen. We recorded the species of the approached butterfly specimen and the bird whenever possible. If no bird approached the offered specimens within 20 minutes, we removed them and presented them again at another point. We compared the approach frequency between the danaid and nymphalid butterfly specimens for each of the eight pairs.

Results

Beak-mark rate

Figure 1 shows the mean beak-mark rate of each family. The beak-mark rate of family Danaidae was significantly lower than those of the Satyridae, Nymphalidae, and Pieridae families (Ryan's multiple-comparison method, $P < 0.05$ in each case) but not for Papilionidae. In contrast, we found no significant differences among the four nonpoisonous families ($P > 0.05$ in each case).

Field presentation experiment

In total, 399 pair-wise presentations were conducted, and 53 specimens were approached by birds. All specimens approached were Nymphalidae butterflies—no Danaidae butterflies were approached. The approach responses of birds were significantly less frequent to Danaidae specimens than to Nymphalidae ones for five of the eight pairs (Fisher's exact test, $P<0.01$) (Fig. 2). The total approach frequency was insufficient for statistical analyses for the other three pairs. In some cases, we could identify the bird species approaching the offered specimen, but precise determination was often difficult. We recorded birds from at least three families (Pycnonotidae, Timaliidae, and Irenidae).

Discussion

Beak marks have been interpreted as evidence of active escape by the prey (Edmunds 1974). If danaid butterflies are unpalatable, then birds that have sampled them may learn to avoid them. Thus, there should be fewer attacks and beak marks on danaid butterflies than on other butterflies. The low beak-mark rate we observed for danaid butterflies suggests that they were attacked less frequently by birds than were other putative nonpoisonous butterflies at this study area. These results are in agreement with those found by Ohsaki's (1995) study conducted in Sabah, Malaysia. However, beak-mark rates in natural populations of butterflies are not only affected by palatability (Edmunds 1974). Thus, we must be careful when interpreting these results.

The low approach frequency of birds to the offered danaid specimens more directly showed that they were avoided by some birds in the wild. Among the birds, most species of Pycnonotidae and some of Timaliidae are known to forage on some insects on trees (Smythies 1999). Therefore, we interpreted the bird's approach behavior as an attempt to prey on the offered specimen. Indeed, the bird caught the specimen in some cases. In many of the cases, the bird most likely noticed the fishing line just before attacking the butterfly and left.

Our results suggest that some insectivorous birds were more reluctant to attack danaid butterflies than other butterflies at this study site. This rejection may be due to unpalatability caused by the presence of some chemical substances in the Danaid butterflies.

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References

Brower JVZ (1958) Experimental studies of mimicry in some North American butterflies. I. The monarch, *Danaus plexippus*, and viceroy, *Limenitis archippus*, Evolution 12:32–47

Brower LP (1969) Ecological chemistry, Scientific American 220:22–29

Edmunds M (1974) Significance of beak marks on butterfly wings, Oikos 25:117–118

Johki Y (1985) Wing damages of butterflies and bird's attacks, Tyo to Ga 35:202–207

Malcolm S, Rothschild M (1983) A danaid mullerian mimic, *Euploea core amymone* (Cramer) lacking cardenolides in the pupal and adult stages. Biological Journal of the Linnean Society 19:27–33

Ohsaki N (1995) Preferential predation of female butterflies and the evolution of batesian mimicry, Nature 378:173–175

Otsuka K (1988) *Butterflies of Borneo*, Tobishima Corporation, Tokyo.

Pollard (1975) A method for assessing changes in the abundance of butterflies, Biological Conservation 12:115–134

Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernandez LM (2001) *Hostplants of the moth and butterfly caterpillars of the Oriental Region*. Southdene Sdn Bhd, Kuala Lumpur

Smythies BE (1999) *The birds of Borneo*, Natural history publications (Borneo) Sdn. Bhd. Kota Kinabalu

Turner JRG (1984) Mimicry: the palatability spectrum and its consequences, In *The Biology of Butterflies*, RI Vane-Wright and PR Ackery eds., Academic Press, London

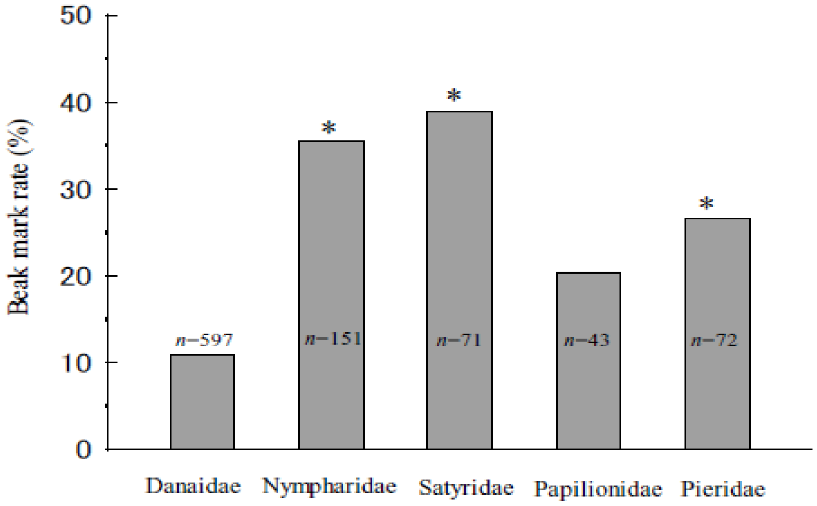

Fig. 1. Percentage of butterflies with beak marks in each families.
* indicates the beak mark rate differes siginigicntly from its Danaidae (Ryan's multiple comparison test $P<0.05$).

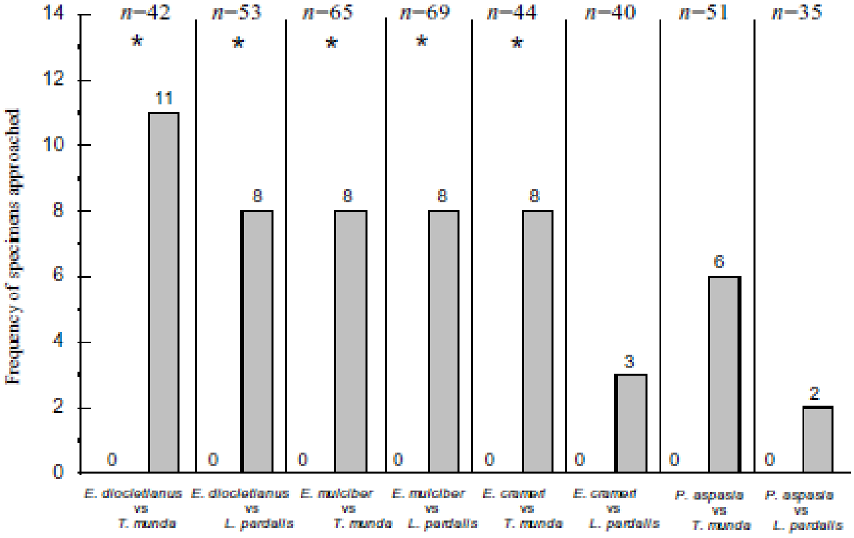

Fig. 2. Number of butterfly speciemens attacked in each pair wise presentation experiment. * indicates significant difference (Fisher's exact test $P<0.01$).

The Morphological and Ecological Characteristics of *Arhopala* Species (Lycaenidae) Utilizing *Macaranga* Species (Euphorbiaceae) as Host Plants in a Bornean Dipterocarp Forest

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Introduction

The Asian butterfly genus *Arhopala* (Lycaenidae) includes 160 species that are distributed from India to Australia. The *amphimuta* subgroup of this genus is known to utilize *Macaranga* species (Euphorbiaceae) as its host plants (Maschwitz et al. 1984; Megens et al. 2005). Genus *Macaranga* includes more than 20 species of myrmecophytes (Whitmore 1969; Quek et al. 2004). These myrmecophytic species develop mutualistic relationships with species-specific specialist ants of the genera *Crematogaster* or *Camponotus* (Fiala and Maschwitz 1991, 1992). These plants provide nesting space for ants in the internodes and produce food bodies in the leaves and stipules that provide a food resource for the ants. The symbiotic ants exclude herbivores by responding to volatile chemicals from injured tissues of the host plant; they quickly aggregate at the injured points, where they attack the herbivores.

Arhopala larvae could feed on such myrmecophytic *Macaranga* if they are capable of evading the aggressive ants. However, studies of the utilization of *Macaranga* as a host plant by *Arhopala* are limited. In the Malayan peninsula, only three *Macaranga* species have been investigated. Each of these species serves as a host for the larvae of one *Arhopala* species, and symbiotic ants do not appear to attack the *Arhopala* larvae (Maschwitz et al. 1984). There is wide variation in the intensity of the mutual dependency in ant–*Macaranga* interactions, ranging from non-myrmecophytes to facultative, transitional, and obligate myrmecophytes (Fiala and Maschwitz 1990; Fiala et al. 1994). In addition, the defenses of *Macaranga* include defense by ants and chemical or physical defenses (non-ant defenses). The balance between ant and non-ant defenses also differs among *Macaranga* species (Itioka et al. 2000; Nomura et al. 2000; Itioka 2005).

Each *Arhopala* species that utilizes *Macaranga* may overcome one or more components of the variation in anti-herbivore defenses by *Macaranga*. However, the relationship between *Macaranga* and *Arhopala* has not been investigated, and as a result, the survival strategy of each *Arhopala* species that utilizes *Macaranga* has not yet been revealed. In the present study, we investigated the relationships between *Macaranga* and *Arhopala* in Borneo, where the highest species richness of *Macaranga* is found. In addition, we describe the morphology and ecology of the *Arhopala* larvae, and especially the interaction between the larvae and symbiotic ants.

Methods

Study site

Our study was conducted in Lambir Hills National Park, Sarawak, Malaysia (4˚2'N, 113˚2'E, 150 to 200m a.s.l.), from the end of May 2006 to the beginning of March 2007. This park is covered primarily by lowland mixed dipterocarp forest. More than 16 *Macaranga* species, including at least 11 myrmecophytic species, occur in the park.

Sampling and rearing

We investigated 11 myrmecophytic and 5 non-myrmecophytic *Macaranga* species to obtain *Arhopala* eggs and larvae. During this collection, we recorded the parts of the plant on which the larvae fed, the location of the larvae, ant behavior in response to the larvae, and the number of attendant ants. The collected eggs and larvae were taken to the laboratory on their host plants for rearing and observation. In the laboratory, the eggs and larvae were maintained in plastic boxes with their host plants until they reached the adult stage. We observed any myrmecophilic organs on the larvae and recorded. The host plants were maintained by cutting the stems and inserting them in sponges used in floral arrangements (i.e., in floral oases).

Results

In total, we recovered 18 eggs and 93 larvae of *Arhopala* from four myrmecophytic and two non-myrmecophytic *Macaranga* species. In the myrmecophytic plants (*M. trachyphylla*, *M. bancana*, *M. beccariana*, and *M. hosei*), each plant hosted the larvae of a single *Arhopala* species; two closely related species (*M. trachyphylla* and *M. bancana*) hosted conspecific *Arhopala*. Two non-myrmecophytic plants (*M. gigantea* and *Macaranga* sp. A) were also utilized by conspecific *Arhopala*. The morphological and ecological characteristics differed among the *Arhopala* species (Table 1).

1. ***Macaranga trachyphylla, M. bancana – Arhopala amphimuta***

Arhopala amphimuta utilized *M. trachyphylla* and *M. bancana* (both myrmecophytes) as its host plant. These two species are closely related. One or two eggs covered with many warts were laid on the underside of fresh leaves (Fig. 1). The emerging light-green larvae rested on the underside of fresh leaves (Fig. 2). Some leaves of *M. trachyphylla* and *M. bancana* developed a red color on their underside. When larvae fed on these red leaves, they tended to develop a red-brown band in the middle part of the green body of the middle-instar larvae (Fig. 3). Larvae that fed on green leaves did not develop this band. All larvae developed myrmecophilic organs (a dorsal nectary organ and tentacle organs; Fig. 4). Symbiotic ants of *Macaranga* did not attack the larvae and instead appeared to tend them (Figs. 2–4). The number of ants that tended a last-instar larva averaged 6.8 ± 0.97 (mean ± SE, $N = 5$). The pupal body color was similar to that of the stipules of the host plant (Fig. 5). A parasitic fly emerged from the body of a prepupa, and an ichneumonid fly emerged from the body of a pupa. 24% of the collected larvae were parasitized by either a parasitic fly or an ichneumonid fly.

2. ***Macaranga beccariana – Arhopala zylda***

Arhopala zylda utilized *M. beccariana*, a myrmecophyte host plant. The whitish-green larvae rested on the underside of fresh leaves, and their body color was similar to that of these fresh leaves (Figs. 6–8). The larvae only developed tentacle organs and did not exhibit a dorsal nectary organ. Symbiotic ants of

Macaranga did not tend these larvae, but they also did not attack the larvae. The pupal body color was similar to that of fresh leaves of the host plants (Fig. 9). 23% of the collected larvae were parasitized by either a parasitic fly or an ichneumonid fly.

3. ***Macaranga hosei* – *Arhopala dajagaka***

   Arhopala dajagaka utilized *M. hosei*, a myrmecophyte host plant. One or two eggs covered with many warts were laid on the underside of fresh leaves (Fig. 10). The larvae had a greenish-yellow color that is similar to that of fresh leaves of the host plant (Figs. 11–13). This species developed two myrmecophilic organs (a dorsal nectary organ and tentacle organs). The larvae of this species appeared to exude more honeydew from their dorsal nectary organ than the larvae of *A. amphimuta*. The number of ants that were tending a last-instar larva averaged 17.5 ± 2.72 (mean ± SE, *N* = 4). The pupal body color was similar to that of the fresh leaves of the host plants (Fig. 14). 25% of the collected larvae were parasitized by either a parasitic fly or an ichneumonid fly.

4. ***Macaranga gigantea*, *Macaranga* sp. A – *Arhopala major***

   Arhopala major utilized *M. gigantea* and *Macaranga* sp. A, both non-myrmecophytes, as its host plant. Only one larva was discovered on *Macaranga* sp. A, thus most of the larvae were discovered on *M. gigantea*, which has very large leaves. One to three eggs covered with many warts were laid on the underside of fresh leaves (Fig. 15). The larvae developed two myrmecophilic organs (a dorsal nectary organ and tentacle organs). Their body color ranged from light green to pale yellow and was similar to that of fresh leaves of the host plant (Figs. 16–18). Many fresh leaves had feeding damage caused by these larvae, but the larvae were rarely discovered on fresh leaves. This is because they usually rested inside stipules during the day (Fig. 17). The pupal body color was very similar to that of the stipules of the host plant (Fig. 19). A braconid wasp emerged from the body of a middle-instar larva, and a parasitic fly emerged from the body of a prepupa. 37% of the collected larvae were parasitized by either a parasitic fly or a braconid wasp.

Discussion

In the Malayan peninsula, three *Arhopala* species have been reported to utilize *Macaranga* species (Maschwitz et al. 1984). These species formed three associations: *A. amphimuta*–*M. triloba*, *A. moolaiana*–*M. hulletti*, and *A. zylda*–*M. hypoleuca*. In the present study (in Borneo), *A. amphimuta* utilized *M. trachyphylla* and *M. bancana*, which are closely related to *M. triloba*. *M. triloba* was not found in Lambir Hills National Park. *Arhopala zylda* utilized *M. beccariana*, which is closely related to *M. hypoleuca*, but *M. hypoleuca* was not utilized by larvae of *A. zylda* in Lambir Hills National Park. The relationship between *Macaranga* and *Arhopala* species may thus exhibit a certain degree of species specificity. The larvae of *A. moolaiana* were not found on *Macaranga* in the present study, but many adults of this species were captured. This suggests that *A. moolaiana* larvae will be found on other *Macaranga* species in the Lambir Hills National Park.

The majority of lycaenids develop associations with ants that can be either facultative or obligate and that range from mutualism to parasitism (Pierce et al. 2002). Ant association has exerted a strong selection pressure on lycaenid larval shape. Thus, the majority of lycaenid larvae develop myrmecophilic organs to protect themselves from ant attack. In the present study, the larvae of *A. amphimuta* and *A. dajagaka* developed two myrmecophilic organs and were tended by symbiotic ants on myrmecophytic *Macaranga*; however, *A. zylda* did not develop a dorsal nectary organ and was not tended by ants on myrmecophytic *Macaranga* (Table 1). Thus, larvae may be tended by the ants because they are attracted by honeydew secreted from the dorsal nectary organ. In addition, the difference in the number of ants found attending a last-instar *Arhopala* larva between *A. amphimuta* and *A. dajagaka* is likely to result from differences in the amount of honeydew provided for the ants.

Despite their lack of a nectary, the larvae of *A. zylda* were not attacked by the ants. These larvae may have evolved a chemical mimicry to penetrate symbiotic ant–*Macaranga* partnerships. The location and parasitoids of the larvae differed between the myrmecophytic and non-myrmecophytic *Macaranga* (Table 1). The larvae of *A. amphimuta*, *A. dajagaka*, and *A. zylda* on myrmecophytic *Macaranga* may protect themselves from braconid wasps by coexisting with the ants, which may defend them from the wasps. On the other hand, the larvae of *A. major* on non-myrmecophytic *Macaranga* may protect themselves from ichneumonid flies by hiding in host stipules. The larvae and pupae of the four *Arhopala* species tended to have coloration and shape similar to those of the fresh leaves or stipules that each species utilizes. The survival strategy of each *Arhopala* species may thus correspond to the specific ant–*Macaranga* symbiosis. The differences in morphological and ecological characteristics among the *Arhopala* species are likely due to differences in the anti-herbivore defense strategy adopted by the *Macaranga* species.

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References

Fiala B, Grunsky H, Maschwitz U, Linsenmair KE (1994) Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. Oecologia 97:186-192

Fiala B, Maschwitz U (1990) Studies on the South East Asian ant-plant association *Crematogaster borneensis* / *Macaranga*: Adaptations of the ant partner. Ins Soc 37:212-231

Fiala B, Maschwitz U (1991) Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: Comparative studies of their possible significance as predispositions for myrmecophytism. Biol J Linn Soc 44:287-306

Fiala B, Maschwitz U (1992) Food bodies and their significance for obligate ant-association in three genus *Macaranga* (Euphorbiaceae). Biol J Linn Soc 110:61-75

Itioka T (2005) Diversity of anti-herbivore defenses in *Macaranga*. In: Roubik DW, Sakai S, Karim AAH (eds) Pollination ecology and the rain forest: Sarawak studies. Springer, New York, pp 158-171

Itioka T, Nomura M, Inui Y, Itino T, Inoue T (2000) Difference in intensity of ant defense among three species of *Macaranga* myrmecophytes in a Southeast Asia dipterocarp forest. Biotropica 32:318-326

Maschwitz U, Schroth M, Hanel H, Pong TY (1984) Lycaenids parasitizing symbiotic plant-ant partnerships. Oecologia 64:78-80

Megens HJ, Jong RD, Fiedler K (2005) Phylogenetic patterns in larval host plant and ant association of Indo-Australian Arhopalini butterflies (Lycaenidae: Theclinae). Biol J Linn Soc 84:225-241

Nomura M, Itioka T, Itino T (2000) Variations in abiotic defense within myrmecophytic and non-myrmecophytic species of *Macaranga* in a Bornean dipterocarp forest. Ecol Res 15:1-11

Pierce NE, Brady MF, Heath A, Lohman DJ, Mathew J, Rand B, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu Rev Entomol 47:733-771

Quek SP, Davies SJ, Itioka T, Pierce NE (2004) Codiversification in an ant-plant mutualism: stem texture and the evolution of host use in *Crematogaster* (Formicidae: Myrmicinae) inhabitants of *Macaranga* (Euphorbiaceae). Evolution 58:554-570

Whitmore TC (1969) First thoughts on evolution in Malayan *Macaranga*. Biol J Linn Soc 1:223-231

Figs.1-5. *Arhopala amphimuta*. 1. Egg of *A. amphimuta* after hatching. 2. First instar larva of *A. amphimuta* underside of fresh leaf. 3. Middle instar larva of *A. amphimuta* attended by some symbiotic ants of *M. trachyphylla*. 4. Last instar larva of *A. amphimuta*. **A**: a dosal nectary organ. **B**: tentacle organs. 5. Pupa of *A. amphimuta*.

Figs.6-9. *Arhopala zylda*. 6. First instar larva of *A. zylda* underside of fresh leaf. 7. Middle instar larva of *A. zylda* on stem. 8. Last instar larva of *A. zylda*. 9. Pupa of *A. zylda* underside of fresh leaf.

Figs.10-14. *Arhopala dajagaka*. 10. Egg of *A. dajagaka* underside of fresh leaf. 11. First instar larva of *A. dajagaka* underside of fresh leaf. 12. Middle instar larva of *A. dajagaka* on leaf stem attended by some symbiotic ants of *M. hosei*. 13. Last instar larva of *A. dajagaka*. 14. Pupa of *A. dajagaka*.

Figs.15-19. *Arhopala major*. 15. Egg of *A. major* underside of fresh leaf. 16. Second instar larva of *A. major* underside of fresh leaf. 17. Middle instar larva of *A. major* inside of *M. gigantea* stipule. 18. Last instar larva of *A. major*. 14. Pupa of *A. major*.

Table 1. Summary of morphological and ecological characteristics of *Arhopala* larvae utilizing *Macaranga*

			Morphological character		**Ecological character**				
***Arhopala* species**	**Host plants**		**The body length of last instar larva**	**Myrmecophilic organs**	**Ant behavior to larvae**	**The number of attendant ants**	**Location of larvae**	**Feeding parts**	**Parasitoid of larvae**
A. amphimuta	**Ant plant**	***M. bancana* and *M. trachyphylla***	**16.5±0.5mm**	**Dorsal nectary organ and Tentacle organ**	**Attendance**	**6.8±0.97**	**Underside of fresh leaves**	**Fresh leaves**	**parasitic fly and ichneumon fly**
A. zylda	**Ant plant**	***M. beccariana***	**12.5±0.5mm**	**Tentacle organ**	**Non attack**	—	**Underside of fresh leaves**	**Fresh leaves and Food-bodies**	**parasitic fly and ichneumon fly**
A. dajagaka	**Ant plant**	***M. hosei***	**24.5±0.5mm**	**Dorsal nectary organ and Tentacle organ**	**Attendance**	**17.5±2.72**	**Underside of fresh leaves**	**Fresh leaves**	**parasitic fly and ichneumon fly**
A. major	**Non-ant plant**	***Macaranga sp.A* and *M. gigantea***	**20±1.0mm**	**Dorsal nectary organ and Tentacle organ**	—	—	**Inside of stipules**	**Fresh leaves**	**parasitic fly and braconid wasp**

Factors Controlling the Composition of Soil Microbial Communities in Tropical Forest Ecosystems

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Introduction

Soil microbial community plays a fundamental role in ecosystem nutrient cycling through the mineralization of detritus organic matter (Chapin III *et al.*, 2002). In ecosystem models, the microbial mineralization process has been described as a function of environmental factors, and microbial community is regarded as a "black box". The role of different taxonomic or functional groups of microbes in ecosystem is therefore virtually unknown. Soil microbes appear to play particularly vital role in the tropics due to its unique geochemical condition. Tropical ecosystems are often maintained on highly weathered soils due to warm, humid climate regime and stability of land surface. Such tropical soils are dominated by reactive, small mineral particles down to tens of nano-meter in size (Birkeland, 1999). These minerals strongly influence biological processes at least by two geochemical reactions: (1) physical/chemical blocking of extracellular-enzyme activity and thus reduction in decomposition (nutrient mineralization) in consequence, and (2) sorption of phosphate, an essential nutrient for biota, and subsequent phosphorus limitation to plants and presumably to soil microorganisms. Observed high productivity and biomass of tropical forests, however, suggest that soil microbes adapted to these tropical soils efficiently mineralize nutrients by overcoming the geochemical constraints. We therefore tested the hypothesis that microbial community composition is controlled by soil mineral factors (e.g., geochemical condition and phosphorus limitation) as well as the availability of substrate (organic resource) using a series of tropical forest soils in Mt. Kinabalu. Based on the identified environmental factors that control microbial community in Mt. Kinabalu, we also speculated on the possible impact of logging on soil microbial community composition.

Methods

We studied soils on the eastern and southern slopes of Mt. Kinabalu (4095 m, 6^{o}05'N, 160^{o}33' E), developed on both acidic sedimentary and ultrabasic igneous parent materials, under the primary rain forests protected as the Kinabalu Park, Sabah, Malaysia. The six selected sites (at ca. 700, 1700, and 2700 m above sea level on the two rock types) are part of a long-term ecological study (Kitayama and Aiba, 2002). Briefly, the climate is humid tropical with weak influences of the Asiatic monsoon. A strong temperature gradient is present along the slope: mean annual air temperature (MAT) decreases with altitude at a mean lapse rate of 0.0055 ^{o}C m^{-1}, with <2 ^{o}C intra-annual variations. Mean annual rainfall is relatively constant (2300-2400 mm yr^{-1}) with elevation. Air and soil moisture generally increase with elevation due to more frequent cloud cover and less evapotranspiration at upper elevations.

We used phospholipid fatty acid (PLFA) biomarkers to assess shifts in microbial community composition. PLFA is a microbial cell membrane constituent and its chemical composition is unique for different broad taxonomic groups. At each site, soil samples were collected from O-horizon, 0-5, and 5-15 cm from three transects. Four to six cores were taken along each transect to make a composite. Soil profiles down to 1 meter depth (or to BC horizon) were described and samples are taken along the profiles at each site. All samples were brought back in cooler box and frozen within 6 hours after the sampling, followed by freeze-drying. The dried samples were sieved (2 mm), ground, and extracted for PLFA following Balser *et al*. (2005). Dried sample masses of 0.3-4.0 g were used for the extraction depending on the total organic carbon content of the sample. Fatty acids were extracted with 10:5:4 volumes of methanol, chloroform, and 0.1 M phosphate buffer (pH 7.0). Following purification, polar-lipid fraction (phospholipids) were isolated by silicic acid columns and subjected to saponification and methylation. Gas chromatograph was used to identify and quantify individual fatty acid methyl esters.

Results and Discussion

General trends

Total microbial PLFA concentration, a sensitive indicator of active microbial biomass, ranged 2.0-2.7 nmol g^{-1} in organic horizon (O-horizon) and 0.2-0.8 nmol g^{-1} in the surface mineral horizon (Fig. 1). These ranges are comparable to those in temperate forest and grassland soils. Corresponding to the variations in the concentration of soil organic matter (i.e. microbial substrate), the PLFA concentration of each broad taxonomic group as well as that of total microbial community decreased in the order: O-horizon > 0-5 cm > 5-15 cm. At 700 m and 2700 m sites where deeper soil samples were analyzed, bacteria showed clearer decline with increasing depth than fungi.

Elevation gradient

We considered two geochemical gradients (elevation and soil depth) to test above hypothesis as the abundance and chemistry of soil minerals predictably change along these gradients. Along the elevation gradient from 2700 m to 700 m, the ratio of gram-positive bacteria to gram-negative bacteria (G+:G- ratio) progressively increased in 0-5 cm mineral soils (Fig. 2) as well as O horizon (data not shown) in the sedimentary soils, while the ratio changed little in the ultrabasic soils. Along the same gradient, the ratio of fungi plus actinomycetes to bacteria consistently decreased at all three depths on both rock types. Fungi:bacteria ratio showed a similar yet less clear trend.

Relatively small standard deviations in these ratios (Fig. 2b) than those in each taxonomic group (Fig. 2a), together with above trends, suggest a significant shift in microbial community composition along the elevation gradient. Bacteria (esp. G+ ones) appeared to increase their relative abundance over fungi and actinomycetes in the surface soils under warmer climate regime where soil organic resources are lower in concentration and poorer in quality due to the protection by active mineral phases compared to the soils under cooler climate.

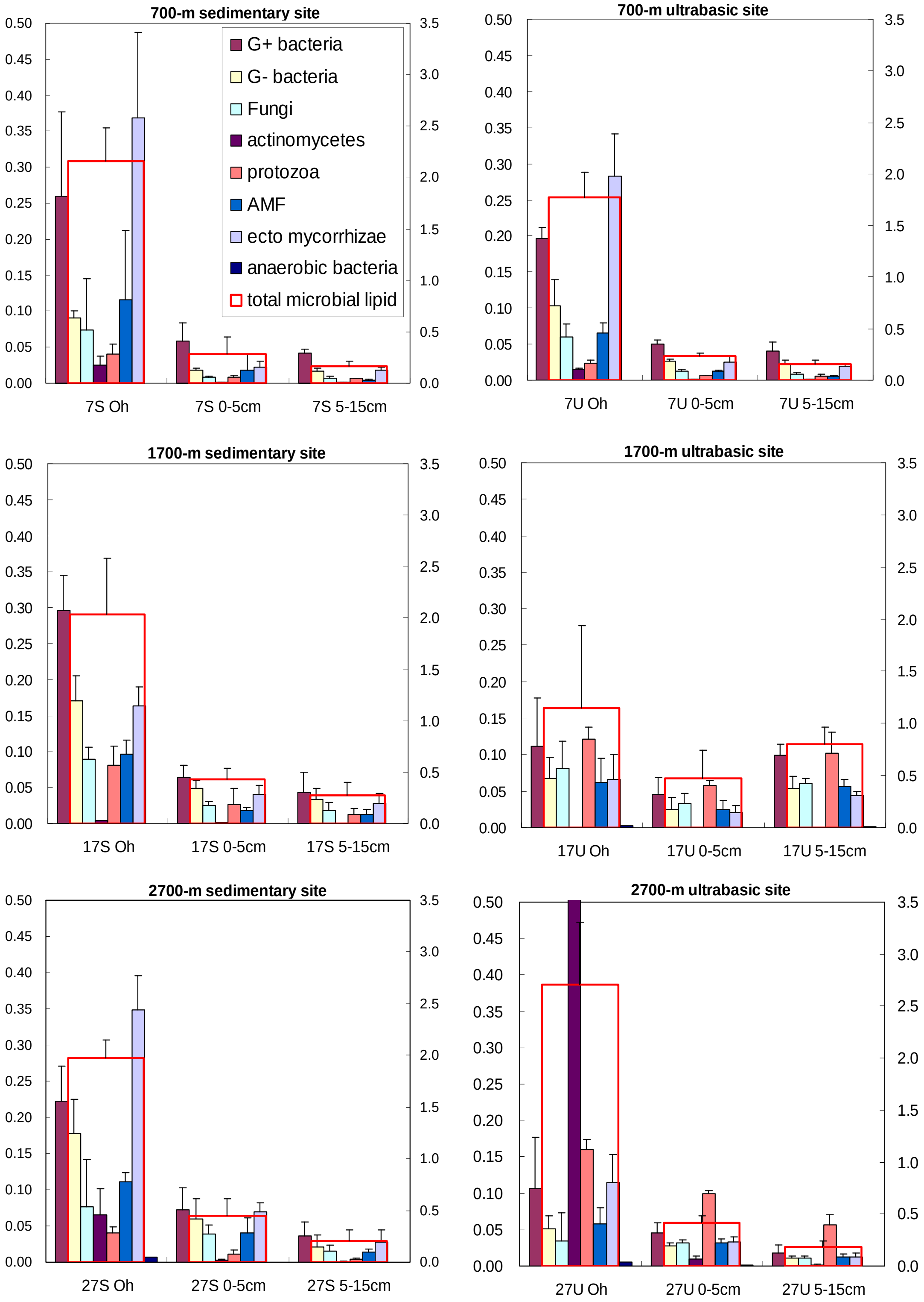

Figure. 1. PLFA concentrations of total active microbial biomass and broad taxonomic groups at each site and depth. N = 3 (error bar = SD). Left axis is PLFA concentrations of individual broad taxonomic group (nmol g^{-1}) and right axis is total microbial PLFA (nmol g^{-1}).

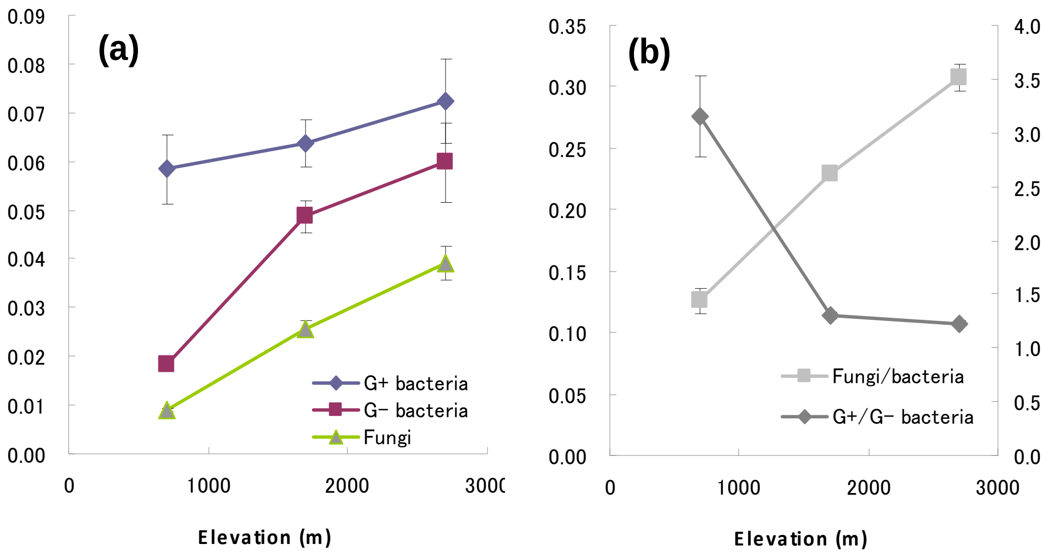

Figure 2. (a) PLFA concentrations of selected broad taxonomic group with elevation (nmol g^{-1}) in sedimentary soils (0-5cm). (b) Ratio of fungi to bacteria (left axis) and gram-positive to gram-negative (right axis) based on (a).

Forest ecosystems at the 700-m elevation are characterized by high rates in plant detritus input (litterfall), rapid decomposition of the detritus in O-horizon, and severe reduction in microbial substrate in mineral horizons due to physical/chemical protection of organic matter by abundant, reactive mineral phases. Our previous work showed that the 700-m soils have the specific surface area of 40-100 m^2 g^{-1} with clay mineralogy of kaolinite and gibbsite at sedimentary site and that of goethite and hematite at ultrabasic site. These mineral phases have significantly greater capacity to adsorb organic substrate and anionic nutrients such as phosphate than upper-elevation soils. Thus microbes in lowland forest soils likely experience rapid changes in physical environment (temperature/moisture) and stochastic pulses of substrate and nutrient input (as litterfall and root death) that are quickly consumed and/or stabilized by soil minerals into unavailable forms. Bacteria appear to be more adapted to these conditions than fungi as the former is capable of rapid growth and dormancy when facing stress (e.g., limitation in substrate and nutrients, draught). Compared to G- bacteria, G+ bacteria hold thicker cellwall, are generally more capable of degrading complex organic substrate and tolerating to stress, and may be more effective in the attachment to soil mineral surfaces. These traits may account for the greater G+ abundance in the 700-m soils.

Depth gradient

Soil samples with depth at each soil pit provide another geochemical gradient in which soil mineralogical characteristics and substrate quality (amounts and chemistry of detritus organic matter) progressively change while macro climate remains constant. With increasing soil depth from surface, the G+:G- ratio among bacteria also increased with depth (Fig. 3a). The ratios for the ultrabasic soils at >60 cm were very high as G+ bacteria was detectable (0.004 nmol g^{-1}) while G- was not detected at all. The fungi+actinomycetes to bacteria ratio showed the lowest values at 10-30 cm and then increased down to 80-100 cm in both sedimentary and ultrabasic soils (Fig. 3b). In a given forest, soils at deeper horizons contain smaller amounts of substrate that are increasingly more stabilized by soil mineral particles and are sparsely located in soil matrix. Fungi and actinomycetes who can extend filaments/hyphae at great extents may thus be more successful utilizing the substrate at depth. Furthermore, fungi (and, to a less extent, G+ bacteria) are capable of producing wider ranges of enzymes to degrade more recalcitrant substrate, which may also account for their relative abundance at depth.

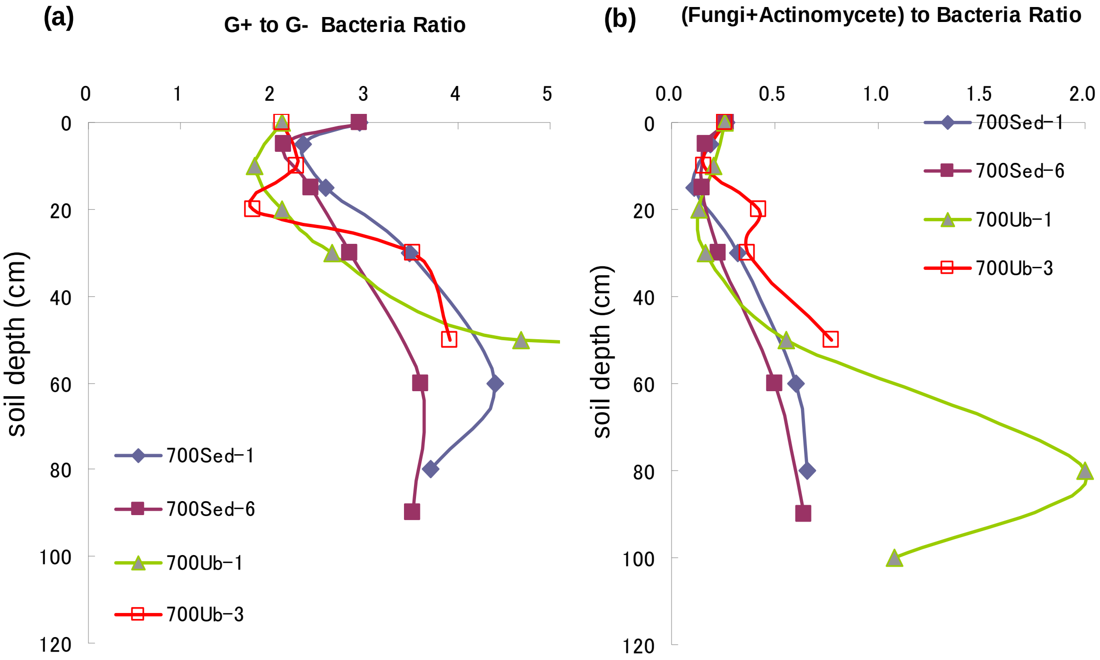

Figure 3. The ratio of gram-positive to gram-negative bacteria (a) and that of fungi plus actinomycete to bacteria (b) along soil profile depth gradients at two 700-m sedimentary soils and two 700-m ultrabasic soils.

Implication for logging impacts

Above results were generally consistent with our hypothesis – the shifts in microbial community composition appeared to be controlled by climate and soil geochemical factors, specifically by temperature, substrate abundance and its interaction with soil mineral particles in the studied ecosystems. Furthermore, we found predictable shifts in microbial community composition corresponding to the changes in climatic and geochemical factors that affect availability of substrate and nutrient. In the environment where organic resources are limited and mineral protection of organic substrate and nutrients is strong, community shifted towards bacterial dominance (particularly G+ ones) over fungi and actinomycetes. Similar shifts in microbial community has been observed along soil depth gradient (down to 2 meter) in Californian grasslands (Fierer *et al.*, 2003).

Then how would soil microbial community respond to the logging of tropical forests? Logging likely causes initial increase and then long-term decline in organic resources due to reduced litter inputs, surface soil erosion, and enhanced decomposition due to disturbance. The prolonged decline in organic resources and enhanced fluctuation in temperature/moisture regime likely result in the community shift towards bacterial dominance. While microbial community hasn't been characterized with respect to logging intensity, two lines of observations in microbially-driven processes suggest significant shifts in microbial community associated with logging activity.

We compared indicators of soil N and P availability between severely-logged site (Tunkulap) and reduced-logging site (Deramakot). Readily-available ammonium and nitrate in surface soils were roughly two-fold higher at Deramakot than Tunkulap when comparing both on skit trails and under forest canopy (Table 1). Similarly, acid phosphotase activity, microbe- and root-derived enzyme that mineralizes organic phosphorus, was about two-fold greater under reduced-logging sites: 4.04 ± 0.71 in Daramakot and 2.24±0.26 μmol hr^{-1} g^{-1} soil in Tunkulap. These results suggest that severe logging likely resulted in a reduction in nitrogen and phosphorus availability in soil, which was presumably accompanied by shifts in soil microbial community.

Table 1. Comparison of soil total C, N, C:N ratio, and readily-available ammonium and nitrate between skit trail and adjacent forested area. Soil samples (0-10cm deep) were taken from 20-meter long parallel transects along each skit trail (A to E).

Location	TOC	Total N	C:N	KCl−extr NH4+		KCl−extr NO3−	
	%	%		μg/g soil	mgN/gN	μg/g soil	mgN/gN
Deramakot							
Skit trail A	1.27	0.092	13.8	8.1	8.8	5.4	5.8
Forested A	1.99	0.122	16.4	15.0	12.3	5.4	4.4
Skit trail B	1.46	0.108	13.5	12.7	11.8	5.8	5.4
Forested B	2.29	0.161	14.2	9.4	5.8	4.3	2.7
Skit trail C	1.81	0.131	13.9	10.3	7.9	6.0	4.6
Forested C	2.05	0.141	14.5	9.0	6.3	4.7	3.3
Tunkup							
Skit trail D	1.28	0.096	13.3	4.9	5.1	3.4	3.6
Forested D	2.77	0.190	14.6	7.4	3.9	2.9	1.5
Skit trail E	0.98	0.085	11.6	2.5	3.0	-1.6	-1.9
Forested E	2.29	0.162	14.1	4.1	2.5	1.1	0.7

Three samples from each transect were mixed for the chemical analysis.
The inorganic N was extracted by 1.5M potassium chloride solution followed by paper filtration.

To understand logging effects on long-term productivity of tropical forests, it is important to establish direct linkage between microbial community and critical ecosystem processes such as mineralization of N and P. Further investigations on the direct controls on microbial community composition as well as the role of different microbial groups on ecosystem processes would help to substantiate the role of soil microbes in ecosystem functioning and maintenance of biodiversity in tropical forests.

References

Baileya, V.L., Peacockb, A.D., Smithc, J.L., Bolton Jr., H. (2002) Relationships between soil microbial biomass determined by chloroform fumigation–extraction, substrate-induced respiration, and phospholipid fatty acid analysis. Soil Biol Biochem **34**: 1385-1389

Balser, T.C., Tresederb, K.K., Ekenlera, M. (2005) Using lipid analysis and hyphal length to quantify AM and saprotrophic fungal abundance along a soil chronosequence. Soil Biol Biochem **37**: 601-604

Birkeland, P.W. (1999) Soils and Geomorphology, 3rd ed., Oxford Univ. Press, New York. 430. pp

Chapin III, F.S., Matson, P.A., Mooney, H.A. (2002) Principles of terrestrial ecosystem ecology. Springer-Verlag

Fierer, N., Schimel, J.P., Holden, P.A. (2003) Variations in microbial community composition through two soil depth profiles. Soil Biol Biochem **35**: 167-176

Kitayama, K., Aiba, S. (2002) Ecosystem structure and productivity of tropical rainforests along altitudinal gradients under contrasting soil P pools on Mount Kinabalu, Borneo. Jap J Ecol. **90**: 37-51

The Influence of Selective Logging to Decomposition of Leaf Litter in Tropical Forest

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Introduction

Lavelle (1997) suggested that the role of soil fauna in ecosystems could be divided into three groups, i.e. ecosystem engineer, litter transformer and microbial food web. Litter transformer and ecosystem engineer enhanced litter decomposition processes through their feeding activities (Yamashita and Takeda 1998) and thus have an important ecosystem function. Forest management may affect biological assemblage of decomposers, which may feed back to decomposition rate. However, the influence of forest management on their function in tropical forests has not fully been reported. In our study, the influence of selective logging on the decomposition of leaf litter in tropical forest was investigated and discussed in relation to soil animal activity.

It has been widely recognized that forest disturbance can affect nutrient cycling (Siira-Pietikäinen et al. 2001; Palviainen et al. 2004) and soil biota (Seastedt and Crossley 1981; Holloway et al. 1992; Siira-Pietikäinen et al. 2003; Negrete-Yankelevich et al. 2007).

Selective harvesting or setting logging roads/skid trails in tropical forest might influence the decomposition processes, because they cause the changes of plant community (Burghouts et al. 1994) and climatic conditions (Siira-Pietikäinen et al. 2001), which lead to the changes of soil microbial or faunal components (Davies et al. 1999). Changes in the relative abundance of some groups of soil and litter invertebrates due to selective logging have been reported (Eggleton et al. 1995; Lima et al. 2000).

Recent studies have demonstrated that the soil fauna (mainly soil microarthropods) have a more profound effect on decay rate in wet tropical forests than in dry tropical, temperate and sub-alpine forests (Heneghan et al. 1998; González and Seastedt 2000). Soil macro-fauna (ex. termite, Isopoda and millipedes) contribute to the disappearance of leaf litter by their feeding activities, and their activity results in the loss of leaf area during decomposition. In contrast, during the early stage of leaf-litter decomposition by microorganisms, leaf area does not significantly decrease but the weight of the litter decreases. Thus, it may be possible to evaluate the contribution of soil fauna (especially termites) by measuring the loss of leaf area in comparison to the loss of weight in the initial stage of litter decomposition.

The objective of the study is to investigate the influence of selective logging and skid trail to the decomposition process of tropical tree leaves, and to evaluate the contribution of soil fauna through the analysis of leaf-area loss during decomposition.

Material and Methods

Our study was conducted in the Deramakot Forest Commercial Forest Reserve, Sabah, Malaysia. The details of the forest are shown in Chapters 2 and 3. We set two quadrates (2 X 2m) at the conventionally-logging forest (Tangkulap), the reduced-impact logging forest and the primary forest in Deramakot forest reserve. At each forest, one quadrate was placed at the edge of a skid trail (the width of the trail was 2.5 to 4m), and one quadrate was placed inside the forest (20m from the edge of the trail).

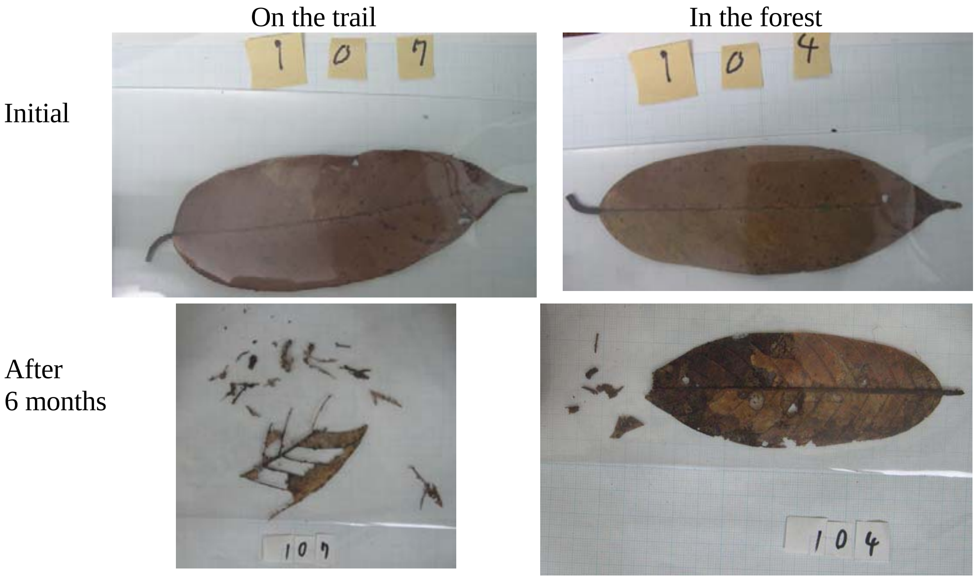

Fig.1 Example of digital photo for leaf area estimation in *Shorea macroptera*

Fresh fallen leaves of *Shorea macroptera* and *Macaranga* sp. were collected from one tree of each species in March 2006. The litter was air-dried and the weight and area of each leaf were measured before placing them into litterbags. The leaf area was analyzed by Image J v. 1.37 (Rasband 2007) using digital image of the leaf. From the 2nd to the 4th March, 2006, we set 10 litterbags of *Shorea macroptera* and *Macaranga* sp. at each quadrate. Litterbags (20 x 20cm) were made of nylon net with a diamond shape mesh (long diagonal line: 4mm, short diagonal line: 2mm). Each litterbag included one piece of leaf for each tree species. On the 30th September, 2006, we collected all of the litterbags. The leaves recovered from the litterbags were measured for wet and air-dried weight as well as leaf area (cf. Fig. 1).

Weight and area remaining were analyzed using two-way analysis of variance (ANOVA) using SYSTAT10.2 (SYSTAT Software Inc., Richmond). The factors were forest type [primary forest (PR), reduced-impact logged forest (RIL) and conventionally-logged forest (CV)] and quadrate placement on the trail (out) and in the forest (in). Data were arcsine transformed before the analysis.

Results

After the 6-month incubation in the field, the percentage of remaining weight relative to the initial weight for *Shorea macroptera* leaf litter ranged from about 16 to 39 %. The percentage of the litter weight in the primary forest was significantly larger than in conventional logging forest and RIL forest (Fig. 2, Table 1). Percentage of remaining weight for Shorea litter was significantly higher within forest than on trail (Fig. 2, Table 1). Significant interaction of two factors was not found (Table1). Percentage of remaining area relative to the initial area for Shorea litter ranged from 33 to 98 %, and it was significantly larger in the primary forest than in the conventionally-logging forest (Fig. 2, Table 1). Percentage of remaining area for Shorea litter was significantly larger within forest than on trail (Fig. 2, Table 1). Significant interaction of two factors was found;

RIL and CV on the trails showed lower percentage of leaf area compared to the other sites (Table1).

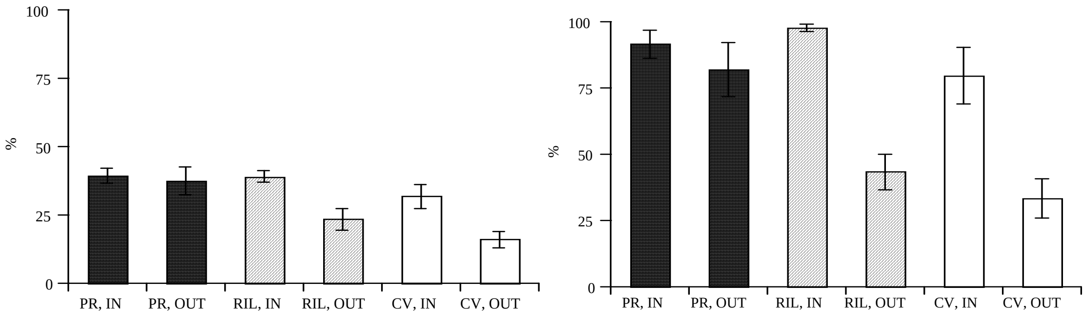

Fig.2 The percentage of remaining weight (left) and area (right) for *Shorea macroptera* leaf litter
PR: Primary forest, RIL: Reduced-impact forest, CV: conventionally-logged forest, IN: within forest, OUT: on the trail. Bars indicate standard errors.

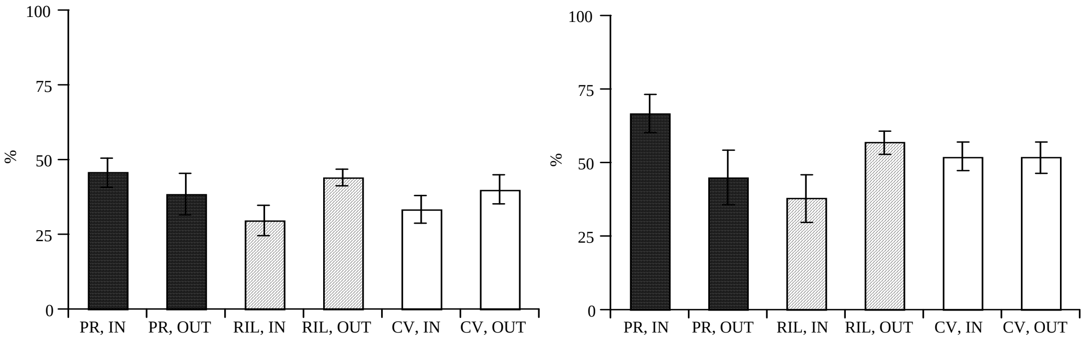

Fig.3 The percentage of remaining weight (left) and area (right) for *Macaranga* sp. leaf litter
Legend as in Fig.2.

Table 1 Results of two-way ANOVA for the effects of forest type and quadrate placement on the weight remaining and leaf area remaining of *Shorea macroptera* litter.

		Shorea macroptera	
		Weight remaining	Area remaining
Forest type	*F*	7.65	9.45
	P	0.001	<0.001
Placement	*F*	13.11	41.18
	P	0.001	<0.001
Forest type X Placement interaction	*F*	2.14	6.76
	P	0.100	0.002

Table 2 Results of two-way ANOVA for the effects of forest type and quadrate placement on the weight remaining and leaf area remaining of *Macaranga* sp. litter.

		Macaranga sp.	
		Weight remaining	Area remaining
Forest type	*F*	0.83	1.20
	P	0.444	0.310
Placement	*F*	1.18	0.12
	P	0.282	0.732
Forest type X Placement interaction	*F*	2.14	4.78
	P	0.128	0.012

The percentage of remaining weight for Macaranga sp. ranged from 30 to 46 %(Fig. 3). No significant difference was found in the weight remaining of two factors and their interaction (Table2). The percentage of remaining area for Macaranga sp. was from 38 to 67 % (Fig. 3). Significant difference in the two factors was not found. However, significant interaction of the two factors was found; the litter placed within the PR forest showed a higher percentage of leaf area than that within the RIL forest (Table2).

Discussion

The percentage of remaining weight after 6months ranged from 16 to 46%. These values are comparable to the previous studies of leaf litter decomposition in tropical forests (Anderson et al. 1983; Yamashita and Takeda 1998; Sundarapandian and Swamy 1999). We expected that the litter of the pioneer species *Macaranga* sp. would decompose faster than that of *Shorea macroptera* because of the physical and chemical characters of *Macaranga* litter (softer texture and higher nutrient concentration). However, the decomposition rate was approximately the same in this study.

On the trail, soil-water content is often lower than in the forest, which likely limits the activity of soil microorganisms. However, the weight loss of *Shorea* leaves was greater on the trail of RIL and CV. The greater weight loss on the trail of RIL and CV was accompanied by the greater rate of the disappearance of leaf area. Activities of soil macrofauna in the litter decomposition involve the loss of weight and area of litter. Therefore, the difference in remaining leaf area may be attributable to macro-faunal feeding activity. The difference in the loss of weight and area between within-forest and trail was more prominent in *Shorea* leaves than in *Macaranga* leaves. Animal feeding habit might have contributed to the different pattern of decomposition between tree species.

In tropical forests, termites are an important faunal component for litter decomposition (Abe and Matsumoto 1979; Petersen and Luxton 1982). Yamashita and Takeda (1998) suggested that the soil animals especially termites accelerated leaf litter decomposition by their feeding in Malaysian tropical forests. Lima et al. (2000) suggested that disturbances such as logging which reduces the abundance of some species of termites could reduce the rate of litter breakdown inside a forest.

In our study area, however, the density of termites was not so high, compared with other sites in tropical area (Abe and Matsumoto 1979; Eggleton et al. 1999; Hasegawa et al. 2006). Burghouts et al. (1992) also suggested that the termite density in Danum Valley in Sabah was smaller than that in the other sites in Asia and Africa. In Borneo, Eggleton et al. (1999) suggested that selective logging appeared to have relatively little effect on termite assemblages, although soil-feeding termites may be moderately affected by this level of' disturbance. In the same study area as our current study, Hasegawa et al. (2006) suggested that the density of termites in the PR site was higher than that in the CV. Thus, the contribution of termites to the difference in decomposition between the PR and CV sites might be less important. However, termite distribution is generally heterogeneous, and they can bring litter to their nests, that might have not been located in our sampling zone. Thus, we might have missed the activity of termites in the CV site. In addition, we did not identify the species of termites. Some important groups of termites (ex. *Macrotermes*) may be included in the CV sites. In contrast, Hasegawa et al. (2006) suggested that isopoda and diplopoda density was higher in the CV sites. Tsukamoto and Sabang (2005) suggested that earthworm and isopods increased in *Acacia* plantation than in mixed Dipterocarps forest. Hassall et al. (2006) also suggested that the relative abundance of individual species of Isopoda was highest in the most disturbed environment. Further ecological study of termites and Isopoda are needed.

In conclusion, conventional logging and the creation of skid trails in this study area might accelerate the decomposition process. Greater litter fragmentation may enhance surface runoff of fragmented litter upon rainfall events. The enhanced runoff may aggravate the condition for the colonization of other soil biota and tree seedling, and may lead to a successive loss of biodiversity in that area (Tsukamoto and Sabang 2005; Ruan et al. 2005).

References

Abe T, and Matsumoto T (1979) Studies on the distribution and ecological role of termites in a lowland rain forest of west Malaysia (3) Distribution and abundance of termites in Pasoh forest reserve. Jap J Ecol **29**:337-351

Anderson J M, Proctor J, Vallack H W (1983) Ecolological studies in four contrasting lowland rain forests in Gunung Mulu national Park, Sarawak. Journal of Ecology **71**:503-527

Burghouts T, Ernsting G, Korthalis G, De Vries T (1992) Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. Phil. Trans. R. Soc. Lond. B **335**:407-416

Burghouts T B A, Campbell E J F, Kolderman P. J. (1994) Effects of Tree Species Heterogeneity on Leaf Fall in Primary and Logged Dipterocarp Forest in the Ulu Segama Forest Reserve, Sabah, Malaysia. J Trop Ecol **10**:1-26

Davies R G, Eggleton P, Dibog L, Lawton H, Bignell D E, Brauman A, Hartmann C, Nunes L, Holt J, Rouland C (1999) Successional response of a tropical forest termite assemblage to experimental habitat perturbation. J Appl Ecol **36**:946-962

Eggleton P, Bignell D E, Sands W A, Waite B, Wood T G, Lawton J H (1995) The Species Richness of Termites (Isoptera) Under Differing Levels of Forest Disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. J Trop Ecol **11**:85-98

Eggleton P, Homathevi R, Jones D T, MacDonald J A, Jeeva D, Bignell D E, Davies R G, Maryati M (1999) Termite assamblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. Phil Trans R Soc Lond B **354**:1791-1802

González G, Seastedt T R (2000) Comparison of the abundance and composition of litter fauna in tropical and sub-alpine forests. Pedobiologia **44**:545-555

Hasegawa M, Ito M T, Kitayama K, Seino T, Chung A Y C (2006) Logging effects on soil macrofauna in rain forests of Deramakot Forest Reserve, Sabah, Malaysia. The second Workshops on synergy between carbon management and biodiversity conservation in tropical rain forests, Workshop proceedings:53-60

Hassall M, Jones D, Taiti S, Latipi Z, Sutton S L, Mohammed M (2006) Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. Eur J Soil Biol 42 (2006) **42,** supplement:197–207

Heneghan L, Coleman D C, Zou X, Crossley Jr. D A, Haines B L (1998) Soil microarthopod community structure and litter decomposition dynamics: A study of tropical and temperate sites. Appl Soil Ecol **9**:33-38

Holloway J D, Kirk-Spriggs A H, Khen C V (1992) The Response of Some Rain Forest Insect Groups to Logging and Conversion to Plantation. Phil Trans R Soc Lond B **335**:425-436

Lavelle, P (1997) Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. Advances in Ecological Research **27**:91-132.

Lima A P, Cordeiro-Duarte A C, Luizao F J, Higuchi N (2000) Effect of selective logging intensity on two termite species of the genus Syntermes in Central Amazonia. For Ecol Manag **137**:151-154

Negrete-Yankelevich S, Fragoso C, Newton A C, Heal O W (2007) Successional changes in soil, litter and macroinvertebrate parameters following selective logging in a Mexican Cloud Forest. Appl Soil Ecol **35**:340-355

Palviainen M, Finer L, Kurka A M, Mannerkoski H, Piirainen S, Starr M (2004) Decomposition and nutrient release from logging residues after clear-cutting of mixed boreal forest. Plant and Soil **263**:53-67

Petersen H, Luxton M (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos **39**:288-388

Rasband W S (2007) ImageJ, V. 1.37 U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/.

Ruan, H., Y. Li, and X. Zou. 2005. Soil communities and plant litter decomposition as influenced by forest debris: Variation across tropical riparian and upland sites. Pedobiologia **49** 529—538.

Seastedt T R, Crossley Jr D A (1981) Microarthropod response following cable logging and clear-cuting in the Southern Apparachians. Ecology **62**:126-135

Siira-Pietikäinen A, Haimi J, Siitonen J (2003) Short-term responses of soil macroarthropod community to clear felling and alternative forest regeneration methods. For Ecol Manag **172**:339–353

Siira-Pietikainen A, Pietikainen J, Fritze H, Haimi J. (2001) Short term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. Can J For Res **31**:88-99

Sundarapandian S M, Swamy P S (1999) Litter production and leaf-litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. For Ecol Manag **123** 231-244

Tsukamoto J, Sabang J (2005) Soil macro-fauna in an *Acacia mangium* plantationin comparison to that in a primary mixed dipterocarp forest in the lowlands of Sarawak, Malaysia. Pedobiologia **19**:69-80

Yamashita T, Takeda H (1998) Decomposition and nutrient dynamics of leaf litter in litter bags of two mesh sizes set in two dipterocarp forest sites in Penisular Malaysia. Pedobiologia **42**:11-21

Chapter 4

CHANGES IN BIODIVERSITY AND ECOSYSTEM SERVICES

Chapter 4 Introduction

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This chapter examines the changes in ecosystem services caused by changes in biodiversity. Ecosystem services were classified into three types—provisioning, regulating, and cultural—following the definitions of the Millennium Ecosystem Assessment. In particular, we focused here on ecosystem services that have close relationships with biodiversity.

Timber supply is one of the most important provisioning services of forest ecosystems, although the tree species available must change according to the change of forest structure caused by forest use system (Seino et al., in this Chapter). Woody material is also important as fuel. Coniferous trees are commercially more valuable in Japan, but broadleaf trees can have value as fuel for locals and for particular products (Oh). Recently, Non Timber Forest Products (NTFPs) have attracted more attention in the context of sustainable forest use (Naito, Kanazawa, in this Chapter). Mushroom and other organisms for livelihood are important NTFPs that depend on the forest type (Yamashita, Kato); thus, changes in the forest ecosystem have caused great changes in the patterns of forest utilization by local people.

We focused on the control of pest animals as a regulating service provided by the forest ecosystem. Some species of parasitoid wasps were found to be abundant in traditionally used landscapes (Maeto & Kitabatake). Agricultural damage cased by deer and monkeys in recent years may have a close relationship with past forest utilization. The rapid increase in young plantations caused an increase in the population of wild animals, which has led to serious damage to agricultural crops (Agetsuma). The negative services in systems with simplified biodiversity were affected by the local landscape (Morino & Koike).

The change in forest ecosystems and the intellectual and cultural changes of local people are an interactive process. An example of such interactions on Yaku Island was documented (Baba). The knowledge of plants and birds varies among local indigenous tribes, but it has changed in recent decades (Aihara & Momose). A diverse landscape is also important for local people, and in turn, it operates to maintain sustainable forest uses (Kaga & Momose).

We succeeded in elucidating some of the influences of the forest ecosystem and biodiversity on ecosystem services, but many remain unclear. The relationships between biodiversity and ecosystem services are not very tight and sometimes depend on local and regional conditions. More studies are required to clarify the relationship between biodiversity and ecosystem services.

Tree Diversity and the Changes of Wood Utilization of Tropical Rain Forest in Borneo

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Introduction

The lowland tropical rain forests of Borneo are characterized by high tree species diversity and the stratification of multiple foliage layers, which exceed 60 meter in height with emergent trees. Above-ground biomass is also high. The lowland forests of Borneo are characterized by many Dipterocarpaceae species and called a mixed dipterocarp forest. The diversity and stand structure of the dipterocarp forest relate with environmental conditions such as soil nutrient, topography and altitude.

Humans use forest products from tropical rain forest as wood in terms of biomass stock, and as tropical fruits and medicinal ingredients in terms of species diversity. With regard to wood utilization, the amount of harvests and the species that are harvested have changed with human activity. As a recent trend, deforested area is increasing and the depletion of the wood resource is expected to rise from increasing demand for resources. In the project "Sustainability and biodiversity assessment on forest-utilization options” by RIHN, we began our research in Deramakot Forest Reserve in Sabah, Malaysia, which introduced low impact selective-logging (Reduced Impact Logging, RIL) method. The policy and aim of forest management in Deramakot Forest Reserve are to establish the harmony between biodiversity maintenance and the sustainable utilization of forest products with the employment of an ecological approach. A strict forest management has been applied to Deramakot Forest Reserve (Lagan et al 2007). Thus, this site is a good model for the research project focused on the relationship between forest ecosystem and historical background of human forest utilization. Here, we report how harvested species changed with the introduction of heavy machinery and how the change was related with the density of wood in the lowland dipterocarp forest.

Method

The study site

The study site (5˚22'N, 117˚25' E, approximately 300 m asl) is located in a lowland forest of the Deramakot Forest Reserve (DFR) in Sabah, Malaysian Borneo. Forests in DFR had been selectively logged in the 1970s (Lagan et al. 2007). DFR was logged again with RIL from the 1990s in contrast with the surrounding areas which were harvested by a more destructive, conventional logging method. Thus, the forests in DFR can be divided into the following three types as the old-growth forests in DFR without any logging records after the 1970s logging, the forests logged with RIL after 1996 in addition to the conventional logging prior to 1996, and the forests continuously logged with the conventional method (Aiba et al. in Chapter 3).

Diversity of wood density

As for the dipterocarp trees, a commercial classification according to the specific gravity of wood is available based on vernacular names (Wood and Meijer 1964). In Sabah, dipterocarp trees were classified as Seraya (including genus *Shorea* and *Parashorea*, approx. 0.50 g cm^{-3} in specific gravity), Selangan Batu (sect. *Shorea* and *Neohopea* of genus *Shorea*, approx. 0.80 g cm^{-3} in specific gravity), Kapur (genus *Dryobalanops*, approx. 0.70 g cm^{-3} in specific gravity), and Keruing (genus *Dipterocarp*, approx. 0.75 g cm^{-3} in specific gravity). We followed the vernacular classification by Wood and Meijer (1964) in our analysis. For the analysis of wood utilisation, and the changes of the frequency distribution of wood density in relation to harvest intensity, data of specific gravity of wood were obtained from Wood and Meijer (1964), Burgess (1966) and Suzuki (1998) (including sapling data), and unpublished data by Seino. We applied those density data to the observed species in Deramakot Forest Reserve in the research plots described by Aiba et al. (in Chapter 3).

Historical background of forestry in Sabah

Historical background of forestry in Sabah was examined from literatures, official reports, and technical documents (Sabah Forestry Department .1989; 2003; Forest Research Institute Malaysia 2001).

Results

Historical background of timber production in Sabah

The first commercial logging in Sabah was started in around 1895 by a UK enterprise, and the Forest Bureau in Sandakan was set up in 1915. Since then, the commercial harvest of forests in Sabah has been developed to a fuller scale. Main mode of the logging at the earliest time was axe cutting of trees and wood transportation was conducted by human power, horse, and rafting. As these methods depended on human power, those trees which were low in specific gravity of wood were preferentially logged due to the limitation of transportation technology and labour. Therefore, harvest was limited to the neighbouring districts of a town and riverside (Sabah Forestry Department 1989). There is a local terminology for this type of logging called “Memingel” in a traditional village in a river bank of Sabah. Memingel is a traditional wood transportation method – the logs cut by an axe on a small scale in upstream forests are naturally transported to the downstream village by floods during a wet season. Illegal encroachments using this method can also occur (Kitayama personal communication).

The amount of harvested wood in Sabah was increased by the major lumber companies especially after the World War II. After the introduction of tractor and mechanical equipments such as trucking, and the establishment of large-scale woodland path and logging road network, a large amount of logs was carried from the forests in central part of Sabah. This was accelerated especially after the

World War II. Moreover, it became comparatively easy to carry trees that were high in specific gravity of wood and a large amount of logs was harvested by improved techniques utilizing chainsaw and motor lorry. The harvest impact and deforestation pressure became higher by increased mechanization with heavier wood increasingly harvested (Sabah Forestry Department 1989; Forest Research Institute Malaysia 2001).

Differences of specific gravity of wood

Fig.1 shows the differences in the frequency distribution of stems for the specific gravity of wood among different logging impacts in Deramakot. The frequency distribution of the specific gravity of wood for the tree species in the natural lowland forest is shown by the normal distribution that has the average value of 0.57 g cm^{-3} in agreement with Turner (2001). Mean specific gravity of individual stems was 0.67 g cm^{-3} in old-growth forest, 0.62 g cm^{-3} in forest harvested by RIL, and 0.49 g cm^{-3} in forest harvested by conventional method, respectively.

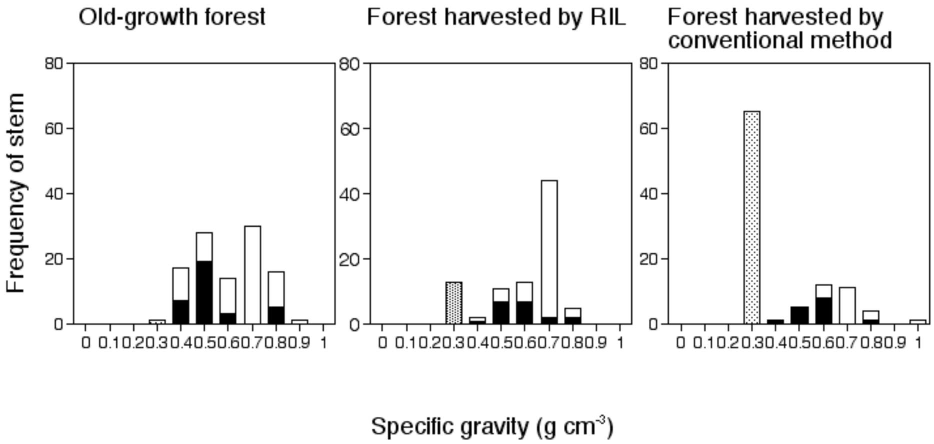

Figure 1. Comparison of the frequency of stems in the classes of the specific gravity of wood among different forest managements in Deramakot Forest Reserve. Closed, shaded, and open bar indicate specific gravity of Dipterocarpaceae, *Macaranga* of Euphorbiaceae, and the other tree species, respectively.

Fig.2 shows the differences of frequency distribution of species number for the specific gravity of wood among different logging impacts. Frequency distribution of the specific gravity of wood was not different among logging impacts (Kolmogorov-Smirnov test, $P > 0.05$). When specific gravity was weighted by species number, mean specific gravity was 0.64 g cm^{-3} in old-growth forest, 0.64 g cm^{-3} in the forest harvested by RIL, and 0.67 g cm^{-3} in the forest harvested by conventional logging method.

Mean specific gravity of the major species of Dipterocarpaceae varies greatly; Seraya group, *Shorea domatiosa* (0.50), *S. macrophylla* (0.50), *S.gibbosa* (0.57), and *S. fallax* (0.56); Kapur, *Dryobalanops lanceolata* (0.69); and Keruing, *Dipterocarps kerri* (0.69 g cm^{-3}, specific gravity). On the other hand, average specific gravity of the pioneer species of genus *Macaranga* (Euphorbiaceae) was low; *Macaranga conifera* (0.40 g cm^{-3}, specific gravity), *M. hypolueca* (0.33), *M. gigantea* (0.36), and *M. pearsonii* (0.39). Logging impact resulted in the increase of the abundance of *Macaranga* trees that are characterized by light wood (approx 0.30 g cm^{-3} in specific gravity) and associated fast growth with their preferential establishment on heavily disturbed area.

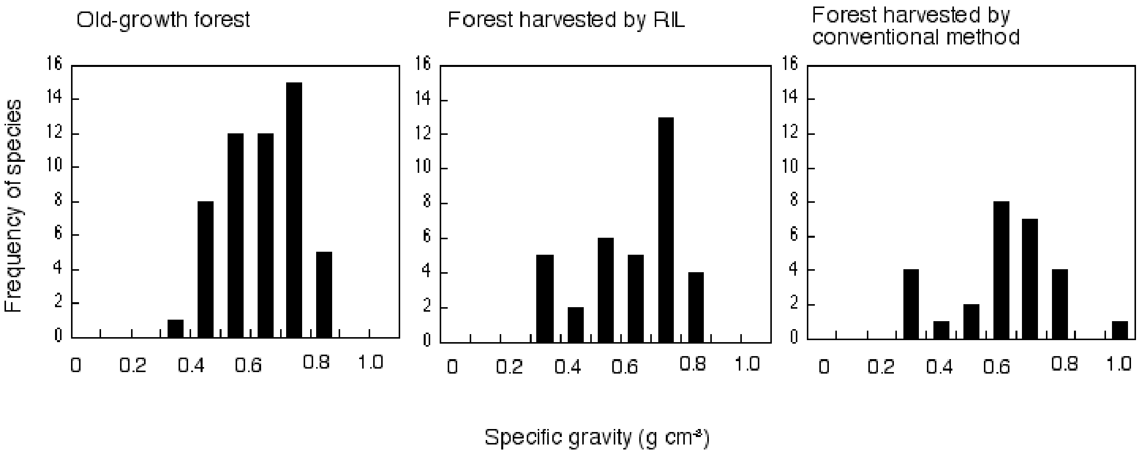

Figure 2. The comparison of the frequency of species in the classes of the specific gravity of wood among different forest managements in Deramakot Forest Reserve.

Discussion

Results from the frequency of stems in the classes of the specific gravity of wood demonstrate the dominance of light wood in the conventionally logged forest primarily due to the dominance of *Macaranga* (Fig. 1). In the old-growth forest, dipterocarp trees of comparatively low specific gravity (light-wood, e.g., Seraya) accounted for roughly 30% of the total basal area, and those of high specific gravity (heavy-wood, e.g., Selangan Batu, Kapur and Keruing) accounted for roughly 10-20% of the total basal area in the Deramakot Forest Reserve. An appropriate logging plan is needed to control the resource depletion of such heavy-wood species. The heavy-wood trees were sparse in their population probably reflecting past harvest and the slow recovery due to the slow growth of heavy-wood species in the forest harvest by the conventional logging. Suzuki (1998) discussed relationship between specific gravity of wood and growth traits. Most of light-wood trees were characterized by fast growth, while heavy-wood trees were characterized by slow growth. Light-wood trees tend to bear a smaller number of vessels with large pore area and heavy-wood trees tend to bear a larger number of vessels with small pore area (Santiago et al. 2004). Santiago et al. (2004) conclude that fast-growing trees needed a large amount of water for photosynthesis and that they sacrificed wood density for hydraulic transportation of water.

Currently, the heavily logged forest outside Deramakot Forest Reserve has the species composition with the dominance of light-wood trees as a result of modern forest practice (Fig. 1). The advancement of the modern technology has lead to the simplification of ecological traits of species such as specific gravity of wood. The usage of Dipterocarpaceae timber is shown in Table 1. The usage is different depending on their wood specific gravity.

The timber with a much greater specific-gravity of wood (heavy wood) such as Borneo ironwood (*Eusideroxylon zwageri*) of Lauraceae is also available and it is used for different purposes such as pillar and roofing tile. On the other hand, the timber with much lighter gravities has not traditionally been used. For instance, the timber of *Macaranga* has no commercial importance. However, the light-wood species that have not been used commercially in the past are being utilized in recent years. The commercial utilization of a pioneer tree *Neolmarckia cadamba* of Rubiaceae is one of such examples (Sabah Forestry Department 2003). *Neolmarckia cadamba* has a light specific gravity and is used for packing materials/boxes. Human exploitation nearly depleted the timber resources of moderate and heavy wood and lead to a diversified use of light wood.

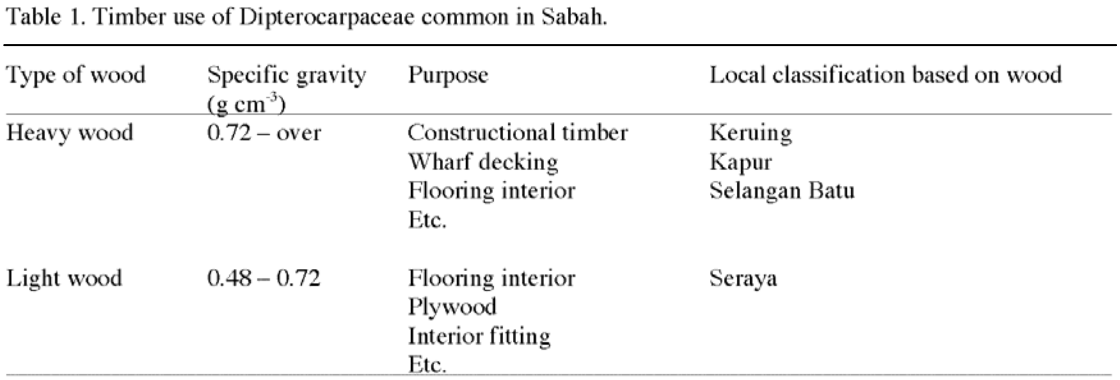

Table 1. Timber use of Dipterocarpaceae common in Sabah.

Type of wood	Specific gravity ($g\ cm^{-3}$)	Purpose	Local classification based on wood
Heavy wood	0.72 – over	Constructional timber Wharf decking Flooring interior Etc.	Keruing Kapur Selangan Batu
Light wood	0.48 – 0.72	Flooring interior Plywood Interior fitting Etc.	Seraya

References

Aiba S, Seino T, Takyu M, Kitayama K, Ong RC (2007) Stand structure, floristic composition and diversity of tropical lowland rain forests in Sabah, Malaysia under different managements. In this report, Chapter 3.

Burgess PF (1966) Timber of Sabah. Sabah For. Rec. No. 6., Forest Department, Sandakan

Forest Research Institute Malaysia (2001) Forestry and Forest Products R&D in FIRM. Forest Research Institute Malaysia.

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Ecol Res 22:414-421.

Sabah Forestry Department (1989) Forestry of Sabah. Sabah Forestry Department.

Sabah Forestry Department (2003) Annual Report 2003. Sabah Forestry Department.

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140: 543-550.

Suzuki E (1998) Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. Ecol Res 14: 211-224.

Turner IM (2001) The ecology of trees in the tropical rain forest. Cambridge University Press.

Wood GHS, Meijer W (1964) Dipeterocarps of Sabah. Sabah Forest Record No.5, Forest Department, Sandakan.

Broadleaf Tree Plantation by the Fishermen in Yakushima Island

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Introduction: the tree planting movement by fishermen

In the 1990s, forest plantations by fishermen were often reported as topical incidents in Japan. Such an activity was also implemented in Yakushima Island. The festival for the plantation was held during 3 years from 1996 to 1998. Over ten thousands of young trees, several kinds of broadleaf trees, were planted covering 5.6 hectares of the national forest where the trees had once been logged. The site is called "the Forest of *Yaku-saba* (Spotted mackerel)". It was the obvious decrease of fishery resources that motivated Fishermen's union to the plantation in the island supposedly rich in "nature".

The Plantation by the oyster farmer at Karakuwa town of Miyagi prefecture was the critical momentum which propagated this movement throughout the nation. The Oyster farmer in the Moune Bay started planting the broadleaf tree, e.g. fagaceae (*Buna*), at the upstream of the Oo River from 1989. Before long, similar activities were taken place across the country, subsequently the integrated resource management has been discussed among the agriculture, forestry and fisheries industry at the regional scale (Tutatani, 1998).

Once in the postwar years of the recovery and following the period of high economic growth in the 1960s, the logging and the plantation of conifers from broadleaf trees were operated in the nationwide scale with the high demand for building materials. Meanwhile, the broadleaf tree became less valuable with the decreasing demand for fuel wood, as the energy revolution progressed. Today, fishermen re-appreciate the broadleaf tree because of its positive effect for fishery resources. These effects have long been known by the people. Such forests which attract fishes are called Uotsuki-rin (魚付き林) and have been existed from the Edo period and protected from cutting. Though further scientific research is required to explain the detail mechanism, functions of the forest, such as supplying nutritional substance into the sea or controlling the outflow of soil and rainwater were widely recognized.

On the other hand, from the stand point of the ecosystem conservation, the coordination among a sort of the cooperatives such as farmers, fishermen and forest owners are encouraged (Tutatani, 1998). Such a social linkage between forest resources and fishery resources which might affect each other are important but yet to be scrutinized.

Exceptionally, the study of Karakuwa town's case indicated the existence of the local background in such conservation activity. The critical factor is the project of the dam construction in progress at the upstream of the Oo River at that time. The fact that the infrastructure development possible to segmentalize the ecosystem urges people to such a conservation movement is significant.

Though it implies the significance to discuss sustainable use of natural resources from the aspect of social linkage, these earlier studies are not accumulated so many enough to develop a kind of theory for explaining the effect between two resources system. So in this study I clarified the context in which the fishermen go beyond their familiar territory of fishery resources to manage the resource system including the forest. For that, first I described the history of the regional fishing industry in Yakushima Island, focusing on the catch of mackerel. Second, I reviewed the cut of the broadleaf trees from the national forest in the past 50 years. Also I introduced some opinion of the local people about this planting. Then, I concluded that fisherman is the one of the actors who recognizes the value of the broadleaf tree. For the forest to remain valuable, fishery resources should be jointly managed in an integrated way in a specific circumstance. The management and the use of diverse fishery resources may be one approach to support the diversity of the forest.

Brief summary of Yakushima Island

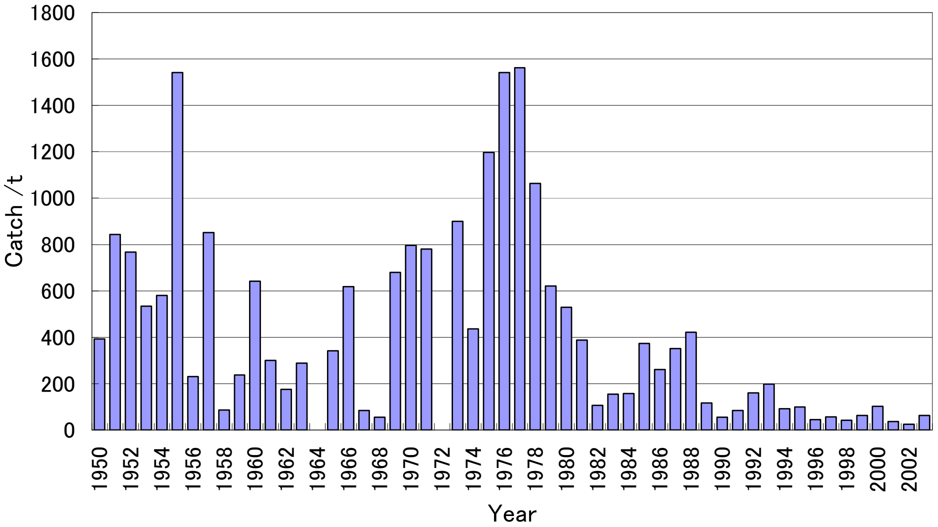
There exist two administrative districts in Yakushima Island, Yaku town and Kamiyaku town. The socioeconomic conditions are different in each district within the island. It partly comes from the difference of the natural conditions, e.g. the marine products. In Kamiyaku town located in the northern part of the island, people catch spotted mackerel in the fishing ground off the island. Isso, one of the villages in Kamiyaku town, had long been the main fishing port along the history of the island. On the other hand, in Yaku town located in the southern part, they catch flying fish in the Tane-Yaku canal. Because the plantation mentioned above was carried out by the Fishermen’s union of Kamiyaku town, this study focused on this district.

The decrease in the catch of Spotted Mackerel (*Gomasaba*)

Fig.1 shows the catch of mackerel from 1950 to 2003. Several characteristics can be mmediately pointed out. First, the catch is inconstant and seems to have several peaks. Second, the ecreasing trend in recent years is remarkable. After the catch marked the highest amount around 1977, it decreased sharply. In contrast, the total catch in Japan from the East China Sea has kept around 50,000 ton with yearly fluctuation. The catch fluctuation depends on two factors under the constant fishing effort, the population size, and the migration and the immigration of mackerel in the fishing ground. Even in consideration for the lowering of fishing effort as the result of aging of fishermen and depopulation, the decreasing fishery stock is serious problem to the fishing industry of Kamiyaku town. The plantation by the fishermen in Yakushima Island was carried out from 1996. In this term the catch kept decreasing without the tendency of recovery. Not only mackerel but other species living in the coastal zone are also decreasing. To realize the background of this drastic change in the catch, the local history was described in detail below.

The Fishing industry in Kamiyaku town has developed based mainly on fishing bonito, mackerel and flying fish. Until the middle of the Meiji period, bonito was the dominant target. The number of bonito fishing vessels had been about 50 in the beginning of Meiji period. Mackerel fishing became a substitute for bonito around 1900 because the fishing ground moved away off the island. The competition against the vessels from the main land also made it difficult to maintain. The fishing of mackerel had developed successfully with the motorization of vessels. The number of the power-driven vessels increased from 36 in 1926 to 80 in 1933 (Committee of Kamiyaku town history 1984). Around 1932, it was told that fishing ground shifted to near the island, and the catch of mackerel became active again. In this term, the amount of dried mackerel production was also increasing. There was the factory which produced about 4,500 ton in a year at this time. We can know that the annual fish catches were periodically changing since a hundred years ago.

Fig.1 The transition for mackerel catch in Kamiyaku Town



In the Post war period, the fishing industry recovered against the background of food scarcity. The total amount of the fish catch in Kamiyaku town marked its maximum (2402.5t) in 1955. Also the population and the number of vessels increased in this period. But soon after the middle of the 1950s, the catch dropped sharply. It is considered that many vessels from the mainland gathered around the fishing ground off the island and the fishery stock deteriorated. It is pointed that the difference of the fishing method is the factor. As compared with the pole-and-line fishing carried out by the islanders, the outsider operated by the seine fishing. The motorization of the vessel and the improvement of the equipment became the disadvantage for the islanders. The end of the regulation toward the fishing area in 1952 was one of the factors that made this area very competitive.

During the period of the economic growth, the catch level stayed unstable, together with the decrease of the labor. From around 1955, the number of the people working away from the island started increasing. The number of the fishermen which increased over 600 in 1955 decreased down to over a hundred until 1975. The fishery industry which was one of the important means to earn cash was noticeably in decay during the economic growth. Against the background of the decreasing population and catch, the modernization of the fishery was in progress. The size of the vessel was getting larger and the equipment improvement was pursuit to rationalize the management. Before that, mackerel fishing is limited with the vessel condition. The increase in the catch experienced from 1970 owed partly to the investment toward the machinery and equipment. At the same time, the oil shocks of the 1970s lead to the concentration of fishing effort in the coastal and offshore fishery. This trend was also backed up by the decay of the deep-sea fishery, following the setting of 200 nautical miles economic zone. These factors are considered to affect the resource stock.

The transition of the Broadleaf Tree Logging in the National Forest

Figure 2 shows the amount of broadleaf tree yields from the national forest. Soon after the end of the war, the operation restarted from 1946, the government enacted the legislations and planed the program to meet the sudden expansion of the national needs for timbers. The yield started increasing especially after 1960s and marked its maximum during the late 1960s. This production increase was followed by the establishment of the public corporation to manage the conifer plantation, and the private company to product the raw material for pulp utilizing the broadleaf woods from the national forest.

In this term, the broadleaf tree was considered as "low quality" and put under the operation of full-scale logging. The effect of this operation can be known by the interview of the elder. When it rained, the muddy stream induced by the clear cutting had colored the mouth of the river in red. It is pointed out that the disappearance of "jiki-tobi", the flying fish which periodically immigrate to the coast to spawn, is attributable to the deterioration of the forest environment.

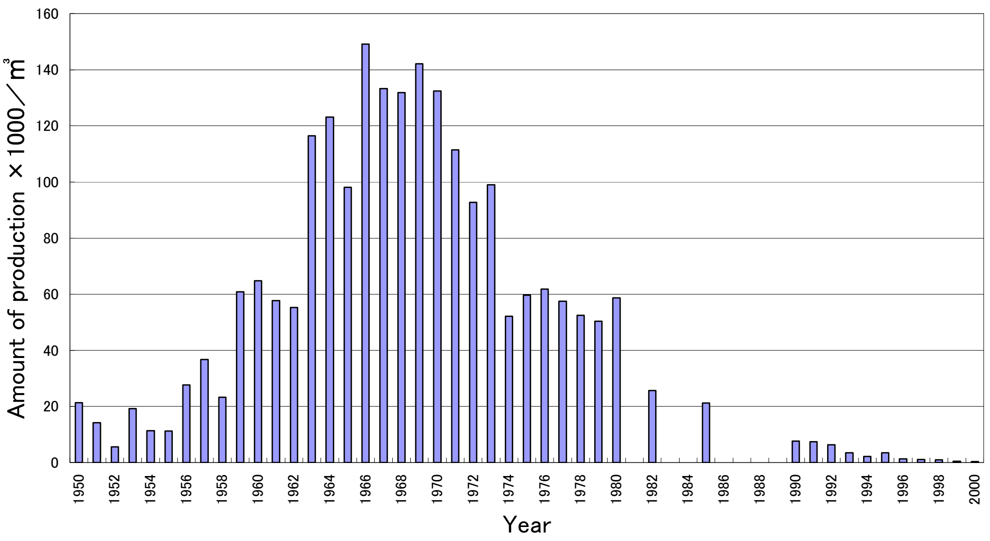


Fig.2 The transition for broadleaf tree production from the national forest

Source: Forest management office data

Forest and the Fisherman

Figure 1 and 2 indicate that the forest and fishery resources have experienced drastic disruption by the economic activity. But the mutual relation between mackerel catch and the amount of the broadleaf tree logging are not obvious. In fact, one interviewee recognized the positive effect of the broadleaf tree toward fishery, but he doubted its effect toward mackerel which is not inhabitant ashore.

Together with the natural fluctuation, current and water temperature variation, over fishing are supposed to be the critical factor to the decrease of the mackerel catch. The decrease of the man power is also one factor affecting the catch. Additionally, the import of the fish decreases the price of domestic fishes. Due to such circumstances, the fishermen directed their attention to the coastal fishery rather than the offshore fishery.

To keep the forest valuable, it is critical to retain the human resource supporting the ecological function. Fishermen are one of the stakeholders who regard the broadleaf tree valuable. The diversity of the stakeholders, especially those who live on the eco-system might keep the diversity of the forest. For that, fishery resource management is essential to forest resource management in Yakushima Island. As the local fishermen know the complicated factors existing in the background of the mackerel decrease, integrated resource management is suitable idea in such a circumstance.

References

Ichikawa, Hideo 1994. ”The Socio-economic Change in Yakushima Island and Local Fishery” *Bulletin Fisheries Economy* Vol.35, No.2, pp.171-191.

Kamiyaku town history Committee. 1984. *The History of Kamiyaku Town.* Kamiyaku Educational Board.

Kawasaki, Akitoshi, 1973. “ The Interviews on Mackerel Fishing in Isso, Yakushima Island―Focusing on between 1930 and 1931―” *South Island Folklore* No.31, pp.65-70.

Obitani, Hiroaki. 2000. ”The Development and Character Change of Planting Movement by Fishermen―From Watershed Area Conservation to Environment and Resource Creation―”*Journal of Environmental Sociology* No.6, pp.148-162.

Shibasaki, Sigemitsu. 1996. ”The Tree Planting Movements by Fishermen and Their Historical Backgrounds ― The Case of Kesennuma District ―” *Review of Forestry Culture* No.17, pp.69-81.

Tsutatani, Eiichi. 1998. “Fish Farming Attaching Weight to Ecosystem, Agriculture and Forestry” *Finance for Agriculture and Forestry* Vol.51, No.2, pp.128-144.

Yoshitake, Takashi. 2004. “Is the study of Uotsuki-rin possible?” *The Mountain Forest* No.1442, pp.56-62.

The Significance of Ecosystem Services for the Livelihood of Local People in Sarawak

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Introduction

Ecosystem services provide many benefits for human beings. In this paper, I focus on the provisioning services, and try to show how it is significant in local people's livelihood. Especially I focus on the food services and its utility for income.

Over the past half-century, the ethnic groups living in inland areas of Borneo, Malaysia, have experienced great environmental changes resulting from large-scale logging. These people, who had previously led a nomadic life in the forest, were forced to settle and turn to hill paddy cultivation (Rousseau 1990).

The common assumption for the displaced hunter-gatherers is that as hunting-gathering activities have declined, poverty has risen due to maladjustment to farming (Hong 1990). But in these previous studies, the significance of the forest resources such as wild plants and animals for their livelihood was not mentioned empirically. So, I try to make clear these points.

Study site

The study area is the one of the former hunter-gatherer community, located in inland area in Sarawak. The village sea level is about 85m and surrounded by mountains. The forest around the village is dipterocarp forest.

They are originally nomads, dependent on the wild sago palm, they began to settle in villages and undertake hill paddy cultivation in the 1960s, acting on a government policy.

Methods

This participant-observation study was conducted for about 11 months from January 2004 to May 2007 in the village. I investigated subsistence activity, mainly by recording activity times and identifying and measuring animals and plants they got. The dietary survey was conducted in one household and included a questionnaire and record of daily food consumption, number of meals, and meal contents. For cash income, I recorded the forest product for sale in the market, the number of sales, and their income from these sales.

Subsistence activity

Their subsistence activities now, contain four kinds of activities, hunting of wild animals, fishing, gathering of wild plants and farming. The farming was introduced according to government projects, such as hill paddy cultivation project in 1960s or vegetable gardening project in 1990s.

Nowadays, they use guns mainly for hunting but the elder generation like to use blowpipe, hunting spear also, and younger generation like to use hunting trap. These are the common technique in other hunter-gatherers in Borneo (Puri 1997). They mainly use casting net or gill net for fishing, and sometimes use 2 types plated rattan fish traps or angling. However men did the hunting and fishing, gathering and farming were done by both of men and women. Gathering wild plants or fruits from the forest was also important for their subsistence. They cultivate not only hill paddy but also some vegetables, like maize, tapioca or long beans in the garden near the village.

Historically, various environmental changes have altered their subsistence methods. In the midst of such environmental change, they have learned to use devices such as catch nets, hunting guns and gill nets, as well as developing more varied hunting and gathering of forest resources.

To obtain food resources, they spent most of their time hunting and fishing, which were regarded as the most important for food. Compared to hunting and fishing, they speared little labor on cultivation. Hunting was more important than fishing, but if they did not get any animals, they often turned to fishing. The same relation held between fishing and gathering. If they did not catch enough fish, they gathered wild plants. Cultivated plants were used only when hunting, fishing, and gathering yielded no food. Thus, their food values place hunted prey at the top and cultivated plants at the bottom.

This can be expressed in other word. Food obtained from hunting and fishing is called *bao* or *lelu ayok* (“big side dish”), whereas food from gathering and cultivation is called *lelu* or *lelu ici* (“small side dish”), which demonstrates the importance attached to these food items.

Significance of forest resources as foods

During June–August 2004, the villagers used 149 types of animals and plants as food. Wild plants comprised the largest percentage, with 67 species. Other foods included 28 fish, 17 mammals, 16 cultivated plants, 9 reptiles, 2 amphibians and 1 insect species (see table 1).

Table1. Food resources appeared in 139meals in 47 days in June to August 2004 at the A village

Category	Times of Use
Wild plants	67
Fish	28
Mammals	17
Cultivated plants	16
Birds	9
Reptiles	9
Amphibians	2
Insect	1
Total	149

I observed 139 meals, comprising 471 dishes, from June to August 2004. Rice totaled 60% of staple foods, whereas sago palm, the former staple, had a low 23% use rate (see Table 2).However, sago palm use was more varied, appearing in ten dishes, whereas rice was used in only three recipes. In particular, sago palm was preferred in a culturally important dish with wild boar meat. The self-support rate of sago palm was 40%, compared to 30% for rice.

For side dishes, the self-support rate was 100%. The use rates were wild plants, 37%; fishes, 34%; cultivated plants, 15%; and animals, 14% (see Table 3).

Table 2. Variety of staple food (In 139 meals consisting of 471 dishes)

Category	Times of eat
Rice	83
Sago	33
Bananas	13
Cassava	6
Taro	2
Yam	2
Noodles	2
Total	141

Table 3. Variety of non- staple food (In 139 meals consisting of 471 dishes)

Category	Times of eat
Wild plants	102
Fishes	95
Cultivated plants	41
Animals	38

Although few mammals were eaten, red meat was regarded as important. The use of animal and vegetable foods was almost equal. Wild plants exceeded cultivated plants, both in number and in kinds of use.

In the total diet, 63% of foods came from hunting-gathering, 21% from farming and 16% from purchases. The cash for purchasing food was earned from selling forest resources obtained by hunting-gathering. Thus, on the whole, nearly 80% of foods were supplied by hunting-gathering.

Significance of forest resources as income

For them, fishing and gathering wild plants remain central for subsistence, food, and cash income. Then I’d like to try to make clear how these resources are important in relation with market economy. The nearest local market was located about 4 km from the village, or 1.5 hours on foot.

According to their income survey, they earned most of their income by selling forest products such as fishes or wild plants. They earned much of their cash income by fishes, wild plants, and baskets or mats made of rattan (see table 4).

Although they have been settled down and hill paddy farming for 40 years, they still rely on hunting and gathering of forest products provide most of their cash income.

Conclusion

Among them, hunting-gathering is important both for food and cash income. Even after 40 years of farming experience, the main subsistence activities remain hunting and fishing. In all, 70% of their diet was supplied by hunting-gathering and 20% by farming. Wild plants were more widely used than cultivated plants, both in number and in kinds of use.

Table4. Sources of cash income (three months from June-August 2004)

Category	Income (RM)
Fishes	643
Petai bean	170
Baskets or Mats of Rattans	165
Durians	136
Fishing trap of Bamboo	90
Flog	32
rattan shoots	26
Huts made of palm	20
Palm leaf	16
Total	1298

* 1RM=33YEN

Although they have settled into village life and are influenced by the market economy, they have adapted their hunting-gathering activities to the market economy. By selling forest products, such as fishes or wild plants, they achieve a steady income. Thus, hunting-gathering has not declined but is, in fact, more focused. This differs from the usual hypothesis, that hunting-gathering by former nomads has declined in favor of farming.

They began the practice of shifting cultivation more than 40 years ago and also engage in periodic wage labor. However, the use of wild plants and fishes predominates over market-economy activities. Because of their proximity to a market, they earn most of their cash income by selling fishes and wild plants and fruits, which are also important to them as food. Thus, they continue hunting-gathering through their engagement with the market economy.

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References

Hong, Evelyne. 1987. Natives of Sarawak : survival in Borneo'svanishing forest.

Puri,R.K. 1995. *Hunting knowledge of the Penan Benalui of East Kalimantan,Indonesia. Diss.* University of Hawaii.

Rousseau, J. 1990 Central Borneo: Ethnic Identity and Social Life in a Stratified Society. Clarendon press, OXFORD.

Mushroom Utilization by the Iban in Eastern Sarawak, Malaysia

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Introduction

Fruiting bodies of macrofungi (mushrooms, stinkhorns, bracket fungi etc) are used not only as food products but also for traditional uses (Spooner and Roberts 2005). It is well known that the dried tissue of one of the bracket fungi, *Fomes fomentarius*, is used as tinder in Europe. In northern parts of America and Europe, other traditional uses of fungi are also seen, such as dyeing, razor stops and perfume. Not only in boreal and temperate zones, but also in the tropics, local people eat wild mushrooms, as seen in reports from, for example, Guyana (Henkel et al. 2004), Mexico (Jarvis et al. 2004; Ruán-Soto et al. 2006), Venezuela (Zent et al. 2004), Cameroon (van Dijk et al. 2003), Ethiopia (Tuno 2001), Zaire (Courtecuisse 1993), Thailand (Desjardin et al. 2004) and Malaysia (Anderson et al. 2003), and also use them for other purposes, such as medicine (Zent et al. 2004).

The local peoples of Borneo have a tradition of utilizing forest products. Christensen (2002) reported that the Iban, the most populous ethnic group in Sarawak, use and give names to 17 species of fungi. Because more than 100 aphyllophoralian species (bracket and shelf fungi, not including agaric mushrooms) are found in our study area, Lambir, Sarawak (Yamashita unpublished data), the large part of fungal use by Iban people is still uncovered. In this study site, Iban villagers cut and burn secondary forests to establish rice fields, and leave the fields for fallow or plant para rubber seedlings on the fields after 1 or 2 years of rice cultivation (Ichikawa 2004). The fungal community structure differs according to type of land use (Yamashita et al. 2007), thus I expected that there would also be differences in the importance of a forest type from the view of fungal use. In this study, I aimed to reveal the recognition and utilization patterns for macrofungi by Iban people.

Methods

From 27 December 2005 to 13 January 2006, I sought fruiting bodies of macrofungi in 29 forest stands within 30 km of Rumah Chabu, Lambir, Sarawak for about 3 hours daily, working with an informant. The informant was an Iban local villager, a man who was about 60-years old and lived in Rumah Chabu. Because he knew much about plants in this region, I expected that he would have substantial information about macrofungi. Study stands included fallows, an oil palm plantations, rubber plantations, isolated primary forest, and primary forest. In addition, we collected all the conspicuously large macrofungi at the roadside or rice field. When we collected each fruiting body, I asked him in Malayan to tell me the Iban name and how it was used. After that, I confirmed the spelling with four Iban villagers who understood English. The fruiting bodies collected were identified to determine the species and preserved as dried specimens.

Results and Discussion

Local knowledge and utilization

A total of 171 fungal fruiting bodies of 49 Iban species were collected (Table 1). Twenty-five species are used as food. Kulat gelang (*Lentinus sajor-caju*) seems to be popular and Kulat sawit (*Volvariella* sp.) is sold in Miri city. Kulat kerang (*Schyzophyllum commune*), which forms rather tough fruiting body, is widely distributed around the world, and some other local ethnic groups, such as the Majangir in Ethiopia, also eat this fungi (Tuno 2001). Furthermore, 10 Iban species were used for purposes other than food. Seven Iban species of bracket fungi, e.g. Kulat batang, Kulat Rajang, Kulat kering and so on (*Earliella scabrosa*, *Ganoderma australe*, *Trametes elegans* and so on) were used as mosquito repellents by putting the fruiting bodies in flames and fumigating. A red-coloured shelf fungi named Kulat dunggul manuk (*Pycnoporus sanguineus*, *Stereum ostrea*), a stinkhorn named Kulat butuh apaisali (*Dictyophora* sp.), and Kulat tusu kamba (*Xylaria* sp.1) are used as medicine for sick fowl by soaking the fruiting bodies in water and letting the fowl drink the water. Some coral fungi, Kulat punas (not identified), are used as medicine to increase fertility by rubbing the fruiting bodies into the lower abdomen. However, nowadays Iban people in the study area normally use fungal fruiting bodies only as food.

Latin names and Iban names

Thirty-nine Latin species were recognized, although the informant named 49 Iban species. This does not mean that Iban people recognize fungal fruiting bodies in detail, because some Iban species obviously include many Latin species. For example, Kulat ipuh contains *Coprinus* sp., Boletaceae, and other agaric fungi. The informant gave the Iban name “Kulat ipuh” to mushrooms that he does not know or eat.

Among 18 Iban species that were observed more than 3 times, 6 Iban species corresponded to one Latin species and rest of them include a number of Latin species. In addition, one Latin species did not always correspond to a single Iban species. For example, Kulat batang includes 11 Latin species. One of these 11 Latin species, *Earliella scabrosa*, was named as Kulat batang, Kulat kering and Kulat rajang. It is not a surprise that Iban people lump many Latin species of bracket fungi into one Iban species, because microscopic traits are very important in order to identify most of the above-mentioned bracket fungi to the Latin species level. On the other hand, *Cookeina* spp. was always named as Kulat mangkok, *Xylaria* sp.2 as Kulat tusu babi, and *Lentinus sajor-caju* as Kulat gelang. The shapes of fruiting bodies of *Cookeina* spp. and *Xylaria* sp.2 were conspicuously different from other fungi. For example, *Cookeina* spp. is named as Kulat mangkok, which means cup-shaped mushroom. In addition, more than 40% of Iban names were based on traits and similes of morphological traits of fungal fruiting bodies. *Lentinus sajor-caju* seems to be one of the most popular fungal foods. These points suggest that recognition of fungal fruiting bodies by Iban people is based on morphological character, and that fungal fruiting bodies which are not important species are grouped into complexes such as Kulat ipuh, Kulat batang and so on.

Effect of land use types on edible and other utilized fungi

The average number of edible fungal species increased with decreasing human activities, although the number in oil palm plantations was higher than the number in isolated primary forest (Fig. 1). The number of Iban species of fruiting bodies with traditional uses was high in isolated primary forest and primary forest, which seemed to reflect the spatial distribution pattern of bracket fungi among forest types (Yamashita et al. 2007).

An oil palm plantation provided economically valuable fungi, Kulat sawit (*Volvariella* sp.). However, other forest types did not always provide economically valuable fungi. We did collect some edible and economically valuable fungi from many forest types, but without a regular pattern emerging. In addition, the informant said that the Iban do not go into forest only to get mushrooms because it is very difficult to know when and where they appear. This indicates that no specific forest type is particularly valuable from the perspective of production of fungal fruiting bodies.

Further implications

Compared to other tropical areas, the study area is characterized by the lack of a dry season. It is well known that the appearance of fungal fruiting bodies is stimulated by rainfall (Yamashita and Hijii 2004). Thus, the lack of a dry season makes it hard to predict when and where fungal fruiting bodies will appear. Tuno (2001) also pointed out the importance of predictability of fungal appearance by stating that the Majangir in Ethiopia also collect their favorite fruiting bodies when they come across them, because of absence of clear seasonality. It is possible that low predictability in the appearance of mushrooms affects the Iban culture of fungal utilization.

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References

Anderson J, Nilsson C, de Richelieu T, Fridriksdottir H, Gobilick J, Mertz O, Gausset Q (2003) Local use of forest products in Kuyongon, Sabah, Malaysia. ASEAN review of Biodiversity and Environmental Conservation (ARBEC) January-March.

Christensen H (2002) Ethnobotany of the Iban & the Kelabit. p384. Joint publication of Forest Department Sarawak, NEPCon, and University of Aarhus. Videbæk, Denmark.

Courtecuisse R (1993) Taxonomy of some fungi used by the Songola people (Zaire). African Study Monographs 16:45-60

Desjardin DE, Flegel TW, Boonpratuang T (2004) Basidiomycetes. In: Jones EBG, Tanticharoen M, Hyde KD (eds) Thai fungal diversity. Biotec, Thailand: 37-49

Henkel TW, Aime MC, Chin M, Andrew C (2004) Edible mushrooms from Guyana. Mycologist 18:104-111

Jarvis MC, Miller AM, Sheahan J, Ploetz K, Ploetz J, Watson RR, Ruiz MP, Villapan CAP, Alvarado JG, Ramirez AL, Orr B (2004) Edible wild mushrooms of the Cofre de Perote region, Veracruz, Mexico: An ethnomycological study of common names and uses. Economic Botany 58 (supplement): s11-s115

Ruán-Soto F, Garibay-Orijel R, Cifuentes J (2006) Process and dynamics of traditional selling wild edible mushrooms in tropical Mexico. Journal of Ethnobiology and Ethnomedicine 2

Spooner B, Roberts P (2005) Fungi. New Naturalist Series. p. 594. HarperCollins Publishers, Suffolk, UK.

Tuno N (2001) Mushroom utilization by the Majangir, an Ethiopian tribe. Mycologist 15:78-79

van Dijk H, Onguene NA, Kuyper TW (2003) Knowledge and utilization of edible mushrooms by local populations of the rain forest of south Cameroon. Ambio 32:19-23

Yamashita S, Hijii N (2004) Relationships between seasonal appearance and longevity of fruitbodies of Agaricales and meteorological factors in a Japanese red pine forest. Journal of Forest Research 9: 165-171

Yamashita S, Hattori T, Momose K, Nakagawa M, Aiba M, Nakashizuka T (2007) Effects of forest use on Aphyllophoraceous fungal community structure in Sarawak, Malaysia. Biotropica: accepted.

Zent E, Zent S, Iturriaga T (2004) Knowledge and use of fungi by a mycophilic society of the Venezuelan Amazon. Economic Botany 58:214-226

Table 1 List of collected mushrooms and other fungi

Iban name	Frequency	Food	Use	Meaning of Iban name
Kulat ampuh bah	7	7	-	ampu(o)h, flood; bah, come on or
Kulat batang	15	-	10	a log
Kulat batang merah	1	-	1	batang, a log; merah, red
Kulat batang repuk	1	1	-	batang, a log; repuk, bad
Kulat bulu	5	5	-	hairy, feather
Kulat burak	7	7	-	white
Kulat butuh apaisali	1	-	1	butuh, penis; Apai Sali, Father of Stupidity
Kulat dunggul manuk	3	-	2	dunggul, a cock's comb; manu(o)k, chicken
Kulat gam	3	-	-	molar teeth
Kulat gelang	3	3	-	a large bracelet
Kulat gupung	1	-	-	gupu(o)ng, a bouquet, large bunch of fruit
Kulat ikan	4	4	-	ikan, fish
Kulat ipuh	9	-	-	ipuh, poison
Kulat ipuh belalang	1	-	-	ipuh, poison, belalang, cobra
Kulat jarum	1	-	-	jarum, needle
Kulat kasut	1	1	-	kasut, a shoe
Kulat kerang	5	5	-	of rattan or sugar-cane
Kulat kering	6	-	5	strong, tough, hard
Kulat kerup	2	2	-	the sound of biting into or chewing upon
Kulat labit manyi	4	4	-	labit, nest; manyi, bee
Kulat lapar	1	-	-	lapar, hungry
Kulat malam	4	-	-	night
Kulat mangkok	7	6	-	a cup or bowl
Kulat mangkok bulu	2	1	-	mangkok, a cup or bowl; bulu, feather, hairy
Kulat mata babi	1	1	-	mata, eye; babi, pig
Kulat mayau	1	-	-	cat
Kulat merah	2	-	2	red
Kulat minyak	7	7	-	oil
Kulat panyun	11	11	-	a large plant

Table 1 List of collected mushrooms and other fungi (*Continued*)

Iban name	Frequency	Food	Use	Meaning of Iban name
Kulat pending chit	2	2	-	pending, ear; chit, rodent or mouse or rat
Kulat pending mayau	3	3	-	pending, ear; mayau, cat
Kulat peril udok	1	-	-	peril, scrotum; udok, dog
Kulat pik	3	3	-	no meaning
Kulat pinang	1	-	-	pinang, the areca palm
Kulat punas	3	-	3	childress
Kulat rajang	7	-	5	epiphytic fern
Kulat rambut	1	-	-	hair
Kulat repuk	5	5	-	repu(o)k, brittle, rotten
Kulat resak	1	1	-	resak, name of tree (tree species)
Kulat rian	4	4	-	durian
Kulat risik	4	4	-	no meaning
Kulat sawit	1	1	-	oil palm
Kulat suntung	2	-	-	cuttlefish
Kulat tapak lelabi	2	2	-	tapak, paddle; lelabi, a freshwater turtle
Kulat telinga gajah	1	-	-	telinga, ear(M); gajah, an elephant
Kulat tukul	4	-	1	tukul, a hammer
Kulat tusu babi	3	2	-	tusu, breast; babi, pig
Kulat tusu kamba	1	-	1	tusu, breast; kamba cf. bunsu kamba, the little

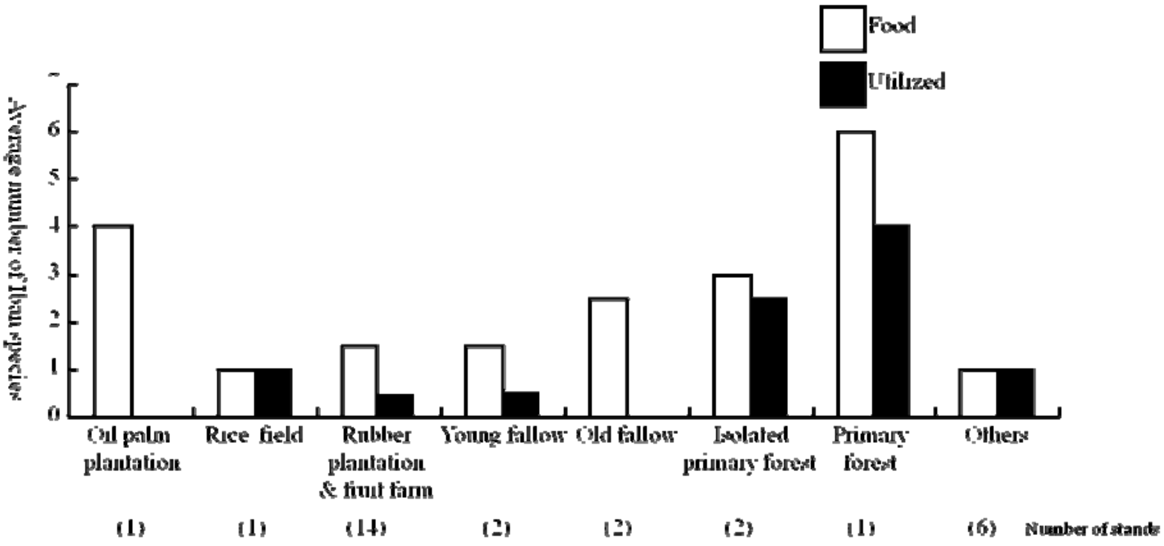

Fig. 1 Number of edible and utilized fungal species in each forest type

Change of Orang Sungai’s Subsistence Activities in the Kinabatangan River Basin in Sabah, Malaysia

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Introduction

Sabah was once the central area for export of tropical timber. Timber logging, increased from the late 1950s, and timber became the largest exporting good to countries such as Japan. Excess logging led to the decrease of forest. Sabah has recently adopted a significant change in its Forest Policy to implement an export regulation on raw timber and decrease timber exports. Palm oil and crude oil are the current main export goods, but forest products such as plywood and sawn timber still play an important role. The Sabah Forestry Department has worked towards sustainable forest management for the remaining forest and has adopted several forest policies such as the implementation of the Forest Certification Scheme from the late 1990s. The Kinabatangan River is the longest river in Sabah, and its basin was once the central area for timber logging.

In the basin of the Kinabatangan River, the indigenous people of Orang Sungai (River People) have long lived by forest product gathering, hunting, shifting cultivation and fishing. The population of Orang Sungai is approximately 40,000, and they are one of the many indigenous groups that live in Sabah. They have received the greatest impact from commercial logging around the Kinabatangan River as they live in wide areas of the river basin.

There have been many studies on forestry or forest policies in Sabah, the forest policy during the colonial period, the royalty system (Tachibana 2000), and socio-economical studies of the logging system and the timber industry. However, there has been no study to show how involvement in the booms and busts of the timber industry has affected the indigenous people, illustrating the topic from the perspective of these people.

The research area is Village W in the basin of Kinabatangan River, Sabah. Research was done through living in the village and interviewing the indigenous people who had been engaged in timber logging and hearing about their life stories and their involvement in the logging industry.

Overview of the Research Area

1. Location of the Village and the Environmental Background

Sabah is 73,000 km^2 by area, which is 22.3% of the total area of Malaysia. The population is approximately 2.6 million (Department of Statistics, Sabah 2000). The Kinabatangan River which runs through the northeastern part of Sabah State is the longest river in the state at 560 km by length and 16,800 km^2 by size of the basin area. The upstream area of the river basin is mainly highlands and mountains covered with forest, and the downstream area is flood plain covered with mixed dipterocarp trees. Many wild mammals and birds can be seen in this area, including orangutans, Asian elephants, and proboscis monkeys (Reza Azmi 1996). However, the environment has changed dramatically due to the recent forestry and oil plantation expansions.

The research area of Village W is located in the midstream of the Kinabatangan River. It is located at the south of Bukit Garam, where the district office of Kinabatangan is located. From Bukit Garam, it is a 30 minutes car drive towards Tawau, turning west into the farm road in the oil palm plantation and driving 60km further. It is now possible to drive directly into the village as the oil palm plantation has been expanded to just south of the village in 2004. The only transportation upstream is by boat, and Village K can be reached by 2 hours by a 30 hp boat.

Village W is located in the downstream section of the Kinabatangan River, so floods are not rare. According to the data from the Forest Department, the annual precipitation of this area is the highest in Sabah at 3,000 to 3,500 mm. The average temperature is 27 degrees Celsius, lowest at 23 and highest at 31. Height above sea level is approximately 200 m. The village is located in the lowlands along the river. As for vegetation, *Shorea leptoclados, Dryobalanops lanceolata, and Dipterocarpus caudiferus* are the dominant species. This area is rich in biodiversity. Endangered species living in this area are Asia Elephants (*Elephas maximus*) and Tembadau (*Bos javanicus*). Orangutan (*Pongo pygmaeus*) also live in this area, and deer, pigtail monkeys, and hornbills are several more examples of the animals that can be observed (Sabah Forestry Department 2005).

2. The Households of Village W

The people of Village W are Orang Sungai, and many of these villagers are Muslims. There is praying in mosques on Fridays, and the Islamic religion has a great impact on the customs of the village. Houses are built along the river and have raised floors for protection against the frequent floods.

The current activities are timber logging, forest product gathering of sawn timber and rattan, hill rice or vegetable cultivation by shifting cultivation, and fishing. In the village are an elementary school, mosque, and an assembly hall.

There are currently 40 households and approximately 250 people in Village W. Each household owns an individual house. Until Second World War, people used to create simple houses and move for shifting cultivation. In this paper, a household is defined as a group of people who live in one house. There is usually one nuclear family per household, but there are cases where a family lives together with a newly married couple or other close relatives. People began to settle down in the current location from the 1940s, and the construction of the elementary school in 1963 accelerated this trend. The number of households reached a peak as timber logging became more popular, and it has been decreasing since. Since 1999, 13 households have moved out of Village W.

Below is the analysis of data gained from 17 households in Village W. The members of Village W are the heads of households, their spouses, and their children. There are only 4 men whose hometowns are not Village W: Mr. H, age 74, from Paitan, Mr. J and Mr. JM, age 68 and 64, originally from Lemag (current Bukit Garam), and Mr. K, age 24, from Bukit Garam. The oldest 3 came to the village for timber logging and married the women from the village. Mr. K, age 24, is still single and came to the village after his sister married a man from Village W. He has a job in Village W.

The women whose hometown are not Village W moved to the village through a marriage with a man from the village: Ms. A, age 41, from Village A, Ms. B, age 3, from Tawau, Ms. C, age 30, from Bukit Garam, and Ms. D, age 26. More women than men have moved to Village W. Although there are some who are new to the village, the majority of the villagers are originally from the village.

3. The Subsistence Activities of the Villagers and their Working Status

Table 1 shows the working status of the villagers. Villagers are involved in various activities such as shifting cultivation, vegetable cultivation, fishing, and forest product collection. Therefore, these activities have been listed as Kerja Kampung (Work in village). The only public facility in Village W is the elementary school. The only activities which receive a Kerja Tamat (fixed income) are teachers at the elementary school, security guards at the elementary school, and village leaders such as Ketua Kampung and JKKK.

Information about Kerja Kampung was collected from observations and interviews in the village. For agriculture, hill rice cultivation is the main activity, but in 2006, only 2 households planted in that year. Some of the reasons mentioned by the villagers were the flood which occurred earlier that year after 6 years of no flood, the unsettled weather, or the sickness of a family member. On the other hand, many households planted their seeds in 2007. They originally planted 3 times a year, in March, July, and October. It changed to twice a year, in March and July. It has recently become only once a year in July and harvest in October. The crops are sweet rice, non-glutinous rice, red-kerneled rice, and black-kerneled rice. Over 5 types of rice were mentioned in the interviews.

Other households purchase rice from stores. It can be purchased at general stores in the village, but most households purchase at stores in Bukit Garam or Sandakan for more reasonable prices.

Vegetables and root vegetables are usually grown in small private farms around each house. They usually cultivate for 1 to 2 years, and when the soil is no longer fertile, they find a different place, log, burn, and plant again. Some vegetables that can be harvested throughout the year are cassavas, Sayur Manis, eggplants, pumpkins, and sweet potatoes. Some vegetables that are planted twice a year are Sawi, corn, okra, and Kacang Panjang. They feed their families and sell the rest. They sell in the village, or sometimes go to the estate or to Bukit Garam.

In Village W, plantation of rattan and fast growing species are popular. They are currently waiting for the next opportunity to harvest.

Fishing is done within the territory of the village for feeding families and selling. There are various methods, such as using fishing nets and fishing poles, but chemical poisoning and the use of electricity are prohibited. Prices of fish are strictly regulated by the village. The distance to the town is the issue for selling outside the village.

4. Education

Table 2 shows the current status of schooling children and educational background of graduates in the village. A kindergarten is run by an NGO based in Sabah that supports voluntary social development of the local people. It is each parent’s decision to send a child to kindergarten for it is not compulsory education. Before the establishment of the elementary school in 1963, villagers went to the downstream village of Pintasan or Lemag (current Bukit Garam, the center of the district) for education, and many villagers did not have this chance. The elementary school was constructed as a result of the demand from the villagers. Junior high school is only available in Bukit Garam, which is 1.5 hours downstream from the village. One has to stay in a dormitory or a relative's house to attend the junior high school. As shown in the figure, many of the graduates are only elementary school graduates, unable to attend junior high school.

Until the 1980s, villagers had to go to Sandakan for high school, but now it is available in Bukit Garam. Even after graduating from high school, many people stay in the village. Connections are said to be more important than educational background in finding a job in the village. Because of financial reasons, only a few have the chance to go to university. It is becoming more difficult to find a job in the village, and at the same time, jobs in town require a certain degree of educational background.

Indigenous People in Forest Use and Commercial Logging

The people of Orang Sungai who live along the Kinabatangan River have experienced the booms and busts of large-scaled commercial logging since the 1950s. In order to illustrate the involvement of the people in Village W in forest use, interviews were carried out to research past subsistence activities and the life stories.

1. Subsistence Activities before Commercial Logging

The basin of the Kinabatangan River was famous during the Sulu Period for non-forest products such as aloewood, ivory, hornbill beaks, and bird nests. Until the 1940s, the people were involved in forest product gathering, especially damar (resin) and rattan gathering, shifting cultivation, and fishing.

Before being involved in commercial logging, many villagers were involved in forest product gathering. They had collected damar regularly from trees in the forest such as Kapur (Dryobalanops spp.). Damar was sold to stores of Chinese brokers in Sandakan. As for rattan, there were several types, an example of which was Rotan sega (Calamus caesius).

In shifting cultivation, hill rice was harvested about 2 to 3 times a year. When there was a shortage of rice harvest, the village moved to other land for shifting cultivation. People cultivated sweet potatoes and cassavas around their houses. Houses were built with bamboo and palms, and were easy to build again.

2. Subsistence Activities during Commercial Logging Period

Until the early 1960s, timber logging was done around Sandakan, but in the late 1960s, it expanded to the downstream of the Kinabatangan River as well as to Lahat Datu (Tachibana 2000). The reasons were that land along the Kinabatangan River was relatively flat, and that rivers were used to carry timber. In the 1970s, the area also expanded into the inland, and in the 1980s, the center of timber logging shifted to the upstream of the Kinabatangan River, which was the area with the richest resources. Logging of secondary forest also began, which was mainly in the coastal areas.

It was after the Second World War when large-scaled timber logging began in the basin of the Kinabatangan River. It was in the downstream area of the river where logging first took place.

In the early 1950s, the British Borneo Timber Company acquired the logging concession in the downstream area of Seguliud-Lokan and began to operate. Logging had long been a monopoly of this company, ever since the colonial period. Saws and axes were used for logging, and timber was carried by Kuda Kuda (a large sleigh for carrying logs), and by railways and tramways.

The news of the beginning of the logging in Seguliud-Lokan soon spread to Village W, and many single men from Village W went out of the village to seek job opportunities. The people traveled down the river in a small rowing boat. The jobs given to the villagers were very simple, such as transporting logs, peeling tree bark, or tying up the logs.

According to Mr. U, age 74, who used to be a Kuda Kuda puller, one Kuda was pulled by a group of 8 men. He pulled from 3 to 5 logs in a day. Pay was in accordance with the pulled distance, and this pay was split amongst the members of the group. The more they pulled, the more pay they received.

Long term logging concessions were only allowed to a few companies, but in the 1960s, they were also given to timber companies run by overseas Chinese owners. A company run by an overseas Chinese owner, gained the long term logging concession in the Forest Reserve nearby Village W, and large scale logging was operated from 1956 to 1977.

As new logging camps opened very close to the village, many villagers became engaged in logging, and this gave a tremendous impact on the subsistence activities in the village. The people who had been working in downstream areas also came back to the village to work in the newly opened logging camp.

Kuda Kuda, railways and tramways were used when logging camps first opened, but the work of logging eventually became automated. In mid 1970’s, logging companies began using chain saws and tractors for logging, and soon the villagers became involved in such machinery work.

There were also many villagers involved in transporting timber from logging camps to log ponds in Sandakan, being hired by the timber companies. They worked as a captain or as crew of the timber transporting ships. Depending on the water level, one round trip took about 1 to 2 weeks, and depending on the amount of the timber, they took about 1 to 3 trips per month. One boat had a captain, an engineer, and a sailor.

Timber logging decreased in the 1980s as the number of trees decreased. After the 1980s, timber companies operated relatively small scale timber logging.

In the 1990s, the scarcity of resources and the prohibition of log exports by the government led to the closure of many logging camps around the village. As a result, many people moved or began working at the Forestry industry as logging camps moved to the upstream of the Kinabatangan River.

3. Current Subsistence Activities

The exit of the logging companies from Village W had a substantial impact on the subsistence activities of the indigenous people. They can no longer sell fish or vegetables to the logging camps. The opening of the oil palm plantations also had a substantial impact. The oil palm plantations expanded at the south of the village. Some villagers opened small oil plantations, and some villagers are working at oil plantations. The work is relatively tough for the amount of pay, and many have quit.

Other sources of income are scrap metal and rattan collection, fishing, shifting cultivation, but there is a limit to the number of activities. Metal scrap gathering involves searching for and digging up the scrap parts of abandoned tractors from the old logging camps. Scrap was sold to a tauke, and more people began to be involved in this activity from 2004 onwards. The tauke then transported the scrap to Sandakan and sold it to metal factories.

The decrease of wage labor in logging industry led to a significant decrease in the job opportunities in the village. More and more households have moved to the downstream of the Kinabatangan River such as Bukit Garam or Sandakan, where county public offices are located.

Conclusion

Orang Sungai people had long been involved in shifting cultivation, fishing, and forest product gathering in the basin of the Kinabatangan River in Sabah. When commercial logging began and many logging camps were opened around the village, many villagers became involved directly as logging workers. Villagers also received indirect financial benefits such as by selling vegetables or fish to these logging camps.

The booms and the busts of commercial logging had a significant impact on the subsistence activities of the villagers. The current subsistence activities of the villagers are shifting cultivation or fishing as before, logging of timber from trees that are currently scarce, plantation of rubber trees or oil palms, or seeking new job opportunities in the cities. They are still searching for new subsistence activities in place of timber logging.

References

Tachibana, S 2000. *Forest Exploitations and Timber Export Restrictions in Southeast Asian countries*, Regional policy research 3 (1). 49-71.

Department of Statistics, Sabah 2000. Year Handbook Statistics Sabah 2000. Kota Kinabalu.

Reza A 1996. Protected Areas and Rural Communities in the Lower Kinabatangan region of Sabah. Sabah Society Journal 13. 1-32

Sabah Forestry Department 2005. Forest Management Plan 2 Deramakot Forest Reserve FMU19. Sandakan.

Table 1: The Subsistence Activities of Villagers and Working Status

Job Type	W village		Outside		Total
	F	M	F	M	
Kerja Kampung	22	29			51
House work			5		5
Oilpalm farming			3	1	4
Imam		2			2
School Safeguard		2		1	3
Kindergarten Teacher	2				2
Village Leader		1			1
JKKK		1			1
Police Officer			1		1
Elementary School Teacher				1	1
Secretary for Political				1	1
Nurse			1		1
Tourist Guide				1	1
Hotel Cook				1	1
Furniture Sales				2	2
Cars Sales			1		1
Selling Staff at Retail				1	1
Oil Palm Plantation				3	3
OfficeWorker			1		1
Weed Cutting				1	1
Others	1	1			2
Unknown				1	1
Total	25	36	12	14	87

Source: Household Survey by the Author

Table 2: Current Status of Schooling Children and Educational Background of Graduates in the Village

Current Students				Graduates			
	Female	Male	Total		Female	Male	Total
Tadika	3	2	5	No	12	5	17
SR1	2	2	4	SR1	0	0	0
SR2	2	0	2	SR2	0	0	0
SR3	2	1	3	SR3	0	0	0
SR4	1	2	3	SR4	0	0	0
SR5	2	1	3	SR5	0	1	1
SR6	0	0	0	SR6	11	12	23
SM1	1	0	1	SM1	2	4	6
SM2	1	1	2	SM2	0	2	2
SM3	1	1	2	SM3	3	13	16
SM4	1	1	2	SM4	0	0	0
SM5	1	1	2	SM5	10	12	22
SM6B	0	0	0	SM6B	0	0	0
SM6A	1	0	1	SM6A	0	0	0
U	0	0	0	U	0	0	0
Total	18	12	30	Total	38	49	87

No: No Schooling, SR: Elementary School, SM: Junior High and High School, U: University. Source: Household Survey by the Author

Distribution and Collection of the Non-timber Forest Product, Gaharu, along the Upper Streams of the Baram River in Sarawak

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Introduction

Gaharu is a forest product from rainforests in India and eastwards throughout Southeast Asia. Some species of trees in the genus *Aquilaria* which belong to the Thymelaeaceae family accumulate resin in parts of their trunks. The resin forms aromatic nodules called gaharu.

Gaharu has a long history as a traded good (Dunn, 1975, Lim and Parid, 2001). A Chinese document from the third century already recorded that gaharu was imported from Southeast Asia. Hong Kong, as its Chinese characters demonstrate, flourished as an entrepot port to deal with aromatic woods.

Gaharu needs to be burned or heated for the fragrance to be released. The fragrance of gaharu can be quite faint and subtle, but profound. In Islam and Buddhism, gaharu in the form of wood chips or incense is necessary for religious acts in order to purify the space. Gaharu is also used as Chinese herbal medicine for asthma and gastrointestinal fragility, because of its calming effect. In Japan, the art of incense ceremony using gaharu became established as Koh-doh in the Muromachi era (1336-1573), and is still performed by enthusiasts today (Morita, 1992).

Gaharu is one of the most expensive forest products in the world. The price of gaharu sold as wood pieces or small chips varies with quality (grade). Long established retail shops in Japan are selling the best gaharu for 10,000 yen (US$ 90) per gram, making it much more expensive than pure gold or platinum. In 2004, all species of *Aquilaria* were subject to trade controls under CITES appendix II. However, because it is relatively easy to carry, a large volume of gaharu is allegedly traded illegally (Soehartono and Newton, 2001: 37).

This paper has four purposes. First, it aims to examine the distribution characteristics of gaharu trees in a community with primary forest. Second, the paper makes a comparison with the distribution characteristics under other land use patterns. Third, the paper shows the methods by which local gatherers extract gaharu. Fourth, it is shown how much the sale of gaharu contributes to the local economy.

Location for Research

The location for this research is Village L, a Penan village in the upper reaches of the Baram River in Sarawak, Malaysia. The Penan is a hunter-gatherer of the Borneo rainforest. Among 6,000 Penan people living along the Baram River, around 300 are nomadic, and the others lead settled or half-settled lives.

In order to reach village L, one must drive along the logging road from Miri, a coastal city, for 10 hours and then walk for two more hours (See Figure 1). Primary forest without any commercial logging is still continuous around the village. The village comprises 28 households and 118 people, with a make-up shown in Figure 2.

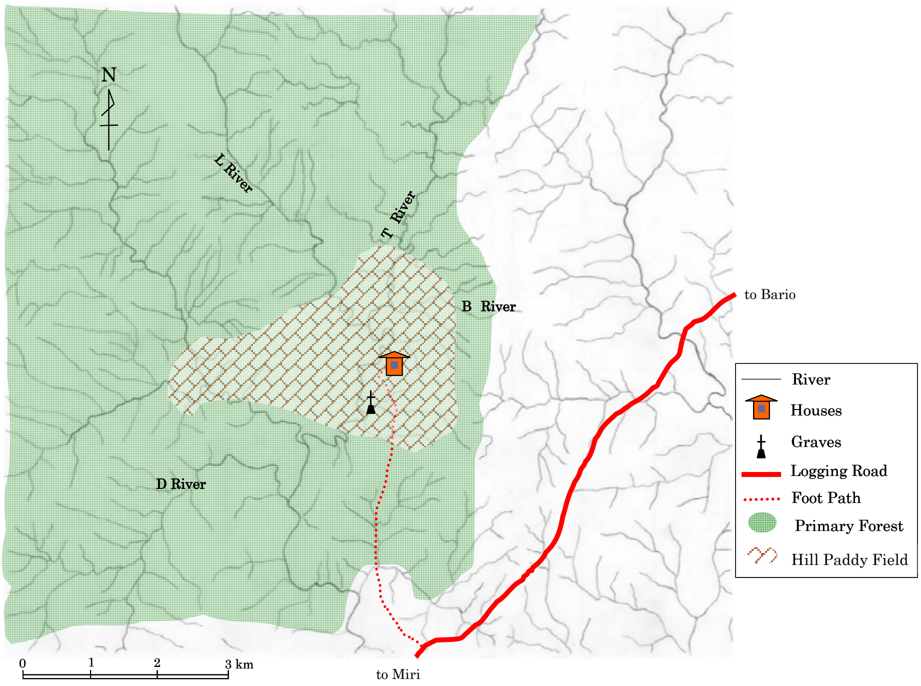


Fig. 1. Map of Village L

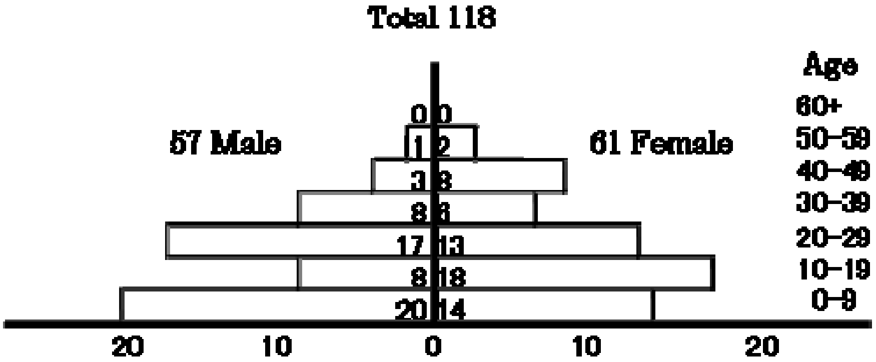


Fig. 2. Population composition of L Village

People in village L live by hunting with blowpipes and gathering, and also by shifting cultivation. The average area for shifting cultivation per household is 2.33 acres. Their relatives living nearby taught agriculture to them, but the relatives themselves had learned agriculture from farming peoples such as the Kelabit and the Saban.

Research Method

The field survey was conducted in August 2004. L Villagers went along and cooperated in the field survey. First, we walked around a total of 90 ha along the B River, D River, T River, and L River in primary forest areas. We used GPS (MAP60-CS-AP) made by Garmin for estimating the geographical position and also PC software (Trip and Waypoint Manager) in order to estimate the size of the area. The reception of GPS signals that we attempted near the trees was about 60%. We took photos and kept records of all individual gaharu trees. We used Vertex III made by Haglof in order to estimate the height of the trees. We used a tape

measure to measure the diameter. As for the degree of decay of felled trees, we used the following four degrees estimated visually:
Degree 1: Immediately after felling, with green leaves
Degree 2: Sapwood is decayed
Degree 3: Heartwood is decayed, sapwood is missing
Degree 4: Most decomposed

In order to make a comparison, we carried out same research in 50 ha of secondary forests eight years after commercial logging and 40ha of secondary forests three- to ten-years after shifting cultivation, and in 10 ha of secondary forests 15 years after shifting cultivation.

I interviewed the villagers as for the amount and quality of extracted gaharu over a month, and was shown actual samples.

Result

Species of Gaharu

Gaharu taken in Village L are of two species: *Aquilaria microcarpa* and *Aquilaria beccariana*, both belong to the Thymelaeaceae family. *A. microcarpa* is called Gaharu Tokong, which means mountain Gaharu in Penan language, and *A. beccariana* is called Gaharu Ba, which means river Gaharu in Penan. *A.* malaccensis can be also seen in other areas in Sarawak, but it does not grow here.

Extraction Method

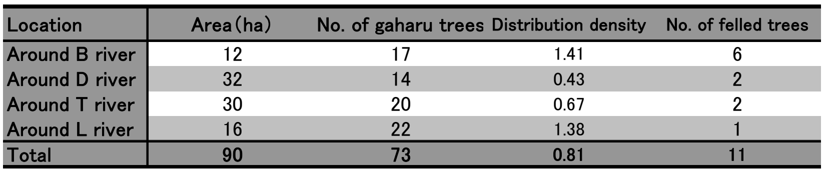
When Penan look for a gaharu tree in the forest, they pay attention to fallen leaves and tree bark. As soon as they find a fallen leaf, they can immediately find the tree nearby. It is reported that in Indonesia, when one finds a gaharu tree, one cuts down the tree whether it contains resin or not (Soehartono and Newton, 2001). However, Penan in village L make a little cut on the tree bark and if they find that there is a little resin, they use an ax or a knife to cut out only the part where resin has accumulated. If a gaharu tree is not cut down, the tree may accumulate resin again. It takes several months or several years to accumulate resin.

Gaharu Trees Distribution

We recorded 73 gaharu trees in the total of 90 ha primary forest around the village (Table 1). They were all *A. beccariana*. Table 2 shows data for tree heights and diameters. The felled trees are also contained in the number. The average tree height was 9.1m and the average diameter was 11.4 cm. Of these trees, 11 that were believed to contain a relatively large amount of resin were cut down by villagers. It turned out that not all gaharu trees generated resin, but only relatively mature trees generated it. All four trees whose height was over 18 m and whose diameter was over 28 cm were cut down. As for the degree of decay, two trees were in Degree1, two in Degree 2, five in Degree 3, and two in Degree 4. If we exclude two felled trees that were decayed so much and did not retain their original forms, the average tree height of the felled trees was 15.5 m and the average diameter was 19.9 cm.

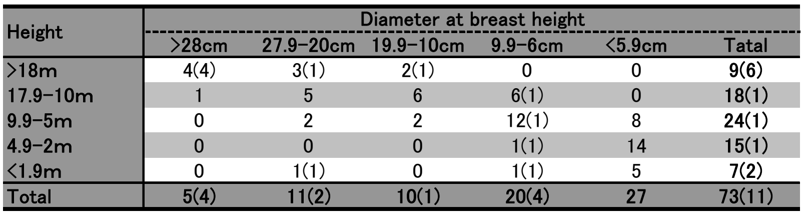
In contrast, as Table 3 shows, in about 50 ha of eight-year commercial logged forest, there were only two gaharu trees. In about 40 ha of secondary forests for three to ten years after shifting cultivation, there was no gaharu tree. In about 10 ha of secondary forests for fifteen years after shifting cultivation, there was only one gaharu tree.

Table 1. Gaharu trees distribution in primary forest



Location	Area (ha)	No. of gaharu trees	Distribution density	No. of felled trees
Around B river	12	17	1.41	6
Around D river	32	14	0.43	2
Around T river	30	20	0.67	2
Around L river	16	22	1.38	1
Total	90	73	0.81	11

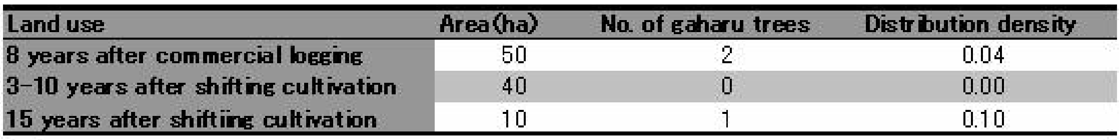
Table 2. Size of the gaharu trees in primary forest



Height	Diameter at breast height					
	>28cm	27.9-20cm	19.9-10cm	9.9-6cm	<5.9cm	Tatal
>18m	4(4)	3(1)	2(1)	0	0	9(6)
17.9-10m	1	5	6	6(1)	0	18(1)
9.9-5m	0	2	2	12(1)	8	24(1)
4.9-2m	0	0	0	1(1)	14	15(1)
<1.9m	0	1(1)	0	1(1)	5	7(2)
Total	5(4)	11(2)	10(1)	20(4)	27	73(11)

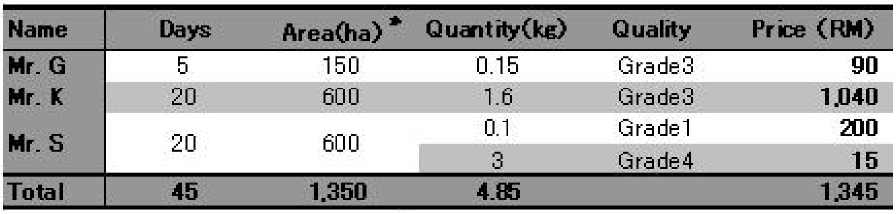
( ) number of felled trees

Table 3. Gaharu trees distribution in secondary forests



Land use	Area(ha)	No. of gaharu trees	Distribution density
8 years after commercial logging	50	2	0.04
3-10 years after shifting cultivation	40	0	0.00
15 years after shifting cultivation	10	1	0.10

Table 4. Villagers' one-month income from gaharu (August, 2004)



Name	Days	Area(ha) *	Quantity(kg)	Quality	Price (RM)
Mr. G	5	150	0.15	Grade3	90
Mr. K	20	600	1.6	Grade3	1,040
Mr. S	20	600	0.1	Grade1	200
			3	Grade4	15
Total	45	1,350	4.85		1,345

* The extraction area per day is presumed to be 30ha.

Income for Villagers

During the month of August 2004, three villagers collected 4.35 kg of gaharu from an estimated 1,350 ha of forest. In reference to the prices that Kayan brokers use (first grade: RM2,000 per kg; second grade: RM1,500 per kg; third grade: RM650 per kg; fourth grade: RM50 per kg; and fifth grade: RM3 per kg), this amount would be equal to RM1,345 (US$366) (See Table 4). For L villagers, Gaharu is the biggest source of income and their rattan handicrafts are second.

Conclusions

73 gaharu trees were distributed in about 90 of ha primary forest around the Village L. Habitat density is lower than one per ha. It turned out that not all gaharu trees generated resin, but only relatively mature trees generated it. When land use such as commercial logging or shifting cultivation is introduced, the habitat of the gaharu trees is subjected to destructive damage. The Penan in village L do not cut down all gaharu trees, but cut out only parts where resin has accumulated with an ax or a knife and let the tree survive. Gaharu is the biggest source of income for the L villagers.

The present situation of the gaharu wood habitat

Today, in Sarawak, except for National Parks and Wildlife Sanctuaries, very few areas of substantial-sized primary forest remain; however, in the upper reaches of the Baram River, a sizable forest without any logging operation still remains. Today, approximately 18,000 ha of primary forest exists within the boundaries of the village that people in Village L recognize. When we apply the distribution density that we have acquired to the 18,000 ha, it is estimated that there should be about 15,000 gaharu trees within the village boundaries.

In October 2004, the Malaysian Timber Certification Council (MTCC) granted a certificate to a private logging company to “manage” the remaining 55,000 ha of primary forest that neighbors Village L. The Penan people living inside are making protests regarding this certified logging because the MTCC certificate does not recognize their native customary rights.

In the forest industry, timber has been recognized as the major forestry product and others as minor. However, it was only a few decades ago that people started focusing on timber in the rainforest. The export of non-timber products, as trading goods, surpassed that of timber until half a century ago. In extracting non-timber products including gaharu, it is possible to ensure certain productivity without necessarily felling the trees. In comparison with timber, these products were traded for much more appropriate prices. As a result, profits have been returned to local gatherers. In order to conserve the rainforest, the lives and cultures using it, it is necessary to review forest values other than timber and to devise policy options to secure sustainable use of forest products.

Acknowledgements

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References

Dunn FL (1975) *Rainforest collectors and traders: A case study of resource utilization in modern and ancient Malaya* (Monographs of the Malayan branch of the Royal Asian Society No.5). MBRAS, Kuala Lumpur.

Lim HF and Parid MM (2001) Non-timber forest product utilization by the local communities in Peninsular Malaysia and policy implication. *International conference on forestry and forest products research*. 308-316.

Morita, Kyoko (1992) *The Book of Incense: Enjoying the Traditional Art of Japanese Scents*. Kodansha.

Soehartono T and Newton ACII: The impact of gaharu harvesting in Indonesia, *Biological Conservation* 97. 29-41.

Underuse of Coppice Woodlands Decreases the Abundance of Parasitoid Wasps, Potential Natural Enemies of Agricultural and Forest Insects, in Central Japan

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Introduction

Coppice woodlands, which have been rotationally harvested for the production of wood, charcoal, fertilizer, and mushrooms, are a typical vegetation cover in satoyama landscapes in Japan (e.g., Takeuchi et al. 2003). Satoyama landscapes include not only woodlands, but also farmlands (rice paddies, orchards, vegetable fields, and other agricultural areas), settlements, and water reservoirs. These landscape elements are mutually connected in terms of ecological processes. Rural woodlands and other semi-natural ecosystems neighboring agricultural fields can be used as temporal habitats of natural enemies that invade croplands and control insect pests (e.g., Altieri and Nicholls 2004; Hajek 2004). Biological control is one of the most sought-after services of insect biodiversity (Samways 2005).

However, the area of regeneration cutting for rotational harvesting has gradually decreased over the last several decades, mainly from considerable changes in energy consumption and fertilizer use in Japan (Takeuchi et al. 2003). This may decrease the abundance and function of indigenous natural enemies in rural agricultural and forest landscapes. Such rural landscape changes and underuse of coppice woodlands have affected a variety of arthropods, including endangered or rare species (Maeto and Makihara 1999; Takeuchi et al. 2003; Inoue 2003; Makino et al. 2006; Maleque et al. 2006), but little is known about changes in the assemblages of parasitoid wasps, which are among the major groups of natural enemies of pest and non-pest insects (e.g., Gauld and Bolton 1988; Hajek 2004). The decline in understory vegetation, which is often observed in old coppice woodlands, may reduce the abundance and diversity of parasitoids, although no evidence is currently available to support this prediction.

The aim of this study was to clarify the effects of underuse, i.e., aging of deciduous coppice woodlands, on the abundance of parasitoid wasps in the understory layers. We focused on the family Braconidae (Hymenoptera), the second largest group of parasitoid wasps. Members of this group have highly diversified host ranges and are very important in bio-control programs of pest insects (Gauld and Bolton 1988; Hanson and Gauld 1995).

Materials & Methods

Study area

This study was conducted in an area of coppice woodlands in Ogawa (580-800m a.s.l.), located at the southern edge of the Abukuma Mountains in Kitaibaraki, Ibaraki Prefecture, central Japan (Makino et al. 2007). In this area, woodlands have been subjected to human activities such as burning, cattle grazing and clear-cutting for fuel wood (Suzuki 2002), and small scale clear-cutting of broad-leaved stands has been ongoing through the present. We selected nine plots in deciduous broad-leaved stands, dominated by

Quercus serrata, *Q. mongolica*, and *Fagus crenata*, representing a chronosequence from 4 to > 100 years after clear-cutting (Table 1).

Table 1 Study plots and collection summary of braconid parasitoids in Ogawa in 2002

Plot code	Age (years)	Area (ha)	Number of braconid subfamilies	Number of braconid individuals
O4	4	5	15	1110
O12	12	4	13	670
O24	24	24	15	797
O51	51	10	14	405
O54	54	14	15	311
O71	71	19	15	408
O128	128	98	13	343
O174	174	11	15	340
O178	178	10	13	368

Sample collection

Parasitoid wasps were collected with Townes-style Malaise traps (Golden Owl Publishers; 180 cm long, 120 cm wide, 200cm high; coarse mesh) in 2002. The traps were placed in study stand to avoid edge effects. Trapped insects were collected every 2 weeks from late April to early November. A mixture of ethanol and propylene glycol was used as preservative in the insect containers of the traps.

Parasitoid wasps

Braconid wasps (Hymenoptera, Braconidae) collected in two traps, 10 m distant from each other, were used for each plot in the following analyses. All specimens were dried, mounted, and identified to subfamily or tribe, and all voucher specimens were deposited at Kobe University (Graduate School of Agricultural Sciences), the Museum of Nature and Human Activities, Hyogo, and the Forestry and Forest Products Research Institute (FFPRI).

Analyses

Data on braconid wasps were pooled for each plot through the seasons. Principal component analysis (PCA) was performed on the abundance of subfamilies (tribes) in each plot to make an ordination of plots and braconid subfamilies. Simple regression of the abundance of parasitoids was analyzed in relation to stand age after clear-cutting. For these analyses, the number of individuals per trap was log-transformed as $\log_{10}(X + 0.5)$. Statistical analyses were carried out with SPSS for Windows, ver. 11.5.1 J (SPSS Inc.).

Results

In total, we collected 4,752 individuals of braconid parasitoids (Table 2). The number of captures increased abruptly in May, remained high during summer, and dropped from mid-August to September (Fig. 1). The specimens belonged to 17 subfamilies, and the major guilds of their host insects are summarized in Table 2. Fourteen subfamilies (including the tribe Dacnusini of the Alysiinae) were presumed to be parasitoids of plant feeders (herbivores), and four subfamilies (including the tribe Alysiini of the Alysiinae) were presumed to be parasitoids of detritus feeders (including wood borers and mushroom feeders). The former group accounted for 74.7 % and the latter for 25.3 % of total captures.

Table 2 Subfamilies of braconid parasitoids collected, and presumed feeding guilds of their host insects

Subfamily (tribe)	Major feeding guild of hosts P – plant feeders D – detritus feeders	Recorded range of host insects* C – Coleoptera, L – Lepidoptera, D – Diptera He – Hemiptera, Hy – Hymenoptera	Number of individuals
Agathidinae	P	Plant-feeding larvae of L	54
Alysiinae (Alysiini)	D (P)	Detritus-, mushroom-, or rarely plant-feeding larvae of D	509
Alysiinae (Dacnusini)	P	Plant-feeding larvae of D	229
Aphidiinae	P	Plant feeders of aphids	8
Braconinae	P (D)	Plant-feeding or occasionally wood-boring larvae of C, L and D	257
Cheloninae	P	Plant-feeding larvae of L	692
Doryctinae	D (P)	Wood-boring larvae of C, or rarely plant-boring larvae of L	326
Euphorinae	P (D)	Plant feeders or rarely detritus feeders of C, He, etc.	50
Helconinae	D (P)	Wood-boring, mushroom-feeding, or seed-boring larvae of C	249
Homolobinae	P	Plant-feeding larvae of L	24
Ichneutinae	P	Plant-feeding larvae of L and Hy	42
Macrocentrinae	P	Plant-feeding larvae of L	72
Meteorinae	D (P)	Wood-boring or mushroom-feeding larvae of C larvae, or plant-feeding larva	118
Microgastrinae	P	Plant-feeding larvae of L	1,392
Miracinae	P	Plant-feeding larvae of L	13
Opiinae	P	Plant-feeding larvae of D	305
Orgilinae	P	Plant-feeding larvae of L	2
Rogadinae	P	Plant-feeding larvae of L	410
Total			4,752

*According to Shaw and Huddleston (1991), Wharton et al. (1997), and literature cited by them

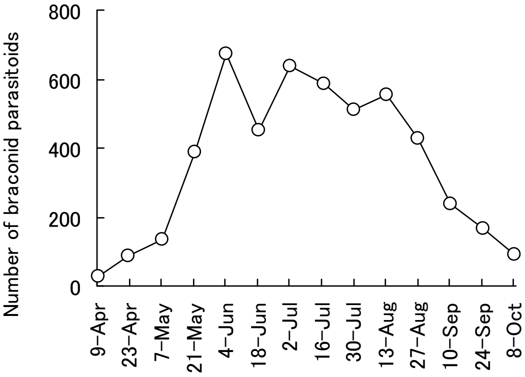

Fig. 1 Seasonal prevalence of braconid parasitoids collected by Malaise traps in Ogawa in 2002

Figure 2 shows the PCA ordination of plots and subfamilies (tribes) with more than 20 individuals. Along the first axis (proportion of variance = 0.462), nine plots were arranged by the age of stands (Fig. 2a; $\tau = - 0.889$, $P < 0.001$, between the first axis score and stand age), and the parasitoids of plant feeders were mostly clustered among younger plots (Fig. 2b). In contrast, the parasitoids of detritus feeders were near the origin of the first PCA axis, indicating no obvious relation to stand age.

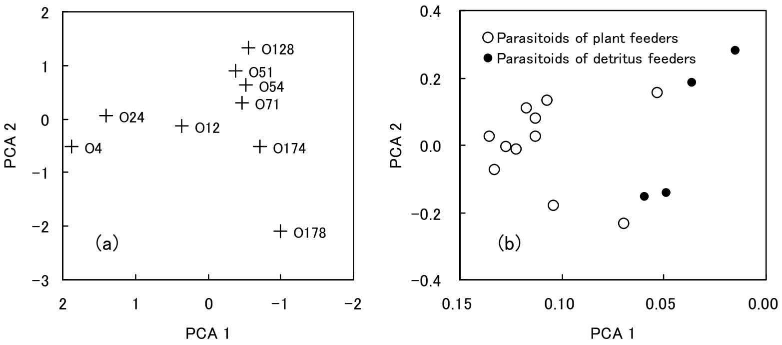

Fig. 2 Ordination of plots (a) and braconid subfamilies (b) by principal component analysis (PCA)

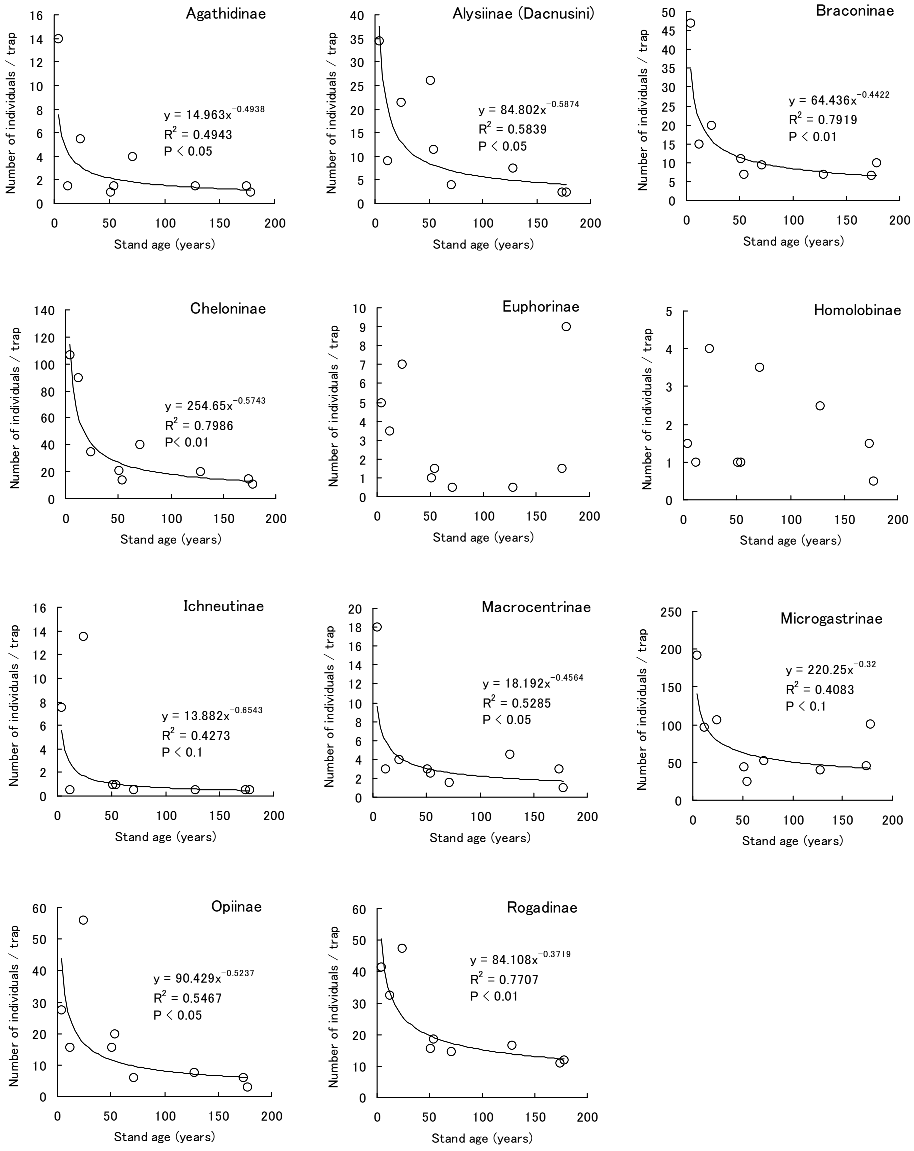

Fig. 3 Relationship between stand age after clear-cutting and the abundance of braconid parasitoids of plant feeders for each subfamily

Figure 3 shows the abundance of the parasitoids of plant feeders in relation to stand age after clear-cutting. The number of captures per trap in most groups except for two small subfamilies, the Euphorinae and Homolobinae, declined markedly with the increase in stand age. In the parasitoids of detritus feeders, however, changes in abundance along with stand age were not consistent (Fig. 4), whereas a temporal increase and decrease in the middle-aged stands were evident for the Alysiinae (Alysiini) and the Doryctinae, respectively.

Data of the parasitoids of plant feeders were pooled. Their collective abundance along with stand age is shown in Fig. 5. Overall abundance of the parasitoids of plant feeders declined steeply for about 50 years after clear-cutting, indicating a power function of stand age.

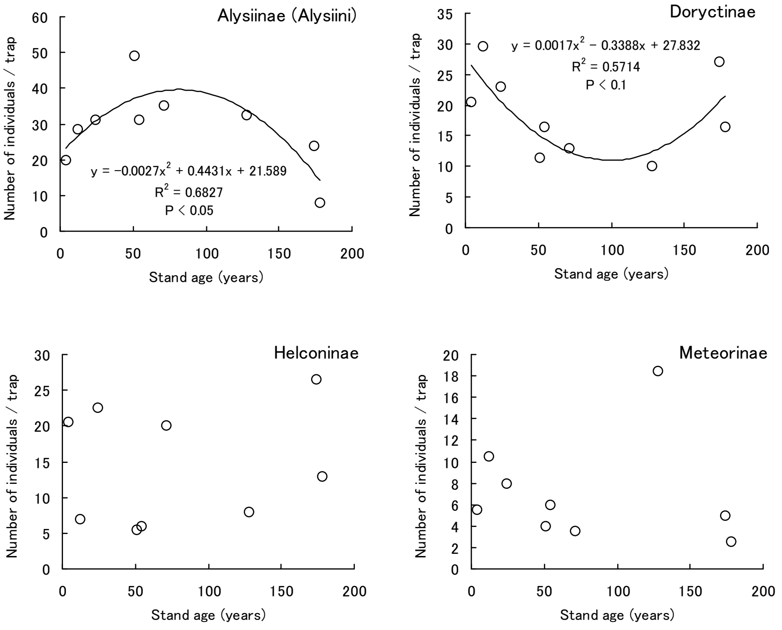

Fig. 4 Relationship between stand age after clear-cutting and the abundance of braconid parasitoids of detritus feeders for each subfamily

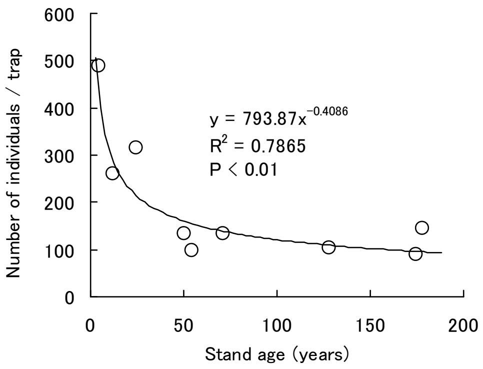

Fig. 5 Relationship between stand age after clear-cutting and the overall abundance of braconid parasitoids of plant feeders

Discussion

In rural landscapes of Japan, old-growth secondary forests provide invaluable habitats for saproxylic insects, such as stag beetles or *Pidonia* longicorn beetles, as well as for some herbivores feeding on flowers and seeds in the canopy (Maeto and Makihara 1999; Maeto et al. 2002; Inoue 2003). Thus, old woodlands free from agricultural or forestry use should be preserved when possible for the conservation of regional biodiversity.

On the other hand, large elements of biodiversity in satoyama landscapes have deteriorated with the abandonment of conventional land use in temperate Japan (Takeuchi et al. 2003; Inoue 2003, 2007; Sueyoshi et al. 2003; Ishii and The Nature Conservation Society of Japan 2005; Makino et al. 2006, 2007). Besides aquatic plants and animals, herbs, grasses, shrubs and herbivorous insects feeding on them are declining in semi-natural grasslands and in the understory layers of coppice woodlands. This not only leads to the extinction of endangered insect species (butterflies), but also weakens ecological functions of rural landscape elements.

In traditional rural ecosystems, semi-natural elements, such as meadows and coppice woodlands, are potential sources of natural enemies for neighboring paddy fields, orchards, vegetable fields, and tree plantations. In the conservation of biological control agents (e.g., Altieri and Nicholls 2004), we expect indigenous natural enemies in semi-natural vegetation to regulate agricultural and forest insect pests. However, our study shows that abandonment or underuse of young coppice woodlands impoverishes the assemblages of indigenous parasitoids of plant-feeding insects and depletes their populations. At least some of them must be potential natural enemies of insect pests in agricultural and forestry fields.

The geographical transition in the abundance of braconid parasitoids of plant feeders in Ogawa and its neighboring area was reconstructed from our data shown in Fig. 5 on a regional forest GIS developed by the FFPRI (courtesy of Dr. A. Miyamoto). It shows that the high-density habitats of parasitoids (over ca. 250 individuals per trap) have been reduced in the last few decades (Fig. 6).

Well-preserved assemblages of indigenous natural enemies in semi-natural elements within rural landscapes make up the base of Integrated Pest Management (IPM), which has been proposed in order to reduce the use of chemical pesticides in pest management (e.g., Pedigo 2002). Modest conventional use of woodlands should be more encouraged in satoyama landscapes for the purpose of environment-oriented agriculture and forestry.

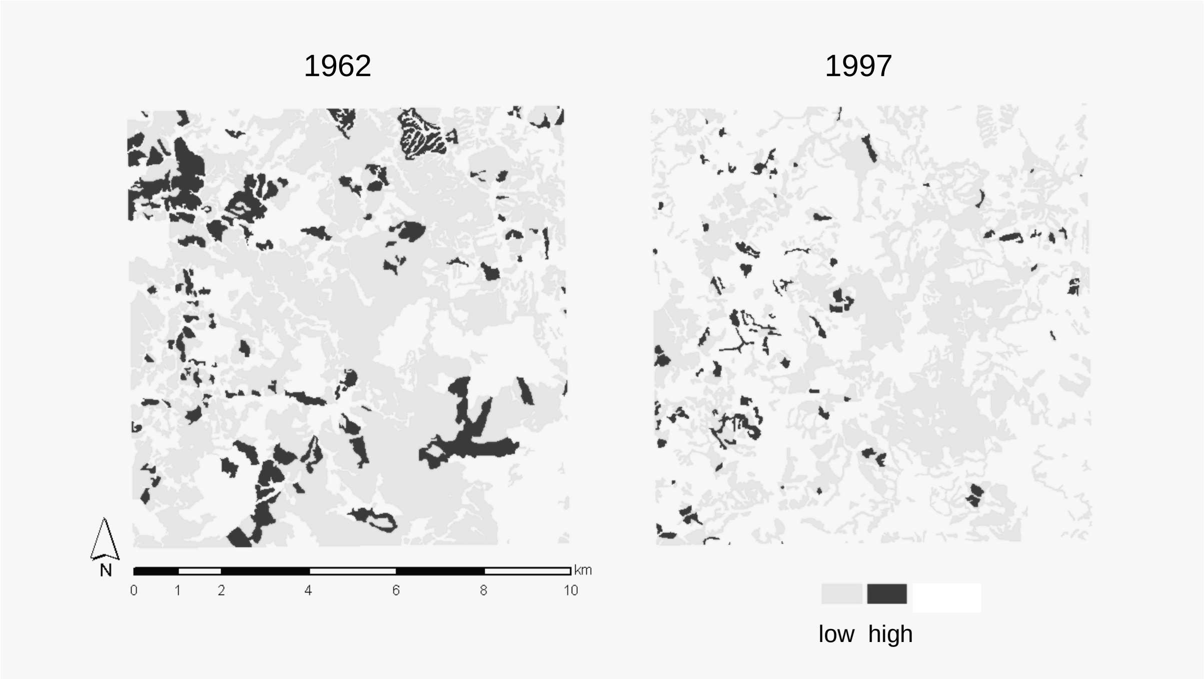

Fig. 6 Reconstructed map of the transition in the abundance of braconid parasitoids of plant feeders in Ogawa and its neighboring area from 1962 to 1997 on a regional forest GIS developed by the FFPRI (courtesy of Dr. A. Miyamoto). Dark and light areas indicate coppice woodlands with more and less than ca. 250 parasitoid individuals per trap, respectively

Acknowledgments

We thank Dr. S. Makino and Mr. H. Goto for field collection of parasitoid wasps with Malaise traps and valuable information about the study area and plots. We are grateful to Dr. A. Miyamoto for reconstruction of the distribution of parasitoids in Ogawa and its neighboring area using GIS.

References

Altieri MA, Nicholls CI 2004 Biodiversity and pest management in agroecosystems, 2nd edition. Food Products Press, New York.

Gauld ID, Bolton B (1988) The Hymenoptera. Oxford University Press, Oxford

Hajek A (2004) Natural enemies – an introduction to biological control. Cambridge University Press, Cambridge

Hanson PE, Gauld ID (eds) (1995) The Hymenoptera of Costa Rica. Oxford University Press, Oxford.

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomol Sci 6: 151-163

Inoue T (2007) Conservation of butterflies in relation to the recent land use change in Japan. Jpn J Soc Grassland Sci 53: 40-46 (in Japanese)

Ishii M, The Nature Conservation Society of Japan (eds) (2005) Nature and conservation of satoyama from the point of view of ecology. Kodansha, Tokyo (in Japanese)

Maeto K, Makihara H (1999) Changes in insect assemblages with secondary succession of temperate deciduous forests after clear-cutting. Jpn J Entomol (NS) 2: 11-26 (in Japanese with English summary)

Maeto K, Sato S, Miyata H (2002) Species diversity of longicorn beetles in humid warm-temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. Biodiv Conserv 11: 1919-1937

Makino S, Goto T, Sueyoshi M, Okabe K, Hasegawa M, Hamaguchi K, Tanaka H, Okochi I (2006) The monitoring of insects to maintain biodiversity in Ogawa forest reserve. Environ Monit Assess 120: 477-785

Makino S, Goto T, Hasegawa M, Okabe K, Tanaka H, Inoue T, Okochi I (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan. Ecol Res 22: 372-381

Maleque MA, Ishii HT, Maeto K (2006) The use of arthropods as indicators of ecosystem integrity in forest management. J For 104: 113-117

Pedigo LP (2002) Entomology and pest management, 4th edition. Prentice Hall, Upper Saddle River

Samways MJ (2005) Insect diversity conservation. Cambridge University Press, Cambridge

Shaw MR, Huddleston T (1991) Classification and Biology of Braconid Wasps (Hymenoptera: Braconidae). Handbooks for the Identification of British Insects, Vol. 7, Part 11. Royal Entomological Society of London, London

Sueyoshi M, Maeto K; Makihara H, Makino S, Iwai T (2003) Changes in dipteran assemblages with secondary succession of temperate deciduous forests following clear-cutting. Bull FFPRI 2: 171-192 (in Japanese with English abstract)

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. In: Nakashizuka T, Matsumoto Y (eds) Diversity and interaction in a temperate forest community: Ogawa Forest Reserve of Japan. Springer-Verlag, Tokyo, pp 27-41

Takeuchi K, Brown RD, Washitani I, Tsunekawa A, Yokohari M (eds) (2003) Satoyama – the traditional rural landscape of Japan. Springer-Verlag, Tokyo

Wharton RA, Marsh PM, Sharkey MJ (eds) (1997) Manual of the new world genera of the family Braconidae (Hymenoptera). Spec Publ Int Soc Hym 1: 1-439

Land Use and Crop Damage by Japanese Macaque on Yakushima Island, Japan

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Introduction

In Japan after WW II, natural broad-leaved forest was extensively converted to artificial coniferous forest (including *Cryptomeria japonica*) for timber production. The Japanese government promoted extensive afforestation throughout the archipelago from the mid-1950s to the mid-1980s. The expansion of farmlands has also altered forests. In particular, some types of fruit have high economic value, and orchards have expanded onto sunny slopes following the clearing of forests. Hence, Japanese forests have changed extensively within a short period.

The ecological aspects of forests have also changed extensively, which should alter the forest ecosystem services available for humans. Wild animals have caused severe crop damage recently, which may be a result of changes in the forest ecosystem. Crop damage is a long-standing source of conflict between humans and wild animals in Japan. However, damage caused by monkeys, deer, wild boars, and other animals has increased extensively since the 1970s. On Yakushima Island, we investigated the spatial elements of land use (including forest use) by humans, which are related to the occurrence of crop damage by monkeys (hereafter monkey damage).

Materials and Methods

We studied two areas on Yakushima Island, i.e., Nagata and Koshima, where there are many orchards, primarily citrus (Fig. 1). Extensive afforestation ensued on the island in the 1960s and 1970s. In 1960, farmlands occupied approximately 40% of the total area. Now, the land is used for forests, farmland, and housing. Orchards expanded from 1960 to 2000 (Fig. 2). In 1980, orchards appeared in the northeastern area where forests had expanded in 1960. Citrus orchards, which have high economic value on the island, have also expanded markedly in other areas since the 1970s.

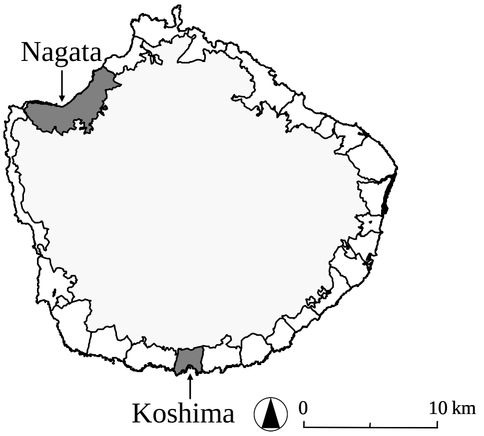

Fig. 1 Location of the study areas on Yakushima Island.

Monkey damage on the island has been severe since the 1980s in the Nagata area, and since the 1990s in the Koshima area. Previous studies investigated the distance between farmlands and forests (Hill 1997; 2000; Naughton-Treves 1998; Saj et al. 2001) and the areas adjacent to farmland (Hill 2000); such spatial elements may affect the occurrence of monkey damage. To elucidate the relationship between land use by humans and the occurrence of monkey damage, however, the spatial elements of land use should be investigated. We performed a questionnaire survey of 11 farmers in the Nagata area and 15 farmers in the Koshima area to determine the extent of monkey damage to orchards in the two areas. The term of the survey was from 1 to 19 September 2003. We selected 12 parameters (Table 1) and used logistic regression to examine the relation between each parameter and the occurrence of monkey damage. In addition, we constructed a risk map of the probability of the occurrence of monkey damage in each area by combining the results of the model and using a geographic information system (GIS).

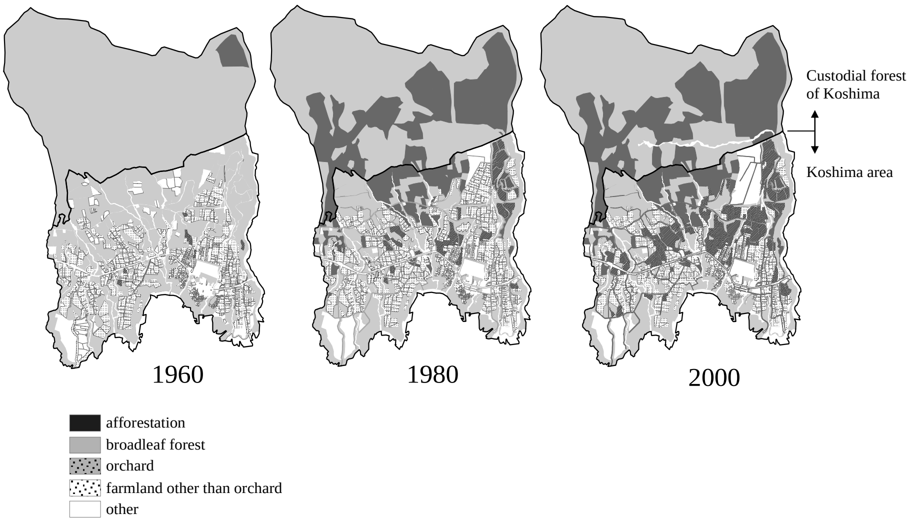

Fig. 2 Land use changes in Koshima.

Table 1 List of parameters considered.

	Name of parameter
dependent parameter	
economic damage to crops caused by Macaque	*Damage*（damage=1，no damage=0）
independent parameter	
distance between forest and orchard (*m*)	*Forest*
distance between housing and orchard (*m*)	*Housing*
distance between road (wide) and orchard (*m*)	*Road* 1
distance between road (middle-wide) and orchard (*m*)	*Road* 2
distance between road (narrow) and orchard (*m*)	*Road* 3
distance between river (wide) and orchard (*m*)	*River* 1
distance between river (middle-wide) and orchard (*m*)	*River* 2
distance between river (narrow) and orchard (*m*)	*River* 3
speceis of fruit tree planted in orchard	*Fspecies* (TANKAN; *Citrus tankan* , HAYATA=1，PONNKAN; *Citrus reticulata* , Blanco=2，TANKAN and PONNKAN=3）
age of fruit tree planted in orchard	*Fage*
whether there is electric fence or not arround orchard	*Fence*（fence=1，no fence=0）
type of forest nearest orchard	*ForestType*（broadleaved forest=1，Japanese cedar forest=2）

Results

The multivariate logistic regression analysis produced probabilities for the occurrence of monkey damage, which are the dependent parameters included in the model. The model was:

$$log\{p(x)/(1 - p(x)) = -1.172 - 0.034 Forest + 0.004 Road1 + B \qquad (1)$$

Nagata: $B = 2.507$

Koshima: $B = 0$

where the primary factors selected were *Forest*, *Road*1, and *B*. The parameter *B* indicates differences in monkey damage between the areas and was significant (p = 0.000); the perceived monkey damage was greater in the Nagata area. Parameters regarding the quality of the orchard showed no significant differences.

We calculated the probability function of monkey damage as $p(x)$. We then constructed two risk maps of monkey damage using the function and GIS (Fig. 3). More than 90% of orchards in the Nagata area and approximately 30% of orchards in the Koshima area might suffer monkey damage, with a risk > 50%.

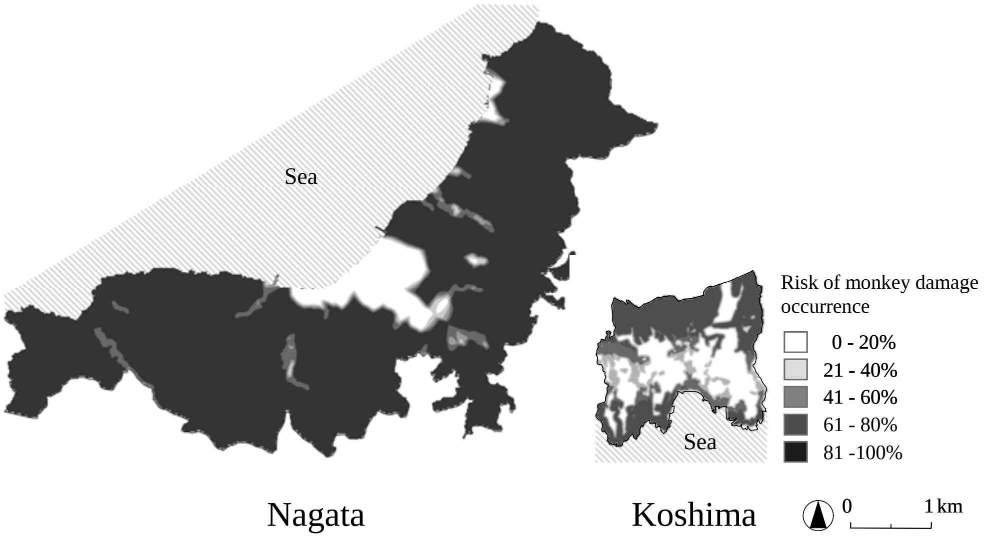

Fig. 3 Maps indicating the risk of crop damage caused by Japanese macaque.

Discussion

The model indicated that the distance between forests and farmlands (i.e., the parameter *Forest*) was negatively correlated with the occurrence of monkey damage. This result supports those of previous studies that suggest similar patterns of occurrence for monkey damage on Yakushima Island (Hill 1997; 2000; Naughton-Treves 1998; Saj et al. 2001). Monkeys are arboreal animals and forest is a space of safety for them. Therefore, when the distance between forests and farmlands is greater, the risk of raiding farmlands might be higher for monkeys. The model also indicated that the distance between roads and farmlands (i.e., the parameter *Road*1) was positively correlated with the occurrence of monkey damage. This road parameter accounts for wide roads, which are prefectural main roads with much traffic. Therefore, monkeys might avoid these roads. These spatial elements of land use, rather than variables related to orchard characteristics, are important in predicting the occurrence of monkey damage on the island.

The distance between forests and farmlands could change with the alteration of forests and large-scale timber extraction. At the study sites, the extent of changes in land use was small, although the forest physiognomy has changed extensively in the last 40 years. Orchards have expanded since the 1970s by the clearing of forest areas. Newer orchards are more likely to be closer to forests and thus are more likely to suffer from monkey damage. We used only the current spatial elements in these analyses. Therefore, it is not possible to predict how previous changes in forest use affected the occurrence of monkey damage. We can only suggest that new farmlands located on newly cleared land would be more likely to suffer damage from monkeys.

Compared to the Koshima area, monkey damage was high in the Nagata area, where the population density of Japanese macaque was higher and the damage began earlier in the season. In other words, farmlands more likely suffer monkey damage in the Nagata area than in the Koshima area, even when the parameters *Forest* and *Road*1 are the same. The parameter *B* may imply variation in the density of monkeys, their habituation to humans, and their habitats. The forest ecosystem would affect the parameter *B* and cause differences in the extent of monkey damage.

References

Hill CM (1997) Crop-raiding by wild vertebrates: the farmer’s perspective in an agricultural community in western Uganda. Int J Pest Management 43(1): 77-84

Hill CM (2000) Conflict of interest between people and baboons: crop raiding in Uganda. Int J Primatology 21(2): 299-315

Naughton-Treves L (1998) Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conservation Biol 12(1): 156-168

Saj TL, Sicotte P, Paterson JD (2001) The conflict between velvet monkeys and farmers at the forest edge in Entebbe, Uganda. Afr J Ecol 39: 195-199

Crop Raiding by Wildlife due to Landscape Modifications: Ecological Function Losses Caused by Forest Development on the Island of Yakushima, southern Japan

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Monotonous forest and deterioration of ecological functions

In primary industries, mass production requires intensive and monotonous land use, especially large-scale logging and commercial planting, such as seen in monocultures of coffee, palm, gum, and sugarcane, which are cultivated widely throughout tropical and subtropical regions (e.g., Nagata et al. 1994; Hartemink 2005). However, such monotonous land use has damaged the ecological functions and services that result from forest ecosystems (e.g., McNeely et al. 1990; Lugo 1997).

In Yakushima, located off the south coast of Japan, monotonous land use has developed mainly as large-scale logging of natural forests and replacement with coniferous trees, in accordance with policies of the Forest Agency that were formulated in 1958 and aimed at increasing wood production. However, forest development has disturbed animal and plant communities (e.g., Aiba unpub. data; Yumoto unpub. data) as well as ecological functions (e.g., Japan Institute of Land and Environmental Studies 1981). On the island of Yakushima, endemic subspecies of Japanese deer (*Cervus nippon yakushimae*) and monkeys (*Macaca fuscata yakui*) have experienced major habitat disturbance. In general, the food supply of herbivores fluctuate widely after logging and planting for about 20 years in Japan (e.g., Koizumi 1988; Sone et al. 1999; Hanya et al. 2005). Logging initially destroys plant production, but it quickly recovers with improved exposure to sunlight. However, it subsequently decreases rapidly to minimum levels, concomitant with growth of trees (Fig. 1). On Yakushima, the extensive forest transformations of the 1960s and 1970s have preceded intensive crop damage by these species in the 1980s and 1990s. Thus, crop raiding by mammals occur after major fluctuations in their habitat caused by monotonous plantations. This paper reviews the processes and factors of agricultural crop raiding by these mammals in relation to forest development on Yakushima, with reference to cases from other locations in Japan.

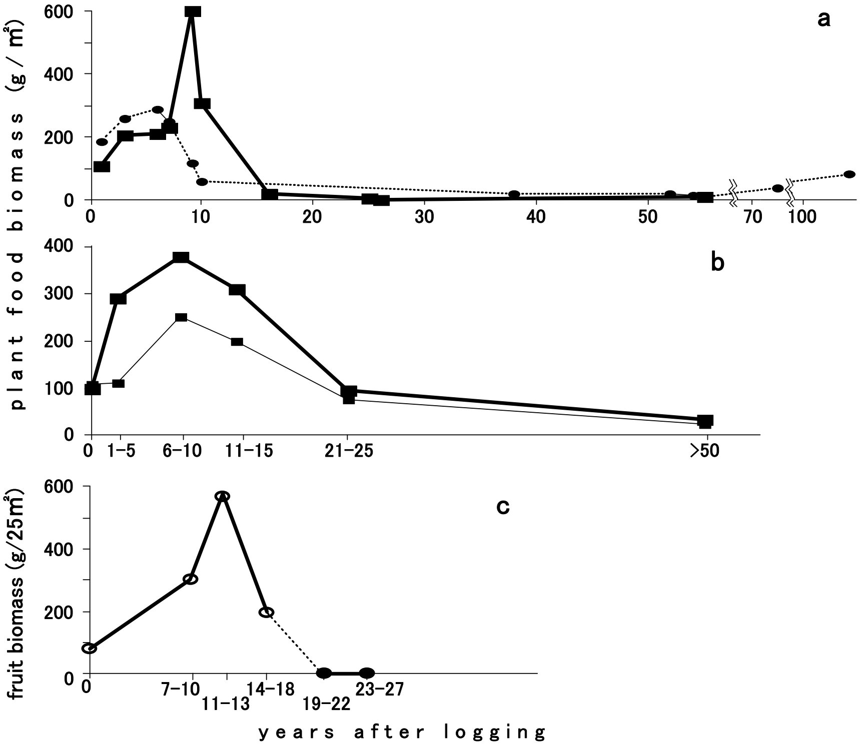

Fig. 1. Food plant biomass (g dry weight/m^2) after clear-cut logging of broad-leaved forests. (a) Food plant biomass for Japanese sika deer under cedar plantations (solid line) and secondary broad-leaved forests (broken line) (modified from Takatsuki 1992). (b) Food plant biomass (g dry weight/m^2) for Japanese serow under conifer plantations in November (solid line) and August (thin line) (drawn from Sone et al. 1999). (c) Fruit biomass (g/25 m^2), as food for Japanese monkey, in primary and secondary broad-leaved forests (solid circles) and cedar plantations (open circles) (modified from Hanya et al. 2005).

Forest development

Yakushima is a circular, mountainous island (ca. 500 km^2) located in southern Japan (30°N, 130°E). Approximately 14,000 inhabitants live in about 20 villages located less than 100 m above sea level (a.s.l.); most other areas are afforested with about 80% being National Forest property. Natural forests, consisting mainly of evergreen broad-leaved trees, occur from 0 to 800 m a.s.l.; between 800 and 1800 m, the forests consist of both broad-leaved and coniferous trees. In addition, many natural Japanese cedars occur, especially over 1200 m a.s.l. (Tagawa 1994). Annual precipitation at lower altitudes is 2500–5000 mm; at higher altitudes, rainfall reaches 7000 mm, and occasionally 10000 mm (Kagoshima Prefecture 1992). At the coast, the annual mean temperature is about 20℃ (Tagawa 1994); above 1000 m a.s.l., the climate is much cooler, with snow cover in winter.

On Yakushima, intensive logging began in the upland regions for cedar. Logging of conifers increased in the 1950s but decreased in the 1960s owing to tree depletion (Fig. 2). However, with increased demand for wood and pulp products, the logging area shifted to broad-leaved forests at intermediate altitudes. Logging volumes of broad-leaved trees increased significantly from 1963, but decreased after 1973 (Fig. 2) with the reduction in the market price of wood (Japan Federation of Bar Associations 1991) combined with increased awareness of nature conservation (Kamiyaku Town 1984). After the logging of broad-leaved trees, Japanese cedar was widely planted in areas that were not the natural habitat of this species (Fig. 2).

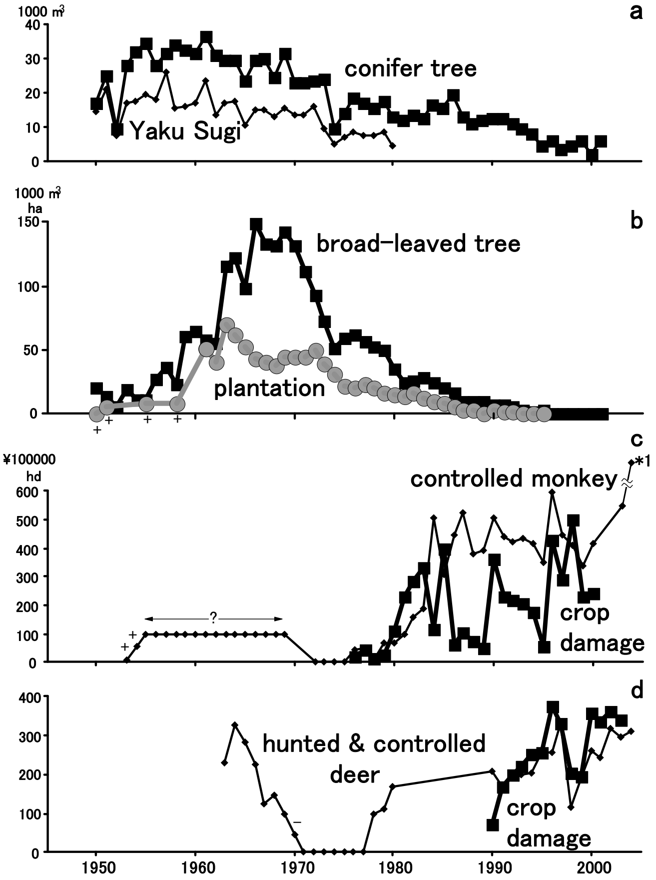

Fig. 2. Annual logging volumes, conifer planting areas, agricultural crop damage by wildlife, and number of hunted animals. Possible underestimated values (+), possible overestimated values (–), and approximate values (?). (a) Logging volume of conifer trees (solid line) (Suwa pers. commun.) and cedar (thin line) (Fujimura 1971; Miura 1984). (b) Logging volume of broad-leaved trees (solid line) (Suwa pers. commun.) and conifer plantation area (gray line) (Kagoshima Prefecture 1992; data of Forest Agency). (c) Amount of crop damage (×\100000, ca. $800) by monkeys (solid line) and number of monkeys culled (thin line) (Azuma 1984; Hirose 1984; Kagoshima Prefecture 1992; Agetsuma 1998). Values of *1 are 833 individuals. Monkeys were captured for experimental use in the 1950s and 1960s. After 1972, all captures were conducted as pest control measures. (d) Amount of crop damage by deer (solid line) and the number of hunted and culled deer (thin line) (Kagoshimaken Shizen Aigo Kyokai 1981; Kagoshima Prefecture 1992; Sueyoshi 1992). Deer hunting was prohibited during 1971–1977. From 1999, deer control has focused in the vicinity of farms.

Land-use changes in lower areas

Below 300 m a.s.l., the inhabitants of Yakushima had deforested the land and cultivated it intensively for traditional practices, such as swidden cultivation, fuelwood, and charcoal (Sprague unpub. data). As a result, the area of "rough land," that is, treeless land, spread extensively in the 1920s (Sprague unpub. data). On Yakushima, monkeys (Agetsuma 1995) and deer (Agetsuma and Agetsuma-Yanagihara 2006) in a natural forest are mainly dependent on the tall trees for their foods; therefore, a “treeless land” may be of little use to them, although deer could utilize herbaceous plants (Takatsuki 1990) and monkeys could feed on the fruit of some shrubs (Hanya 2004). In addition, increased human activity in farming areas would discourage the use of such places by these animals. However, fuel and fertilizer revolution occurred. In addition, because of the shift in the industrial structure of the island, the area of farmed land and number of farmers decreased significantly between 1950 and 1975 (Fig. 3). Then, some areas of treeless land and farmed areas were converted to orange groves in the 1970s through the promotional efforts of local governments (Agetsuma 1998). Although, most treeless lands were abandoned and subsequently reverted to broad-leaved forests after 1970s (Sprague unpub. data), thereby providing renewed resources for wildlife. Consequently, in lower areas, an overall decrease occurred in treeless lands with a simultaneously increase in broad-leaved forests and orange groves. Production of oranges has increased greatly since 1980 (Fig. 3).

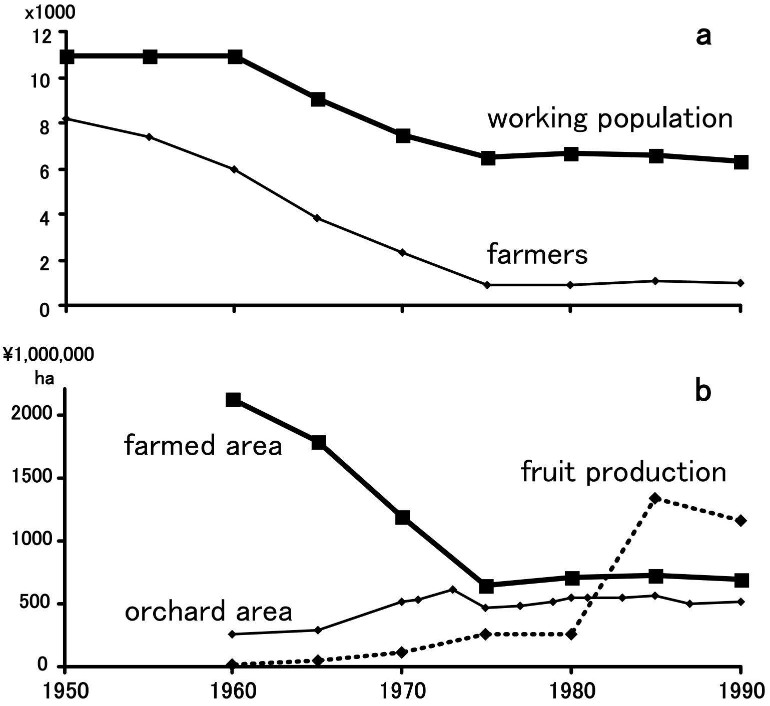

Fig. 3. Working population, farmland area, and fruit production (×\1000000, ca. $8000) in Yakushima. (a) Total working population (solid line) and numbers engaged in agriculture (thin line) (Kagoshima Prefecture 1992). (b) Farmed areas of the five main crop items (solid line), orchards (thin line), and fruit production (broken line) (Kagoshima Prefecture 1992; Agetsuma 1998).

Outbreaks of crop raiding and pest control

Monkeys damage oranges, other fruits, and sweet potatoes (data of Kamiyaku Town). On the island of Yakushima, crop raiding by monkeys was reported before 1950 (Itani 1994), but the amount of damage increased greatly after 1980 (Fig. 2). After 1978, in response to crop raiding, local governments implemented pest control on monkeys. However, between 1978 and 1983, even though the number of controlled monkeys increased, crop damage still increased (Fig. 2) and the high level of damage is continuing, even though 300–600 monkeys have been culled every year since 1984. In spite the fact, many assume that increases in the monkey population have been averted by culling. However, the numbers have not been determined scientifically but have been influenced mainly by voluntary efforts of local hunters and the availability of bounties from local governments. Therefore, it would be purely coincidental if the number of monkeys culled equalled the number required to halt population growth. It is more likely that the population has increased to match the number culled, thereby maintaining a constant population size.

On Yakushima, severe raiding of agricultural crops by deer has been recorded from the 18th century (Kamiyaku Town 1984). However, over the last 60 years, crop raiding by deer greatly increased in the 1990s (Fig. 2). Crops damaged were mainly orange trees by bark stripping (data of Kagoshima Prefecture), sweet potatoes, and rice (Sueyoshi 1992). Deer hunting has been conducted traditionally in Yakushima, and during the 1950s, more than 1000 deer were killed annually (Kamiyaku Town 1984). The number of hunted deer, however, rapidly decreased between 1964 and 1970 (Fig. 2), and ultimately, deer hunting was banned in 1971. It was reintroduced in 1978 as a pest control measure, but damage to crops and forestry seemed not to be widespread during this period (Tagawa 1987). Deer control was implemented over the whole island, and thus deer with no association to crop damage were also controlled. However, from 1999, deer control was limited to around farmland in an effort to target actual raiding deer. After 1980, the number of culled deer remained at 200–300 (Fig. 2). Thus, raiding deer were controlled more intensively than pre-1999, but no reduction in crop damage occurred.

From the empirical data, two common trends in crop raiding by both mammals are recognizable. One is the timing of the rapid increase in crop raiding, which occurred after a delay of approximately 20 years from the logging peak of broad-leaved forests (Fig. 2). The other is the ineffectiveness of pest control in reducing crop damage.

Impact of forest development on mammal ecology

The impact of transforming natural forests to monotonous conifer plantations on the ecology of wildlife includes alteration in diet, habitat use, and other behaviors (Gill et al. 1996). To evaluate the impact, population density is used as an easily measurable index. On Yakushima, the density of monkey groups has tended to decrease with the spread of plantations (Hill et al. 1994) and correspond closely to the food production of forests (Hanya et al. 2004, 2005). Ohsawa et al. (1995) and Agetsuma et al. (2003, unpub. data) surveyed deer density in forests at different degrees of planting. These studies showed that deer densities in heavily planted sites were much lower than those of relative undisturbed sites (Fig. 4). The impact cannot be minimized, even several decades after planting. Deer hunting and cull statistics suggest that the deer population declined soon after intensive logging. Numbers of hunted deer decreased greatly in the 1960s (Fig. 2), which may indicate a population decline. Similar decreases in population densities caused by food depletion due to the establishment of conifer plantations have also been reported in roe deer (*Capreolus capreolus*) (Gill et al. 1996) and Japanese serow (*Capricornis crispus*) (Sone et al. 1999). It is probable that the monkey and deer populations decreased owing to lowered productivity through logging and planting. Subsequently, they gradually recovered, in tandem with renewed production, mainly in naturally regenerating forest stands.

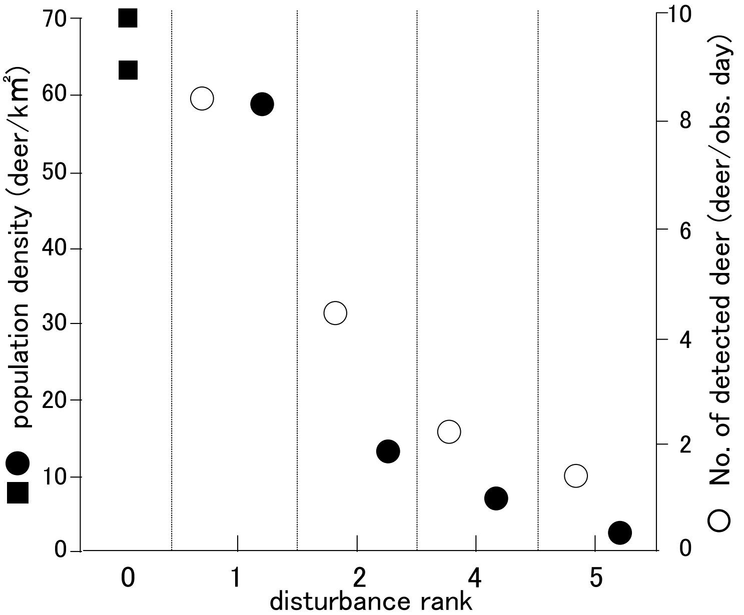

Fig. 4. Relative deer population density at six sites in Yakushima. Solid squares indicate estimated population densities in two lowland natural forests (50–200 m a.s.l.) almost without plantations in 2001 (Agetsuma et al. 2003). Solid circles indicate the estimated densities in 2004 (Agetsuma et al. unpub. data) and open circles denote the number of detected deer per observation day in 1994 (Ohsawa et al. 1995) at four sites, including plantations at intermediate altitudes (300–700 m a.s.l.). Sites with higher disturbance ranks have more areas of younger plantation. Disturbance rankings 1–5 are from Hill et al. (1994).

Relationship between crop raiding and habitat transformation

In Hyogo Prefecture, a positive relationship was found between the occupancy of conifer plantations and crop damage by deer (Sakata et al. 2001). In addition, crop damage by monkeys was greater in regions with 40–50% areal coverage by conifer plantations (Japan Society for Preservation of Birds 1988). These statistics imply some negative influences of plantations regarding the prevalence of crop raiding. On Yakushima, crop raiding increased rapidly with fluctuations in food resources after logging and conifer planting. However, the populations might have been lower than the pre-intensive logging period, which means that a population eruption cannot explain the onset of intensive crop raiding. Crop raiding is possibly influenced by specific ecological and behavioral changes; otherwise, more incidences of raiding would have been previously recorded (i.e., in the1950s) when the animal population was higher and the area of farmland greater than in the 1980s (Fig. 3). Ambiguous or inverse relationships between herbivore densities and damage to crops, forestry, or natural vegetation have been reported (e.g., Oi and Suzuki 2001; Sakata et al. 2001). Ochiai (1996) suggested that damage to plantation trees by serow commenced before the increase in population density. These data suggest that functional responses, such as a shift in ecological strategies, play an important role in crop raiding, rather than simply wildlife density.

The reasons why animals change ecological strategies might be explained as adaptations to fluctuations in habitat. Different ecological strategies has been understood as adaptations to habitat stability and unpredictability (e.g., Begon et al. 1986). Such adaptations would explain interspecific differences of ecology. Similarly, the same species and even individuals within their respective ranges of capability must change their ecology in relation to habitat stability. To confirm the shift in ecological strategies of mammals due to habitat disturbance, it is necessary to further analyze the history of habitat disturbances in relation to crop raiding.

Changes in landscape structure would facilitate crop raiding. At the intermediate altitudes on Yakushima island, forests have been transformed into low-productivity conifer plantations. In contrast, at lower altitudes, low-productivity treeless terrain has reverted to broad-leaved forest (Sprague unpub data). The natural resources for wildlife have changed inversely from "middle to low altitude" to "low to middle altitude". This shift in landscape structure encourages raiding and makes it difficult to defend crops. The problem is a result of ecological function loss due to landscape modification. Therefore, appropriate landscape management strategies are required to resolve the issue of crop raiding by wildlife.

References

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): The influence of food availability and temperature. Int J Primatol 16:611–627

Agetsuma N (1998) Crop damage by wild Japanese monkeys on Yakushima Island, Japan (in Japanese with English abstract). Jpn J Conserv Ecol 3:43–55

Agetsuma N, Agetsuma-Yanagihara Y (2006) Ecology of Yaku sika deer in the island of Yakushima (in Japanese). In: Ohsawa M, Tagawa H, Yamagiwa J (eds) World Heritage, Yakushima. Asakura Publishing, Tokyo pp 143–149

Agetsuma N, Sugiura H, Hill DA, Agetsuma-Yanagihara Y, Tanaka T (2003) Population density and group composition of Japanese sika deer (*Cervus nippon yakushimae*) in ever-green broad leaved forest of Yakushima, southern Japan. Ecol Res 18:475–483

Azuma S (1984) Monkeys, forests and people (in Japanese). Monkey 28:94–102

Begon M, Harper JL, Townsend CR (1986) Ecology: Individuals, populations and communities (3rd edition). Blackwell Science, Oxford

Fujimura S (1971) Forest development and nature conservation (in Japanese). Water-Utility Research Institute Japan, Tokyo

Gill RMA, Johnson AL, Francis A, Hiscocks K, Peace AJ (1996) Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. For Ecol Manage 88:31–41

Hanya G (2004) Diet of a Japanese macaque troop in the coniferous forest of Yakushima. Int J Primatol 25:55–71

Hanya G, Yoshihiro S, Zamma K, Matsubara H, Ohtake M, Kubo R, Noma N, Agetsuma N, Takahata Y (2004) Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. Ecol Res 19:485–493

Hanya G, Zamma K, Hayaishi S, Yoshihiro S, Tsuriya Y, Sugaya S, Kanaoka MM, Hayakawa S, Takahata Y (2005) Comparisons of food availability and group density of Japanese macaques in primary, naturally regenerated, and plantation forests. Am J Primatol 66:245–262

Hartemink AE (2005) Plantation agriculture in the tropics. Environmental issues. Outlook Agric 34:11–21

Hill DA, Agetsuma N, Suzuki S (1994) Preliminary survey of group density of *Macaca fuscata yakui* in relation to logging history at seven sites in Yakushima Japan. Primate Res 10:85–93

Hirose S (1984) Hunters of Yakushima (in Japanese). Monkey 28:82–87.

Itani J (1994) Nature and people in Yakushima (in Japanese). Seimei No Shima 30:25–29

Japan Federation of Bar Associations (1991) Consideration of future forests (in Japanese). Yuhikaku Publishing, Tokyo

Japan Institute of Land and Environmental Studies (1981) Research on mudslides in Kamiyaku Town, Kagoshima Prefecture (in Japanese). Kokudo Mondai 22:1–86

Japan Society for Preservation of Birds (1988) Survey on measures to control damage by wildlife: Japanese monkey and common cormorant (in Japanese). Environment Agency, Tokyo

Kagoshimaken Shizen Aigo Kyokai (1981) Survey of distribution of Yaku sika deer (in Japanese). Kagoshimaken Shizen Aigo Kyokai Chousahoukoku 5:1-34.

Kagoshima Prefecture (1992) Master plan of the Yakushima Environmental Culture Village (in Japanese). Kagoshima Prefecture, Kagoshima

Kamiyaku Town (1984) Chronicle of Kamiyaku Town (in Japanese). Kamiyaku Town, Kamiyaku

Koizumi T. (1988) Management of sika deer in Hokkaido. The effects of forest management and hunting on the deer populations (in Japanese with English summary). Res Bull Hokkaido Univ For 45:127–186

Lugo AE (1997) The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. For Ecol Manage 99:9–19

McNeely JA, Miller KR, Reid WV, Mittermeier RA, Werner TB (1990) Conserving the world's biological diversity. IUCN, Gland, WRI, CI, WWF-US, The World Bank, Washington, DC

Miura K (1984) Nature conservation of Yakushima (in Japanese). Monkey 28:64–69

Nagata S, Inoue M, Oka H (1994) Forest utilization pattern in the course of economic development. In an inquiry of the U-shaped hypothesis of forest resources (in Japanese with English summary). Rural Culture Association, Tokyo

Ochiai K (1996) Effects of forest management on Japanese serow populations in relation to habitat conservation for serows (in Japanese). Mammal Sci 36:79-87

Ohsawa H, Yamagiwa J, Hill DA, Agetsuma N, Suzuki S, Vadher SKA, Biggs AJ, Matsushima K, Kubo R (1995) Disturbances of ecology of wildlife by cedar plantation in Yakushima Island, WWF-J Report (in Japanese). Yakushima Wildlife Conservation Project, Inuyama

Oi T, Suzuki M (2001) Damage to sugi (*Cryptomeria japonica*) plantations by sika deer (*Cervus nippon*) in northern Honshu, Japan. Mammal Study 26:9–15

Sakata H, Hamasaki S, Kishimoto M, Mitsuhashi H, Mitsuhashi A, Yokoyama M, Mitani M (2001) The relationships between sika deer density, hunting pressure and damage to agriculture in Hyogo Prefecture (in Japanese with English abstract). Hum Nat 12:63–72

Sone K, Okumura H, Abe M, Kitahara E (1999) Biomass of food plants and density of Japanese serow, *Capricornis crispus*. Mem Fac Agric Kagoshima Univ 35:7–16

Sueyoshi M (1992) Damages by sika deer on Yakushima, Kagoshima Prefecture (in Japanese). For Pests 41:33–35

Tagawa H (1987) Researches on dynamics and management of Biosphere Reserves (in Japanese). In: Researches on Dynamics and Management of Yakushima Biosphere Reserve, Research team of "Dynamics and management of Yakushima Biosphere Reserve," Kagoshima, pp 1–11

Tagawa H (1994) Natural World Heritage, Yakushima (in Japanese). Japan Broadcast Publishing, Tokyo

Takatsuki S (1990) Summer dietary composition of sika deer on Yakushima Island, southern Japan. Ecol Res 5:253–260

Takatsuki S (1992) Sika deer living in the north (in Japanese). Dobutsusha, Tokyo

Factors Affecting Wild Resource Use: Actual Use of Wild Resources by the Penan Benalui of East Kalimantan

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Introduction

Many studies have shown that local people know numerous useful wild species (e.g., Boom 1987; Milliken et al 1992; Balée 1994; Christensen 2002). Long inventories of useful wild species are usually considered to express the importance of biodiversity to local people. Some (or even many) species on such a list, however, are hardly used (e.g., Dwyer 1990, 122; Koizumi & Momose 2007). Actual use of species is determined by availability, preference, need, and other factors.

This paper examines use of wild species by the Penan Benalui, a former hunter-gatherer group of East Kalimantan, Indonesia. Among 713 species of wild plants examined in a previous study (Koizumi & Momose 2007), 540 species are reported useful by the Penan Benalui. According to them, however, only 212 species are of good quality, often used, or important for a certain purpose(s) (ibid.). I describe two examples of wild resource use here. One is wild species used for food during a three-month survey. In this example, several species were intensively used. The other is rattan species used for basketry. Changes in the use from 2002 to 2007 are described. I then summarize factors affecting actual use of species and discuss the advantage of knowing currently less or rarely used but potentially useful species.

Penan Benalui

The Western Penan is a Bornean hunter-gatherer group, and the Penan Benalui is a subgroup of the Western Penan (Needham 1972; Hildebrand 1982; Brosius 1992, 52–55, 60–68; Puri 2005, 2–6). About 2900 Western Penan, not including the Penan Benalui, live in Sarawak, Malaysia (Brosius 1999), and about 450 Penan Benalui live in East Kalimantan, Indonesia. Traditionally the Western Penan were essentially self-sufficient in obtaining food, eating forest products such as sago palms, fruits, bearded pigs, leaf monkeys, and palm shoots, though they also interacted with farmers for trade and protection from raids (Brosius 1991; 1992, 111–96).

According to the Penan Benalui, farmers encouraged the Penan Benalui to live in their villages and to learn how to farm. Behind this encouragement was pressure from Indonesian bureaucrats and pastors on the farmers to persuade the Penan Benalui to settle and farm (Puri 1997, 78; 2005, 56). The Penan Benalui gradually adapted to sedentary life from the mid-1950s (Puri 1997, 77–78; 2005, 55–56). The present Penan Benalui are practicing a mixed subsistence economy. They, however, largely depend on forest products for cash income as well as for food and material culture.

Methods

Fieldwork was conducted in the village of Long Belaka (2°41´ N, 115°43´E), a Penan Benalui community, in East Kalimantan, Indonesia from 2002 to 2007. The residential site of the village is located about 300 m above sea level and surrounded by mountains. The forest around the village is mainly lowland dipterocarp forest.

Plants were collected with informants in mature and secondary forests and along riversides around the village at about 300–600 m above sea level (Koizumi & Momose 2007). During these collections, informants were interviewed about ethnobotanical information including plant names and uses. The informants were ten men and two women between the ages of about 30 and 60 who were relatively knowledgeable about plants. I made a list of plants for each use mentioned in the field. For each use category, one or two (or three) villagers were asked to name plants associated with that use. I also asked which plants were often used, were of good quality, or were considered important for each use category.

The food survey was conducted from September to November 2004 for a total of 20 days (Dounias et al 2007). At each house of the study village, I conducted interviews about foods the inhabitants had eaten. I asked the names of dishes, ingredients of the dishes, and asked who hunted, collected, or harvested the ingredients. There were 20 houses in the village at the time of the survey. Data was collected for 346 day-houses. I could not interview at some houses on some days because the people were staying at a downriver village or swidden field. I analyzed the times of use of each kind of ingredient. If an ingredient was used at a house for a dish at a meal, it was counted as "1 time."

Voucher specimens were identified by me and other botanists. Voucher specimens are mainly deposited in Herbarium Bogoriense (Indonesia) and the Kyoto University Museum (Japan).

Results

(1) Wild plants and animals appeared in the food survey

Only 16 or 17 species of wild plants appeared in the food survey (Table 1), though the Penan Benalui know at least 193 edible species (Koizumi & Momose 2007). One of the reasons for this is that forest fruits were not available during the survey period. Some food resources, especially fruits and fungi, are not available throughout the year.

Although the Penan Benalui knew about 10 edible ferns, *Diplazium esculentum* (Retz.) Sw. was almost exclusively used. The species was abundant in open places around the village, especially on moist soil along rivers. The fern was thus easy to collect and considered a delicious fern by the villagers. The fern, however, was a far less favored food than meat, especially when oil was not available and the leaves were just boiled. Nevertheless, the species was often collected when meat was not available.

Sago starch was processed only from *Arenga undulatifolia* Becc., though the Penan Benalui know eight kinds of wild sago palms. Distribution, abundance, and taste of the palms account for the use of the species. Four palms are not found near the study village. Two palms grow near the village, but they are not very abundant. Two species, *A. undulatifolia* and *Eugeissona utilis* Becc., are abundant around the village. According to the villagers, the starch of *A. undulatifolia* is sweet, while that of *E. utilis* is bitter unless it is cooked with fat. The processing of sago starch requires much effort, and the villagers processed the starch only when they did not have rice. Furthermore, many villagers preferred to earn money to buy rice rather than to process the starch.

The shoots of *A. undulatifolia* and *E. utilis* were similarly often used. They were abundant, as explained above, and have large shoots. The shoots of the two species have different tastes, but the villagers liked both of them. According to a villager, eating the shoots of *Oncosperma horridum* Scheft. is a good remedy for headache. Although it was not asked in the survey, the shoots were collected and eaten not only for its good taste but also for the medicinal property.

Leaves of *Albertisia* sp. were pounded and cooked with other ingredients like monosodium glutamate. The plant was not abundant but not rare in the forest around the village. Although monosodium glutamate was usually used, villagers said that palm shoots tasted better when they were cooked with the leaves.

Table 2 shows wild animals appeared in the food survey. (The villagers used wild meat bought in a downriver village at two times, but they are excluded from Table 2.) The bearded pig (*Sus barbatus*) was used far more often than any other animals. It was the most favored food for most villagers. When adult bearded pigs were hunted, the meat was distributed to all families of the village. The sambar deer (*Cervus unicolor*) is also a large animal, but the villagers did not value the meat so much as that of the bearded pig. The sambar deer is one of the pest animals, and they were usually hunted around swidden field. In general, when men went hunting with a spear and dogs or with a shotgun, they and other villagers hoped that they would get the bearded pig. Some men sometimes went hunting with a blowpipe to hunt the gray leaf monkey (*Presbytis hosei*) when the bearded pigs were scarce. The people may also hunt other animals that they happen to encounter (Puri 1997, 2005).

(2) Depletion of a rattan species and change in rattan use

During the study period, a change in use of rattans was observed. *Calamus caesius* Blume is the most valued rattan species for fine basketry in the study area. The villagers of Long Belaka were frequently producing **bukui**, a kind of rattan basket, made from *C. caesius*. In 2003 and 2004, they had bad rice harvests and worked hard to collect and process forest products to earn money to buy rice. Rattan baskets were among the most common forest products they sold. Some women even newly learned how to weave **bukui**. In 2005 or 2006, however, some families stopped producing rattan baskets made from *C. caesius*. According to an elder, his family stopped producing the baskets because the rattan was depleted. (Conversely, another man about 40-year old said that rattan was still abundant. Being asked further, he answered that the rattan was depleted around the village, but was still available at places which could be reached by 3–4-hour walk from the village.) The villagers started to produce **kavung**, a different model of rattan basket, for sale in 2006. They learned the model from the Kayan, swidden agriculturalists. The baskets can be made from *Calamus javensis* Blume and *Korthalsia* cf. *hispida* Becc., both of which are most common species around the village.

Discussion

(1) Factors affecting actual use

In the above examples, availability of resources in time and space affected actual use (Fig. 1). Availability in time or seasonality controls the possibility of use. It is impossible, for example, to collect the fruit of a certain species when it is not fruiting time. Seasonal resources, however, contribute to people’s livelihoods when available. Availability in space, in terms of distribution, habitat, and abundance, is closely related to searching costs. Searching costs can be reduced if two or more resources are collected at the same time.

There are also collecting and processing costs, which are related to morphological, chemical, behavioral, or other characters of resources. The costs can be reduced or increased by collecting and processing techniques. The possibility to use a resource may even depend on whether a community or an individual has a proper technique or not.

The decision to use a resource depends on the balance of perceived costs and benefits. The perceived costs partly depend on the perception of effort by individuals. The same work, for example, can be a relatively easy task for young men and a hard task for elders. The benefits that can be gained from a resource are related to quality and amount of the resource. At the same time, however, it is not determined by the resource itself. People judge the benefits according to their perception of the quality, preference, and need. The need for a resource changes according to the situation of each individual, household, community, and of the outside world (e.g., the market).

(2) Advantage of knowing potentially useful species

People usually know several or many species for a certain purpose. In general, different species have different availability and quality. This will result in people's perception of different costs and benefits of using these species. (As I have explained, the costs and benefits here are determined not only by objective factors but also by subjective factors.) The species of a better cost-benefit balance will more likely to be used. As far as there is a highly available or highly valued species, the species is intensively used and others are less or not used. It is not surprising that people know seasonally available resources and resources used for special occasions (such as eating a certain food, etc. when someone is sick, when someone becomes tired), though they may not be used at all during a short period. Rare resources may not be searched for specially, but they will be collected or hunted when people happen to encounter them. What, however, is the advantage of knowing species of perceived inferior quality?

The situation can change. Availability of a good quality resource may be depleted by overuse, as in the rattan case in this paper. An alternative resource then exhibits a better cost-benefit balance than the depleted one. An inferior resource can even become a best resource if a new way of use or new technique is introduced, or if the people's preference changes. The informants often introduced a plant by saying, "This is used for ——— (a certain purpose) if there is no ——— (a plant name)." People are prepared, to some extent, for changing situations. Knowledge of alternative species or resources will help people to quickly adapt to a new situation.

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References

Balée WL (1994) *Footprints of the forest: Ka'apor ethnobotany: The historical ecology of plant utilization by an Amazonian people*. Columbia University Press, New York.

Boom BM (1987) *Ethnobotany of the Chácobo Indians, Beni, Bolivia*. Advances in Economic Botany 4. The New York Botanical Garden, New York.

Brosius JP (1991) Foraging in tropical rain forests: The case of the Penan of Sarawak, East Malaysia (Borneo). *Human Ecology* **19**:123–50.

——— (1992) The axiological presence of death: Penan Gang death-names. Dissertation, University of Michigan.

——— (1999) The Western Penan of Borneo. In *The Cambridge encyclopedia of hunters and gatherers* (ed. B. Lee and R. Daly), pp. 312–16. Cambridge University Press, Cambridge.

Christensen H (2002) *Ethnobotany of the Iban & the Kelabit.* Forest Department Sarawak, Kuching; NEPCon, Aarhus; University of Aarhus, Aarhus.

Dounias E, Selzner A, Koizumi M & Levang P (2007) From sago to rice, from forest to town: The consequences of sedentarization on the nutritional ecology of Punan former hunter-gatherers of Borneo. *Food and Nutrition Bulletin*, supplement **28**: 294–302.

Dwyer PD (1990) *The pigs that ate the garden: A human ecology from Papua New Guinea*. The University of Michigan Press, Ann Arbor.

Hildebrand HK (1982) Die Wildbeutergruppen Borneos (The collector groups of Borneo). Dissertation, Ludwig Maximilians University of Munich.

Koizumi M & Momose K (2007) Penan Benalui wild-plant use, classification, and nomenclature. *Current Anthropology* **48**: 454–459.

Milliken W, Miller RP, Pollard SR, & Wandelli EV (1992) *The ethnobotany of the Waimiri Atroari Indians of Brazil*. Royal Botanic Gardens, Kew, Richmond.

Needham R (1972) Penan. In *Ethnic groups of insular Southeast Asia*, vol. 1. (ed. F.M. LeBar), pp. 176–80. Human Relations Area Files Press, New Haven.

Puri RK (1997) Hunting knowledge of the Penan Benalui of East Kalimantan, Indonesia. Dissertation, University of Hawai'i.

———. (2005) *Deadly dances in the Bornean rainforest: Hunting knowledge of the Penan Benalui.* KITLV Press, Leiden.

Table 1
Wild plants appearing in meals of 346 day-houses in September to November 2004 at Long Belaka

Category	Species	Habitat	Times of Use
Green leaves (ferns)	*Diplazium esculentum* (Retz.) Sw.	Open place	69
	Pteris tripartita Sw.	Open place	1
Green leaves (seed plant)	*Piper* sp.	Forest	2
Starch (sago palm)	*Arenga undulatifolia* Becc.	Forest	40
Starch (tuber)	Sp. 1	Village site	1
White shoots (palms)	*Arenga undulatifolia* Becc.	Forest	13
	Eugeissona utilis Becc.	Forest	13
	Oncosperma horridum Scheft.	Forest	3
	Daemonorops fissa Blume	Forest	1
	Licuala sp.	Forest	1
	Not asked		1
White shoots (ginger)	*Etlingera foetens* (Blume) R.M. Sm.	Forest	1
White shoots (bamboo)	Sp. 2	Open place?	1
Condiment	*Albertisia* sp.	Forest	12
Ginger flowers	*Etlingera. elatior* (Jack) R.M. Sm. and/or *E. pyramidosphaera* (K. Schum.) R.M. Sm.	Forest	2
Fungi	Sp. 3	Forest	1
	Sp. 4	Open place	1
Fruit	*Passiflora foetida* L.	Village site	1
	Total		164

Table 2
Wild animals appeared in meals of 346 day-houses in September to November 2004 at Long Belaka

Animals	Times of Use
Bearded pig (*Sus barbatus*)	316
Sambar deer (*Cervus unicolor*)	25
Barking deer (*Muntiacus muntjac* and/or *M. atherodes*)	9
Mouse-deer (*Tragulus javanicus* and/or *T. napu*.)	9
Malayan softshell turtle (*Dogania subplana*)	3
Bushy-crested hornbill (*Anorrhinus galeritus*)	2
Common porcupine (*Hystrix brachyura*)	2
Gray leaf monkey (*Presbytis hosei*)	1
Pig-tailed macaque (*Macaca nemestrina*)	1
Asian leaf turtle (*Cyclemys dentata*)	1
Rough-necked monitor (*Varanus rudicollis*)	1
Palm weevil (species not studied)	1
River shrimp (species not studied)	1
Fishes (species not distinguished)	165
Total	537

	Necessary conditions	**Costs**			**Benefits**
		Searching	Collecting Hunting	Processing	Use (domestic use or sale)
Biological factors	· Phenology (Availability in time)	· Distribution · Habitat · Abundance (Availability in space)	· Morphology · Behavior	· Physical character · Chemical character	· Quality and amount
Human factors	· Technique · Physical ability	· Technique (knowledge, experience) · Physical ability · Perception of effort			· Perception and evaluation of the quality · Preference · Need (domestic, market)

Fig. 1 Example of factors affecting wild resource use

Importance of a Mosaic of Vegetations to the Iban of Sarawak, Malaysia

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Introduction

Human disturbance has been creating habitat mosaics (Smith and Wishnie 2000), and swidden agriculture is one kind of human disturbance. In swidden agriculture, a piece of forest is cut and burned, and the land is used for farming for one year or for a few years (or more), then left fallow until forest grows again (e.g., Conklin 1957; Chin 1985). A mosaic of farming land, young to old fallows, and primary forest are usually found around swidden farmers' settlements (e.g., Colfer 1997; Wadley, Colfer, and Hood 1997). The land can regain nutrients during the fallow period (Szott, Palm, and Buresh 1999), and weed seed banks are reduced (De Rouw 1995). Furthermore, fallows are actually abundant in useful plants for local people and are actively used by them (Balée 1994, Colfer 1997; Chazdon and Coe 1999; see also Voeks 2004). In addition, early successional species are adopted to open environments created by disturbance (Bazzaz and Pickett 1980). This implies that they are less likely to become extinct by use pressure. Overexploitation of primary forest may be avoided by effective use of secondary vegetation (see also Momose 2005). The traditional swidden agriculture is not a destructive practice, nor are swidden fallows themselves a threat to biodiversity.

This study examines use and classification of plants in primary and secondary environments by the Iban living near the Lambir Hills National Park in Sarawak, Malaysia. The Iban is the largest indigenous group of swidden farmers in Sarawak (Ichikawa 2004). Around an Iban village, a mosaic of swidden fields, young to old fallows, rubber and pepper gardens, orchards, and fragmented primary forests is found (Ichikawa 2004). According to ecological studies conducted in Lambir Hills National Park and the area surrounding it, primary forest has higher diversity of plant species than secondary forest (Momose et al. in this report). Primary forest, however, is decreasing, and secondary forest after logging and farming as well as oil-palm plantations are increasing around Lambir Hills National Park and in Sarawak (Ichikawa 2007). We have to understand the importance of primary and secondary forests for local people as well as their biodiversity to consider the consequence of the land use change. By examining the use and recognition of plants and forests by the Iban, we will show differences in importance of primary and secondary vegetation to the local people who are creating and using the mosaic environment.

Methods

Fieldwork was conducted in the territory of an Iban village Rumah Chabu (4°10´ N, 114°01´E) near Lambir

Hills National Park, Sarawak, Malaysia in 2003. A vegetation survey in 0.1 ha (10 × 100 m) plots in various environments was conducted as part of a larger ecological project. For our purpose, the vegetation of trees and vegetation on the forest floor was investigated. The vegetation of trees was surveyed in 11 plots: three in fragmented primary forests, two in old fallows (more than 20 years after abandonment), three in young fallows (5 years after abandonment), and three in rubber gardens. All trees ≥ 10 cm dbh (diameter at breast height) were tagged, mapped, measured, and identified. Vernacular names were identified by two Iban informants, who were men about 60 years old.

The vegetation of the forest floor was surveyed in 16 plots: three in fragmented primary forests, five in young fallows, four in new fallows (1 year after abandonment), and four in rubber gardens. Within each plot, small woody and herbaceous plants on the forest floor were identified in forty 1 × 1 m subplots. Vernacular names were identified by the Iban informants.

For an ethnobotanical survey, we collected specimens with the Iban informants and asked them about vernacular names, uses, and places to collect the plants during the vegetation survey and other occasions. We also asked about classification of vegetation types and about traditional belief and stories about forests and plants. Voucher specimens collected in the vegetation and ethnobotanical survey were stored in the Herbarium of the Forest Research Center, Sarawak.

To evaluate the abundance of useful trees ≥ 10 cm dbh, basal area (m^2/ha) and density of individual trees (number of individuals/0.1 ha) of all useful species for each use category (Fig. 1) in each vegetation type were calculated. Species that were used for two (or more) categories were included for both of the categories.

For plants of the forest floor, the number of subplots (n_i) where a useful species i for a certain use category (Fig. 2) appeared was counted. The sum total of n_i (N) for all useful species for each use category in each vegetation type was then calculated. The density of useful plants was expressed as N per 40 subplots. One plot was counted twice (or more times) for a certain use category when the plot had two (or more) useful species for the category. Species that were used for two (or more) categories were also included in both of the categories.

For analysis of vernacular names (Iban names), primary and secondary names were distinguished. A primary name is a single expression to indicate a taxon, and a secondary name is formed from a primary name by adding a modifier (Martin 1995, 210). Three name types were distinguished (Fig. 3), and the number of species and percentage of individual trees (as found in the vegetation survey of tree ≥ 10 cm dbh) having each name type in each vegetation type were calculated.

Results

(1) Useful trees ≥ 10 cm dbh

Figure 1 shows basal area and density of useful trees ≥ 10 cm dbh. The fragmented primary forests showed much higher basal area of timber species than plots of other vegetation types (Fig. 1A). More timber species were found in the fragmented primary forests (25 species in three plots) than in the old fallows (10 species in two plots), the young fallows (6 species in three plots), and the rubber gardens (4 species in three plots). The Dipterocarpaceae (13 species) contributed 82.7% of basal area of timber species in the fragmented primary forests.

The old fallows showed the second highest basal area and density of food species, while the rubber gardens showed the highest values (Fig. 1). In the rubber gardens, however, rubber trees (*Hevea brasiliensis* Müll Arg.), whose seeds and leaves can be (but were only occasionally) eaten as vegetables, comprised 75.5% of basal area or 77% of individuals of food species. If this species is excluded, food plants were most abundant in the old fallows. There were nine species of food plants found in the old fallows, and five of them were *Artocarpus* spp. These *Artocarpus* spp. produce edible fruits and accounted for 72.3% of basal area or 55% of individuals of food species in the old fallows. *Artocarpus* spp. were also abundant in the rubber gardens and the young fallows. In the old fallows, *Shorea amplexicaulis* Ashton, from whose seeds cooking oil is processed, was also commonly found (13.8% of basal area or 20% of individuals of food species in old fallows).

One of the most common *Artocarpus* spp. in the old and new fallows and the rubber gardens was *A. elasticus* Reinw. The species contributed the most to basal area and density of species used for crafts in these vegetation types. Strong fiber can be obtained from the inner bark of the species and is used for rope. The latex was also often used for birdlime.

The people most often used *Vitex pinnata* L. for firewood. The plant was a dominant species in the new fallows and also abundant in the old fallows and the rubber gardens.

Larger basal area of plants for religious and magic purposes in fragmented primary forests and old fallows than other vegetations were mainly due to *Xylopia* spp. and *Euodia malayana* Ridl., respectively. Branches of *Xylopia* spp. may be burned with *Goniothalamus* spp. (see the fifth subsection of the results) to keep the fire burning longer. *Dillenia suffruticosa* (Griff.) Mart. was also found in old fallows. Branches of *D. suffruticosa* were cut and stuck in rice fields to drive rats and mice away.

(2) Plants of the forest floor

The vegetation survey of the forest floor included ferns, herbaceous seed plants, rattans, and shrubs as well as saplings of many tree species. Many more species were recorded than in the survey of trees ≥ 10 cm dbh. Many of the species, however, were not used by the Iban. The density of the useless species was excluded from Figure 2.

Vegetable species were most abundant in the young fallows (Fig. 2). Most commonly found vegetable species in the young fallows were *Nephrolepis biserrata* (Sw.) Scott, a fern species especially favored after giving birth, and *Stenochlaena palustris* (Burm.) Bedd., the most favored fern species in the study village. *Gnetum gnemon* L. (leaves as well as fruit and seeds were eaten) and rattans (shoots were eaten) were also common. In the new fallows, *N. biserrata* was similarly abundant, but rattans were rare and *G. gnemon* was not recorded. Vegetable species found in the rubber gardens were similar to those of the young fallows, but their density was lower. *N. biserrata* and *S. palustris* were not recorded in fragmented primary forests, though rattans were common and *Gnetum* spp. were not rare.

The density of medicinal species[1] was similar among the plot types (Fig. 2), but species composition was different. *Lygodium* spp., for example, were very common in the young fallows and also found in the new fallows and the rubber gardens, but not in the fragmented primary forests. The plant was believed to cure a headache in the morning by tying the stem around the head. *Merremia* spp.[1] were abundant in the new fallows, but not recorded in other vegetation types. The plant was used to cure sexually transmitted disease by shamans. *Spatholobus* spp. were found in all vegetation types, but the density was relatively high in the fragmented primary forests and the rubber gardens and rare in the new fallows. When people get injured, they may cut the stem and drink the sap so that the bleeding would stop (but larger stems were used).

In the use category of crafts (Fig. 2), *Dicranopteris linearis* Und., *Melastoma malabathricum* L., rattans, and some other plants were included. *D. linearis*, a fern species, has fiber used for crafts. The species was most common in the rubber gardens and not recorded in the new fallows. *M. malabathricum*, a weedy shrub species, was abundant in the new fallows, but not found in the fragmented primary forests. The fruit was used as a black dye. Rattans were commonly found except in the new fallows. *Archidendron clypearia* (Jack) I. C. Nielsen, whose leaves were used as a blue dye, was commonly found in the rubber gardens (but the leaves were usually collected from lager trees).

The higher density of species of the religious & magic category in the young and new fallows than in the other vegetation types (Fig. 2) was due to high density of *Dillenia suffruticosa* and *Merremia* spp.[1], respectively.

Saplings of timber species showed high density in the new fallows and the fragmented primary forests (Fig. 2). Species composition, however, was different. In the new fallows two pioneer species *Alphitonia excelsa* (Fenzl) Reiss. and *Macaranga gigantea* Müll Arg. contributed 85% of the density value, while five species of the Dipterocarpaceae contributed 51% of the value in the fragmented primary forest.

(3) Classification of plants

Three types of names can be distinguished among Iban names of plants. They are defined as follows: (1) a primary name including one scientific species (type 1 name; e.g., **tekalong** for *Artocarpus elasticus*, **selangking** for *A. nitidus* Trécul), (2) a secondary name including one (or rarely two) scientific species (type 2 name; e.g., **resak kerubong** for *Dipterocarpus geniculatus* Vesque, **resak ensulai** for *D. palembanicus* Slooten), and (3) a primary name including two or more species, but with no secondary name to distinguish them (type 3 name; e.g., **seladah** for *Dacryodes rostrata* (Blume) H. J. Lam, *Santiria laevigata* Blume, and *Scutinanthe brunnea* Thwaites).

The number of species appearing in the survey of trees ≥ 10 cm dbh greatly varied according to plot type, but the number of species which were labeled by type 1 names was almost the same (Fig. 3A). These species accounted for many of individuals in the young fallows (79%) and the rubber gardens (88%) (Fig. 3B).

Type 1 and 2 names distinguish plants to the scientific species level. Most individuals in the young fallows (92%) and the rubber gardens (91%) had type 1 or 2 names (Fig. 3B). This means that most individuals in these vegetation types were linguistically recognized with the same distinctions as scientific species. (We have to add, however, that *Vitex pinnata* and *Hevea brasiliensis*, both of which had a type 1 name, accounted for 42% of individuals in the young fallows and 58% in the rubber gardens, respectively.) In the fragmented primary forests and the old fallows, the percentage of individuals having type 1 or 2 names were only 49% and 53%, respectively.

(4) Management and use of the vegetations

Fragmented primary forests were called **pulau,** and were secured to conserve timber for house construction or to protect graves by the study people (timber reserves and cemetery forests are given different names by the Iban of other areas [e.g., Wadley, Pierce, and Hood 1997]). Timber may be logged from cemetery forest when needed. The people did not go to **pulau;** probably because the places were somewhat far from the longhouse. Although not included in the vegetation survey, the people called large primary forest outside their living area (in Lambir Hills National Park) **kampong**. They rarely entered **kampong** because they believed there were lots of spirits, though shamans sometimes went to **kampong** to obtain magical power. An exception was made in the fruit seasons, when other people also went (but not often) to **kampong** to collect fruits and hunt bearded pigs.

The people did not consciously manage fallow vegetations, but usually went to fallows for collecting vegetables, firewood, materials for crafts, and offerings for annual events as well as for hunting. They called fallows one to three years after abandonment **jérami'**, about five years after abandonment **temuda'**, and after many years and with large trees **pangérang**. To collect vegetables, **temuda'** near the longhouse were most often used.

Rubber has not been tapped in the last 20 or 30 years because of low selling price of the latex. When the rubber was tapped, the undergrowth was cut to make the tapping work easier for the villagers, but today there are lots of small trees and grasses covering the rubber gardens. Some fruit trees were planted at edges of rubber gardens.

(5) Beliefs and stories about forest and plants

Although not appearing in the vegetation survey, **Ara** (large strangling *Ficus* trees, such as *F. kerkhovenii* Koord. & Valeton) was believed to host spirits and was feared by the people. Some men, however, were said to communicate with spirits on **Ara** to get strong magical power that can absorb other people's vitality and provide an ability like that of **Ara** strangling other trees. The plant was found in (fragmented) primary forest. An Iban story about **Ara** goes like this: A man lost his way in forest. Someone called him, and he followed the voice and found a longhouse. He entered and stayed at the longhouse. In the morning, he found himself on **Ara** and could not get down.

The people used **Selokai** (*Goniothalamus* spp.) for protection from spirits in the forest and the longhouse. The plants were abundant on the forest floor of primary forest (in Lambir Hills National Park). The people believed that lots of evils would come if it rains while the sun is shining. They would put leaves on their ears or burn leaves and branches so that spirits could not see them. They also burned the bark in the longhouse to protect pregnant women and babies from evils. There was a story about **Selokai**: A man went out to hunt bearded pigs. He met a man carrying a bearded pig. They made a fire to bake the pig to eat together, but the man who had been carrying it suffered from the smoke and ran away. The pig turned into a man. There was **Selokai** in the firewood. The man was a spirit and had tried to have the first man eat a human. For another example of a talisman, the people planted **Kemali** (*Leea indica* Merr.) at the border of a cemetery forest after they buried a dead person there so that the ghost of the person would not come out of the forest.

There was a story about **Kuang-Kapong** (Indian Cuckoo, *Cuculus micropterus*; Aihara 2007) and **Kemunting** (*Melastoma malabathricum*). **Kuang-Kapong** made trees fruit in the past. One day, however, **Kemunting** said, “I am the king from today. Plants other than me should not fruit very often.” Plants in forest thus do not fruit very often. On the other hand, **Kemunting** likes rice, so rice fruits well.

Discussion and conclusion

Fragmented primary forests were conserved by the study people, and the people were getting timber for house construction from there. Actually, the vegetation type had a large basal area of timber species, and they were regenerating well. At the same time, (fragmented) primary forests were not safe places for the Iban because there were lots of spirits. Some plants were used to control or drive away spirits.

In contrast, secondary vegetations were used in everyday life. The young fallows, where the people usually collected vegetables, had rich vegetable flora both in terms of the number of species and their density. A good firewood species was also abundant in the young fallows. There were more fruit trees in the old fallows and the rubber gardens. Plants producing materials for crafts were also abundant in secondary vegetations. For the study people, secondary vegetations were places for humans and their livelihood. **Kemunting** was one of the symbolic plants of the human area, and it helps rice to crop.

The abundance of useful plants in secondary vegetations is probably the result of both natural and cultural factors. The vegetations compared here had different species composition, and thus it is natural that they had different importance to the people. Different cultures, however, may recognize different useful plants in the same vegetation (Voeks 2007). In general, there were more useful plants used in everyday life by the study people in secondary vegetations than in primary forest. This implies that the people have developed more knowledge about plant use of secondary vegetations than of primary forest. By using plants near their settlement, people can save effort to collect plants. The knowledge or use pattern may also be ecologically reasonable. For example, collection of vegetables and firewood from early successional, fast growing species would not seriously threaten the species.

Land use is changing around the study village, and primary forest is decreasing. If primary forest disappears, it will become difficult for people to find large timber for construction. The disappearance of primary forest also means, to the Iban, the disappearance of the place of spirits. Conversely, the secondary forests are now increasing. But if they disappear because of plantation development, people will become unable to find necessities that were once abundant around the village and will have to buy them. As long as the people depend on natural products they collect by themselves, they will conserve primary and secondary forests to the extent that fulfill their needs.

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Endnote

1. The distinction between medicinal plants and religious and magic plants was not always clear, but the study people distinguished between plants used to cure disease and plants used in religious or magic ceremonies. The former plants were included in the use category of medicine. *Merremia* spp., however, was used to cure disease only by shamans and was included both in the medicinal category and the religious and magic category.

References

Aihara Y (2007) Ranbiru kokuritu-kouen oyobi shuuhen niji-rin no chourui-sou to yakihata-min Iban ni yoru tori no riyou to ninsiki (Composition of bird species and their use and recognition by the Iban of Lambir Hills National Park and nearby secondary forests). M.A. thesis, Ehime University.

Balée WL (1994) Footprints of the forest: Ka'apor ethnobotany: the historical ecology of plant utilization by an Amazonian people. Columbia University Press, New York

Bazzaz FA, Pickett STA (1980) Physiological ecology of tropical succession: a comparative review. Ann Rev Ecol Syst 11:287–310

Chazdon RL, Coe FG (1999) Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of Northeastern Costa Rica. Conserv Biol 13:1312–1322

Chin SC (1985) Agriculture and resource utilization in a lowland rainforest Kenyah community. The Sarawak Museum Journal 35, special monograph 4

Colfer CJP (1997) Beyond slash and burn: building on indigenous management of Borneo's tropical rain forests. Advances in Economic Botany, vol. 2. The New York Botanical Garden, New York

Conclin HC (1957) Hanunóo agriculture: a report on an integral system of shifting cultivation in the Philippines. Food and Agriculture Organization of the United Nations, Rome

Ichikawa M (2004) Relationships among secondary forests and resource use and agriculture, as practiced by the Iban of Sarawak, East Malaysia. Tropics 13:269–286

Ichikawa M (2007) Degradation and loss of forest land and land-use changes in Sarawak, East Malaysia: a study of native land use by the Iban. Ecol Res 22:403–413

Martin GJ (1995) Ethnobotany: A method manual. Chapman & Hall, London

Momose K (2005) Yasei-seibutu wa donoyouna jooken-ka de jizoku-teki ni riyou-sarete iruka: houfu-na seibutu-tisiki to seibutu-tayoosei no kouka (Conditions for sustainable use of wild organisms: roles of rich ethnobiological knowledge and biodiversity). Kagaku 75:542–546.

De Rouw A (1995) The fallow period as a weed-break in shifting cultivation (tropical wet forests). Agriculture, Ecosystem and Environment 54:31–45

Szott LT, Palm CA, Buresh RJ (1999) Ecosystem fertility and fallow function in the humid and subhumid tropics. Agroforestry Systems 47:163–196

Wadley RL, Colfer CJP, Hood IG (1997) Hunting primates and managing forests: the case of Iban forest farmers in Indonesian Borneo. Human Ecology 25:243–271

Smith EA, Wishnie M (2000) Conservation and subsistence in small-scale societies. Annual Review of Anthropology 29:493–524

Voeks, RA (2004) Disturbance pharmacopoeias: Medicine and myth from the humid tropics. Annals of the Association of American Geographers 94:868–88

Voeks RA (2007) Penan ethnobotany: subsistence strategy and breadth of knowledge. In: Sercombe P, Sellato B (eds) Beyond the green myth: hunter-Gatherers of Borneo in the twenty-first century. NIAS Press, Copenhagen, pp 262–288

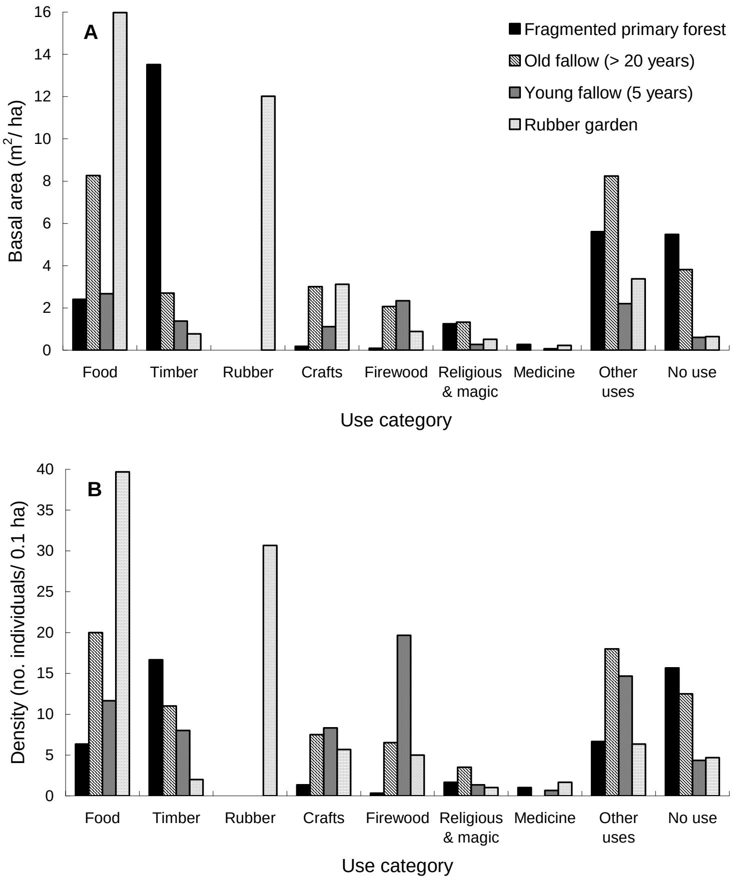

Fig. 1 (A) basal area (m^2/ha) and (B) density (number of individuals/0.1 ha) of useful and useless trees ≥ 10 cm dbh in four types of vegetations.

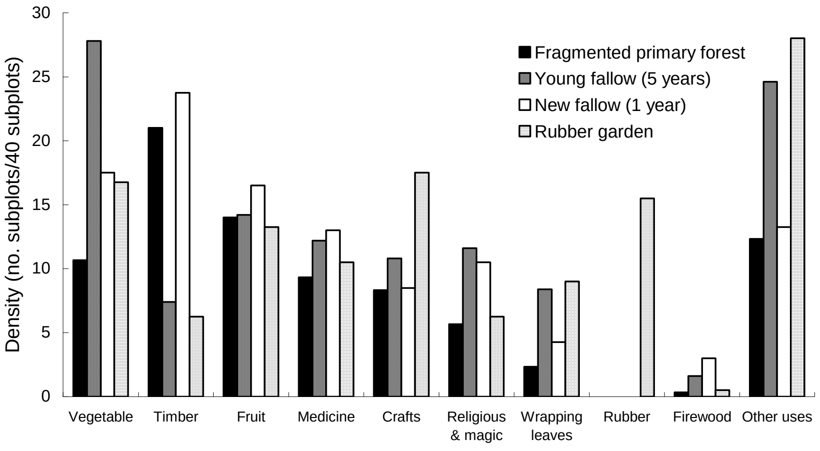

Fig. 2 Density (number of subplots/40 subplots) of useful plants on the forest floor in four types of vegetations.

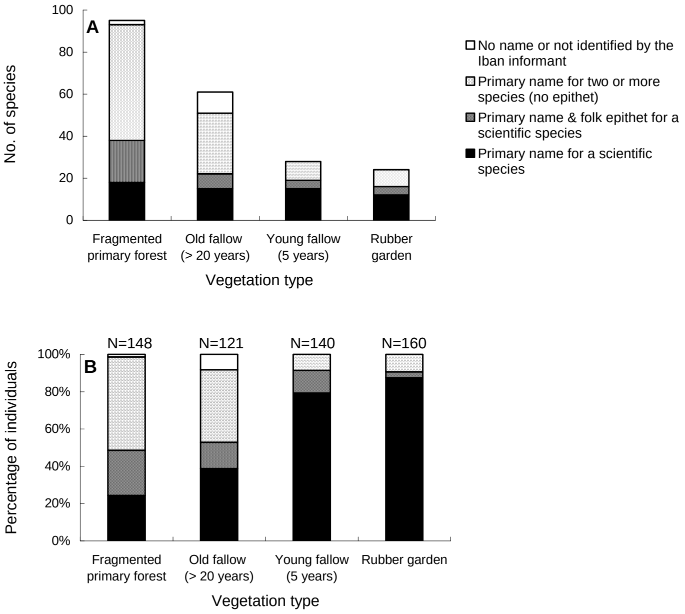

Fig. 3 (A) Number of species and (B) percentage of individuals (appeared in the survey of trees ≥ 10 cm dbh) having different types of names in the four vegetation types. Data from three 0.1-ha plots are compiled for each of fragmented primary forests, young fallows, and rubber gardens. Data from two 0.1-ha plots are compiled for old fallows.

Iban Knowledge of Wild Birds in a Habitat Mosaic

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Introduction

Birds play important roles in people's culture. Birds often have symbolic meanings and are related to traditional culture and belief systems (e.g., Feld 1988; Hagiwara 1996). In Borneo, people practice bird augury, and it affects people's activities (e.g., Hose and McDougall 1901; Richards 1971; Jensen 1974; Sather 1984). Birds also economically contribute to people's life. Bird's nests and hornbill's casques, for example, have been traded by local people of Borneo to Chinese traders (Freeman 1999).

Birds contribute to people's culture and economy and at the same time use habitats created by human activities. Traditional coffee agroforests have proved to create a complex habitat and support a rich avifauna. (Moguel and Toledo 1999). Different human management of lands results in different compositions of birds even under the same area (Kataoka, Iwata, and Prawiradilaga 2006).

This paper reports on the importance of birds to the Iban living near Lambir Hills National Park, Sarawak, Malaysia. Primary and secondary environments in the area are analyzed for the number of bird species and individuals having cultural importance to the Iban. The objective of the study is to show how the Iban recognize the importance of birds in a habitat mosaic created by their subsistence and economic activities.

Methods

Fieldwork was conducted in Lambir Hills National Park, Sarawak, Malaysia (4°12´ N, 114°02´E at the headquarters) and Rumah Chabu, an Iban village (4°10´ N, 114°01´E at the longhouse), from April to July and from September to October 2005 and from September to October 2006. The main vegetation type of Lambir Hills National Park is lowland mixed dipterocarp forest (Yumoto and Nakashizuka 2005). Rumah Chabu is situated 4 km from an edge of the national park and has a population of about 400. Around the village, swidden fields, swidden fallows, wet rice fields, rubber gardens, orchards, fragmented primary forests, and some other environments were found.

The plot census method (Yui 1997) was used to estimate composition of wild bird species in different habitats. Thirty-two 10 × 100 m plots in seven vegetation types were used. In primary forest of Lambir Hills National Park, five plots were located on the forest floor and two plots were located along a walkway at a height of 20 m. In and around Rumah Chabu, nine plots were in fragmented primary forests, five plots were in rubber gardens, five plots were in old fallows (more than 20 years after abandonment), three plots were in middle-aged fallows (about 7 years), two plots were in young fallows (about 3 years), and one plot was in a village open space. The fragmented primary forests were protected by the villagers as timber reserves and spiritual places. The rubber gardens were not used for tapping rubber during the study period, and fruit trees and herbs were also abundant. In the old fallows, small and large trees were found. In the middle-aged fallows, there were small trees, but herbaceous plants were still abundant. The young fallows were covered by herbaceous plants and shrubs. The village open space was almost bare, but some herbaceous plants were found. Each plot was surveyed three (or two) times between 0700 and 1200 hours, and birds seen or heard were counted. (Detailed information concerning these vegetation types is reported by Momose et al. and Kaga et al., and detailed ecological results of this census are included in Itioka et al. in this report.)

To collect ethnoornithological information, birds were observed in various habitats in and around the Lambir Hills National Park and Rumah Chabu with an Iban informant (key informant), who was a man about 60 years old. For observed wild birds, the informant was asked for Iban names, uses, and other information. Additional information was collected from five informants (the key informant and four other men above 50 years old) by showing pictures in a field guide to birds of Borneo (Francis 1984) They were selected as informants because of several dozens of villagers interviewed, they were the only people who were knowledgeable about birds. Uses of birds were also observed in the study village.

For analysis of cultural importance of birds to the Iban, importance categories shown in Tables 1 and 2 and Fig. 1 were distinguished. They include not only practical importance but also spiritual importance. Furthermore, pests were considered to be culturally “important” in the sense that they had negative roles in people’s lives.

For analysis of names, primary and secondary names were distinguished. A primary name is a single expression, even if composed of more than one constituent (e.g., **Tandok-ulat** [lit. ‘antenna of caterpillar’] for Common Iora, *Aegithina tiphia*), and a secondary name is a name formed from a primary name by adding a modifier (Martin 1995, 210). In terminal rank, some species were labeled by primary names and others by secondary names. Primary and secondary names in terminal rank are called terminal names in this paper. The number of species that were labeled by a terminal name was also analyzed. The number was judged from the present study, and thus the number of species that were distinguished to the species level by Iban names can be an overestimate.

Results

(1) Cultural importance of birds to the Iban

A total of 150 species were observed during the study. Among them, 126 species appeared in the plot census, but 24 species were observed only in other occasions. According to the ethnoornithological information, 85 species (57%) were culturally important to the Iban, and 65 species (43%) were not (Table 1). Three species had two kinds of importance to the Iban, while the rest of the culturally important species had one.

Thirty-nine species were related to the Iban belief system and stories. According to informants, for example, if people hear the song of **Bubut** (Greater Coucal, *Centropus sinensis*), someone would die at their longhouse. **Jerruit** (tailorbirds, *Orthotomus* spp.) is **udok antu** (spirit dog) of **Antu Gerasi** (giant spirit that hunts humans), and people would not be able to return home and would die if they followed the song of **Jerruit** in forest. If people hear the song of **Beragai** (Scarlet-rumped Trogon, *Harpactes duvaucelii*) when they are in forest for hunting, they hunt bearded pigs. At **Gawai** (Iban ceremony or festival), two men sang about **Lang sengalang** or **Lang laut** (Brahminy Kite, *Haliastur indus*), a spirit of a war chief, and other six bird species, which were said to be sons-in-law of **Lang sengalang** (a lot of literature [e.g., Jensen 1974] has reported seven sons-in-law of **Lang sengalang**, but we recorded only the six). These birds were **Ketupung**

(Rufous Piculet, *Sasia abnormis*), **Beragai** (Scarlet-rumped Trogon), **Papau** (Diard's Trogon, *Harpactes diardii*), **Nandak** (White-rumped Shama, *Copsychus malabaricus*), **Panguas** (a woodpecker species), and **Bejampong** (Crested Jay, *Platylophus galericulatus*). In a ceremony of constructing a new house in September 2006, eight packages of rice in leaves were prepared for the seven birds and **Antu Petara** (favorable spirit). Ten sticks of trees called **Paung burong** were also buried at the base of pillars after blood of a chicken and a pig was poured to the ground. To prepare **Paung burong**, the key informant went to forest before dawn on the ceremony day and waited until **Nandak** started to sing at dawn. He then pulled out saplings about 30 cm in height by his right hand on hearing the song (any species of tree can be used). According to the key informant, **Paung burong** is used to avoid **Antu Gerasi** coming to the house, avoid bad dreams, cure disease, get a lot of money, and so on.

According to informants, all but the seven species related to the ceremonies above may be eaten, but **Empulu** (bulbuls, *Pycnonotus* spp.) and **Puna** (Pigeons, *Treron* spp.) are usually eaten. We included 34 species, the reported species and some others that were observed to be eaten during the study, in the category of food. Birds were caught by birdlime, net, and gun. Birdlime was most often used to hunt smaller birds during agricultural activities. Birdlime was made from the latex of *Artocarpus elasticus* Blume and attached to the top of a wooden stick about 30 cm long. The stick would be put near a small stream or pool in the forest to hunt birds coming for bathing. The technique was said to be effective when it had not rained for three or more days. Birds were usually baked and eaten in the field. **Engkeruak** (White-breasted Waterhen, *Amaurornis phoenicurus*) was often found at ridges between wet rice fields. According to informants, villagers mimic the call of the bird to attract them and then hunt. The birds are usually eaten by whoever hunted them, but can be sold at a market near the village at a price of 10 Malaysian Ringgit (RM).

Two species were used for decoration. A hat decorated with plume of **Ruai** (Great Argus, *Argusianus argus*) was observed on the last day of **Gawai** held in July 2005. In the night after dinner, one villager wearing the hat danced around a pillar decorated with banana leaves and fruits and sweets and finally cut off one of the fruits or sweets. He handed the hat to another man, and then the same performance was repeated again and again. Great Argus is a protected species (Appendix II of CITES), but the longhouse was keeping the plume so that it could be used in the future. The hat was stored as soon as the ceremony was finished. For another example, villagers put plumes of **Bruie** (Black Hornbill, *Anthracoceros malayanus*) in frames and vases.

Entalik (Blue-crowned Hanging Parrot, *Loriculus galgulus*) and **Bayan** (Long-tailed Parakeet, *Psittacula longicauda*) can be sold. These species are favored as pets because they have beautiful colors and an interesting habit of hanging upside down from a twig. The villagers have not been catching them in recent years, but they used to be caught in September and sold at the price of 20 RM and 10 RM, respectively.

Eleven species were recognized as pests by villagers. Flocks of **Pipit** (munias, *Lonchura* spp.) were observed at rice fields, though the damage was not serious. When a flock of **Tiong batu** (Hill Myna, *Gracula religiosa*) was eating the fruit of **Kemayau** (*Canarium* sp.), villagers made fire to drive them away by the smoke. **Manaul** (hawks) eat chickens that villagers keep, and villagers sometimes shoot **Manual** so that they would not come. As far as the key informant knew, villagers shoot about 10 individuals a year. **Banggau** (egrets of white colors, two species of *Egretta*) can be both pests and beneficial birds. They eat fish in ponds.

Villagers threw rocks when they saw the birds in ponds. They, however, also eat pest insects in swidden and wet rice fields. The key informant said that he was waiting for **Banggau** to come. The birds usually come to the study area in September. Although **Achang** (Domestic Pigeon, *Columba livia*) was not included in the study, villagers did not like the birds because they lived in the longhouse and soiled it.

(2) Iban names of birds (classification of birds)

Among 150 species studied, 139 species (93%) had Iban names and 11 species (7%) did not (Table 1). Informants said that they did not know the 11 bird species without an Iban name. The 139 species were labeled by 94 different names in terminal rank (65 primary names in initial rank). We distinguish four types of Iban names of birds by the number of species included in a terminal name (one or more species) and the structure of the name (primary or secondary name) (Table 1). First, some species were distinguished to species by a primary name (e.g., **Bubut** for Greater Coucal, *Centropus sinensis*; **Entekop** for Lesser Coucal, *C. bengalensis*). Percentages of bird species labeled in this way were 35% for culturally important species (for detailed categories, 44% for species related to Iban belief system and stories, 21% for food species, etc.) and only 12% for culturally unimportant species.

Second, some species were distinguished to species by a secondary name (e.g., **Puna bedidi** for Large Green Pigeon, *Treron capelli*; **Puna bagau** for Thick-billed Pigeon, *T. curvirostra*; **Engkechong lilin** for Chestnut-winged Babbler, *Stachyris erythroptera*; **Engkechong kubok** for Black-throated Babbler, *S. nigricollis*). Among the birds studied, 55% of culturally important species were distinguished to species either by primary or secondary names, while 31% of culturally unimportant species were distinguished to species.

Third, some species were labeled only by primary names and not distinguished to species (e.g., **Banggau** for Chinese Egret, *Egretta eulophotes* and Little Egret, *E. garzetta*). Names that were included in this name type usually included two or three species. Exceptions were **Engkechong**, which included 12 species of babblers (culturally unimportant species; but some abundant babblers were distinguished by secondary names, and their names were included in the second type), **Tagerih**, which included 5 species of woodpeckers (culturally unimportant species), and **Kangan**, which included 4 species of flycatchers (food species). Twenty-six species or 40% of culturally unimportant birds had this type of name.

Lastly, some species were labeled by secondary names, but not distinguished to species (e.g., **Puna mayang** for Little Green Pigeon, *Treron olax* and Pink-necked Pigeon, *T. vernans*; **Empulu betul** for Olive-winged Bulbul, *Pycnonotus plumosus*, Red-eyed Bulbul, *P. brunneus*, and Cream-vented Bulbul, *P. simplex*).

(3) Habitat types and cultural importance of birds to the Iban

The birds were not evenly observed among different habitats. In the village open space and the young fallows, fewer species were observed than in forested habitats (Table 2). The number of individuals, however, generally declined as the succession progressed (Fig. 1A). In the rubber garden, both the number of species and the number of individuals were high.

In the rubber gardens, culturally important birds were also rich in the number of species and number of individuals (Table 2, Fig. 1A). The number of culturally important birds was largest in the village open space and second largest in the young fallows (Fig. 1A), though they include a limited number of species (Table 2). This is because some culturally important species were abundant in these habitats. The smallest number of individuals of culturally important birds was observed in the primary forest (Fig. 1A). In the primary forest, five species that appeared in the plot census did not have an Iban name (Table 3). A total of 11 species observed during the whole study period did not have an Iban name, and seven of them were found only in primary forest of Lambir Hills National Park. The rubber gardens were richest in the number of species, but all the species had Iban names (Table 3).

The number of species related to the Iban belief system and stories was largest in the rubber gardens (Table 2). Among forested habitats, the number was smallest in the primary forest. The primary forest also had the smallest number of individuals in this category (Fig. 1B). The number of individuals was largest in the village open place. The most often observed species of the category in the village open place was Chinese Egret (*Egretta eulophotes*; 3.64 individuals/0.1 ha, 5 h).

Regarding birds for food, the number of species was similar among forested habitats, though the number was somewhat smaller in the middle-aged fallows (Table 2). The number of individuals of food species was more abundant in the young fallows and the rubber gardens than in other habitats (Fig. 1B). Villagers often hunted birds in orchards and rubber gardens during the study period.

Rhinoceros Hornbill (*Buceros rhinoceros*) has an important symbolic meaning in the Iban culture and is used for decoration (Hose and McDougall 1901; Freeman 1999), but the species was not observed during the study. According to the key informant, recently the species is rarely seen, even in Lambir Hills National Park. He said this was because trees of their favorite fruits were disappearing. Plumes of other hornbills are also used for decoration by the Iban (Freeman 1999), but only Black Hornbill was observed in the study. The birds came out from primary forest in the morning and used various habitats during daytime. Great Argus, another species for decoration, was observed in various forested habitats.

Among the two species for pets, a small flock of Blue-crowned Hanging Parrot was observed only once in the canopy of primary forest (but not in the plot census). The people used to catch the birds in fragmented primary forests, but they ceased to catch and sell them because the species were rare and small and thus difficult to catch. Flocks of the other species, Long-tailed Parakeet, were often observed in rubber gardens.

More pest species were found in the rubber gardens than other habitats (Table 2). The number of individuals of pest species was largest in the village open space, followed by the young fallows and the rubber gardens (Fig. 1B). The most common pest species in the village open space and the young fallows were Philippine Glossy Starling (*Aplonis panayensis*; 10.8 individuals/0.1 ha, 5 h) and Dusky Munia (*Lonchura fuscans*; 4.75 individuals/0.1 ha, 5 h), respectively.

Discussion

Importance of birds in the Iban belief system has been reported in many studies (e.g., Richards 1971; Jensen 1974; Sather 1984). The results of the present study further supported this importance. The number of bird species included in the category of belief and story was larger than other cultural importance categories, and nearly half of the bird species in the category were named to species by a primary name. Religious practices related to birds were often observed during the study. Birds also had some importance as food. Villagers hunted birds during agricultural activities and ate them as snacks, though they were not for main meals.

Some birds were recognized as pests. However, they were not causing serious damage to the Iban life, and the people dealt with pest birds, except for hawks, in simple ways such as making smoke and throwing rocks. Furthermore, people knew that some pest species help agriculture by eating pest insects.

Different vegetations had different importance to the Iban in their avifauna. The primary forest was less rich than other types of forest in the number of culturally important species. It is difficult to observe birds in primary forest because of limited sight and the height of the canopy. Furthermore, the Iban do not usually enter primary forest (Kaga et al. in this report). They only have very limited chances to observe bird species that are mostly found in the canopy. The relationship between the Iban and birds in primary forest is not so strong. Some species, especially hornbills, however, have special importance to the Iban culture.

Fragmented primary forests and primary forest around Lambir Hills National Park have similar vegetation structure (Momose et al. in this report), but the composition of bird species was different. Birds observed in the former habitat were usually using a habitat mosaic, while about a half of bird species observed in the latter habitat were found only in primary forest. The fragmented primary forests were somewhat richer than the primary forest in the number of species and number of individuals of birds related to the Iban belief system and stories. The result in the old fallows was similar to that of the fragmented primary forest. In the middle-aged fallows fewer species and more individuals were observed than in the old fallows, but the proportion of bird species and individuals of each importance category was similar.

The rubber gardens were richest in the number of species having cultural importance. Individuals of culturally important birds were also relatively abundant. Rubber was not being collected during the study period because of the low price. Villagers, however, were growing fruit trees, collecting wild vegetables, and hunting birds there. Rubber gardens had a mixed vegetation of trees and herbs. Fruit orchards are probably playing a similar role for birds to rubber gardens; birds hunted by villagers in orchards were similar to those hunted in rubber gardens.

Most of the birds seen in the village open space and the young fallows had some importance to the Iban, though only limited species were coming to these habitats. Birds can easily be observed in these habitats, and people often pass these habitats. This may help people to develop cultural recognition of the birds there. Pests were abundant in these habitats and rubber gardens. They are probably attracted to the habitats made by human activities.

Conclusions

Secondary environments were important both for the Iban culture and for the biodiversity of birds. Many bird species and individuals were utilizing habitats or a habitat mosaic made by human activities, and the Iban readily recognized the birds in their living places and the birds that were important to Iban culture and life. On the other hand, primary forest was generally less important for the Iban culture related to birds, though there were some culturally important species there.

A relatively large area of primary forest around the study site is protected as Lambir Hills National Park. Land use of secondary vegetations, however, changes according to social circumstances and people’s decisions. A plantation company was inviting the study village to make oil palm plantations in the village land. Leaders of households were discussing the invitation. The land use pattern of oil palm plantation is different from that of orchards and rubber gardens in its monocropping over a large area. If the land use changes the avifauna, it will also affect the Iban culture.

Furthermore, the key informant worried most that present young people did not want to go to the forest and that they could not learn about birds. The young generation is attracted to city life, and only some old people in the study village knew birds well. Social change itself is affecting the Iban culture.

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References

Feld S (1988) Tori ni natta shoonen (Sound and sentiment: Birds, weeping, poetics, and song in Kaluli expression), trans. Yamaguchi O, Yamada Y, Shimeda T, Fujita T. Heibonsha, Tokyo.
Freeman JD (1999) A note on the Gawai Kenyalang, or Hornbill Ritual of the Iban of Sarawak. In: Birds of Borneo, by Smythies BE. Natural history publications (Borneo), Kota Kinabalu, pp 123–127
Francis CM (compiler) (1984) Pocket guide to the birds of Borneo, based on 3rd edn, by Smythies BE. The Sabah Society and WWF Malaysia, Kota Kinabalu.
Hose C, McDougall W (1901) The relations between men and animals in Sarawak. The Journal of the Anthropological Institute of Great Britain and Ireland 31:173–213.
Hagiwara H (1996) Ine to tori to taiyou no michi (A road of rice, birds, and the sun). Taishukan-shoten, Tokyo.
Jensen E (1974) The Iban and their religion. Oxford University Press, Oxford.
Kataoka M, Iwata A, Prawiradilaga DM (2006) Relationship between the bird community and human activities in a mountainous area adjacent to Gunung Halimun-Salak National Park, West Java, Indonesia. In: McNeely JA, McCarthy TM, Smith A, Olsvig-Whittaker L, Wikramanayake ED (eds) Conservation biology in Asia. Society for Conservation Biology Asia Section and Resources Himalaya Foundation, Kathmandu, pp 173–182
Martin GJ (1995) Ethnobotany: A method manual. Chapman & Hall, London
Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Cons Biol 13:11–21
Richards A (1971) Iban Augury. The Sarawak Museum Journal 20:63–82.
Sather C (1984) Iban agricultural augury. The Sarawak Museum Journal 34:1–36.
Smythies BE (1999) Birds of Borneo. Natural history publications (Borneo), Kota Kinabalu
Yui M (1997) Chourui no kotai-suu no shirabe-kata (How to survey bird numbers). In: Yamagishi S (ed) Choorui seitai-gaku nyuumon: Kansatsu to kenkyuu no shikata (An introduction to bird ecology: Observation and research methods). Tsukiji-shokan, Tokyo, pp 63–73
Yumoto T, Nakashizuka T (2005) The canopy biology program in Sarawak: Scope, method, and merit. In: Roubik DW, Sakai S, Hamid AA (eds) Pollination ecology and rain forest Sarawak studies. Springer, New York, pp 13–21

Table 1 Cultural importance of birds to the Iban and their Iban names

	Number of species					
	Named to species		Not named to species			
Importance	By primary name	By secondary name	By primary name	By secondary name	No name (not known)	Total
Culturally important						
Belief and story	17	7[b]	9[c]	6	0	39[bc]
Food	7	6	14[c]	7	0	34[c]
Decoration	2	0	0	0	0	2
Pet (sold)	2[a]	0	0	0	0	2[a]
Pest	3[a]	5[b]	2	1	0	11[ab]
Subtotal	30	17	24	14	0	85
Culturally unimportant	8	12	26	8	11	65
Total	38	29	50	22	11	150

Note: Data are compiled from the plot census and other observations during the study.
For the total and subtotal, a species included in more than one category is counted as one.
[a] One species is included in the categories of "pet (sold)" and "pest."
[b] One species is included in the categories of "belief and story" and "pest."
[c] One species is included in the categories of "belief and story" and "food."

Table 2 Habitat types and bird species having different cultural importance to the Iban

	Number of species						
Importance	Primary forest	Fragmented primary forest	Rubber garden	Old fallow	Middle-aged fallow	Young fallow	Village open space
Belief and story	14[a]	23[ac]	29[ac]	21[ac]	18[a]	6[ac]	8[c]
Food	20	18[c]	22[c]	19[c]	15	8[c]	5[c]
Decoration	2	2	2	2	2	0	0
Pet (sold)	1[b]	1[b]	1[b]	0	0	0	0
Pest	2[ab]	4[ab]	9[ab]	4[a]	4[a]	4[a]	3
Not used	27	27	28	24	18	4	1
Not known	5	2	0	1	0	0	0
Total	69	74	88	69	56	20	16

Note: Data are compiled from the plot census. For the total, a species included in more than one category is counted as one.
[a] One species is included in the categories of "belief and story" and "pest."
[b] One species is included in the categories of "pet (sold)" and "pest."
[c] One species is included in the categories of "belief and story" and "food."

Table 3 Habitat types and the Iban names of birds

	Number of species						
Name type	Primary forest	Fragmented primary forest	Rubber garden	Old fallow	Middle-aged fallow	Young fallow	Village open space
Named to species							
By primary name	17	23	27	19	18	1	6
By secondary name	15	20	23	17	16	7	4
Not named to species							
By primary name	22	17	22	20	14	6	5
By secondary name	10	12	16	12	8	6	1
No name (not known)	5	2	0	1	0	0	0
Total	69	74	88	69	56	20	16

Note: Data are compiled from the plot census.

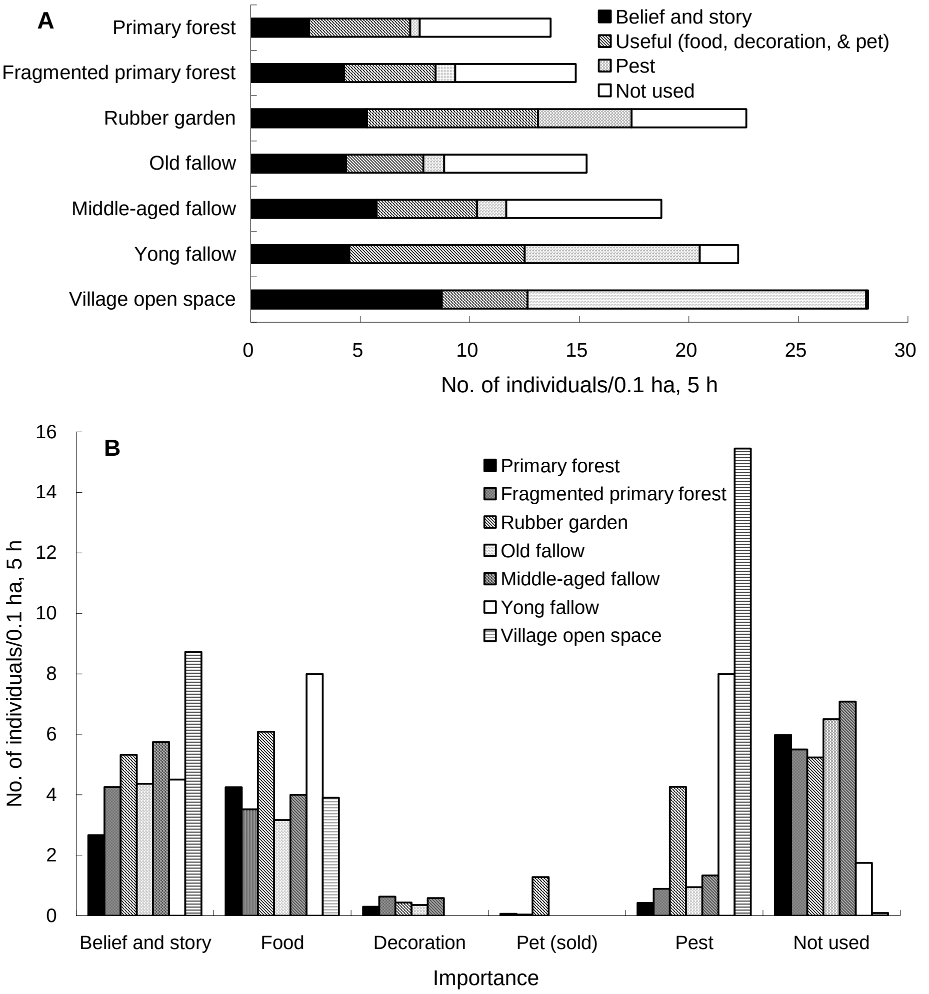

Fig. 1 Habitat types and abundance of birds having different cultural importance to the Iban, sorted by (A) habitat types and (B) cultural importance categories.

Chapter 5

INSTITUTIONS AND THEORETICAL FRAMEWORKS ON SUSTAINABLE USE OF FOREST AND BIODIVERSITY

Chapter 5 Introduction

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Up to this point in the book, we have examined how human activities affect forests and biodiversity, and as a result, how the ecological services of the forests have changed. In this chapter, we analyze various institutions and schools of thought on the sustainable uses of forests and biodiversity.

In section 5.1, two papers examine institutions at the local community level. Ichikawa discusses the local institutions of the Iban, who are indigenous to Sarawak, focusing on land and natural resource tenure. Although their tenure system has changed as the socioeconomic conditions surrounding them have changed, it still contains mechanisms for maintaining sustainable resource uses. Momose discusses how the Iban use natural resources. He argues that, if local residents have abundant knowledge of their natural resources in a region with a high level of biodiversity, they will not cause resource degradation because they have a greater understanding of the various options to utilize them. Unfortunately, after accomplishing so many great things, Dr. Momose passed away in 2007 due to illness. All of the project members admire his achievement and pray for this prominent scholar.

In section 5.2, there are four papers on national and international institutions. In the first, Baba examines the changes in forest management policies on Yaku Island as they relate to natural, social, and economic factors from the 1920s until today. In the second, Morishita looks at commercial logging in Sarawak and explains the relationship between a Chinese log trader and a politician. In the third paper, Fujita explains the changes of forest policy in Sarawak, which have been affected by European NGOs fighting against commercial logging in the 1980s. Fujita also describes the background for the introduction of forest certification in Malaysia. Looking at CITES, Onuma examines how a trade ban can successfully help conserve biodiversity.

In section 5.3, the theoretical framework and methods of evaluating biodiversity are examined from an economic perspective. Akao et al. try to identify the conditions under which finite-time exhaustion of renewable resources would be optimal. In the second paper, Akao discusses methods of evaluating intangible and unpriced values and measuring the achievement of biodiversity conservation. Hasegawa then examines methods of economic evaluation for forest values, using Kinabalu Mountain as a case study. In the final paper, Moreno indicates the strong relationship between people’s awareness and forest conservation.

We obtained, from the results of this project, abundant and broad-based information on local, national, and international institutions. The results described in this chapter provided valuable data for examining institutions for sustainable forest and biodiversity uses in Chapter 6.

Institutions and Rules on Forest Use and Management by the Iban of Sarawak

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Introduction

Sustainable forest use by natives in the tropics, who have been using forest resources for a long time, has been recently gained attention from the viewpoint of biodiversity conservation. Regarding the Iban, a native people of Sarawak, Freeman characterized their forest use by shifting cultivation as being destructive (Freeman 1955). Researchers after him, such as Padoch (1982), Sather (1990) and Ichikawa (2004), clarified that the Iban's land use was rather sustainable, supported by their social institutions and rules on forest use and management. This paper deals with 2 types of rules on forest use and management. One is rules on the tenure of natural resources, such as land, fallow forest, and fruit trees. The other is rules on the inheritance of land and forest.

Regarding the former rules, I point out that there are significant differences between the rules reported by this research and those reported by previous studies (Cramb1986; Wadley1997; Sather1990), and I describe how the differences are caused. I examine how forest use and management by the Iban are affected by the changes of the rules. Regarding the inheritance rules, there have been few studies so far. I describe a case of application of the rules and examine how Iban inheritance rules are related to their forest use and management.

Rules on tenure of natural resources according to previous studies

It has been known that in the native people's institution, their adat, land ownership cannot be permanently held. For example, in cases in Borneo, a holder of a fallow forest has a right to make a rice field there, and then before the harvest he/she can exclusively manage the land and also the plants growing on it. In contrast, in the fallow period, the fallow forest is recognized as common property and natural growing plants in the forest may be taken by any longhouse members (Cramb 1986).

If a member of a longhouse moves to another longhouse, he/she loses his/her rights to lands in the former longhouse (Wadley 1997; Cramb 1986), and those lands sometimes become common properties of the longhouse (Cramb 1986). That means that lands belong to not only individuals but also to the longhouse community.

For fruit trees, in a case of the Iban, the holder is not necessarily the holder of the land on which the fruit trees grow, but is the person who planted the trees (Sather 1990). Since that holder right is evenly inherited to all children of the planter, the holder is not necessary single person (ibid.). This rule makes difficult for a land holder to make drastic changes to land use on it by only his/her independent decision, because the holder of the land and the holder of the fruit trees are different, and because there may be more than one holder (ibid.). The characteristic of land as property of the longhouse community, as mentioned above, is also thought be effective in preventing disposal and development of lands by the decision of only a single individual.

Methods

For the study on natural resource tenure, I conducted interviews with persons knowledgeable on the adat in several longhouses in the study areas shown in Figure 1. In total, I visited 15 longhouses and interviewed 16 persons. I asked the questions listed below. For the inheritance study also, although I conducted interviews in the 15 longhouses, the description in this paper is mainly a result of interviews of a person living in the Bakong Basin. The interviews were conducted in March and April, 2005.

Questions I asked on rules of natural resource tenure are as follows:

1. Regarding holding of lands and fruit trees:

(i) Can fruit trees be planted in an area held by other household members?

(ii) Two brothers planted fruit trees in lands of their parents when the brothers were still single and lived together as member of their parents' household. Later, the younger brother married and became independent from the parent's household. The parents handed over him a piece of land. There were fruit trees planted by the elder brother on the land. Who holds the right to those fruit trees?

(iii) In the harvest season for fruits, can persons other than those with holding rights for the fruit trees harvest them?

2. Regarding natural useful plants:

(i) Can natural useful plants, such as rattans, palms, ferns, mushrooms, etc., grown in fallow forests, rubber gardens and fruit groves be collected by those who do not hold those lands?

3. Regarding land rights and dealing in lands of persons who move to another longhouse

(i) In a case where all members of a household move to another longhouse located in a different territory, how are their lands dealt with?

Results

I describe only an outline of the results here because of space limitations.

1. Changes of rules on natural resource tenure

(i) Changing of tenure rules as a result of commercialization of natural resources

Table 1 is a summary of the results of interviews on natural resource tenure. There are several significant differences observed between descriptions of tenure rules in previous studies, and the results of this paper. According to previous studies, the fruit tree holder is the planter of the tree, so the holders of the tree and of the land where the tree grows are not necessarily the same. On the contrary, in this research some 60% of the interviewees answered that today the fruit trees belong to the holder of the land, regardless of who planted them. This means that the holder of the land and the holder of the fruit trees are coincident. Most of them said that the rule changed during the last 2 or 3 decades, although some said the rule was always the same from a long time ago. In short, the planter used to be the holder, but now the rule has been changing so that the fruit trees belong to the land holder.

Similar changes are observed for usufruct of natural useful plants. According to the previous studies, natural useful plants growing in fallow forests can be freely taken by anybody from the longhouse community. On the contrary, in this research, many interviewees answered that the usufruct belongs to the holder of the land on which the plants grow. That is to say, the rights of the land holder have become strong regarding using and holding fruit trees and natural useful plants.

Concerning lands, if one moves from a longhouse to a longhouse of another territory, his/her land rights used to be lost. However, according to this research, some signs of changes are observed. Today, the person moving may be able to continuously hold the rights to the land.

The changes, such as the coincidence of holder of land and fruit trees and natural useful plants, and the continuous holding of land rights by persons moving out from the longhouse, could be said to be due to the Iban's institution assimilating to a modern tenure system. A commonly-observed background to the changes is commercialization of the natural resources.

According to the interviews, the commercialization started in the latter half of the 1960s. In Sarawak, trunk roads passed in the middle and lower parts of major river basins where the Iban mainly live, and road networks were developed based on the trunk roads. The roads provided connections to urban areas such as Kuching, Sibu, Bintulu and Miri, and those towns also started developing in that period. The urbanization accelerated particularly after the 1980s. Under those conditions, the value of lands located near roads increased in urban areas, and growing demand for fruits and natural useful plants were observed in urban areas. As a result, problems such as land disputes and stealing of fruits and natural useful plants started happening.

(ii) Differences of recognition of the rules according to the longhouse and to individual people

Although we say the “Iban” institution or rule, details varied from longhouse to longhouse. Even between persons who before lived in a same longhouse, and even between persons living in the same longhouse who are also recognized as people with a good knowledge of their adat, the answers were different.

In order to examine why those differences occur, we need to know the learning process for the rules. Although that point was not examined in detail in this research, on the basis of interviews, I made inferences regarding the reasons why the differences happen, as explained below.

In Sarawak, where fundamentally the population density is low, access to the fruits, natural useful plants, and lands was more open before commercialization than it is today, according to some interviewees. They said that rules on use and belongings were also less stringent.

However, as the value of those commodities increased, disputes and conflicts on holdings and on their use began to occur. The disputes and conflicts have been resolved by building consensus through discussion at the individual level, in meetings of a longhouse, and sometimes through meetings between longhouses. In case the problems were not resolved at those levels, the Iban go to the *Punghule* and to the native court in the sub-division, which are the higher levels for settling problems. In the interviews, interviewees sometimes explained their rules, referring to how problems that had occurred in and near their longhouses had been resolved. That is to say, the Iban's rules are changing and reconstructing; and there are actual cases of introducing new consensus made in various levels of groups as a result of the process of resolving problems. In particular, rules on natural resources tenure, which is the topic handled by this paper, have been undergoing drastic changes, affected by recent commercialization. Therefore, different recognitions are heard according to the longhouse or the individual.

2. Land inheritance

(i) Principles of land distribution

Figure 2 shows a case of an Iban household and how they share their lands. The lands are divided into “old lands” (1 in Fig.2) and “new lands” (*tanah baru*) (2). The “new lands” are lands acquired by the “husband” and “wife” themselves after they married. Figure 2 shows a case where the “husband” inherited his parents’ household and the “wife” came into husband’s household from the same village. Therefore, the “wife’ has land(s) as *pemai* (minor inheritances) (3) from her parents. In Figure 2, although lands (1), (2) and (3) are shown as blocks, they actually represent actually several pieces of land dispersed over the village territory. The size of each piece would be 1 to 3 hectares. Almost all of the lands are covered by natural secondary forest, while a part is agricultural land such as para-rubber garden, fruit grove or pepper garden.

In the case of the household shown in Figure 2, the lands are principally shared as explained next. In the “new lands”, 6 shares were recognized: 2 for husband and wife, 1 for each of the 3 children, and 1 for the household. For example, if there are 12 pieces of land in the “new lands” and each of them have almost the same size, 1 share is equivalent to 2 pieces of land. Supposing that Child 1 will succeed to the household, Child 2 and Child 3 will each be able to receive 1 share of land when they become independent from their parents’ household. Here, after Child 2 and Child 3 of Figure 2 move to independent households, in principle they do not have any rights to use and inherit any lands acquired by this household of Figure 2 after they move. This is because the rights apply only to lands acquired while they are still members of the household. Child 1 remains in the parent’s household and takes care of his/her parents, and manages funeral ceremonies after they die. Child 1 receives 4 shares of land: 1 share for himself/herself, 2 shares for the parents, and 1 for the household, from the “new lands”.

(ii) Inheritance of “old lands” and heritage lands

Concerning “old lands”, *pemai* lands (3) will be normally received by only Child 1 who takes care of the “wife” until she died. “Old lands” (1) from the “husband” side are desirably not divided and are all inherited by Child 1, because the lands are evidence for continuity of the household from ancestors. If “old lands” are abundant and/or “new lands” are few, the “old lands” may be divided to Child 2 and Child 3. However, heritage lands (*tanah pesaka*) in “old lands” are never divided, and must be taken over by Child 1. Land type and recognition regarding the heritage lands differed from village to village. In the study village, the heritage lands consist of fruit groves (*pulau buah*) and rubber-gardens (*getah ekar*) registered by government in the 1960s. The villagers recognized the registered rubber-gardens as high value lands because of their official registration. The fruit groves are lands like islands (*pulau*) with various kinds of fruit trees which were planted by ancestors and grown from seeds dropped from the fruit trees. Although Child 1 inherits the heritage lands, the villagers consider that he does not possess them only by himself, but only manages them. For example, Child 2 and Child 3 hold almost same rights as Child 1 for tapping rubber and collection of fruits in the heritage lands. If Child 1 wishes to sell the heritage lands, he must first consult Child 2 and Child 3 and get agreement from them.

(iii) Strong rights held by children

In the Iban society, sons and daughter have stronger rights for lands. An example of that situation is observed in divorce cases. In case a couple divorces through fault of the husband, their children usually follow their mother. The couple's "new lands" are handed over to the wife and the children. In this case, the Iban sometimes explained that the children, even they are still small, have rather stronger rights for the lands than their mother's, because the children are related to both the husband and wife by blood, and they are those who will inherit household properties.

In the above case, according to a custom of another Iban village, sometimes even "old lands" of the husband must also be handed over to his children. All rights on these lands belong only to the children. The wife has no rights on lands that originated from her husband's ancestors, because she has no blood relations with them.

Conclusion

Regarding the rules on natural resource tenure, their rules observed in this paper have been changing, especially in these recent decades, and the content has been assimilating to that of modern institutions. For example, many interviewees answered that the right of using plants growing on a land is held exclusively by the land holder. Also, although there were not so many cases, some explained that even after one moved to another longhouse, he/she can continue to retain his his/her holding right for the lands of his/her original longhouse. The background to those changes includes the fact that lands, natural useful plants and fruits have become more valuable as commodities than before as urbanization and construction of roads which connect Iban longhouses and the urban areas have progressed. In the future, the value of those commodities would increase under progressing urbanization and under development of the road network in Sarawak. Such changes observed in this paper would work negatively for maintaining land use that serves for biodiversity conservation.

However, I still consider that the way changes occur to the Iban's rules retains positive factors for maintaining their land use. As described above, in the process of changing rules, conflicts of tenure problem occur between people who have different recognitions of tenure rules. In that case, they look for resolutions not by majority rule, but by making consensus between them, principally by discussion. Hence, consensus building takes a long time. As this kind of process happens in various Iban areas, their institution as a whole will gradually change, being reconstructed in a form that is more applicable for their daily lives. That change does not happen drastically in the whole of Iban society at once. Therefore, although the functioning of the Iban's rules of natural resource tenure for biodiversity conservation has been decreasing, it still continues having power to prevent drastic land-use changes in whole Iban areas on a large scale all at once. The changes in the Iban's land-use will be slow and small-scale, contrasting with the change by mono-crop plantation development.

For the Iban, lands are important for rice production, not only for its material value but also for its spiritual value. The reason why *pemai* lands are given to newly independent couples is in order for them to be able to produce rice. Their parents hand over *pemai* lands to their children from the "new lands" which they acquired by themselves. The Iban are proud of "old lands" as proof of long continuity of their household. They consider it is better that “old lands” be handed over to decedents as a property without dividing them. Heritage lands, in particular, are never divided. The Iban’s way of thinking on land inheritance differs partly from the modern concept of land tenure. The Iban consider a land is not only for a person by himself/herself. The land should be managed well by him/her and then handed over to his/her descendants. Decision of ways of land use would not be done considering not only short-term benefit, but longer-time benefit, also considering the holder’s descendants. It is therefore considered important to secure sustainable uses of their lands. In the Iban society, lands are seen as a common resource among generations.

Today in Sarawak, development of large mono-crop plantations is rapidly progressing. Iban land use that sustains the forest based mosaic landscape and that is supported by the Iban institution and rules will become increasingly important for biodiversity conservation.

References

Cramb, RA 1986. *The evolution of Iban land tenure*. Working paper No. 39. Department of Economics, Monash University.

Freeman, JD 1955. *Iban Agriculture: A Report on the Shifting Cultivation of Hill Rice by the Iban of Sarawak.* London: H.M.S.O.

Ichikawa, M 2007. Changes and diversity on rules of natural-resource tenure by the Iban of Sarawak, East Malaysia: An evaluation from viewpoint of biodiversity conservation. *TROPICS*. (in submission).

Ichikawa, M 2005. Inheritance of Natural Resources and their Sustainable Use by the Iban of Sarawak, East Malaysia –Lands as a Common Resource among Generations-. Full paper submitted to International Symposium on “Eco-Human Interactions in Tropical Forests” organized by JASTE.

Ichikawa, M 2004. Relationships among secondary forests and resource use and agriculture, as practiced by the Iban of Sarawak, East Malaysia. *Tropics* 13 (4). 269-286.

Padoch, C 1982. *Migration and its Alternatives among the Iban of Sarawak*. Leiden: KITLV.

Sather, C 1990. Trees and tree tenure in Paku Iban society: the management of secondary forest resources in a long-established Iban community. *Borneo Review* 1 (1). 16-40.

Wadley, RL 1997. Variation and changing tradition in Iban land tenure. *Borneo Research Bulletin* 28. 98-108.

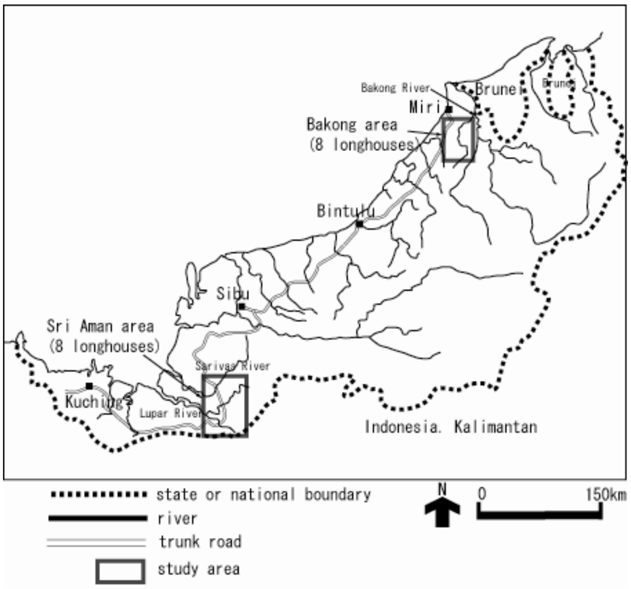
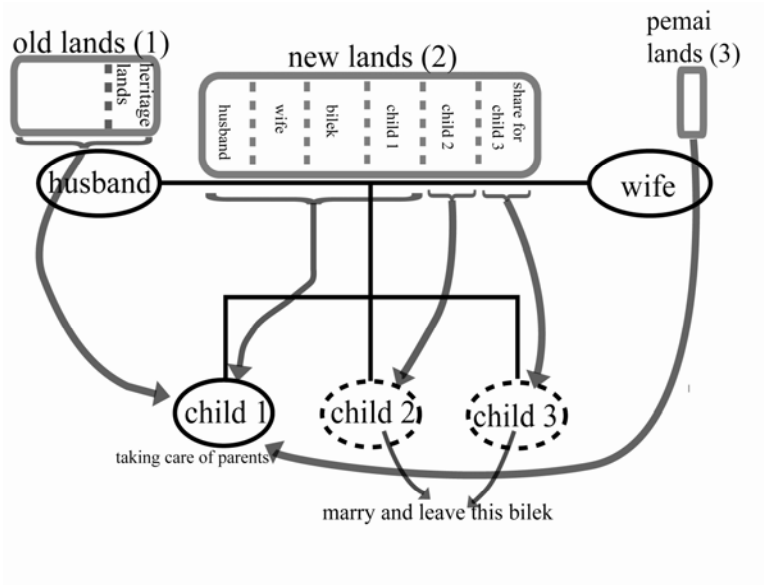


Figure 1 The study area



source: Interviews in fielwork by the author

Figure 2 Inheritance and sharing of lands according to the Iban custom

Table 1 Summary of the interviews (unit: persons)
Source: Ichikawa 2007

Questions	Answers	Bakong area	Sri Aman area	Total
1. Fruit trees and fruit (i) Can you plant in another *bilek*'s land?	Impossible now. But in the past, yes. Planter was the holder.	4	3	7
	Impossible now and even in the past	4	5	9
(ii) Who do fruit trees planted by elder brother in his younger brother's land belong to?	Elder brother	2	2	4
	In the past, elder brother. Now, younger.	3	0	3
	Younger brother, both now and in the past	3	4	7
	Other answers	0	2	2
2. Natural useful plants (i) Can you freely take them from fallow forests of another *bilek*?	Possible even now	3	3	6
	In the past, possible. Now impossible.	5	2	7
	Impossible both now and in the past	0	3	3
(ii) Can you freely take them from rubber gardens and fruit trees groves of another *bilek*?	In the past, possible. Now impossible.	4	2	6
	Impossible both now and in the past	4	6	10
3. Lands of those who move from one longhouse to another	Give them to any relatives.	5	6	11
	Give them to only parents and brother, sister.	2	1	3
	If newly-pioneered lands, the longhouse chief manages them.	1	1	2

In What Kind of Conditions Are Wild Species Used Sustainably?
-Abundant Knowledge of Biology and the Effect of Biodiversity-

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Introduction

Even if people were to live in a “traditional” manner, there is no reason to expect that wild species would be used sustainably. Before modern times and even in the pre-agricultural age, human activities have brought extinctions of wild species. Although not impossible, through all ages and in all countries, it has been difficult to prioritize medium- or long-term profit for a group of people over short-term profit for an individual person. This is not always related to interfusion of money markets or to advancement or modernization.

This paper points out that in biodiversity-rich areas, if the people have a wealth of knowledge of biology, they will tend to use wildlife sustainably without any contradiction associated with short-term profit for individual persons.

Wild species use may be a typical case of the tragedy of the commons(2)(3). Assuming that there is a useful wild species, if the people harvest the species in a self-restrained manner with an attention to the reproductive capacity of the wild species, they are likely to be able to use it continually in the future. However, most of the people would want to collect a large quantity and consume it themselves. The people who put this into practice can take much more utility than those who collect self-restrainedly in view of future use. If many such people appeared, the wild species would be collected exhaustively and eventually become extinct.

In the use of wild species, there are three ways to avoid falling into the tragedy of the commons and to make usage sustainable. Firstly, extinction can be avoided because the quantity required is limited, even if the people consume the wild species as much as they want. In other words, the utility function is saturated at a lower level than the destructive collection intensity that brings the wild species to extinction.

In fact, this is the most familiar and very important way of being able to achieve sustainable use. Although researchers pay little attention to this reason due to its commonness, we must not overlook it. This is because the relative positions of the saturation point of the utility function (maximum collection intensity when the people try to use the wild species as much as they want) and the destructive collection intensity which brings the wild species to extinction can change under conditions where people are able to choose a certain kind of wild species out of several candidates.

In the case when the more that people collect a wild species, the more they achieve unlimited utility (for example, in a situation where they collect the wild species for sale in an external market), or when the collection intensity that causes the extinction of the wild species is at a lower level than the saturation point, some measures to avoid excessive use are needed.

If the useful wild species were plants or animals of scarce mobility, people would divide the common land, so as to manage useful wild species within one’s own land. Such privatization of resources is the second way of being able to achieve sustainable use of wild species.

Thirdly, people can improve their social or political institutions to control the pursuit of an individual’s short-term profit, for example by setting a hunting period, restricting hunting or fishing methods, or by setting a limit to the amount of collection per person. In previous studies on the sustainability of wild species use, the discussions were mainly focused on this third way of achieving sustainability. This is certainly an important way of achieving sustainability, but it is not the only way.

What is density-dependent resource selection?

Biodiversity provides redundancy in useful wild species. If there is an abundance of species, one useful species can be replaced by another that grows in the same place. In cases where one of the three conditions mentioned below is satisfied, people tend to use the most abundant species, choosing it from numerous interchangeable candidates. Then, when the chosen species becomes scarce, people replace it with other useful species. This phenomenon is described here as density-dependent resource selection.

(Condition 1) Skill that is particularized by species

With techniques like trapping or ambush, seen in hunting and fishing, it is essential for people to refine their skills according to the target animal’s behavior pattern, home range, incentive method, etc(4). Thus, if a particular skill is required for collecting a particular species, people’s targets would concentrate on a single and more abundant species. Then, if that species became scarce, they would refine another skill, in order to collect an alternative species which has similar utility but different behavior or distribution range.

(Condition 2) Quality unification

Materials often need to be collected in large amounts at a time, such as building materials (in Southeast Asia, large scale construction such as construction of a longhouse involving an entire village is common), bamboo and rattan for making tools, furniture and house walls, bark and vines as rope or fiber material, several kinds of roofing materials, resin, glue, dye, sap for sugar, seasoning and so on. Such collection might be impracticable unless the materials collected have the same qualities. In such situations, people choose the single most abundant species from among the candidates. If species collected becomes scarce, another will be adopted to ensure uniformity of the material collected.

(Condition 3) Weak habituation

There are quite a lot of effective herbal medicines for the same symptom. People always apply the herbal medicine that they are most accustomed to, as long as that species is abundant and accessible. However, if it decreased in abundance, another species would become the standard one to use.

Furthermore for edible fruits, spice, side dishes, and natural ornamentation, people will use the same species repeatedly while they are abundant, demonstrating similar weak habituation to these species. But when the species become less abundant, the collectors shift to other species rather than collecting the original species excessively.

In contrast, in cases of strong habituation, a completely opposite effect is observed, and the species quickly run short. However, the continuance of wild species use rarely occurs, because wild plants with palatability such as tobacco, hemp, poppy, betel palm, betel, and durian are domesticated sooner or later due to their strong habituation.

Abundant knowledge of wildlife and effect of density-dependent resource selection

Let us consider which case enables sustainable use of wild species to be achieved easily; either when the density-dependent resource selection is practiced or not.

N stands for the total number of individuals of wild species having the same utility, and it is changeable with time. Individual numbers of each species having the same utility are n_1, n_2, ... ,n_k (at first, $n_1 > n_2 > ... > n_k$), which are also changeable with time.

$N = n_1 + n_2 + ... + n_k$

It is assumed that people use a total number of u individuals per hour.

Here, I consider three situations as follows;

(Case 1) Situation where a particular species is in use: This will occur when people do not have enough knowledge of useful wild species. In this case u individuals of single species h (invariable number) are used.

(Case 2) Situation where density-dependent resource selection is in effect: This will occur when the people have enough knowledge, and at least one of the three conditions mentioned earlier (skill which is particularized by species, quality unification, and weak habituation) is satisfied. In this case, among j $(j = 1, 2, ... , k)$ species, u individuals are used from species 1, and none is used from species 2 to k. However, when the order of numbers of individuals changes, u individuals of the species which newly occupies the first place will be used.

(Case 3) Situation where all species are in use without any distinction: This will occur when people have enough knowledge of useful wild species, but none of the three conditions for density-dependent resource selection is satisfied. In this case the individual number of species j that are taken is unj/N.」

Ecological study offers various mathematical models on community composition and population dynamics(5)(6). By applying the above cases to the mathematical models, we could examine in which conditions the extinction of wild species are most unlikely to happen. The details are due to be reported in another thesis, so here I will describe only the brief conclusion in qualitative terms without using mathematical formulas.

First, it is easily understood that extinction is most likely to happen in case 1. Although the biodiversity is high, extinction of species is caused easily when people do not have enough knowledge of useful wild species. So, the comparison between case 2 and case 3 comes into focus. Here, I will consider the issue in two distinct situations; one where species having the same utility are in competition over common resources such as food or space, and the other where there is no such relationship between the species.

Species with the same utility tend to have similar life style, and they are usually in a competitive relationship. When density-dependent resource selection is practiced (case 2), extinction is less likely to happen than when it is not practiced (case 3). Moreover, in case 2, the risk of extinction of rare species decreases compared to the natural state where there is no human use.

This reason is as follows. In case 2, the species with the highest competitive capacity declines under human impact, causing the number of individuals of suppressed species to increase. Therefore, human activities make the rare species in a natural state relatively resistant to extinction.

Resilience in number of individuals is the most important factor for the unlikeliness of extinction under the pressure of human use. From this viewpoint it is assumed that density-dependent resource selection automatically chooses the species most resistant to extinction. It is not that the people use a particular species intensively because they know it has high resilience. They are each pursuing individual profit based on one of the three conditions of density-dependent resource selection (ie; skill which is particularized by species, quality unification and weak habituation). The species most resistant to extinction is selected as a result.

Next is the situation where there is no competitive relationship between species having the same utility. For example, small grass species used for medicines or seasonings are not always competing within their community despite having the same utility or taste. In this situation, unlike the situation with a competitive relationship, extinctions of particular species will not decrease compared to the natural state. However, even in this situation, the process of the species with high resilience of number of individuals being automatically selected for standard use is almost the same as with the competitive relationship situation mentioned above. Therefore, extinction occurs less often in a situation where density-dependent resource selection is practiced (case 2) than in a situation where it is not practiced (case 3).

Where there is no competition, the initially dominant species is the one with high carrying capacity (expressed as an number of individuals K when the condition is stable enough and there is no human use). Because there is a trade-off between the carrying capacity K and the resilience in number of individuals (expressed as r), the initially dominant species tends to be a species without high value in r. Species with small values of r are not suitable for intensive use over the long term, but as a result of dominant species replacing each another as an effect of density-dependent resource selection, species with relatively high r come into standard use.

The effect of biodiversity

Rich biodiversity and poor biodiversity; in which situation can wild species use be sustainable? Following is the formulation of how species are used, in the situation of poor biodiversity.

(Case 4) Situation where biodiversity is poor: Suppose that there is only one species having some kind of utility, and its number of individuals is determined as N. As above, assume that people use u individuals per hour. The number of individuals N was previously divided into k species according to difference in competitive capacity, carrying capacity (K) and resilience in number of individuals(r), but here there should be no difference among N.

From this formulation, the ease of extinction can be compared with case 1 to case 3 above, all of which are situations in which biodiversity is rich. A detailed examination applying the various mathematical models on community composition and population dynamics is due to be reported in another thesis, so here, again, I will describe only the brief conclusion in qualitative terms.

The possibility of extinction occurrence, even in single species, is highest in case 1, where although biodiversity is rich, people's knowledge is poor. Of the rest, the next highest possibility of extinction occurring is with case 3, where although both biodiversity and people's knowledge are rich, density-dependent resource selection is not acting, followed by case 4, where biodiversity is poor and then case 2, where biodiversity is rich and the density-dependent resource selection is acting.

The reason why case 4 is lower than case 3 is that there are few individuals of each species, and in case 3, the species with low value in r, which is most likely to be extinct, is used continually. The reason why case 4 is higher than case 2 is that the species with high r is automatically selected as a standard use species in case 2, whereas in case 4 there is no such selection.

The possibility that usable species die out completely becomes lower in order from case 1, case 4, case 3, and then case 2. Here, in case 3, only species with a low value for r would become extinct, and species with a high value for r would be likely to remain alive, so case 3 replaces case 4 in the order.

Furthermore, the possibility that species potentially having value of use die out completely becomes lower in order from case 4, case 3, case 2, and then case 1. In case 1, species other than h are not used, so they are likely to survive.

Limitations of density-dependent resource selection

Species are less likely to become extinct and the risk of extinction may be even less than in the natural state (where there is no human use) when biodiversity is rich, people have enough knowledge of usable species, and at least one of three conditions for density-dependent resource selection (ie. skill which is particularized by species, quality unification and weak habituation) is satisfied. Looking over the examples mentioned above and limiting the discussion to self-sufficient resources, there are hardly any wild species resources that do not satisfy any of these three conditions for density-dependent resource selection.

From this viewpoint, there are two important conditions for likeliness of achieving sustainable resource use: (i) Usable resources have redundancy due to rich-biodiversity. (ii) The level of redundancy is not fixed, but can be enhanced by people having greater knowledge of useable species.

Lastly, the limitations of sustainable resource use through density-dependent resource selection should be considered. As I mentioned earlier, this paper discusses only the situation when the utility function is saturated. This is a quite general assumption if the wild species resources are used for subsistence. However, if the situation is that the more people collect wild species, the more they profit from high utility, then the assumption collapses completely, which means that density-dependent resource selection cannot contribute to the sustainability of resource use.

Such a situation (in which the utility function is not saturated) is assumed when the wild species resources became a target of commercialization. In this situation, either privatization of resources or communal management should be adopted to maintain sustainability of resource use. In fact, for example, fishermen who sell their catches have severe internal restrictions, and access to the resource by external persons is also limited. By contrast, there are few reports on communal resource management in collectives where diverse wild species are used for subsistence. I believe that communal management is not needed in such cases because density-dependent resource selection is available.

For maintaining biological knowledge

The idea of density-dependent resource selection is still new, so there is still a need to examine a lot of subjects both theoretically and verifiably. Although it seems risky to make many suggestions at this time, I would at least like to mention a certain point. For wild species use in biodiversity-rich area, commercial trade must be restricted but the collection and the use of species should not be excessively restricted. In such area rather they could be encouraged. People’s abundant knowledge not only allows sustainable resource use, but also may result in some species having an even lower risk of extinction than in the natural state without human use. Such indigenous and abundant knowledge structures are only inherited and improved upon by continuing the habit of collecting and using the species. I would like to add that people's abundant knowledge of biology is valuable in various ways, and the aspect emphasized in this paper is just one aspect. The biodiversity, people’s knowledge of biology, and their lifestyle of using abundant species, in which lies the basis of their knowledge, have to be conserved together, and this is in fact an efficient approach.

References

(1) M. Alvard: Current Anthropology, 36, 789 (1995)
(2) G. Hardin: Science, 162, 1243 (1968)
(3) E. Ostrom: Governing the commons, the evolution of institutions for collective action, Cambridge University Press (1990)
(4) K. Momose: Southeast Asia Studies, 40, 85 (2002)
(5) Y. Iwasa: Introduction to mathematical biology, HBJ Publ. (1990) (in Japanese)
(6) E. Renshaw: Modeling biological populations in space and time, Cambridge University Press (1991)

Transition of the Forest Management in Yakushima, Japan

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Introduction

Yakushima, which is a part of Kirishima-Yaku National Park of Japan, forms bountiful and unique nature. Since it contains significantly unique ecosystem even in the world level, a part of island was designated to the world heritage. Since then, numbers of tourists visited to see the distinctive nature, and ecotourism, focusing on the forest, has been the most flourished industry in the island. In fact, it has been only 20 years since the forest began to attract many tourists. The worth of forests in Yakushima had been recognized early on, but the abundant nature was also the important resources in several developments in Yakushima. For instance, the forest has been utilized for forest development and generation of electricity. In other words, people have obtained the various benefits and services from the forest.

Therefore, the transition of the forest management could represent and reveal the attitudes people had towards the forest, the background of the shifted managements, and the interactions among different managements. Moreover, the discussion will be focused on the incidents after 1920s and it is because that people started to utilize the forest in the large scale in 1920. In this paper, the term, the forest management indicates the large scale forest managements that are influential to numbers of people. The term doesn’t include the small scale usage of the forest. For example, it doesn’t include firewood or charcoal use of the forest by local people.

The transition of forest management in Yakushima

There are four categories of major forest managements in Yakushima since 1920. Three direct managements are the forestry, the electricity generation, tourism, and an indirect management is the natural preservation.

Forestry (1921 to present, the peak was during early 1960s to early 1970s.)

In Yakushima, the national forest project was officially started at the area where became the public property in 1885. The Basic Plans of National Forest Management in Yakushima was published in 1921, and the logging was operated with an understanding that Yakusugi has the significance in both the academic field and the natural legacy. Also, a part of the national forest was chosen for an academic forest reserve for Yakusugi. Up to the beginning of the World War Ⅱ, the forest management had a strict standard that prohibited to cut living tree of Yakusugi.

Nevertheless, the management plan shifted towards the one with a focus of increasing the production yields in Post World War Ⅱ era. One of the main driving forces was a high domestic demand of the timber for the reconstruction and for the Korean War in 1950. Another reason was that the national forest began to use a self-supporting accounting system. In consequence, even the depth of the forest became a part of the logging area: in addition to that, clear cutting and artificial regeneration were operated in order to increase the production. The introduction of a chainsaw and a bulldozer also improved the efficiency of logging; as a result, clear cutting was expanded rapidly. Furthermore, the public management of Yakusugi encouraged the logging. In the Plan of National Forest Production Improvement in 1957, for example, the treatment of

Yakusugi was lowered to the level of the ordinary trees. Moreover, Yakushima Forestry Development Plan was established in 1961 and a large quantity of logging began. The large scale logging, supported by the technological innovation was operated for several years (Figure 1).

The large scale national forest project, however, started to decline because of the energy revolution in 1950s and the resulted industrial component transition. Also, cheap foreign timber took over the Japanese forestry, and the Kosugi-dani office, which was the center of logging, was closed in 1970. The outcomes of large scale logging were not only the landscape destruction but also the disasters such as drought and an avalanche of rocks and earth. At the same time, natural conservation movement was growing in Japan, and there were numbers of petitions for natural protections were submitted to the government. (Kagoshima Natural Protection Agency. in 1968, The Botanical Society of Japan, Ecological Society of Japan, The Nature Conservation Society of Japan in 1969.) In 1971, the second regional management plan responded to the petitions, and it enlarged the forest conservation area and settled the Yakusugi recreation forest. In the forth regional management plan, which was established in 1981, it strengthened the forest conservation standing point, and the forest management was shifted from clear cutting with artificial regeneration to group selection cutting, which is better alternative. Another remarkable change was the reintroduction of the policy that mandates the preservation of the living Yakusugi trees permanently. In addition, utilizing the multiple functions of forest, including the recreational use, became the foundation of the forest management. The plan changed its name to the Management Control Plan in 1991. In 1995, two district forestry offices that were in charge of the forest management were consolidated to Yakushima forestry office and it carried the logging. The forest environmental protection center was also settled, and it carries the forest management.

Power Generation Development (1953 to 1960s)

In the post war era, not only the timber but also the electricity was in high demand. There were some coal mines in Hokkaido and Kyushyu; however, the long distance transportation caused high cost. As a result, hydroelectric power generation gained the attentions in Japan. In order to utilize the high precipitation in Yakushima, the water power plant, Senpiro-daki waterfall water power plant was built in 1953. With the support of the electricity, factories of carbide, abrasive, and firebrick were in work in 1960s. This period was described as the daybreak of the coal mining island.

Tourism (before the war time, and the after)

In this paper, the term, ”tourism development” includes the all sorts of required developments that support tourism. In the beginning of the Showa era, the rich and diverse forest in Yakushima gained the attention from the tourism industry. The Law of National Park was enacted in 1931, and Kagoshima prefecture funded for researching tourism development in 1935. In the later investigations, the rich forest was recognized and the forest was in consideration as the national park in 1954. It became a national park as a part of Kirishima-Yaku National Park ten years later. At that time, national parks were selected for its potentials of demonstrating the Japanese unique beauty and attracting foreign tourists (Hatakeyama, 2004.) There are major three reasons why it took long years to become the national park. First, Yakushima is far from the main land. Second it didn’t have sufficient port facility (Fujimura, 1971). Finally, it took years to balance the forest development and electric power generation (Itoga, 1974.)

Even before the Yakushima forest became the national park, the tourism industry from outside paid attentions to the values of the Yakushima forest. After the nomination to National Park, tourism facilities such as the mountain lodges, the hiking trails, the accomodations, were improved, and Yakushima tourism conference was established. In 1968, Kagoshima prefecture included Yakushima in the area of important marine and mountain recreational development. It was a part of their long-term program, called "Next 20 years in Kagoshima." Moreover, Yakushima became famous by the discovery of Jyomon-sugi and following the conservation movement. In addition to that, essential infrastructure, for example, an airport, a port for ferries, and accomodations for tourists were developed for the foundation of tourism industry. The designation of the world heritage in 1993 and the ecotourism trend have contributed to increase the numbers of tourists in Yakushima (Figure 1).

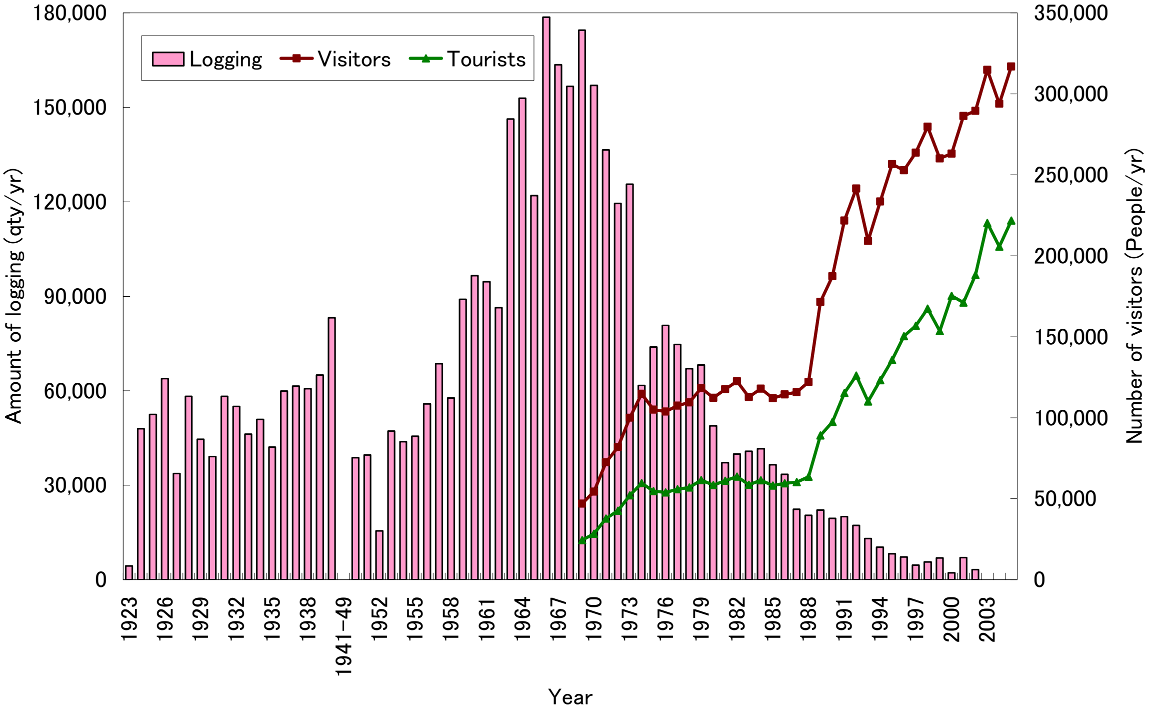

Figure 1. The amount of logging and the number of visitors in Yakushima.
Source: Kumage Branch Office, Kagoshima Prefectural Office

Natural Conservation Movement (from 1960s to present)

The forest of Yakushima was an icon of the natural conservation movement (Iseki and Harashina, 2006). The rapid economic growth in Japan, caused severe pollutions, and the awareness for the environment developed as a result. There were many natural conservation movements against the deforestation and the environmental degradation. Since Yakushima became the national park in 1964, it also promoted the natural conservation movements. The groups of scientists and local people requested the government to reconsider the forest managements such as the national forest project plan and the conservation forests. Moreover, Jyomon-sugi, which found in 1966, showed Yakusugi's distinctive feature that is a remarkable long life, and also it demonstrated the rich environment in Yakushima. When Yakushima became the world heritage, Yakushima and Yakusugi appealed the significance of the natural conservation.

Transition of the forest usages before and after the large-sized logging

Four forest usages were influenced and transformed by the social demands and the interrelated relationship among four usages. For example, an extensive logging was operated in early 1960s to early 1970s. It is assumed that this large scale logging affected to other forest usages. Therefore, it is important to understand how other usages were affected and how those usages were interrelated with each other.

In early 1960s to early 1970s, Japan went through the rapid economic growth and the large-scale logging period. In the meantime, the National Forest Project shifted to clear-cutting in order to meet the high domestic timber demand. The excessive logging and the electricity generation, which triggered watershed alteration, were problematic to tourism development and the natural conservation.

As a result, both the tourism industry and the natural conservation movement sometimes opposed to the forest development and the electricity generation. For example, there was a disagreement between the Forestry Agency, which supported the forest development, and the Ministry of Health and Welfare, which supported tourism development. Especially, Yakusugi was a controversial theme. In 1951, the Forestry Agency lowered the protection level of Yakusugi in the forth forest management plan so that Yakusugi was felled. At the first place, the Forestry Agency and the Ministry of Health and Welfare were recognizing the value of the Yakusugi forest as the tourism attraction that could compete with giant sequoia or the forests in Yosemite National Park in the United States. In one hand, the Ministry of Health and Welfare claimed that all Yakusugi trees should be protected because it is an unrenewable resource. In the other hand, the Forestry Agency claimed that there was no need to protect all Yakusugi trees as long as there are sufficient areas of the Yakusugi forest left for tourism (Shibatate, 1964.) In short, it is assumed that these conflicts caused the late designation as the national park.

During the period of large-scale logging, it was also found a conflict between the Forestry Agency and the local groups that supported the natural conservation. For instance, it was seen in the large gap in existing tree numbers of Yakusugi, which has lived a thousand years, and Kosugi, which has lived less than a thousand years. The Forestry Agency claimed that there were 145,000 Yakusugi and Kosugi trees in total (11,600 trees of Yakusugi and 133,400 trees of Kosugi); on the other hand, the local conservation group claimed that there were only thousand trees of Yakusugi and Kosugi (Aragaki, 1974). There was a huge gap in their understandings. It could be because they gave the numbers that could support their points, but it showed that both sides didn’t have enough discussion over the topic.

Next, there are also some corporative relationships among different forest usages. First of all, the forest development and electricity generation demonstrated a good example. Electricity that generated from Senpiro-daki waterfall water power plant supported the daily life of people who worked for developing the forest and transporting lumbers. Second, the natural conservation movement and tourism development also had a cooperative relationship. For instance, Kagoshima prefecture, local towns, scientific groups and local groups altogether submitted the petition of the natural conservation to the Forestry Agency. Also, the Ministry of Health and Welfare requested to conserve natural and tourism resources to the Forestry Agency. It is presumed that the natural conservation movement and tourism industry were worked together against the forest development.

During the period of the declined forestry, opposing and cooperating positions kept changing. An article, “Visiting the Natural Forests in Yakushima” in the Forestry News (Fukura, 1970), contains comments such that “It is important to support the Yakushima local community by assisting their tourism development from the positions as the Forestry Agency and or the district forestry office.” and “Both district forestry offices were constructing the forest road and contributing for the tourism development.” At first, the Forestry Agency had no need or intent to support the tourism industry, but they began to provide assistance. It could be that the Forest Agency’s attempted to justify the forest development by demonstrating the contribution to the tourism development. According to Shibatate (1964), “the road infrastructure is an essential part of tourism development, and it was improved because of the Forestry Agency.” It applied in the case of Yakushima, and tourists obtained the access to the deep forest. Moreover, the port facility that used to transport timbers contributed to the tourism.

Conclusion

In this paper, the main focus was on the transition of the forest usages in Yakushima because it may help to assume the reasons and backgrounds that the forest usages shifted largely before and after the extended logging. Also, it could help to see the interdependent relationships among four forest usages.

The Yakushima forest that contains rich and diverse flora has been providing the resources to the tourism industry and forestry. However, the landscape and natural resources were degraded because of the expansion of logging in responding to the domestic lumber demands. The most of land in Yakushima was the national forest so that the forest management plans and policies had strong influence over the forest. With the growing environmentalism and natural conservation movement, the preserved forest and recreational forest were arranged. At the same time, the timber production was declined due to the introduction of cheap foreign timbers and the energy revolution in Japan. In short, we have gained the provisioning service of nature such as the timber, but the excess demand caused several problems. As a result, we recognized the significance of the natural conservation and also realized the value of the forest in the cultural service of nature such as recreational use. Moreover, the Forestry Agency changed their standing point from supplying the domestic timber demands to contributing for the island industry in responding to the people’s concerns and awareness.

The forest development resulted environmental degradations. The crisis of Yakushima forests due to large scale logging drawn attentions from the nationwide, and it led to the recognition of bounty nature in Yakushima. However, the tourism industry is also depending on the forest developments. Housing and transportation infrastructure are essential for the tourism industry, and they were developed by the expansion of the forestry. Moreover, the history of logging and forestry became an important part of tourism attraction. For example, the development of forestry and traditional ways of life in the forest in Yakushima are demonstrated in the exhibitions in Yakusugi Museum and in the eco-tour.

The several forest usages have coexisted and transformed with the social needs. Those usages were also influenced with each other. The history and whole transitions of the usages have contributed to develop the present social and geographic environment in Yakushima.

Reference

Aragaki, H., 1974. Visiting a Yakushima Island. National Park 297/298, 21-22 [in Japanese]

Fujimura, S., 1971. Forest Development and Natural Conservation. Institute of Water Facility and Science, Tokyo. [in Japanese]

Fukura, T., Tsuchiya, K., Aikawa, S., Fukuda, S., 1970. Visiting the Natural Forests in Yakushima. Forestry News 17(2), 12-24 [in Japanese]

Hatakeyama, T., 2004. Lecture of the Natural Conservation Law (revised edition). Hokkaido University Press, Sapporo. [in Japanese]

Iseki, T., Harashina, S., 2006. A Study on Relationship between Nature Oriented Tourism and Other Nature-Use-Activities: A Case Study of the Old Famous Cedar Tree, Jyomonsugi in Yakushima Island. Environmental Information Science 35(2), 43-52 [in Japanese]

Itoga, R., 1974. The Issue of Natural Conservation in Yakushima Island. National Park 297/298, 1-4 [in Japanese]

Shibatate, Y., 1964. Story of Yakusugi. The Nishinippon Shimbun, Fukuoka. [in Japanese]

Politico-Business Relationships in Sarawak's Timber Industry

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Introduction

Around 66.1 percent (8.22 million hectares) of the total land of Sarawak, a state of East Malaysia, is categorized as forest area, and by 1985 as much as 60 percent of the forest had been given away for timber concessions (Brown 2001). Those who have made huge profits from logging operations are a handful of top local politicians and local businessmen who succeeded in making close links with the politicians. This paper focuses on Tiong Hiew King, one of those successful businessmen and shows how political patronage is important for business success in the region, especially in the timber sector.

Background

Logging concessions have been issued by the state Minister of Resource Planning, a position which Chief Minister of Sarawak Taib Mahmud has held since 1985. Most concessions were granted to local politicians and their relatives, friends and political associates. The concession holders subsequently subcontracted logging work to local timber companies. As a result, local businessmen have to make good relations with the concession holders, that is, local politicians and their families, in order to gain subcontract work. Under such conditions, five powerful business groups have grown in the region. They are Samling, Rimbunan Hijau, KTS, WTK and Shin Yang (Brown 2001). The founders are all local Chinese, and these companies have grown nationally and even internationally today. How did they make their links with the politicians and become successful in business?

Rimbunan Hijau and its Political Partners

Rimbunan Hijau (RH) is the most multinational and the second largest of the five business groups1. Tiong Hiew King is the founder and chairman of RH, and he was ranked the 8th richest person in Malaysia and the 746th richest in the world in 2006 (Forbes 2006a, 2006b). His personal net worth was said to be more than two billion ringgit (800 million US dollars) in 1995 (Malaysia Business 1995). How has he achieved such a great success?

Tiong Hiew King was born in 1935 to a poor family in Sibu, a Chinese dominant town in Sarawak. He belongs to the second generation of the Foochows who migrated to the region in the early 1900s. After graduating from a local high school, Tiong took up a correspondence course with a Chinese university and also began his career at his uncle's timber company, the WTK group. In 1975, Tiong set up his own company, Rimbunan Hijau, along with his brothers. RH got its start as a timber contractor in Sibu and now operates as far away as New Zealand, central Africa, Papua New Guinea, Vanuatu and Russia. Other than timber exports and timber processing, his business has also expanded to cover finance, media, IT, mining,

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[1] According to Brown (2001), the biggest company is Samling in terms of the total area of concessions in Sarawak.

aquaculture, oil palm plantation, trading, and property development (Malaysia Business 1995, China Daily 2005).

Tiong experienced political hardships during his early business days. In the early 1970s, he was jailed by Sarawak’s Chief Minister at the time, Abdul Rahman Yakub, on a charge of being a communist. After being released, Tiong tried to creep into Rahman's favor, even making a special trip to Taiwan to serve as his golf umbrella-holder. Rahman however continued to abuse his relationship with Tiong. For example, Rahman suspended Tiong's federal senatorship, despite it being promised by the Secretary General of the Sarawak United People’s Party (SUPP), Wong Soon Kai, in exchange for a substantial bribe (Brown 2001). The SUPP is the Chinese-based party of Sarawak’s coalition government and Wong is a Sibu-born Foochow politician (Brown 2001).

In 1981, Rahman Yakub stepped down and his nephew Taib Mahmud assumed the position of Chief Minister and subsequently also Minister of Resource Planning. Tiong moved quickly to build up new political connections not only at the local level but the national level this time. Top national and local politicians or their family members became board members in Tiong’s listed company Jaya Tiasa. These include Abdul Rahman Abdul Hamid (former federal Chief of Defense Force) and Abu Talib bin Othman (former federal Attorney-General). RH also owns around a 40% share in Limbang Trading, the other share of which is owned by a senior local politician, James Wong Kim Min, who is former Minister of Environment and Tourism in Sarawak and owns huge areas of logging concession in the eastern part of the region (Brown 2001, Malaysia Business 1995, Forest Peoples Programme 1994, Malaysia Today 2005)

Under the Taib administration, Tiong’s political ally Wong Soon Kai became the SUPP president, appointing him as Deputy Chief Minister in 1994. Tiong’s younger brother Tiong Thai King was then appointed as Senator in 1995. In order to make further political connections at the national level, Tiong also established an optical fiber company Opcom in Kuala Lumpur in partnership with Mukhriz Mahathir, a son of the Prime Minister at the time (Brown 2001).

Tiong’s Failure in Retaining Political Connections

Opcom, however, failed to make profits and the Tiong family resigned from the company board in 1994. After the Tiongs’ withdrawal from the partnership, Mukhriz Mahathir brought a lawsuit against Tiong. Tiong tried to arrange a meeting with Prime Minister with the help of Wong Soon Kai, an old medical school classmate of Mahathir. The Prime Minister, however, refused to meet with Tiong. It is also said that federal Inland Revenue Service agents were sent to raid the RH headquarters (Ibid). Tiong’s attempt to make a strong connection with the top national politician then broke down.

Tiong’s political links have further withered away since Wong Soon Kai stepped down as the SUPP president after his defeat in the 1996 election. A Miri-born doctor, George Chan, then assumed the party leadership. Today, George Chan is Deputy Chief Minister of Sarawak, and his daughter married a son of the

Chief Minister. It is likely that this was the time when RH was overtaken by Samling, which has close links with the top local politicians including George Chan. Furthermore, another local Chinese businessman, Ting Pek Khiing, has also gained economic strength rapidly since early 1990s. He went into not only the timber industry but also non-timber businesses such as chemical and construction companies in partnerships with powerful politicians at both the national and local levels, including former federal Minister of Finance Daim Zaunuddin. Ting is also said to have obtained the trust of then Prime Minister Mahathir by his very quick completion of the five-star hotel construction project in Langkawi. Moreover, Ting once competed against Sarawak's Chief Minister over a gigantic dam project, but he was able to gain control of the project through ties to these top national politicians (Brown 2001).

While being upstaged by newly emerging business groups and individuals in Sarawak, RH became active and influential in the timber industry in other countries, particularly Russia and Papua New Guinea. The company has been operating in the Russian Far East since 1997 when it acquired the rights to harvest 305.000 hectares of State forest (Greenpeace 2004). In PNG, RH is said to have made close connections with national and local politicians with bribery, including former Deputy Prime Minister, Minister for Internal Security, a provincial Governor and two Parliament members, and as a result succeeded in gaining control of close to 50 percent of PNG's log exports (Greenpeace 2006). Although RH's international operations have been accused of deforestation and illegal logging by Greenpeace and other international NGO groups, it is likely that Tiong can more easily conduct legal and illegal timber business in collusion with politicians in those "weak states" than in Malaysia where his political connections have become weak at both national and local levels.

Conclusion

Through the story of Tiong Hiew King, timber businessmen in Sarawak can be characterized by the following four features. Firstly, Sarawak's forest concession has been controlled by the top local politician, and therefore local Chinese businessmen have depended totally on political patronage for their business success. Secondly, such politico-business connections are likely established along ethnic and regional lines at the beginning but are not necessary divided along these lines at end. Tiong's closest political ally is Wong Soon Kai, who is a Foochow and from Sibu the same as Tiong. He started to make his political links with Wong before other politicians of different ethnic groups. Thirdly, local businessmen who have links with both national and local politicians are likely more competitive on regional business matters than those having links only with local politicians. As described in Ting Pek Khiing's case, he was able to win the competition with Sarawak's Chief Minister over the dam construction project through his close connection with top national politicians. Finally, logging operations by Sarawak's businessmen have recently expanded internationally. Some of them have become notorious as actors in illegal logging and environmental problems, especially in PNG rather than in Sarawak. Collusion between the businessmen and politicians makes such problems difficult to solve.

References

Newspapers and Magazines:

China Daily (2005) Tan Sri Datuk Tiong Hiew King: The World of Rimbunan Hijau, May 17, 2005.

Forest Peoples Programme (1994) Malaysian Loggers Come Out of the Woodwork: Timber Boom drives Malaysian Companies onto the Stock Exchange, September 26, 1994.

Malaysia Business (1995) A Tale of Timber, July 1, 1995.

Malaysia Today (2005) Logging in East Malaysia, 27 May, 2005.

Websites

Forbes (2006a) “Malaysia’s 40 Richest.” (online), available from < http://members.forbes.com/global/2006/0605/035.html>, (accessed July 9, 2007).

Forbes (2006b) “#746 Tiong Hiew King.” (online), available from < http://www.forbes.com/lists/2006/10/CTPL.html>, (accessed July 9, 2007).

Papers and Books:

Brown, DW (2001) Why Governments Fail to Capture Economic Rent: The Unofficial Appropriation of Rain Forest rent by Rulers In Insular Southeast Asia Between 1970 and 1999. PhD Dissertation. University of Washington.

Greenpeace International (2004) The Untouchables: Rimbunan Hijau’s World of Forest Crime & Political Patronage. Amsterdam: Greenpeace International.

Greenpeace International (2006) Forest Crime File, Rimbunan Hijau Group: Thirty Years of Forest Plunder. Amsterdam: Greenpeace International.

In Search of Sustainable Forest Management and Social Solidarity in Sarawak

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Introduction

The tropical forest in Southeast Asia is regarded as important on a global scale because it is one of the world's richest eco-systems in terms of biological diversity. Despite various efforts, however, the area of forest has continuously decreased due to commercial logging and conversion to farmland or plantations.

In Sarawak, anti-logging movements by the native communities since the late 1980s led to international campaigns against commercial logging in Sarawak. The campaigns are now quieter than in the early 1990s, although NGOs are still active both in Malaysia and foreign countries. Many studies also stress a history of endangerment to native people's customary rights and access to forest resources (Hong 1987), and exploitation of the forest resources by timber industries in cooperation with local politicians (Jomo el al. eds. 2004; Fadzillah 1999; Ross 2001; Leigh 1998).

However, both governmental sectors and NGOs are found to have undergone considerable policy changes, though the basic relationships between stakeholders as described above are maintained. Government introduced a 'Sustainable Forest Management' (SFM) policy. NGOs and native people's groups now pursue their struggle with court cases demanding recognition of their 'native customary rights' rather than with blockades of the logging roads.

This article evaluates these changes from the viewpoint of sustainable forest use as a means of promoting biological diversity and social stability.

Forest Management in Sarawak

Legal Framework of Forest and Land

Modern land ownership was first introduced under Brooke rule in Sarawak, and has developed step by step since then. Customary land use by the native people that has been practiced since before the Brooke period is also recognized in the modern land law system to a certain extent: provisions of the Land Code of Sarawak of 1958 are currently applied. The Land Code of 1958 provides for the following categories: 1) Mixed Zone Land, in which both native and non-native people can obtain the ownership of the land, 2) Native Area Land, in which only native people can obtain the ownership of the land, 3) Native Customary Land, in which Native Customary Rights had been established by 1958, 4) Reserved Land, which the government reserved for various purposes, including Permanent Forest Estates for sustainable timber production and Totally Protected Areas as National Parks and Wildlife Sanctuaries, and 5) Interior Area Land, the area not falling into the other categories. Native Customary Land, Reserved Land and Interior Area Land are categorized as State Land.

The most controversial is Native Customary Land. This area is due to customary land use of the native people following their customary law and beyond modern land ownership. Ambiguous boundaries and ambiguity of proof often cause conflicts with outsiders.

Forested areas within the State Land as above are under the control of the Forest Department of Sarawak State. The Forestland is classified into three categories: 1) Totally Protected Area, which includes National Parks and Wildlife Sanctuaries, 2) Permanent Forest Estate (PFE), the forest utilized for long-term sustainable timber production, and 3) State Land Forest, other forest area within the State Land. PFE comprises of Forest Reserves and Protected Forests provided for by the Forest Ordinance of Sarawak of 1953. The Permanent Forest Estates, however, are not limited to natural forests. Therefore, afforestation of, for example, *Acacia mangium* can also be included.

Forestry Operation

Forest areas within State Land are supposed to be utilized for timber production, and logging licenses are issued to those forests. For the Forest Management Units in Permanent Forest Estate, long-term licenses are issued and the logging operation follows the scheme developed by FAO's recommendations in the 1970s[1]. Other State Land Forests are subject to more short-term logging operation, not supposed to be reserved as forested areas, and might be converted into plantations of oil palm or rubber. As discussed below, reduced-impact logging with more attention to local people's welfare is also practiced in some pilot projects.

Forestry and Society

Forestry has long been the most important industry in Sarawak. According to the provisions of the Malaysian Constitution, forest and land, unlike other natural resources as oil, is under the State's control. In addition, Sarawak and Sabah are privileged in that they do not necessarily have to accept recommendations by the Federal Government's experts on the issues of forest and land. Therefore, the Sarawak State Government has an almost free hand over its forest resources. It is often pointed out that the forest resource is among most important rent for local politicians. Logging license holders' names are not open. Even officials responsible for logging management in Sarawak Forestry Corporation (SFC) do not know who owns the licenses[2]. However, it is commonly believed that a small number of local politicians hold the vast majority of licenses. The licenses are rented out for logging by the logging companies.

Anti-logging Movement

Blockades

Commercial logging and plantation development increasingly affected the lives of local native people largely dependent on the forest resources. They started to protest against commercial logging within the areas they had been utilizing since ancestral time[3]. In particular, the Penan people's blockades of logging roads, which started in 1987, became a matter of international concern.

Malaysian NGOs conducted interviews with Penan people in Upper Baram area during 1994 and 1995. Testimony by the local people in the report (IDEAL 1999) describes the various processes of blockade

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[1] Interview at Sarawak Forestry Corporation (SFC) and Sarawak Timber Association (STA). The details of FAO's recommendation are not clear.

[2] Interview at SFC.

[3] Detail history is not clear.

struggles: When the logging company first came to their areas, the local people demarcated the forests from which they appropriated resources for daily life. They negotiated with logging companies not to fell in the demarcated areas and petitioned governmental authorities. Sometimes the logging companies agreed. But when such protests were neglected, they decided to blockade the logging roads following discussion among the neighboring communities. Blockading logging roads became clearly criminalized by the amendments of Forest Ordinance made in 1987. The government sent police to dismantle the blockades. Though there were no cases of serious bloodshed, a lot of local people were arrested. Logging companies might have offered to give 'goodwill money' in exchange for acceptance of logging. But local people did not accept it. Some groups continually constructed new blockades as soon as the old ones were dismantled by the police.

International Bashing

Blockade of logging roads to protest against commercial logging was not carried out solely by the local people. Foreign environmental activists like Bruno Manser as well as Malaysian domestic NGOs such as Sahabat Alam Malaysia (SAM) provided much assistance to the local people[4]. James Ritchie (1994) describes the detail the process from the point where the Penan people in Upper Baram first decided to carry out blockade until its expansion into a worldwide bashing campaign, especially with regard to engagement by outsiders. At the very beginning, Bruno Manser played a role as an organizer: He first facilitated meetings of Penan communities' headmen[5]. After that, in cooperation with SAM, an Australian activist released a Penan public statement to the international mass media demanding an immediate stop to logging and warning that if logging did not stop they would blockade the logging roads. The blockade was implemented on 23 March 1987, the date previously announced. After that, foreign activists secretly visited the site and donations were made from Western countries and Japan to support the movement. The international campaign finally led to a boycott of Malaysian timber in the EU (Ross 2001; Kanazawa 2005).

Impacts of the Movement

The anti-logging campaign was much dependent on the support of outside environmental activists, especially in Western countries. Accusations from international society fueled by the activists might have been a pressure for Sarawak government to amend its policy to pursue 'sustainable forest management'. But it is quite doubtful that these movements substantially improved local people's livelihoods.

Indeed, there was a divergence between foreign environmental activists and local Penan people in terms of what they saw as the main concern. For Penan people, securing the necessary resources for daily subsistence was the main issue. They demanded the government recognize their native customary rights over the forest resources following the Land Code as a tool for survival. Penan do not refuse development projects by the government regarding agriculture, education, public health and so on, which is not related to acceptance of logging (IDEAL 1999). Some communities even accepted collateral financial support or development programs from the logging companies (Samling Plywood n.d.).

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[4] The local people's testimony above (IDEAL 1999) did not refer to outsiders' assistance. Those cases did not occur in the initial stage in the late 1980s, but in the 1990s. Therefore, it is not clear if outsiders also assisted those cases.

[5] Bruno denied his direct involvement in the blockades (Harago 1989).

On the other hand, foreign environmental activists' concern is mostly about the conservation of rich nature, tropical rainforests. When the movement was most active in the late 1980s and the early 1990s, the activists did not seriously consider the Penan people's actual benefits and the improvement of their livelihood. For example, in 1991, a Penan village headman and his vice-head visited 31 Penan villages to collect their opinions on the blockade. The main answer was that Penan did not want blockades and, if assistance were available, they would like outsiders to instruct them in farming methods. A volunteer group consisting of three members from Canada and Australia working in that village reported this result to the activists committed to the anti-logging campaign. However, the activists responded that they knew the Penan did not want blockades but that was not a problem (Richie 2004). In short, the Penan were symbolized as nature loving for the purpose of promoting an international environmental campaign.

Changing Movement

Increasing Court Struggle

Today, the international campaign against the logging in Sarawak is still continued by environmental NGOs in the West and in Japan. However, when we look at domestic NGOs, especially Sarawak-based ones, significant changes can be found. Recently, conflicts over forests or land between native communities and outsiders such as companies or the government are increasingly brought before the court rather than pursued through illegal means such as blockades. The natives legally claim the native customary rights following the Land Code of 1958. More than 100 cases are now in court[6].

The Land Code of 1958 (Part II Section 5) provided that native customary rights may be created in accordance with the native customary law in Interior Area Land before the 1st day of January, 1958 by the following methods: (a) the felling of virgin jungle and the occupation of the land thereby cleared, (b) the planting of land with fruit trees, (c) the occupation or cultivation of land, (d) the use of land for a burial ground or shrine, or (e) the use of land of any class for rights of way. Regarding the natural forestlands, the history of the land usage for agriculture or residence is critically important. The major interpretation, followed by the government as well, has been that the native customary rights cannot be claimed over the forestlands that do not have such history. But the native people have challenged this interpretation: utilizing natural forest resources without clearing the land would be included in 'the use of land of any class for rights of way'.

'Rumah Nor' Case

Many cases regarding native customary rights, as with any other kinds of court cases, are pending in the court for long periods because there are not enough judges. So far, only three cases of native customary rights have reached decision by the court. Among them, the judgment of the 'Rumah Nor' case by the High Court in 2001[7] was epoch-making. Pulp and plantation companies acquired the land title over the forestland issued by the Land and Survey Department, which included 'pemakai menoa' forest, the forest customary used for hunting and gathering. The High Court ruled for the native customary rights over pemakai menoa

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[6] Interview with lawyer Baru Bian.

[7] Suit no. 22-28-99-I.

land as well. Principally this decision was in accordance with the native people’s interpretation of the clause ‘the use of land of any class for rights of way’ as shown above. The Appeal Court reversed this decision in 2005, and now the case is still in the Federal Court. But the High Court’s decision has an impact to all sectors concerned by showing the possibility that various kinds of forest usages can be recognized as native customary rights.

Involvement of Domestic NGOs

The court struggle as a way for the native people to protect their customary rights was first put into practice in 1989 in a Lun Bawan community in Limbang Division. Baru Bian made the initiative. He was working as a lawyer in Kuala Lumpur but returned home to assist his homeland community. The case of his community was settled out of court in the end. Afterward, native communities confronting disputes with companies or the government regarding native customary rights all across Sarawak asked him for legal assistances. He is now based in Kuching, handling over half of the total of more than 100 cases regarding native customary rights currently in court[8].

Three more lawyers other than Baru undertake native customary rights cases. Three of the four, including Baru, are from the native communities. Harrison Ngau is one of them. He founded the Sarawak branch of SAM in 1981 and played an important role in assisting the Penan communities’ blockades and other related activities in anti-logging campaigns during the later 1980s and the early 1990s. He was elected a Member of Federal Parliament in 1990 until 1995. Then he studied law and became a lawyer in 2001[9]. Harrison’s switch of career symbolically reflects the change of characteristics of the movement, especially of domestic NGOs. Substantial benefits for the local people are now given more emphasis than global advocacy of environmentalism. The legal struggle is above all not illegal. Even though it might take time, fighting in the court can lead to the most secure protection of rights, and a court decision in favor of the local people would have a significant social impact.

Domestic NGOs, such as, Borneo Research Institute (BRIMAS) and SAM, are now committed to assisting the native communities’ legal struggles. They have been carrying out projects to instruct the local people in ‘community mapping’ using GPS instruments. Community mapping figures out local people’s customary land or forest uses in a way that can be used as proof in the court. The change from physical protests to legal struggle means a triumph for resolving the problems of Sarawak within Sarawak society.

‘Sustainable Forest Management’

From ITTO Mission until MTCC

The Sarawak government changed its forest policy with the introduction of ‘sustainable forest management’ in 1990s. This change was partially a response to international bashing and to efforts to restore the image of Sarawak forestry.

The policy change began with the mission sent to Sarawak by the International Tropical Timber Organization (ITTO) in 1989. The Malaysian government, in informal consultation with the Sarawak

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[8] Interview with Baru Bian.
[9] Interview with Harrison Ngau.

government, decided to request ITTO to send a mission. As the result of the field investigations by the mission during 1989 to 1990, the mission report recommended reducing annual felling from the existing 1,300m^3 to 920m^3 and expanding Permanent Forest Estate (PFE) (Mission Established Pursuant to Resolution I (IV) 1990). The Sarawak government started to follow this recommendation. However, annual felling has never fallen below the recommended level of 920m^3 (Graph 1). According to an interview at ITTO, annual felling in the PFE area has been less than 920m3[10]. The area of PFE has been expanded from 4.50 million ha in 1989 to 5.2 million ha in 2000. The government has a policy for further expanding the PFE area to six million ha and TPA to one million ha (Poore 2003).

Furthermore, the government made it policy to obtain certification of sustainable timber all over the State. This policy has been under debate since the early 1990s, but, as logging companies did not easily agree, the policy was not realized until 2002 when each of six major companies set up a pilot site, applying for certification from the Malaysian Timber Certification Council (MTCC). MTCC developed its own scheme in cooperation with the Forest Steward Council, one of the most popular timber certification organizations in the world. MTCC's latest 'Malaysia Criteria and Indicators 2002' (MTCC 2002) provides for concrete guidelines for certification by applying the FSC's principles to Malaysian social, legal and ecological contexts. MTCC requires almost the same standards as FSC in the aspects of the relation to indigenous people or local societies, biological diversity and tracking back of the origin of timber. These, however, are basically within the existing legal framework, such as, the recognition of native customary rights. Thus NGOs are opposing MTCC as shown below.

After preliminary implementations of MTCC's guidelines, the first certification was given in 2004 for the Sela'an Linau area operated by the Samling group. In that area, zones for nature conservation and local community utilization are reserved, and reduced-impact logging is practiced. Some NGO staff and local people have also recognized the differences from conventional logging However, some communities within the area are still refusing any kind of logging and protesting by blockade. The company does not operate in the disputed area, and is trying to negotiate with those communities against the logging.

Logic of the Logging Companies

'Sustainable forest management' policy conflicts with logging companies' interests. In particular, sustainable timber certification requires them to incur more costs for reduced-impact logging and measures to cope with the local communities as well as for third-party inspection. Despite this, the international timber market does not pay a sufficient price premium for certified timber to cover these costs. There are several reasons why the logging companies agreed to apply for certification, even though it only covers a small portion of their total logging sites.

First, they aimed to improve their international image. If certified as sustainable timber, they could expand their market to Europe where Sarawak timber was boycotted. Beyond a few Western countries, the global market still demands as cheap timber as possible regardless of its origin[11]. Thus the company's image restoration is more motivating than the market expansion for them.

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[10] Interview at ITTO.

[11] Interview at Sarawak Timber Association (STA).

Apart from this, there was a pressure for sustainable forest usage from the government or within the timber industry. The government would like to secure loyalty and revenue in the future through assuring sustainable forest resource use by certification. Within the industrial sector, plywood companies that are not group companies of logging companies also demanded certification for securing future timber supplies[12]. The logging companies decided to pay the additional cost to respond to the pressures from international society, and from the government and industrial sector within Sarawak. At present they can put up with this situation because applications for certification only cover a small portion. The remaining conventional logging can cover the loss from certified areas. However, the government really wishes to go ahead with having certification cover the whole State, not by enforcement but on a voluntary basis by the companies. However, this might not be achieved if the market does not change to pay a sufficient price premium for certified timber.

Opposition to MTCC by NGOs and Local People

Native people and the NGOs supporting them are opposing the MTCC scheme. They insist that the scheme does not give enough respect to native's customary rights, and that the opinions and interests of those native people who would be directly affected by the logging were not well represented when building up the MTCC scheme. Since MTCC was established in 1998, NGOs representing native people and supportive NGOs network, 'Jaringan Orang Asal – NGO Tentang Isu Hutan (JOANGOHutan)', participated in the debate over setting up the MTCC scheme. They continuously stressed native customary rights over the forest resources, but such opinion was rejected as unrealistic. Finally, in 2001, JOANGOHutan dropped out of the argument, as they felt their participation might have been utilized to legitimize the MTCC process (JOANGOHutan n.d.). They also pointed out that MTCC was dependent on the governmental sectors financially and for personnel, and thus, tended to support the government or companies' side. After this NGO exited, other native group organizations were invited as the representatives of native people. However, they were organizations working for traditional arts and cultures, and did not really represent the stakes of the natives affected by logging. Progressive ideas on native customary rights by the court as shown above are neglected. Considering these facts, JOANGOHutan insisted that the MTCC scheme only looks after sustainability of timber production and dismisses sustainability of society and culture. JOANGOHutan demands complete realization of the FSC's principles, such as ensuring that representatives of local people who are substantially affected by logging are involved in the process of certification and assessment, and insisting that logging needs informed consent in advance by those local people really affected (JOANGOHutan 2004).

Conclusion

Examining the socio-political structure surrounding forest resources as above reveals part of the reason why Sarawak had to suffer from such enormous bashing by international society. In short, only foreign environmental activists were reliable in supporting Penan people against the logging, and could appeal to the Sarawak government and to international society. No politicians, even from other native groups, paid

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[12] Interview at STA.

attention to Penan. There were domestic NGOs like SAM within Sarawak. But they are quite minor in Sarawak and Malaysian society, and have been strongly oppressed by the government. In Malaysia, ‘urban middle class’ people are divided by ethnic group, such as, Malay, Chinese, and Indian in the case of Peninsular Malaysia, and Malay/Melanau, Chinese, and other non-Muslim natives (Dayak and Orang Ulu) due to the Bumiputra policy, which, in fact, treats the Malay better than others. Otherwise these middle class people could be sympathetic with the Penan’s protest as a human right concern. If the government had been more tolerant with social activism within the State and the middle class people united to share a public debate on social justices, various controversies could be resolved within the country and much less international bashing would arise. That might have been much more beneficial for both the Penan and for all other people in Sarawak.

The situations are now changing. Both the government and NGOs have changed their policies. Even though the principal policy and legal framework is not changed, sustainable forest usage began to be taken into consideration, and the local people’s livelihood began to be respected to some extent. Because the government still refuses full recognition of native’s rights over the forests they are claiming, bashing by both domestic NGOs and international society does not stop, but is quieter. On the other hand, NGOs and the native people also changed, now taking legal measures in their struggle with the companies and the government instead of blockades, although these have not yet totally disappeared. Involvement of foreign environmental activists is now smaller than the domestic NGOs’ assistance for the native people in legal struggles or in negotiations with the companies and the government.

These changes reflect the triumph of resolving conflicts within Sarawak society without utilizing international pressure. Substantial and practical improvement of the native people’s living environment is addressed rather than the ideological progression of human rights or nature conservation. But there is still a large gap between the local people supported by NGOs and the government. Local people stick to full recognition of their native customary rights over the vast area of forests. The government and the companies insist on existing laws. This conflict might be resolved only by the court decision. But social solidarity cannot be restored by legal judgments. What is most needed is a place for continuous dialogue in an equal partnership. Every stakeholder should be involved, to think about the most meaningful usage of forest resources in both an ecologically and socially sustainable way. A built-in conflict resolution system in the society is the most important infrastructure for sustainable forest management.

References

Fadzillah M. Cooke. 1999. The Challenge of Sustainable Forests: Forest Resource Policy in Malaysia, 1970-1995. Honolulu: University of Hawaii Press.

Harago, Yuta. 1989. Nettairin no boken: sarawaku no senjumin wo tazunete (Adventure of Tropical Forest: Visiting the Natives in Sarawak). Tokyo: Yosensha. (in Japanese)

Hong, Evelyne. 1987. Natives of Sarawak: Survival in Borneo's Vanishing. Institut Masyarakat.

Integrated Development for Eco-friendly and Appropriate Lifestyle (IDEAL). 1999. Tanah Pengidup Kitai: Our Land Is Our Livelihood. Sibu: IDEAL.

JOANGOHutan. 2004. Malaysian Indigenous Peoples Reject the MTCC Timber Certification Scheme (Indigenous Peoples’ Media Statement on the MTCC: IIFB at COP7 on CBD OWTC, KL, 19 February 2004).

JOANGOHutan. n.d. The Malaysian Timber Certification Scheme and the FSC.

Jomo KS, Chang YT, Khoo KJ eds. 2004. Deforesting Malaysia: The Political Economy and Social Ecology of Agricultural Expansion and Commercial Logging. Zed Books.

Leigh, Michael. 1998. Political Economy of Logging in Sarawak, Malaysia. In Hirsch P. & Warren C. eds. The politics of environment in Southeast Asia, resources and resistance. London: Routledge.

Malaysian Timber Certification Council (MTCC). 2002. Malaysian Criteria and Indicators for Forest Management Certification [MC&I 2002].

Mission Established Pursuant to Resolution I (IV). 1990. The Promotion of Sustainable Forest Management: A Case Study in Sarawak, Malaysia. (Report Submitted to the International Tropical Timber Council, ITTC (VIII)/7, 7 May 1990).

Poore, Duncan. 2003. Changing Landscapes: The Development of the International Tropical Timber Organization and its Influence on Tropical Forest Management. Earthscan Publications.

Ritchie, James. 1994. Bruno Manser: The Inside Story. Singapore: Summer Times Publishing.

Ross, Michael L. 2001. Timber Booms and Institutional Breakdown in Southeast Asia. Cambridge: Cambridge University Press.

Samling Plywood (BARAMAS) SDN BHD. n.d. Samling’s Contributions to Communities within / Adjacent Certified FMU in Baram Sela’an-Linau.

Sarawak Forest Department Annual Report (AR) 1965-2000.

Black Markets and Trade Bans: Can Bans Reduce Illegal Production?

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Introduction

Despite the fact that their consumption is not, by their nature, harmful to people, transactions of some goods are prohibited by law. Key examples include endangered species or derivatives of them. In these cases, “production”, not consumption, is the main focus of the law implemented; to try to increase production of these goods is considered damaging to nature or human society.

Although prohibited, the purchase of the goods in question is still possible to some extent through “illegal markets” or “black markets”. It is extremely difficult to completely wipe out such markets from society, especially in developing nations, despite the efforts of governments and other authorities. In general, it is assumed that the black market would shrink if legal trade were prohibited, since this would reduce demand for the goods and make laundering impossible. Thus, a trade ban is thought to be a useful way of reducing illegal production. This assumption provides the basic case for banning trade, or for not lifting trade bans.

CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) is the main multilateral framework legal framework aiming at preventing species extinction, banning trade of those species that are listed in CITES Appendix I. However, it is pointed out that the CITES trade ban is not always effective in protecting threatened species. For example, according to 'tSas-Rolfes (2000), the ban seemed to work for protecting African elephants, but it failed to stop the extinction of rhino species such as black rhino, because it sharply raised the price in the black market and boosted poaching. That is, a trade ban may have adverse effects, far from the desirable ones expected, and illegal production (i.e., poaching) may not always decline under a trade ban. It could, on the contrary, increase[1].

In the literature in terms of economic theory, Bergstrom (1990) shows in a simple supply and demand model that reducing legal supply of elephant tusks and rhino horns could increase poaching. Barbier and Swanson (1990) and Heltberg (2001) also point out that a trade ban might be ineffective, since it could stimulate the illegal trade through increasing the incentive for poachers, using a model where the demand for ivory declines by the introduction of the ban.

Fischer (2004) gives a microfoundation for considering the effects of a trade ban. In addition, Fischer neatly includes laundering activity, which is crucial in considering the effect of lifting the ban. With this inclusion of laundering, Fischer links the legal and illegal markets and deals with the interaction between the two markets. The result is that a trade ban reduces poaching where laundering is present, and will minimize poaching if it can be assumed that other conditions remain unchanged. That is, a trade ban fails only if laundering would not occur under legal trade.

However, laundering might be inevitable under legal trade, especially in a commodity in great demand

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[1] For the detail of these facts, see Onuma (2006).

like rhino horn. In the rhino horn case, the CITES trade ban was not successful. Thus, whether a trade ban is effective may not be determined by the question of whether laundering would occur in legal trade. A trade ban may still fail even if there is laundering under legal trade. This research aims at clarifying this point, regarding the legal and illegal markets as being interdependent.

In Fischer's analysis, the two markets are kept virtually separate; there exist two groups of people, one consisting of completely immoral people who purchase goods from the black market whenever the price there is lower than that in the legal market. The other consists of completely moral people, who never resort to the black market. Thus, the two markets interact only when the two market prices are identical, or when launderers act as intermediaries between the two markets.

However, it might not be realistic to think that the legal and illegal markets are separate. There may be many people who resort to the black market if the price there is relatively low, but who abide by the law and purchase from the legal market if the price difference between the markets is small enough.

Based on this understanding, this paper provides a simple general equilibrium model in which both legal and illegal markets exist interdependently, and examines whether a trade ban is effective in preventing the endangered species from becoming extinct.

The Model

We assume an economy where the transaction of a commodity is either completely prohibited or permitted only if it is certified by the authorities. We call the former case a "trade ban". However, in each case there exists a black market, where the goods are illegally traded. The goods are produced by illegal activities such as poaching. Let us denote the illegal output by X and its price in the black market by P_B. We assume a representative producer who maximizes his profit defined by, as in the literature,

$$\pi_X = rP_B X - C,\ 0 \le r \le 1 \ .$$

Here r represents the rate of the output that is not confiscated by the authorities, and C is the cost of illegal production. $1-r$, which is the rate of confiscation, is a proxy for the efforts of the authorities to eradicate illegal trade and production.

At the same time, we assume that the cost of illegal production C is dependent only on X as $C=C(X)$ with $C'>0, C''>0$. Thus, the producer's profit maximization leads to $rP_B=C'$.

On the other hand, we assume that there is a representative launderer. Fischer (2004) characterizes laundering behavior as a launderer buying black-market goods and laundering them for subsequent sale in the legal market. The authorities detect this laundering, and confiscate a part of the goods that the launderer tries to sell in the legal market. Let $(1-\phi)$ be the rate of confiscation from laundering. So ϕH represents the supply from the launderer to the legal market. $G(H)$ denotes the cost of laundering behavior, with $G'>0, G''>0$. So the launderer's profit π_H must be defined by $\phi P_L H-G(H)-P_B H$.

Consumers gain utility from the goods in question. There is no difference for each consumer between the goods from the black market and from the government. That is, legal goods and illegal goods are perfect substitutes. However, each consumer feels more or less morally guilty if he or she purchases illegal goods.

Let y and z express the quantity of legal and illegal goods purchased, respectively. The net utility to consumers is represented by

$$V(y,z,\alpha) = U(y+z) - (P_L y + P_B z) - \alpha z, \quad 0 \le \alpha \le \overline{\alpha}$$

where U represents the utility gained from consuming the goods and P_L the price of goods in the legal market. We assume $U'>0$ and $U''<0$. On the other hand, αz is the disutility that arises due to the purchase of illegal goods. We call this disutility “moral pain” and refer to α as the moral pain coefficient. We assume that U is identical across consumers, but that α differs across the same consumers. The number of population with α is denoted by $f(\alpha)$ with $\int_0^{\overline{\alpha}} f(\alpha)d\alpha = 1.$ A consumer's behavior is described by the following expression:

$$\max_{y,z} U(y+z) - (P_L y + P_B z) - \alpha z \quad .$$

Three types of consumers are possible: consumers who purchase only legal goods, consumers who purchase only illegal goods, and consumers who are indifferent between legal and illegal goods. We refer the third type of consumers “marginal moralists”, since they move to the black market if the price difference between legal and illegal markets expands even slightly.

Market Equilibrium

Let Y and Z express aggregate demand for legal and illegal goods, depending on P_L and P_B. We can show that

$$\frac{\partial Y}{\partial P_L} < 0, \frac{\partial Y}{\partial P_B} > 0, \frac{\partial Z}{\partial P_L} > 0, \frac{\partial Z}{\partial P_B} < 0, \left|\frac{\partial Y}{\partial P_L}\right| > \frac{\partial Z}{\partial P_L}, \frac{\partial Y}{\partial P_B} < \left|\frac{\partial Z}{\partial P_B}\right| \quad .$$

These properties come from the role of marginal moralists.

Legal supply from the authority is $\overline{Y}$. In this economy, the market equilibrium is expressed by

$$\begin{aligned} Y(P_L, P_B) &= \overline{Y} + \phi H \\ Z(P_L, P_B) &= rX - H \\ rP_B &= C'(X) \\ \phi P_L &= P_B + G'(H) \end{aligned}$$

where P_L , P_B, X, and H are determined endogenously, given $\overline{Y}$, r and ϕ.

Two Policy Measures

The authority has two policy instruments to control illegal production. One is to change the confiscation efforts in the illegal market and with regard to laundering, i.e., changing r and ϕ. The other is also changing the level of legal supply $\overline{Y}$. Investigation of a trade ban is mainly related with the latter instrument.

A Trade Ban

Under the above model, a trade ban is characterized as $\overline{Y}=0$ so that H=0 in the equilibrium. We are interested in the level of X under $\overline{Y}=0$ and that under $\overline{Y}>0$. Thus, X can be expressed by $X(\overline{Y})$. We compare $X(0)$ with $X(\overline{Y})$. We say that a trade ban should not be lifted or a trade should be banned if

$$X(0) < X(\overline{Y}),\ \forall \overline{Y} > 0\ .$$

On the other hand, if it holds for some $\overline{Y}$ that $X(0) > X(\overline{Y})$ and that level of $\overline{Y}$ is feasible for the authority, a trade ban should be lifted.

Result without Laundering

If laundering is not possible, that is, if H=0 at any level of $\overline{Y}$, then we have

$$X(0) > X(\overline{Y}),\ \forall \overline{Y} > 0\ .$$

In this case, a trade ban maximizes illegal production, so the ban should be lifted. However, the result changes considerably if we include the aspect of laundering.

Result with Laundering

Let us suppose that laundering occurs, i.e., H>0 at any level of $\overline{Y}$.

We can show that there exists a $\overline{Y}_T$ such that

$$\begin{aligned} X(0) &< X(\overline{Y}_T),\ \text{if } \overline{Y} < \overline{Y}_T \\ X(0) &= X(\overline{Y}_T),\ \text{if } \overline{Y} = \overline{Y}_T \\ X(0) &> X(\overline{Y}_T),\ \text{if } \overline{Y} > \overline{Y}_T \end{aligned}\ .$$

This relationship is depicted in Figure 1. From this property, we can say that, with laundering, trade bans can become effective if legal supply is sufficiently small, and that a ban has a desirable effect because illegal production is worse under the supply. In this case, lifting a trade ban might worsen the situation, so that it should be maintained. Only if there is sufficient legal supply is it appropriate to open up the legal market. We call $\overline{Y}_T$ a “threshold” in the sense that it divides a legal supply into either harmful or effective with respect to reducing illegal production.

A Sufficient Condition for a Trade Ban to be Successful.

We do not know the exact level of the threshold legal supply. However, we can give a sufficient condition for a legal supply to be less than the threshold. The condition is:

$$\overline{Y} \leq (1-\phi)H \quad .$$

That is, if the legal supply is small enough to be less than the confiscated laundered goods $(1-\phi)H$, then it is judged that the legal supply is strictly less than the threshold $\overline{Y_T}$, so that a trade ban should not be lifted or the ban should be shifted in this case.

According to our results, the CITES trade ban on ivory trade that was enforced in 1989 is judged a success if the actual ϕ then was less than 0.8. For, in the 1980s, it is estimated that about 80% of ivory trade was in fact illegal and laundered[2]. Under this estimation, $\overline{Y} = 0.25\phi H$. In this case, $\overline{Y} \leq (1-\phi)H$ is equivalent to $\phi \leq 0.8$. That is, if more than one out of five laundered goods were confiscated before the enforcement of the ban, we can say that the ban was effective for reducing the poaching of elephants.

A Policy Mix to Discourage Incentives for Illegal Producer and Launderer

To increase confiscation efforts is not always desirable. The increasing efforts have desirable effects if dX/dr and $dX/d\phi$ are positive, implying that illegal production declines. Also, $d\pi_i/dr$ and $d\pi_i/d\phi$ should be positive, which means that incentives for illegal producers and launderers decrease. However, this is not always the case, as can be seen from the following results.

$$\text{sign}\,\frac{dX}{dr} = \text{sign}\,(\varepsilon_B - \theta_1)$$
$$\text{sign}\,\frac{dX}{d\phi} = \text{sign}\,(\varepsilon_L - \theta_2)$$
$$\text{sign}\,\frac{d\pi_X}{dt} = \text{sign}\,(\varepsilon_B - v_t), (t = r, \phi)$$
$$\text{sign}\,\frac{d\pi_H}{dt} = \text{sign}\,(\varepsilon_L - w_t), (t = r, \phi)$$

where both θ_t and v_t and w_t are positive values that depend on the functional forms. On the other hand, ε_B and ε_L are the price elasticities of demand in the black and legal markets, respectively. As can be seen from these properties, if the price elasticity is low enough, then there can be an adverse effect.

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[2] For example, see p.51 in Barbier et al. (1990).

However, let us consider the following policy mix under a legal supply: let us raise the rate of confiscation directed at laundering by $d(-\phi)>0$. Note that increasing the efforts means to reduce ϕ. On the other hand, legal supply is increased by $Hd(-\phi)>0$. This policy focused on the detection of laundering will reduce both the illegal production and the producer's profit. Moreover, it will decrease the launderer’s profit. That is,

$$\begin{gathered} \frac{dX}{d\phi} > 0, \\ \frac{d\pi_X}{d\phi} > 0, \quad . \\ \frac{d\pi_H}{d\phi} > 0 \end{gathered}$$

As we have seen before, the effects of detecting laundering are not definitive, so that it could be harmful. But by mixing this detection of laundering with an increase in legal supply, desirable effects are always achieved on both illegal production and profits in the black market. This policy can be carried out only if a legal supply is feasible, which is considered to be another merit of allowing legal trade.

Summary

Our results suggest, in the context of biodiversity conservation, how a “sustainable use” policy, coupled with the lifting of trade bans, should be evaluated in terms of poaching when laundering is possible. The question of whether “sustainable use” policies aggravate poaching is under dispute (see, for example, Hutton and Webb (2003)). From our results, we see that a “sustainable use” policy can contribute to species conservation

if the level of sustainable supply is large enough, but it may on the contrary accelerate species decline if the level is too small. Thus, a one-sided view of “sustainable use” policies is not appropriate. Whether the policy is beneficial or not depends on how much legal supply is feasible.

Apart from trade bans, legal supply seems to be a very useful instrument for authorities to wipe out illegal production, when the option of legal supply is available. If it is politically necessary for the authorities to strengthen the detection of illegal business, the policy mix can achieve this goal without raising illegal production.

References

Barbier, E.B. et al. (1990) Elephants, Economics and Ivory, Earthscan Publications Ltd., London.

Barbier, E.B. and T.M.Swanson (1990) Ivory, the case against the ban. New Scientist 17: November 52-54.

Bergstrom,T.(1990) On the economics of crime and confiscation. Journal of Economic Perspectives 4: 8-171.

Fischer, C. (2004) The complex interactions of markets for endangered species products. Journal of Environmental Economics and Management 48: 926-953.

Heltberg, R. (2001) Impact of the ivory trade ban on poaching incentives: a numerical example. Ecological Economics 36: 189-196.

Hutton, J. and G. Webb (2003) Crocodiles: legal trade snaps back. in Oldfield, S. ed. The Trade in Wildelife: Regulation for Conservation, Earthscan Publications Ltd., London.

Onuma, A. (2006) Economics of conserving endangered wildlife species. Environmental Science 19: 573-585.

(In Japanese)

'tSas-Rolfes, M. (2000), Assesing CITES: Four Case Studies, in Hutton, J. and B.Dickson (eds.) Endangered Species Threatened Convention: The Past, Present and Future of CITES, Earthscan Publications Ltd., London.

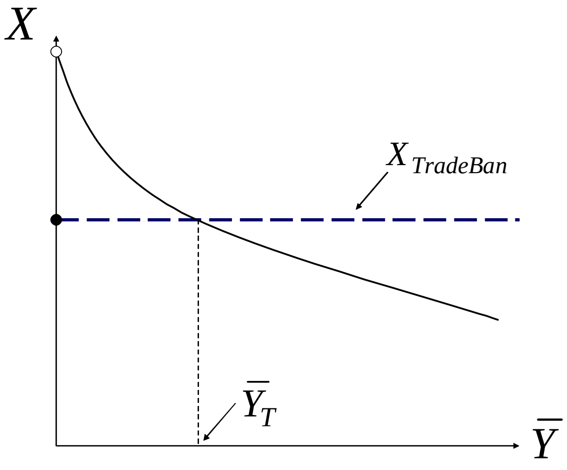

Figure 1

Forest Development and Firewood Shortage in Yakushima Island

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1 Introduction: The Shortage of Firewood in the 1980s

The shortage of firewood occurred in Yakuhsima Island around 1980. The manufactures of dried fish which is a traditional industry in the island suffered from the occasional difficulty to obtain it. The firewood of broadleaf tree is essential supplies to smoke their products. The pulp industry of the island also began to withdraw from the business due to the insecurity of raw material. This shortage means the decrease of broadleaf trees which are part of dominant vegetation in the island.

This island has been designated as a World Natural Heritage site in 1993, and since then, became well-known as an island of thousands-year-old cedar trees and rich natural environment. More than 100 thousand tourists visit each year to see the deep forest of the island (Hirata 2005). Having its rich forest in the Japanese sixth largest island (about 500 hectare) where over 90% of the area is mountainous and forest region, how could a shortage happen?

Although the shortage in a particular resource does not mean its depletion, natural resource that is not severely-depleted can be lacked. As Zimmermann has already pointed out in 1933, “natural resource” does not mean a natural thing itself, but the complex of culture, nature and human beings. He clearly indicated that it is important to focus on social aspects in “resource science” because “resource” could be enhanced or reduced by human activities (Hunker 1964). According to his suggestion, the context of this shortage once happened in this island seems to be worth studying to obtain a valuable insight for the paradigms about the sustainable use of forest resource and the conservation of forest diversity.

The firewood shortage was claimed by the manufacturers of dried fish around 1980 (Isso Brokers Union 1981). At that time, the island had been in the chronic shortage of broadleaf wood. There were two major industries utilizing broadleaf tree. One was the wood chip industry supplying hardwood chip as the raw materials of pulp, and another is the dried fish industry using it for smoking fishes. Even though both industries had suffered from the material insecurity, I focused on the latter, the manufactures of dried fish in this study. The reason of focusing more on the dried fish industry is because the main interest of this research is to examine the traditional utilization of broadleaf tree, which can give us more insights about the sustainable use of natural resources. From the past, the islanders had made their livelihood manufacturing the dried fish of mackerel or bonito and have utilized the broadleaf tree, i.e. oak, to smoke boiled fish (Miyashita 2000, pp.354).

2 The History of the Dried Fish Production

The dried fish of Yakushima Island have been a well-known commodity product since a long time ago. For example, Figure 1 shows the order of the ranking list of dried bonito of Japan in 1822 during the Edo period. The product from the island, called yakushima-bushi , was ranked the first grade, Ozeki. Clearly, this fact shows the tradition of the industry and also the competitiveness of its product, despite of the disadvantages in locality condition and the economic backwardness of the island. Richness in several sorts of natural resources, such as forest, fishery and water, is the major reason for this industrial development. These factors are indeed the gift from natural conditions. Because the island is located on the stream of the Black Current, there were many excellent fishing grounds off the island. In addition, plenty of moisture brought by this warm current has fostered the rich and varied flora (Yumoto 1995).

諸國鰹節番附表

文政五年

行司

世話方

勧進元

紀州

日向

加太

Fig. 1 The ranking list of dried bonito of Japan in 1822.
Source: Miyashita (2000, pp.315)

The average amount of the dried bonito production from 1878 to 1880 in Kamiyaku town, one of two administrative districts of the island, was calculated to be about 16.8 ton. Then in the Meiji period, their products eventually shifted from dried Bonito to dried mackerel because the catch of bonito started decreasing with fishing ground moving away from the island and the competition with the fishing vessels from the mainland. In 1919 of the Taisho period, the amount of production in Kamiyaku town was 149.4 ton for dried bonito, and 341.8 ton for dried mackerel, respectively (Committee of Kamiyaku Town History 1984, pp.463). According to this statistics, the production had increased by more than 10 times compared to that in the Meiji period.

In 1981, the dried mackerel manufacturers asked the branch office of Forest Agency to supply firewood during their 4th local management plan on forest development, starting from 1982. According to the petition, there were eight processors in the island at that time and each processor was considered to consume about 400 m3 to 600m3 of firewood in a year (Isso Brokers Union 1981). And in total, about 3500 m3 to 4000 m3 was estimated necessary for the whole industry to run for a year. In order to maintain the sustainable supply, about 667 hectare of broadleaf forest was calculated to be needed. This area corresponds to just around 1% of the whole forest land in Yakushima Island. The production of dried mackerel was roughly estimated to be less than 700 ton in the early 1980s (Statistical Research Office of Kagoshima Prefecture 1981). Compared to that of the Taisho period, dried fish production had not been increasing very drastically. Therefore, the production itself could not have been the reason for the depletion of broadleaf tree.

Then what could have been the reason for this shortage? We have to scrutinize what happened in the forest resource which had provided goods to the islanders continuously up to that time.

3 The History of the National Forest Management and Change on the Value of Broadleaf Tree

Local people had experienced the drastic change of forest utilization in the Meiji period. Before that, they were allowed to use the forest resources of the mountainous region behind their villages routinely. While the Meiji government fixed the property right of forest area across the nation, large part of the forest area in Yakushima Island, including the place once available for the local, had been transferred under the government control in 1882 (Committee of Kamiyaku Town History 1984, pp.302-303). Therefore, in order to find out how local people adapted to this institutional change, it is necessary to understand the forest resource utilization of the national forest which covers almost 78% of the forest area in this island.

Figure 2 shows the amount of broadleaf timber yield from the national forest after the post war era between 1950 and 2000. Soon after the end of World War Ⅱ, the operation in the national forest restarted from 1946. In the postwar years of the recovery, the logging of conifer was operated in the nationwide scale with high demand for building materials. Meanwhile, the broadleaf trees became less valuable temporarily as the demand for fuel wood decreased due to the progress of energy revolution. But in the late 1950s, the raw material of pulp began to change from pine tree to broadleaf trees with the technological development in pulp industries.

In 1963, Yakushima Forest Development Company was founded to operate logging to provide raw material for pulp. The pulp material replaced the dominant use of broadleaf tree from the fuel wood at this time. The yield of broad leaf timber doubled from the year before and started increasing in the middle of the 1960s, then marked its maximum during the late 1960s. In this term, the national forest was put under the operation of full-scale logging (Kumamoto Forestry Office 1982 & Makita 2005).

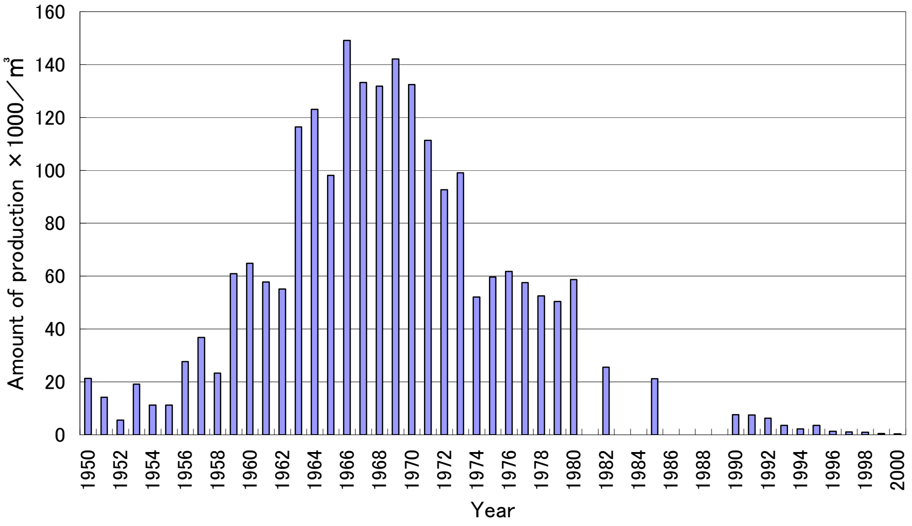

Fig. 2 The transition of the broadleaf tree production from the national forest

Source: Forest management office data

After 1970, the amount of broad leaf timber production started to decrease rapidly. This is partly because of the rise of the environment conservation movement in Japan. Forest Agency gradually changed their operation policy to selective cutting from full scale logging. Under the severe pressure of the movement, the island also re-examined the operation plan, which resulted in changing the target amount of logging. For example, compared with that of the 3rd management plan, 168×103 m3 between 1967 and 1971, the average amount of annual target decreased drastically to 41×103 m3 in the 4th local operation plan starting from 1981. Later, it became 19.4×103 m3 in the 5th local operation plan (Committee of Forestry History of Kagoshima Prefecture 2003). This drastic fall in the amount of broadleaf timber yield caused the price of broadleaf timber to increase in the market of the island.

4 The Progress of Cedar Plantation and the Fluctuation of Fishery Resources

During the drastic increase of the broadleaf timber yield, cedar plantation was also carried out intensively, following the establishment of the public corporation to manage the plantation (Committee of Kamiyaku Town History 1984, pp.506-507). Figure 3 shows the transition of the forest area behind Isso village where most of the manufacturers of dried mackerel are located. This result indicates the increase of cedar plantation which is equal to the decrease of broadleaf tree. The cedar plantation began gradually after 1960 and progressed intensively between 1967 and 1975. These plantations were implemented at a kind of community forest (Kyoyo-rin) behind the villages. This kind of community forest had been allocated by the Meiji government as a compensation for the nationalizing the forest. In this area, local people could obtain timber or fuel wood with a cut rate price through the management of Forest Agency.

Then after the energy revolution, local people decided to plant cedar for selling as building material in the future, instead of leaving it as the secondary forest which could provide the firewood of broadleaf tree. The demand for pulp material also enhanced the transition from the secondary forest of broadleaf tree (Committee of Kamiyaku Town History 1984, pp.507-508). After all, the area of cedar plantation had increased to 317 hectare by 1980. The places where were able to access easily had turned into the cedar forest in the 1980s.

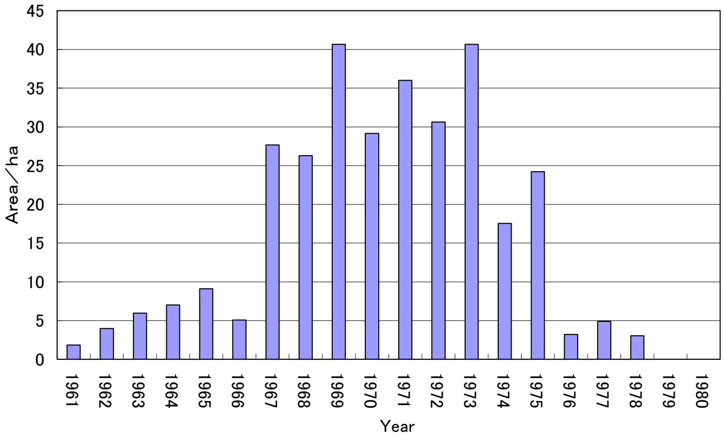

Fig. 3 The transition of cedar plantation area behind of Isso village.

Source: Committee of Kamiyaku Town History (1984, pp.511-512)

In such a circumstance, the islanders have experienced the transition of mackerel catch during the past century (Committee of Kamiyaku Town History 1984, pp.522). Figure 4 shows the statistics of mackerel catch and dried fish production between 1950 and 2003. The ups and downs of the catch have repeated periodically. The annual amounts of dried mackerel production are shown together with mackerel catch mainly after 1979. The figure shows the tendency of correlation between the catch and the production. It could be said that the amount of the firewood which is demanded for dried fish production was also not constant. When the catch became the maximum around the 1970s, it is reasonable to guess that both of the dried fish production and the consumption of firewood was increasing.

Until the beginning of the bumper years of the catch around 1970, the logging at the national forest had been carried out eagerly, and there must have been no worry about the shortage of broadleaf timber during those years. The logging from the national forest was plenty enough to ensure the needs of the pulp companies and the dried fish manufactures. As a result, it leaded to the forestation of cedar tree from broadleaf tree for future income of the villages. This means that the forest resource of the community was exchanged to the specific property, not kept as “resource” to be ready to supply the material for their traditional industry. It was hard to expect the future shortage of broadleaf timber due to the shrinkage of logging in the national forest.

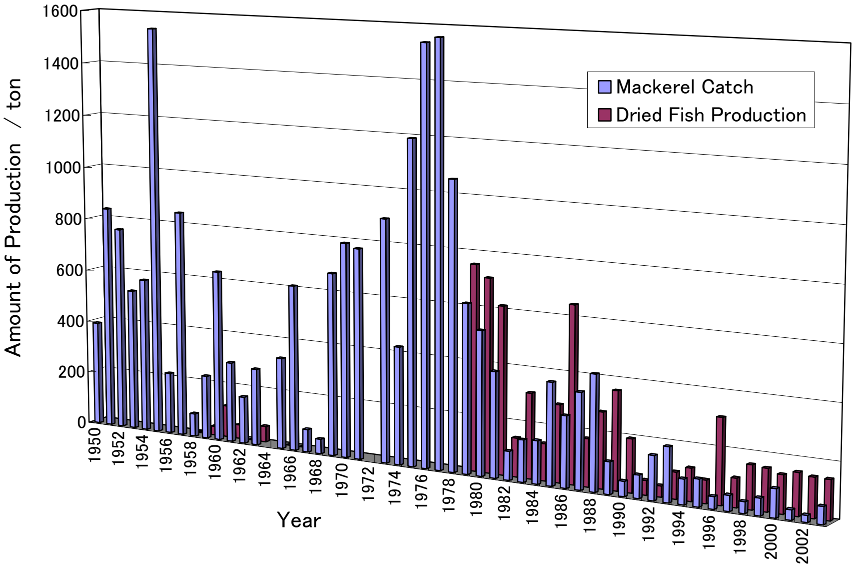

Fig. 4 The transition of mackerel catch and dried fish production in Kamiyaku town.
Source: Statistical Research Office of Kagoshima Prefecture & Tsutsumi (1959)

5 Sustainable Use of Broadleaf tree in Dried Fish Production

As described above, the shortage of broadleaf tree was induced by the logging of broadleaf forest and the plantation of cedar tree in the national forest. Focusing on the dried mackerel production, two major rich natural resources of the island is used for dried fish production. The sustainable use of resources means the sustainable supply of broadleaf tree and mackerel. By the historical perspective, it could be said that this traditional industry was easily affected by the changes occurring to natural resources. In this case, the value of broadleaf tree has been affected by the change of the national and local demands. The villagers once had managed their forest utilization themselves, started relying on the resource distribution system covering the national forest after the Meiji era. As a result of that, the shrinkage of the logging in the national forest induced the shortage of firewood and had left them cedar forest which is unsuitable to smoke. This event clearly shows the social aspect of “resource” which is needed to provide a particular good from a natural thing. And it is casting doubt on the sustainability of national forest management, suggesting the better management of “local” resource.

We could also point out that the sustainable use of broadleaf tree could be affected by marine resources in this case. Because the need for broadleaf tree is correlated with the catch in mackerel in terms of dried fish production, so the decrease in the catch might induce the immediate decrease in the value of broadleaf tree, just as the energy revolution induced the abandonment of the firewood once in the past. If we consider that the variety of forest use which demand many kinds of tree species is the basic condition to enhance the conservation of forest diversity in a society, this case implies the marine resources is one of the critical factors to keep the diversity of the forest use through the traditional industry in this particular circumstance. This expanding causal linkage among natural things and social development indeed shows what “resource” is. It suggests that forest policy needs to be discussed together with marine resource conservation somehow in a particular situation.

Reference

Committee of Forestry History of Kagoshima Prefecture (2003) The History of Forestry of Kagoshima Prefecture (in Japanese). Committee of Forestry History of Kagoshima Prefecture.

Committee of Kamiyaku Town History (1984) The History of Kamiyaku Town (in Japanese). Kamiyaku Town Educational Board.

Hirata K (2005) Multiple Use and Management of Forest-Case Example in Yakushima Island (in Japanese). Journal of Forest Economics Vol.51, No.1, pp.15-26.

Hunker H (1964) Zimmermann’s Introduction to World Resources (in Japanese). Sanryosyobo, Tokyo.

Isso Brokers Union (1981) Petition to sustainable supply of firewood (in Japanese).

Kawasaki A (1973) The Interviews on Mackerel Fishing in Isso, Yakushima Island (in Japanese). South Island Folklore No.31, pp.65-70.

Kumamoto Forestry Office (1982) Forest management of National Forestry of Yakushima (in Japanese). Kumamoto Forestry Office.

Miyashita A (2000) Dried Bonito (in Japanese). Hosei University Press, Tokyo.

National Institute for Japanese Islands (2004) SIMADAS (in Japanese). National Institute for Japanese Islands, Tokyo.

Statistical Research Office of Kagoshima Prefecture (1981) Annual report for Statistics on Agriculture, Forestry and Fisheries of Kagoshima Prefecture (in Japanese).

Tsutsumi H (ed) (1959) Report of the Survey on Agriculture, Forestry and Fisheries (in Japanese). Kamiyaku Town.

Yumoto T (1995) Yakushima (in Japanese). Kodansha, Tokyo.

When Is It Optimal to Exhaust a Resource in a Finite Time?*

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Introduction

Although it may sound paradoxical, in order to realize sustainable resource use, we have to consider the rationale for *un*sustainable resource use. It is important to understand under what conditions a *rational* agent chooses unsustainable resource use, because an effective policy for sustainability should be one that removes the very conditions that render unsustainable use rational. This study identifies the conditions under which finite-time exhaustion of a renewable resource is optimal.

As well known, there is a great deal of debate on how to define sustainability, sustainable development, and sustainable resource management (See, for example, Pearce et al., 1990). However, finite-time exhaustion obviously defies sustainability. As the source of finite-time resource extinction, we discuss the following aspects: (a) the discounting of future benefits, (b) uncertainty about the future of the resource stock, (c) nonconvexity of natural growth function, (d) socio-psychological aspect of work incentives, and (e) strategic interaction among resource users. The policy implications are also discussed.

Intrinsic growth rate and uncertainty

Consider a bio-economic model:

$$\max_{c(t)\geq 0}\int_0^\infty u(c(t))e^{-\rho t}dt \tag{1.a}$$

$$\text{subject to } \dot{x}(t)=f(x(t))-c(t), \tag{1.b}$$

$$x(t),c(t)\geq 0,\ x(0)=x_0 \text{ given}, \tag{1.c}$$

where x denotes the stock of a renewable resource. The natural growth of the resource is described by function $f(x)$. Variable $c(t)$ denotes the amount of harvest at time t. $\dot{x}(t)$ denotes the time derivative of $x(t)$. The consumption of harvest yields utility to the resource user according to the utility function $u(c)$. The *effective* discount rate ρ is the sum of the user's time preference rate and the hazard rate for a fatal event such as complete destruction of the ecosystem or confiscation of the property right.

Under the assumption that the natural growth function is concave, if the intrinsic growth rate $f'(0)$ is too low or if the effective discount rate ρ is too high, then resource extinction is an optimal policy. It is worth noting that instability of the social system and/or ecosystem increases the hazard rate of a fatal event and thus the effective discount rate ρ. Therefore, for sustainable resource use, it is important to achieve institutional, political and economic stability as well as to maintain ecological resistance and resilience.

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[*] Summary of K. Akao and Y.H. Farzin (2007) When is it optimal to exhaust a resource in a finite time? *Ecological Research* **22**, 422—430.

Convex-concave growth function and the initial stock level of the resource

Assume that the natural growth function exhibits a convex-concave shape due to, for example, the Allee effect. (See Figure 1.) Also, assume that the marginal growth rate at origin is less than the effective discount rate. Given these assumptions, there is a threshold of the stock level x_C such that if the initial stock level is smaller than the threshold, then resource extinction is an optimal policy. (See Figure 2.) This implies that if resource degradation is overlooked, eventually sustainable resource management will no longer accord with social welfare maximization.

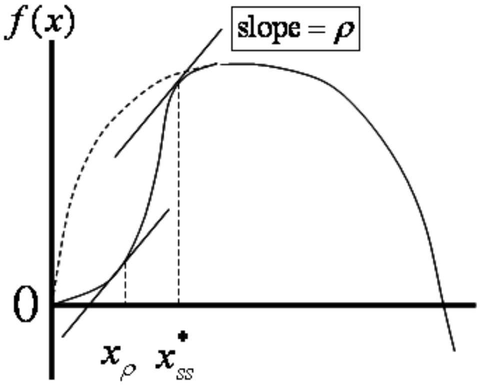

Figure 1 Convex-concave natural growth function.

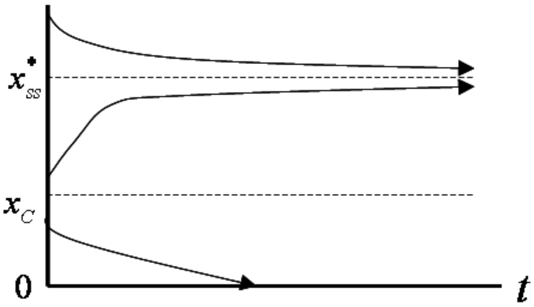

Figure 2 Optimal paths when the natural growth function is convex-concave.

Non-pecuniary value of employment

We modify the utility function in (1.a) to take into account that the people gain their utility not only from consumption but also from working. Formally, we assume:

$$u(c,E),\ E \in [0,\bar{E}],\ E = \text{ working time. } \partial u / \partial E > 0, \partial u^2 / \partial E^2 < 0.$$

If the resource extraction sector is the only industry in the economy and the harvest technology is a concave function in efforts ($E = E(c),\ E' > 0,\ E'' > 0$), then resource extinction with the maximal harvesting effort is optimal, independent of the magnitudes of discount rate and the initial stock level of resource. We will refer to this situation as *full-employment obsession*. For detailed analysis and discussion, see Farzin and Akao (2006).

Ill-defined property right

The “tragedy of the commons,” a problem of a common property resource used by multiple resource users, emerges when the property right of the resource is ill-defined and the resource is freely used by the resource users. The simplest formulation of the problem is as follows:

$$\max_{c(t)\geq 0}\int_0^{\infty} u(c(t))e^{-\rho t}dt \tag{2.a}$$

$$\text{subject to } \dot{x}(t) = f(x(t)) - (n-1)\sigma(x) - c(t), \tag{2.b}$$

$$c(t) \in [0, \bar{h}],\ x(0) = x_0 \text{ given,} \tag{2.c}$$

where $\sigma(x)$ is the common harvesting strategy of all other users, which is assumed to depend only on the resource stock, and in particular, to be time independent. Therefore, in this simplest case, we assume that every user adopts the same stationary Markovian strategy. If the solution of the above problem is given by the same strategy as other users’ strategy $\sigma(x)$, then no player has an incentive to change the strategy. A profile of such a strategy is called a (symmetric) Nash equilibrium. A Nash equilibrium strategy describes the resource use realized by rational resource users.

Under the condition $f(x) < n\bar{h}$ for all $x \geq 0$, the strategy with the users’ maximal harvesting efforts:

$$\sigma(x) = \begin{cases} \bar{h} & \text{if} \quad x > 0 \\ 0 & \phantom{\text{if}} \quad x = 0 \end{cases}, \tag{3}$$

leads the resource to extinction at the most rapid speed and is called the *most rapid extinction strategy*. The most rapid extinction strategy constitutes a Nash equilibrium if the following inequality holds:

$$u'(\bar{h}) \geq \frac{u(\bar{h})}{n\bar{h} - f(x_{ss}^*)}\exp\left[-\rho\int_0^{x_{ss}^*}\frac{dy}{n\bar{h} - f(y)}\right]. \tag{4}$$

This result, which is proved by Sorger (1998), implies that the resource is exhausted at the most rapid speed if any of the following conditions is satisfied: (a) the time discount rate ρ is high; (b) the users are greedy in the sense that the marginal utility $u'(\bar{h})$ is high; (c) the aggregate harvest ability $n\bar{h}$ is high. This is a theoretical representation of Hardin’s (1964) “tragedy of the commons.”

Even in this simplest case, it is known that there are multiple Nash equilibria. Not only the most rapid finite time resource extinction, but also sustainable resource use can be a Nash equilibrium under condition (4). Therefore, the tragedy of the commons may not be inevitable for a common property resource. However, it is hard to predict which equilibrium arises. This indicates that for two communities with identical resource stock and individual preferences, one may use its natural resource in a sustainable way, whereas the other may exhaust its resource at the most rapid speed. It is also possible that a community that has been using its resource in a sustainable way for a period of time may suddenly switch to a ruinous resource use path without any evident trigger.

Policies to Avoid Unsustainable Resource Use

The risk of a fatal event for resource management raises the effective discount rate and a high discount rate brings finite-time resource extinction. To prevent such a situation, we need to mitigate the risk caused by socio or ecological instability. For the socio-economic dimension, political stability matters. For a fragile ecosystem, unsustainable resource use is more likely to become a rational choice, and thus careful attention is required.

If the growth function of the resource exhibits nonconvexity and the resource is being degraded, a policy to mitigate the risk of a fatal event should be implemented early on, because when the resource has been already degraded, extinction is more prone to be an optimal resource use policy, even with a low discount rate.

Non-pecuniary value of employment may make people give priority to full employment over sustainable resource use. Farzin and Akao (2006) show that the remedy is none but to create alternative employment sources to absorb labor force which is excessive from the viewpoint of sustainable resource use. They also suggest that earlier policy implementation is more prudent, since when the resource is more degraded, higher wage rates may be necessary to prevent resource exhaustion.

A direct solution to the problems stemming from an ill-defined property right of resource is privatization. However, this solution may be physically difficult for some resources such as the global atmosphere and migratory animals. Even if privatization is possible, Dasgupta and Mäler (1997) give a caution that it may bring further resource degradation. This is due to the existing inequality in a rural community. If the resource is not favorably distributed to the poor, they cannot help but to encroach on the resource. As for other policy measures, Akao (2007) shows that among standard economic policy measures, a tax on harvest fails to avoid an unsustainable Nash equilibrium, whereas a system of tradable permits or quotas works well to realize sustainable and efficient resource usage.

Finally, resource-sector technological assistance and income assistance may not help to prevent finite-time extinction. In particular, if technological assistance improves harvesting efficiency, and hence the maximum harvesting ability, it may even accelerate resource extinction.

References

Akao K (2007) Tax schemes in a class of differential games. Economic Theory (Available online. doi.org/10.1007/s00199-007-0232-9).

Dasgupta P, Mäler KG (1997) The resource-basis of production and consumption: an economic analysis. In Dasgupta P, Mäler KG (eds) The Environment and Emerging Development Issues, vol.1. Clarendon Press, Oxford, pp 1—32

Farzin YH, Akao K (2006) Non-Pecuniary Value of Employment and Natural Resource Extinction. FEEM Working Paper 24.06, Fondazione Eni Enrico Mattei, Milano

Hardin G (1968) The tragedy of the commons. Science 162: 1243—1247

Pearce D, Barbier EB, Markandya A (1990) Sustainable development: economics and environment in the third World. Edward Elgar, Aldershot

Sorger G (1998) Markov-perfect Nash equilibria in a class of resources games. Economic Theory 11: 78—100

Economic Analysis of Biodiversity Conservation: Two Challenging Problems*

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Introduction

Why does biodiversity conservation matter? What will happen if we do not take action to conserve it? Can we be sure of protecting an ecosystem and keeping it as we want? These are oft-asked questions in research and practice of biodiversity conservation. From the viewpoint of economics, this study identifies novel and challenging problems behind these questions and suggests directions for future research.

Two Challenging Problems

Why is biodiversity conservation important for our society? A simple reason is that biodiversity is useful. We know that biodiversity increases the long-run average productivity of bio-resources, works as insurance against diseases and insect pests for agricultural products, and provides models for medicines and industrial chemicals. At the same time, we know that our motivation to preserve biodiversity comes not only from its practical usefulness, but also from its aesthetic value and from ethical considerations such as stewardship. To make the right decisions about conservation/development of an ecosystem, those values need to be taken into account. How, though, can we evaluate those intangible and non-economic values? This is the first problem we investigate.

The second problem concerns uncertainty. Several policy measures for biodiversity conservation have been proposed and implemented. But, do such measures actually ensure conservation? What would happen without such measures? No one has been able to answer these questions convincingly because there is formidable uncertainty between human intervention and its consequences for an ecosystem. Expectation calculation, a conventional method in decision theory, may be unable to tame this type of uncertainty because we may not be able to choose a plausible probability distribution, even in the subjective sense. How can we develop a decision theory approach for this situation? This is the second problem we investigate.

Diversity Function

The first question mentioned above motivates recent study on *diversity functions*. A diversity function maps a set of species to a nonnegative number that is interpreted as the *existence value* of the ecosystem consisting of the species. The term “existence” signifies that the value is not derived from the practical usefulness of the species, but generated just because they exist.

In his seminal paper, Weitzman (1992) took a course in which the value of diversity was calculated based on the data of the existence value of each species and the *dissimilarity* between two species. Let $V(i)$ be the existence value of species *i* and $d(i, j)$ be the dissimilarity of species *i* for species *j*, which

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[*] Summary of the Japanese article by Ken-Ichi Akao: 赤尾健一(2006) 生物多様性の経済分析－多様性関数と不確実性に関する最近の研究－, 環境経済・政策学会年報 11, 136—147.

is a pseudo distance in the sense that $d\left(i, j\right) \neq d(j,i)$ in general. Then the existence value $V(\{i, j\})$ of the set of species $\{i, j\}$ is defined by:

$$V(\{i, j\}) = V(\{j\}) + d(i, j) = V(\{i\}) + d(j,i) .$$

Weitzman defines the *distinctiveness* of species *k* for the set of the species *S* by:

$$d(k,S) = \min\left[d(k,s) \mid s \in S\right].$$

We obtain the diversity of the set $\{i, j, k\}$ as follows:

$$V(\{i, j,k\}) = d(k,\{i, j\}) + V(\{i, j\}) .$$

The diversity of a set of four species is derived in a similar way using the diversity of the subset of three species and the distinctiveness of the remaining species. This recursive method enables the diversity to be obtained for any set of species. Weitzman’s diversity function has been used in empirical research, including research by Weitzman (1993) and Oka et al. (2001). As the dissimilarity, Weitzman (1993) employs the genetic distance and Oka et al. (2001) use the sum of years with which two species evolved from their common ancestor.

Nehring and Puppe (2002) take another approach. They assume that each species has its own valuable attributes. Their diversity function is constructed by summing up the values of the attributes contained in the set of species under consideration. Let species *i*, *j*, *k* be flowers. Suppose that species *i* has the attributes “fragrant” and “gorgeous,” *j* has “fragrant” and “exotic,” and *k* has “gorgeous” and “exotic.” Denote the values of the attributes “fragrant,” “gorgeous” and “exotic” by λ_f, λ_g and λ_e, respectively. Following Nehring and Puppe, the diversity of the set of three flowers is calculated by:

$$V(\{i, j,k\}) = \lambda_f + \lambda_g + \lambda_e .$$

In general, the diversity of a set of the species *S* is defined by

$$V(S) = \lambda\left(\{A_1,..., A_m\}\right) = \sum_{j=1}^{m} \lambda\left(\{A_j\}\right),$$

where $\{A_1,..., A_m\}$ is the attributes contained in *S*.

Nehring and Puppe show that:

(a) their diversity function is a kind of Neumann-Morgenstern utility function, so that expected utility approach is applicable;

(b) their “attributes” approach replicates Weitzman’s diversity function as a special case; and

(c) Weitzman’s diversity function is too restrictive to express our evaluation of biodiversity.

The last finding is exemplified by the case of flowers above. When we lose species *i* from the three flowers, we do not lose the diversity of attributes and thus the loss of diversity is zero. However, Weitzman’s diversity function suggests a diversity loss. Although the example is quite artificial because in the real world each flower species has its own individuality, the point is that Weitzman’s diversity function may face a logical contradiction. Nehring and Puppe clarify that Weitzman’s diversity function is well behaved only if the attributes are located on a line (one dimensional attribute case).

While the attributes approach by Nehring and Puppe is more comprehensive than Weitzman's approach, it allows too many attributes to be included in the diversity function, so it seems difficult to find a plausible functional form. Due to this difficulty, the attributes approach has not been applied to empirical research.

Ambiguity

The second problem, the issue of how to develop a decision theory approach, has been studied from several perspectives. Among them, much interest has been attracted by a generalization of the expected utility hypothesis. Gilboa and Schmeidler (1989) assume that an agent cannot specify a probability of an uncertain event, but can have a set of possible probability distributions (multi-priors) and can assign a probability to each prior in the set. In other words, this is a situation in which an agent considers a lottery of a lottery. This type of uncertainty is called *ambiguity*, or *Knightian uncertainty*, after Frank Knight, the great economist of the early twentieth century who distinguished risk and true uncertainty; the former is defined as randomness with knowable probabilities and the latter as randomness with unknowable probabilities.

In addition to the axioms for expected utility hypothesis, they posited the axiom called *uncertainty aversion*: an agent weakly prefers the average distribution of priors to the set of priors. Then, the agent makes a decision such that it maximizes the expected utility under the *worst* prior in the sense that the expected utility is minimized. The utility is called the maxmin expected utility (*MEU*).

The formal illustration is as follows. Consider a two period model covering today and tomorrow. Suppose an ecosystem consists of n species. There are 2^n possible states for the situation of the ecosystem tomorrow. Let diversity function $V(s)$ express the present value of the biodiversity in monetary terms when state $s \in S \equiv \{s_1, s_2, ..., s_{2^n}\}$ is realized. A prior ϕ on conservation is represented by a probability distribution of the states $p^{\phi}(s;c)$, where c denotes conservation effort invested today. Denote by Φ the set of the priors. An agent then solves:

$$MEU(\Phi, p^{\phi}, V) = \max_{c \geq 0} E\left\{\min_{\phi \in \Phi} \sum_{s \in S} p^{\phi}(s;c)V(s) - c\right\}.$$

This is the maxmin expected utility. The maxmin expected utility is not as optimistic as the expected utility (*EU*):

$$EU(p^{\phi}, V) = \max_{c \geq 0} E\left\{\sum_{s \in S} p^{\phi}(s;c)V(s) - c\right\} \geq MEU(\Phi, p^{\phi}, V).$$

On the other hand, the maxmin expected utility is not as pessimistic as the maxmin utility (*MU*):

$$MU(\Phi, p^{\phi}, V) = \max_{c \geq 0}\left\{V(\underline{s}(c)) - c\right\} \leq MEU(\Phi, p^{\phi}, V),$$

where $\underline{s}(c) = \arg\min_{s \in S}\left\{V(s) \mid p^{\phi}(s;c) > 0, \phi \in \Phi\right\}$. Therefore, decision making based on the *MEU* cares about a possible bad event more than the EU, but less than the MU. Note that the MU suggests an extremely deliberate decision such as "do not go out because you may have a traffic accident."

The main difficulty of the maxmin expected utility is that there is no plausible assumption about the set of priors Φ . Prevailing assumptions such as rectangularity (Chen and Epstein, 2002) are employed to keep a model analytically tractable, but the economic justification is difficult.

Perspective for future research

Recent developments in the theory of diversity function and the treatment of uncertainty provide greater insight into the theoretical grounds of biodiversity conservation. However, further research is necessary before being able to apply these insights in practice, particularly to decision making for conservation/development. The standard decision tool is cost/benefit analysis (CBA). These new approaches suggest that conventional CBA should be modified by incorporating the existence value of diversity as a benefit of conservation and by replacing the expectation operation with one of maxmin expected utility. However, the problems set out above make it quite difficult to fully satisfy both tasks.

A promising strategy is to seek a feasible modification of a conventional CBA that underestimates the expected value of benefit of biodiversity conservation in comparison with the ideal CBA which incorporates the existence value of biodiversity and ambiguity. A conservation project that passes the CBA is a project most likely to be worthwhile implementing.

References

Chen, Z, Epsitein L (2002) Ambiguity, risk, and asset returns in continuous time. Econometrica 70: 1403—1443

Gilboa I, Schmeidler D (1989) Maxmin expected utility with non-unique prior. J Math Econ 18: 141—153

Nehring K, Puppe C (2002) A theory of diversity. Econometrica 70: 1155—1198

Oka T, Matsuda H, , Kadono Y (2001) Ecological risk-benefit analysis of a wetland development based on risk assessment using ‘expected loss of biodiversity.’ Risk Analysis 21: 1011—1023

Weitzman ML (1993) What to preserve? An application of diversity theory to crane conservation. Quart J Econ 108: 157—183

Weitzman ML (1992) On diversity. Quart J Econ 107: 363—405

Application of Environmental Economic Evaluation to Forest Policies in Sabah, Malaysia

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Introduction

Figure 1 shows relationship between forest conservation policies and their evaluation systems. Among them, the current research takes up the Forest Certification project and the Clean Development Mechanism (CDM) project for afforestation and reforestation, to apply the environmental economic evaluation system. In particular, we have studied what kind of roles the environmental economic evaluation performs for internalization of environmental benefits and costs through cost-benefit analysis of these projects, as trying evaluations of natural ecosystem in Sabah including the Kinabalu Park as well as the Deramakot Forest Reserve Area.

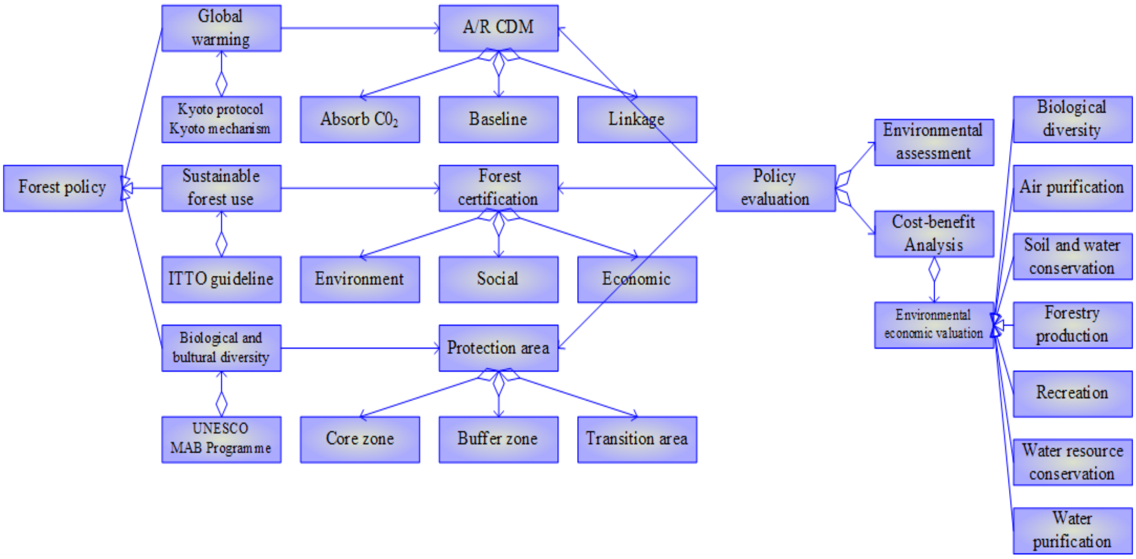

Figure 1 Relationship between Forest Conservation Policies and Evaluation Systems

Necessity of Environmental Economic Evaluation for Forest Policies

In carrying out the project as forest policy, calculating environmental values provides objective evaluation standards. It will support in preserving good forest ecosystem, formulating regulations/laws for forest preservation, zoning nature preservation areas and controlling land use for amenity preservation. Further, it can provide basic data to carry out public or private projects, which have a high economic efficiency from the environmental standpoints. The social loss occurs as precious forest resources decrease. Environmental economic evaluation can make contributions to the policies as follows ;

1) Switch from policies only for economic growth by plantation or clear-cutting toward policies with environmental preservation functions such as water resources conservation and flood control,
2) Promotion of policies which increase environmental values at the expense of efficient and fair

operation/maintenance costs,

3) Development of policies which improve overall social welfare considering public services such as amenity, biodiversity and local culture, not only for national economic growth or private sector's profits, and
4) Formulation of policies actively aiming at environment-oriented land use and social structure for urban area with little natural resources and degraded.

Cost-benefit Analysis

The cost-benefit analysis is a technique to prioritize policies or projects by evaluating social costs and benefits in monetary terms, and comparing the cost with validity. Public infrastructure or private-sector projects have been usually evaluated only with the direct benefits and costs that are so-called "internal economic effects". However, when the target policies/projects are more concerned with environmental impacts or services, it is also needed to internalize the "external effects" of environment and natural resources. If such environmental damages and contribution are estimated as social costs and benefits, it would be possible to duly evaluate the policies/projects not only from the viewpoints of economic efficiency but also from social and environmental ones through the analysis. Table 1 shows a cost-benefit analysis model to calculate a typical evaluation parameter "Net Present Value" for forest policies. Calculating value of the external benefit (*Be*) and the external cost (*Ce*) can realize economic internalization of environmental aspects, leading to fair and social evaluation of the forest policies.

Table 1 Cost-benefit Analysis Model for Forest Policy

$$NPV = B_d + B_e - C_d - C_p - C_e$$

NPV = net present value
Bd = direct benefit from the forest policy
Be = external benefit (including environmental services)
Cd = direct cost to implement the forest policy
Cp = cost for counter-measures to prevent environmental loss
Ce = external cost (including unavoidable environmental damage)

Application of Environmental Economic Evaluation to Forest Certification Project

(1) Background of Forest Certification Project

The competition with non-certified cheap woods hinders the spread of forest certification system. Under the system, marketable woods and their commercial usage have been limited due to their youngness. Therefore, it is a task to manufacture various marketable products using the certified woods. Prices of the certified products are 10 – 20% higher than non-certified ones, although quality is not different between them. So the problem is how to appeal to consumers for environmental significance attributed to the certified products.

At the Deramakot Forest Reserve Area managed by Sabah Forestry Department, tree-cutting have been controlled with the RIL (Reduced Impact Logging) method which is a model for sustainable forest management. It minimizes the environmental damage relying on natural regeneration function and duly considering biodiversity in the forest. Because of such background, the RIL area was first in Sabah certified as sustainable management forest by FSC (Forest Stewardship Council) in 1997.

However, the forest certification system has not been commonly applied in Sabah, because the system necessitates extra techniques and additional cost for preliminary survey and forest management. Economic benefit covering such additional cost is uncertain and environmental contribution is not recognized in wood market. Commercial forests in Sabah have been mostly logged in a short period with a cost-saving productive method. In addition, impacts on society and culture have to be evaluated as management change of commercial forests and setting-up of reserve area affect employment opportunity and life resources for local people.

(2) Cost-benefit Analysis of Forest Certification Project

Table 2 presents typical elements to be included into the cost-benefit analysis model. Improvement of public service functions as well as reduction of environmental and social impacts are required to obtain the forest certificate. Compared with non-certified forests, the certified forests therefore need additional cost to monitor environmental and social impacts on logging area. The model has to cover such additional costs and benefits, reflecting local people's values for project impacts on social and cultural aspects.

Table 2 Typical Costs and Benefits of Forest Certification Project

Bd = value of certificated woods
Be = social and environmental benefit (improvement of biodiversity, flood control, water resources conservation, creation of local employment, etc.)
Cd = direct cost for certification procedure, forest management, logging, etc.
Cp = cost for environmental and social conservation (monitoring, counter-measures, etc.)
Ce = unavoidable social and environmental damage (degraded biodiversity, income reduction, etc.)

(3) Cost for Certification

Cd varies depending on the size of forests. For example, the cost to obtain the certificate is US$0.01-1.3/ha/year under the FSC system while that for Swiss imported woods under the CoC (Chain-of-Custody) system is estimated from US$500 to 1% of the wood price. In case of the SGS which is a FSC certification organization, the cost of certification is US$4,000-100,000/case depending on forest area. Because the direct cost for certification is thus a financially large burden to private foresters, external social and environmental benefits from the certification system should be clarified to wood products consumers so that the higher prices of the certified woods could be well acceptable in market.

(4) Price of Certified Woods

Be is reflected to the price of certified woods and processed products, so that the certified products are sold with 10-20% higher market prices than non-certification products. These prices will further increase for profitability with a small demand because marketable species, diameter and age are limited. If the consumers purchase more Malaysian certified woods, it will help to reduce illegal logging and excessive deforestation in Malaysia. In addition, the wood-mileage evaluation should be reflected on the international and domestic market prices to promote environment-oriented forestry all over the world.

Application of Environmental Economic Evaluation to CDM Project

(1) Background of CDM Project

The CDM projects have positive effects not only on air quality by absorbing CO_2 and producing O_2 but also on total ecosystem. They also contribute in improving flood control function and water resource conservation as usual afforestation projects. But, at the same time, afforestation/reforestation activities will have negative impacts on natural ecosystem and local community when mono-species plantation of fast-growing or exotic trees is introduced.

A difference to the CDM projects from the usual afforestation activities is additional cost for acquisition of the credit. Its example is the cost to monitor and prevent the "linkage", which means incremental CO_2 emission at the tree-cutted agricultural area newly cultivated by farmers who are forced to move from the CDM project sites. As such, social environmental consideration is strictly required under the CDM projects. When the CDM system is introduced in Sabah with a large population and natural environment, impacts of the projects should be fully assessed.

(2) Cost-benefit Analysis of CDM Project

In addition to benefit from air purification function of CO_2 absorption, other *Be* and *Ce* should also be internalized for evaluation of the CDM project. And monitoring and preventive costs for the linkage are to be included as *Cp*. Values of forestry resources are usually estimated through market prices. When these values are increased or reduced, they are regarded as *Bd* or *Cd* respectively. But, if local people consume forest resources for fuel materials, building materials and food not through the market, they should be evaluated as *Be* or *Ce* to be internalized into the cost-benefit analysis model. In addition, social benefit or cost accrues from the CDM project's impact on local people , such as employment opportunity and community disturbance by the forest management. Typical costs and benefits of the CDM project is shown in Table 3.

Table 3 Typical Costs and Benefits of CDM Project

Bd = increased wood products
Be = absorbed CO_2, flood control, water resources conservation, local employment, etc.
Cd = cost of afforestation management (investigation, monitoring, afforestation, logging, road maintenance, etc.)
Cp = cost of social and environmental preservation measures
Ce = unavoidable social environmental damage (degraded biodiversity mono-plantation of fast-growing or exotic species such as eucalyptus, influence to traditional culture, etc.)

(3) Credit Period

Because the credit period affects the credit price, the credit period is the important matter for the entrepreneurs. In COP9, the credit period was set to 60 years at the longest (renewable 20 years twice) or 30 years (no renewable). This relatively longer period has been determined, considering difference of growth period by species and area. However, unlike power station construction or energy-saving projects, afforestation does not have permanence to absorb CO_2 in the future. It is a problem that CO_2 will be emitted again when trees are cut or caught in fires.

Monetary Evaluation Methods for Environmental Values

In actually applying the cost-benefit analysis models presented in the previous chapters, elements more unfamiliar and difficult to evaluate in monetary terms are *Ce* and *Be*. So, in this and following chapters, methodological framework to evaluate typical environmental values ("cost" when it is lost, and "benefit" when it is conserved or improved) is studies, and actual measurement is tried for natural forest, commercial forest and agricultural land in Sabah. Environmental functions are major targets under the current study. The main purpose to apply the monetary evaluation methods is to quantitatively measure the benefits. Envisaged benefits could be largely classified into 9 categories as follows :

1) Fostered water resources,
2) Conserved water quality,
3) Erosion and flood control capacity,
4) Air purification,
5) Aesthetic and recreational amenity,
6) Biodiversity services
7) Forestry resources,
8) Fishery resources, and
9) Agricultural resources

Potential methods for estimating the monetary value of natural resources and environmental benefits are examined. The next table presents a menu of valuation techniques which have been developed so far in environmental/resource economics, as well as typical examples of the evaluated effects. These are largely divided into two categories (OVA and SVA), based on their extent of objectivity or subjectivity.

Table 4 Menu of Valuation Methods for Environmental Effects

Valuation Method	Typical Effects Valued
Objective Valuation Approaches (OVA)	
1) Change in Productivity	Productivity
2) Cost of Illness	Health (morbidity)
3) Human Capital	Health (mortality)
4) Replacement (Restoration) Cost	Capital assets, and natural resource assets
Subjective Valuation Approaches (SVA)	
1) Preventive (Mitigative) Expenditure	Health, productivity, capital assets, and natural resource assets
2) Hedonic Approaches	
- Property (Land) Value	Environmental quality, and productivity
- Wage Differential	Health
3) Travel Cost Method (TCM)	Natural resource assets, and touristic assets
4) Contingent Valuation Method (CVM)	Any effects including biological and aesthetic values
5) Conjoint Analysis	

Source: Economic Analysis of Environmental Effects

Objective Valuation Approaches

The first set if methods in the table are the Objective Valuation Approaches (OVA) that are based on physical relationships that formally describe cause and effect relationships and provide objective measures of effects resulting from various causes. OVA use “damage functions” which relate the level of offending activity to the degree of physical damage to a natural or man-made asset, or to the degree of health impact. OVA in general provide measures of the gross benefits, in the sense of losses avoided, of preventive or remedial actions. The important assumptions for OVA are :

- The net value of averting damage is at least equal to the cost which would be incurred if the damage actually occurred ; and
- Rational individuals, in order to prevent some damage from occurring, would be willing to pay an amount less than or equal to the costs arising from the predicted level of environmental effects.

Subjective Valuation Approaches

In contrast to OVA, the second set of approaches in the table, the Subjective Valuation Approaches (SVA), are based on more subjective assessments of possible damage expressed in real or hypothetical market behavior. Using revealed behavior involves examination of real markets for goods or services which are affected by environmental impacts, such as air or water pollution, in which people actually make trade offs between the environmental impact and other goods or income. In other cases environmental impacts cannot be valued, even indirectly, through market behavior. The alternative is to construct hypothetical markets for various options to reduce environmental damages, and to ask directly a sample of people to express how much they would be willing to pay for various reductions in environmental impacts. These are the so-called “Contingent Valuation Methods” (CDM) and “Conjoint Analysis”.

Applicable Evaluation Framework

The selection of a particular method of measurement obviously depends on what is being measured. Selection procedure starts with any environmental impact and determines whether or not there is measurable change in production, or if the primary effect of the impact is change in environmental quality. According to availability of necessary data for monetary calculation, the more applicable evaluation methods for the above-mentioned 9 kinds of benefits brought from the forest ecosystem could be selected as below :

(1) Fostered Water Resources

It is assumed that development water discharge (incremental water discharge usable during the dry season) is equal to an average outflow of groundwater fostered by incremental vegetation. Therefore, benefit of the water fostering function of the incremental vegetation is evaluated with costs necessary to obtain the same development discharge from irrigation dams (construction and O&M costs of irrigation dams).

Natural vegetation in the watershed fosters groundwater for use in the watershed area and the downstream. And the fostered water flows into rivers and lakes, contributing to stabilization of discharged water amount there. So, loss of the vegetation affects the groundwater utilization and river discharge, decreasing products of agricultural and fishery sectors using water as key input. These industrial production losses can be taken as value of the water fostering function of the vegetation.

Increased water resources → Change in environmental quality → Human habitat
→ **Replacement Cost Method**
[Benefit] = [Incremental vegetation] x [Average unit groundwater outflow of vegetation]
x [(Annual construction cost of irrigation dam per unit development discharge)
+ (Annual O&M cost of irrigation dam per unit development discharge)]

Increased water resources → Measurable change in production → Non-distorted market prices
→ **Change in Productivity Method**
[Benefit] = [Incremental vegetation area] x [Fostered groundwater per unit vegetation]
x [Contribution rate of unit groundwater to each sectoral production]

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(2) Conserved Water Quality

The value of water quality is assumed to be equivalent to the incremental cost of treating the water so that it is suitable for downstream uses. The level of treatment depends on the downstream use. For example, irrigation water does not require the same level of purity as drinking water, so the cost of treating water for use in agriculture would be less than drinking water supply. The incremental cost could be calculated as the extra alum or lime, filter capacity, treatment plant operation costs, etc. needed to treat the excess water pollutants.

Conserved or improved water quality → Change in environmental quality → Water quality
→ **Replacement Cost Method** or **Preventive Expenditure Method**
[Benefit by preventive expenditure method]
= [Reduced water pollutants]
x [Unit cost for construction and O&M of water filter plant to remove the pollutants]

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(3) Erosion and Flood Control Capacity

In case there is stripped area without vegetation in the watershed, severe erosion would occur under heavy rainfall and its downstream water quality is degraded. So value of the vegetation's erosion control function is evaluated using construction costs of check dams to control and mitigate the washed-away soil.

Strengthened erosion control capacity → Change in environmental quality → Water quality
→ **Replacement Cost Method** or **Preventive Expenditure Method**
[Benefit by preventive expenditure method]
= [Amount of soil erosion without vegetation]
x [Unit cost for check dam construction to control or mitigate the washed-away soil]

Watershed degradation contributes to increased flooding in two ways. First, tree cutting and other land disturbance reduce the water holding capacity of the soil, causing larger peak flows of drainage after rain storms. Second, the sediment that erodes from the stripped or disturbed land fills the beds of rivers and lakes, allowing flood water to rise above the river and lake banks. The value of flood damage resulting from watershed degradation could be estimated as the value of the incremental amount of increased flooding or decreased flood control capacity.

Strengthened flood control capacity → Change in environmental quality → Human habitat
→ **Replacement Cost Method**
[Benefit] = [Reduced cost to rehabilitate damages due to mud-slide and flooding]
= [Cost to restore damaged land and building] + [Cost to remove mud and water]
+ [Repair cost of paddy dikes] + [Cost to rebuild or relocate damaged infrastructure]
+ [Other expenditure in rehabilitation]

When land and buildings are damaged, the measure of damage should be calculated as the cost to restore them to their original condition. The restoration activities might include removal of mud and dust, repairing of buildings and paddy dikes, and finding temporary accommodation while the buildings are being repaired. Roads, bridges, pipelines, electrical power lines and other public infrastructure could be damaged by mud slides and flooding associated with land disturbance activities in the watershed. The value of the damage in these cases could be calculated as cost to rebuild or relocate the damaged infrastructure.

The next equation reflects that the loss of revenue from lost farm production is a value of the strengthened erosion- and flood-control capacity when agricultural land is covered by mud slides.

Strengthened erosion and flood control capacity → Measurable change in agricultural production
→ Non-distorted market prices → **Change-in-Productivity Method**
[Benefit] = [Agricultural area protected from erosion]
x [Incremental products] x [Unit market price of product]

(4) Air Purification

Oxygen supply function of the incremental vegetation is evaluated by calculating the oxygen weight discharged from the vegetation based on the existing research data, which is multiplied by unit market price of the industrial oxygen. And amount of CO_2 absorbed by the incremental vegetation is estimated for calculation of a total cost to remove them alternatively. This total cost is regarded as an economic value of the air purification function of the incremental vegetation.

Improved air quality → Change in environmental quality → Air quality
→ **Replacement Cost Method**
[Benefit] = [Amount of incremental vegetation]
x {[(Annual net O_2 discharge per vegetation) x (Unit market price of O_2)]
+ [(Annual net CO_2 absorption net vegetation) x (Unit removal cost of CO_2)]}

(5) Aesthetic and Recreational Amenity, and

(6) Biodiversity Services

The value of the aesthetic quality of the natural environment is difficult to calculate in monetary terms, because it depends on the subjective preference of each individual person. One approach to assigning a monetary value to aesthetic qualities is to estimate how much the people living in and around the area would pay to preserve them (willingness to pay, WTP). The cumulative regional WTP could be interpreted to be equal to the overall value of restoring the aesthetic quality of the environment. In addition, It is likely that Malaysian and international tourists who visit the National Park would also be willing to pay some small amount of money such as a surcharge on hotel room rates for preserving the aesthetic quantities of the Park.

Aesthetic and biodiversity quality → Change in environmental quality → Aesthetics, biodiversity
→ **Contingent Valuation Method**
[Non-use benefit including existence value]
= [Average WTP of non-use value of local households] x [Number of local households]
+ [Average WTP of non-use value of tourists] x [Number of tourists]

Conserved or improved aesthetic quality → Change in environmental quality → Recreation
→ **Travel-Cost Method** or **Contingent Valuation Method**
[Use-benefit by travel cost method]
= [Average travel cost of tourists] x [Incremental number of tourists]
+ [Average travel cost of local visitors] x [Incremental number of local visitors]
Where [Travel cost] = [Transportation fee] + [Time cost] + [Opportunity cost of stay]
[Use-benefit by contingent-valuation method]
= [Average WTP of use value of local households] x [Number of local households]
+ [Average WTP of use value of tourists] x [Number of tourists]

Tourism accounts for a part of the trade of goods and services in and around the National Park. A majority of tourists visiting the Park could be classified as “Adventure and Eco-tourists” enjoying the natural landscape of the area.

Conserved or improved aesthetic quality → Measurable change in tourism production
Non-distorted market prices → **Change in Productivity Method**
[Benefit] = [Incremental tourists due to environmental improvement or conservation]
x [Incremental net profit of tourism sector per tourist]

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(7) Improved Forestry Resources

Forests provide several valuable goods and services, including wood products, flood control by stabilizing soil, aesthetic quality and habitat for wildlife. Potential methods for calculating the value of the loss of flood control and aesthetic quality are mentioned in the above sections, respectively. The value of loss of timber and other wood products could be estimated as the overall income that would be derived from harvesting, processing, and selling the products on a sustainable logging on land of similar area, tree types, proximity to roads and factories, etc. where watershed management has been well done.

Improved forestry resources → Measurable change in forestry production
→ Non-distorted market prices → **Change in Productivity Method**
[Benefit] = [Incremental forest land] x [Amount of incremental forest goods]
x [Unit market price of forest goods]

---

(8) Conserved or Improved Fishery Resources

Siltation of river/lake beds and other fish habitat is the main source of environmental damage that poor watershed management causes to fishery resources. Top soil is eroded during heavy rain, and the sediment drains into these sensitive aquatic areas decreasing their ability to support fish life. The value of the damage to fishery resources might be estimated as the loss of fishing income caused by the siltation of fish habitat.The loss of fishing income might be estimated directly or indirectly. If historical records were available, it might be possible to directly estimate the reduction in fishing income. But these results might be unreliable because such factors as improved fishing techniques and boats, increase in the sale price of fish, and increases in the number of people who work in the fishing industry must all be considered. In addition, this direct estimate might unfairly bias against the watershed management, because the other factors such as over-harvesting and pollution from the inland fishery itself might have contributed to the decline in fishing. Consequently, an indirect method of comparison would probably give better results.

Conserved or improved fishery resources → Measurable change in fishery production
→ Non-distorted market prices → **Change in Productivity Method**
[Benefit] = [Improved or conserved water area]
x [Amount of incrementally caught fish and other fishery products]
x [Unit market price of such fishery products]

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(9) Improved or Conserved Agricultural Resources

The extension program of agroforestry technology would increase productivity of the existing agricultural land. This could be a major benefit, so that the incremental agricultural products between with-project and without-project are evaluated with non-distorted market prices.

Improved agricultural resources → Measurable change in agricultural production
→ Non-distorted market prices → **Change in Productivity Method**
[Benefit] = [Amount of incremental agricultural products]
x [Unit market price of the agricultural products]

---

8. Results of Economic Evaluation for Natural Ecosystem in Sabah

In accordance with the existing data and information available, the most appropriate evaluation methods were selected and economic values for various environmental functions have been measured for such typical ecosystems in Sabah as natural forest, commercial forest and agricultural land. As shown in Table 5, annual overall value of the natural forest seems much higher than the other two ecosystems, although their non-use value of biodiversity services could not be calculated due to lack of data.

“6. Biodiversity services” for the natural forest has been calculated with statistical data (Table 6) collected through questionnaire survey to tourists and local residents around the Kinabalu Park. In order to measure the value for the commercial forest and agricultural land, another questionnaire survey should be carried out to apply the contingent valuation method, furthermore “conjoint analysis” which had been also tried under the current study but resulting in statistically insignificant outputs unfortunately.

Table 5 Economic Values of Environmental Functions

Environmental Functions	Evaluation Methods	Economic Value (RM/ha/year in 2003 price)		
		Natural Forest	Commercial Forest	Agricultural Land
1. Fostered water resources	Replacement cost	91	102	21
2. Conserved water quality	Preventive-expenditure	29,693	7,423	Not related
3. Erosion & flood control	Replacement cost, Change-in-productivity	21,391	5,348	Not related
4.Air purification (including CO_2 absorption)	Replacement cost	24,006	27,828	Little data
5. Aesthetic & recreational amenity	Travel cost	8,735	Not related	Not related
6. Biodiversity services (non-use)	Contingent valuation	112,024,000	Little data	Little data
7. Forestry resources	Change-in-productivity	Not related	51～89	Not related
8. Agricultural resources	Change-in-productivity	Not related	Not related	1,917～19,940
9. Improved fishery resources	Change-in-productivity	1.45	0.36	Not related

Table 6 Average Value for Biodiversity Services

Subject	Unit	Foreign Tourists	Malaysian Tourists	Local Residents
Number of Samples	person	97	76	24
1. Biodiversity of natural forest	$/ha/year	58	10	5
2. Biodiversity of commercial forest	$/ha/year	37	9	6
3. Average value for flora	$/species/year	0.9	0.2	0.1

Note） US$ 1＝RM 3.8

9. Contribution to Forest Policy/Project by Environmental Economic Evaluation

CO_2-absorption function of forest resources is expected as incentive to prevent decrease of a tropical forest. Actually, the forest certification, CDM and ISO14001 has become powerful systems to implement so-called “corporative social responsibility”(CSR). However, the CDM project and the forest certification project should not be managed only as CO_2 absorption source, but also for sustainable forest management. For example, further environmental consideration should be taken such as targeting secondary forests rather than natural forests when a plantation expands.

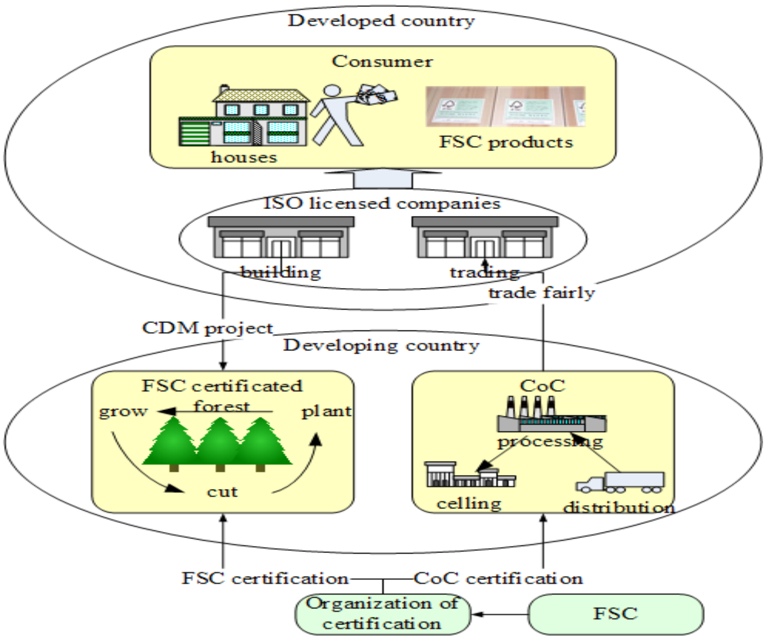

Figure 2 Structural Example of Sustainable Forest Management

As Figure 2 shows, additional value can be added to the certified woods by means of putting the certification labels because of the recent activation of green consumerism. Private foresters can improve their social images through selling eco-friendly certified products. The certified forests help prevent environmental destruction by afforestation managed with technical standards regulating logging methods, tree species and maintenance of logging roads for biodiversity and security of the employment. Environmental value of the certified woods has already been internalized, for example setting the price of certified woods at 20% higher than the non-certified woods.

In activating more and more such environment-oriented forestry systems, the environmental economic evaluation approach focused in this study is quite useful clarifying the objective environmental values of the systems and persuading both foresters and consumers to be actively involved into the sustainable forestry and environmental conservation.

Forest Use and Awareness of Environmental Conservation in Yakushima, Japan

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Introduction

When considering forest conservation measures, it is important to understand how local residents perceive forests. Residents of Yakushima, an island south of Kyushu, Japan, distinguish forest areas as “maedake” and “okudake,” and have utilized these areas in distinct ways. Maedake forests contain broadleaved trees and are located at altitudes below 1200 m. Okudake are covered by coniferous or broadleaved trees and occupy higher altitudes. Almost all residents of Yakushima inhabit the coastal area and traditionally used maedake for fuels and fertilizers. In contrast, the islanders have long regarded okudake as sacred places and have prohibited resource extraction from these forests. Since the Edo period at the beginning of the seventeenth century, the island’s forests have also been known for providing timber from giant, ancient Japanese cedar trees called Yaku-sugi (lit. Yaku cedar).

In 1993 UNESCO designated part of Yakushima Island as a World Heritage Site, and residents have increasingly recognized the non-use values of their forests (e.g., as related to heritage and the existence of nature). Research by Kuriyama (2000) has also demonstrated that the value of Yakushima’s forests is mainly comprised of non-use values. In this study, we looked at how residents of Yakushima value local forests and examined their motivations for forest conservation. We classified respondents into three groups, based on their valuation of maedake, with the aim of clarifying which groups are most motivated to conserve the forest.

Methods

From the population of all households in Yakushima (N = 3167, in 2002), we used simple random sampling from the telephone book to choose a subset of 1095 residents. We then mailed or directly distributed 1095 questionnaire sets in July 2002; of these, 263 sets were returned, for a response rate of 24 %. To analyze the relationship between valuation of maedake and awareness of forest conservation, we classified the respondents into three groups and compared these groups with respect to conservation awareness, frequency of forest use, and type of use.

Results

Of the 263 respondents, 234 (89%) answered that the forest should be preserved. The survey then asked why the forest should be preserved. Respondents were allowed to choose two reasons from a list of six. The most frequent answer was that “it is natural that forest exists” (Fig. 1). We divided these reasons into two categories: use value and non-use value. The reasons “daily needs,” “tourist attraction,” “own property,” and “plants/trees for money" were classified as use values, while "it is natural that forests exist" was classified into the non-use value. The results showed that local residents recognized both types of value.

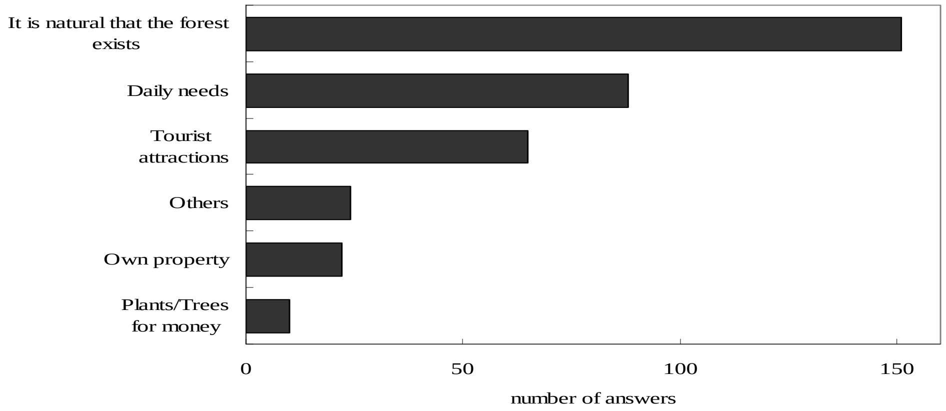

Fig. 1 Reasons why broadleaved forest should be preserved

Next, we divided the respondents into three groups, based on how they valued the forests.

(1) The non-use value group (NUV group): respondents who selected reasons classified as the non-use value.

(2) Use value group (UV group): respondents who selected reasons classified as use value.

(3) Both value groups (BV group): respondents who selected both non-use value and use value reasons.

We compared these groups based on replies to "Would you prefer that the area of maedake be increased?" The five answer choices ranged from "strongly agree" to "strongly disagree." This question was designed to determine whether the respondent felt positive with regard to broadleaved forest conservation. Compared to the NUV group, the UV and BV groups were more positive with regard to increasing the forest (Fig. 2). The BV group used forests more frequently than the UV or NUV groups did (Fig. 3). Figure 4 shows present and past use of the broadleaved forest. Classifying use into two categories (direct use and indirect use) showed that the UV group tended to use the forest more directly, while the NUV group tended to use the forest more indirectly (Fig. 5).

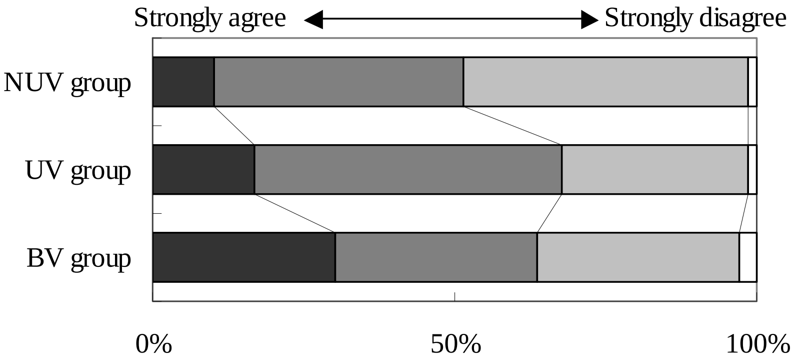

Fig. 2 Replies to "Would you prefer that the area of maedake be increased?"
NUV group: respondents who selected reasons classified as the non-use value;
UV group: respondents who selected reasons classified as the use value;
BV group: respondents who selected both non-use value and use value reasons.

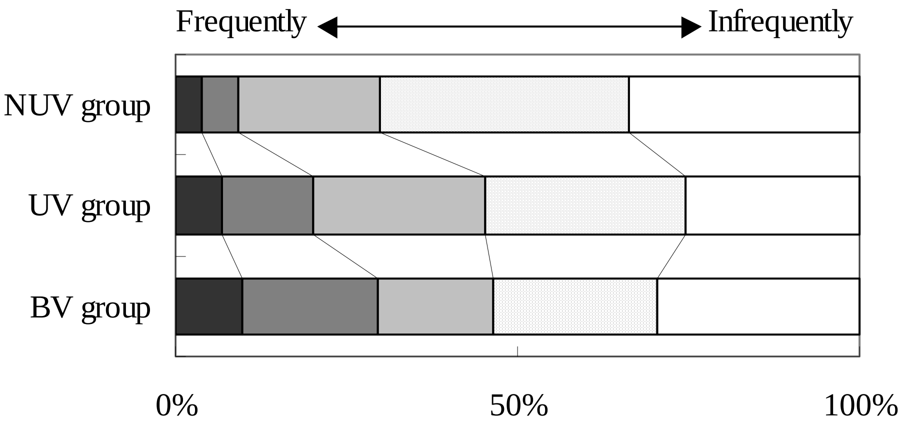

Fig. 3 Frequency of present use of broadleaved forest.
NUV group: respondents who selected reasons classified as the non-use value;
UV group: respondents who selected reasons classified as the use value;
BV group: respondents who selected both non-use value and use value reasons.

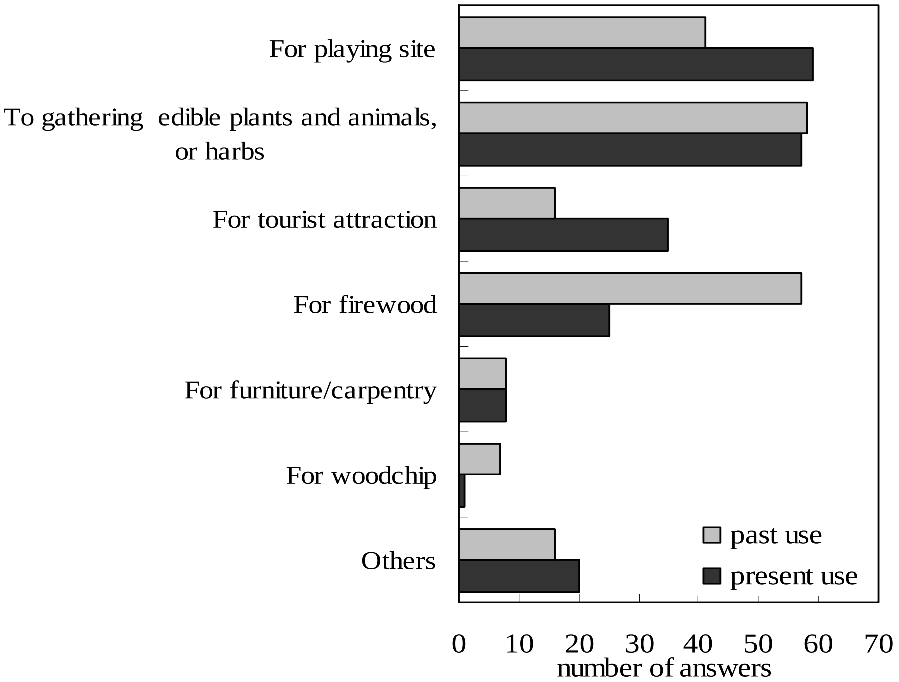

Fig. 4 Change of maedake use

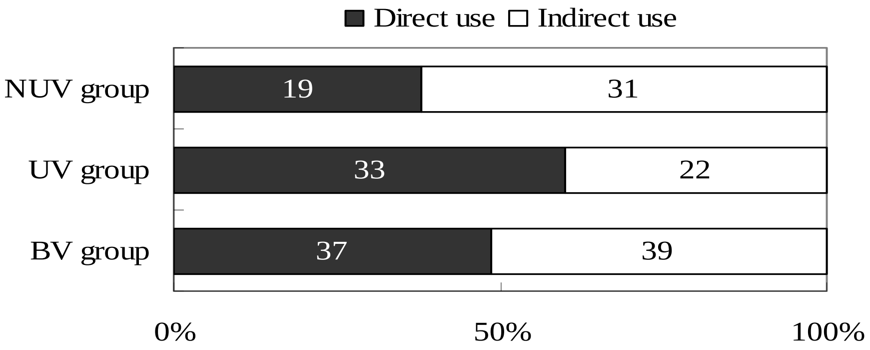

Fig. 5 Direct and indirect uses of maedake.
NUV group: respondents who selected reasons classified as the non-use value; UV group: respondents who selected reasons classified as the use value; BV group: respondents who selected both non-use value and use value reasons.

Discussion

Classification of respondents based on how they valued use and non-use of the forest revealed lower awareness of forest conservation in the NUV group than in the UV and BV groups. This result suggests that local residents have greater awareness of forest conservation when they recognize its use value. As noted above, almost all residential and agricultural areas of Yakushima are near the broadleaved forest. Furthermore, village residents have used forests according to the needs of the times. These results indicate that use value is essential for developing positive feelings with respect to preserving or increasing the forest. On the other hands, local residents, who recognize only non-use value, have not directly used forests. They therefore would not try to change forests even if the area of forests then increase.

The results also reveal that the kinds of use values have changed over time. In the past, most residents used broadleaved forest for firewood or woodchips, but today they mainly use the forest for recreation or in connection with tourism. The residents should aim to preserve the forest depending on their uses. Therefore, future studies should clarify how the residents would preserve the forest.

Some residents still used the forests in traditional ways, such as for obtaining edible plants and animals. This implies that the islanders' lives are still closely connected to the natural forests. At present, firewood use is rare in Japan. However, 10 % of the respondents from Yakushima reported that they still obtain firewood from the forests. Forest policy should reflect such local characteristics of forest use.

Reference

Kuriyama K, Kitahata T, Ooshima Y (2000) "Economics of World Heritage." Keiso shobo (in Japanese)

Chapter 6

CONCLUSIONS

An Integrated Assessment for the Sustainable Use of Forest Ecosystems and Biodiversity

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6.1. Introduction

In this chapter, we propose a methodology for the integrated assessment of sustainable use of forest ecosystems and biodiversity. This assessment is a synthesis of the project results, including the history of forest use, changes in biodiversity and ecosystem services, and socioeconomic mechanisms behind them, which are presented in Chapters 2 to 5.

The aims of the integrated assessment are (1) to evaluate the sustainability of the utilizations of forests and biodiversity by analyzing historical changes in the target regions; (2) to estimate the future forests, biodiversity, and ecosystem services under various scenarios; and (3) to provide possible policy and management options to decision-makers. Every region has specific conditions, and people in those regions make decisions about future forest uses according to the information they have. Our goal in creating this assessment was to provide decision-support tools as well as potential options and their projected consequences.

6.2. Steps in the assessment

6.2.1. Overall process

The assessment process includes the following steps: (1) analyze historical changes in forest use, (2) identify and quantify the driving forces responsible for the changes, (3) analyze the consequent changes in biodiversity and ecosystems, and (4) evaluate the effects of biodiversity on ecosystem services. Through these four steps, we can evaluate how past changes in forest use and biodiversity have affected ecosystem services. We can also identify the types of forest use that caused specific changes in biodiversity and ecosystem services. The assessment has two additional steps: (5) evaluate existing institutions that operate to utilize forest ecosystems and biodiversity in sustainable ways, and (6) propose future forest uses, including potential options and the projected consequences (Fig. 1). The first four steps are well documented in Chapters 2 to 5. In this chapter, we focus on the final two steps.

6.2.2. Historical changes in forest use

As documented in Chapter 2, past forest conditions can be detected using land-use maps, aerial photographs, satellite images, and other related tools. The changes in forest use can then be summarized into transition matrices and analyzed quantitatively.

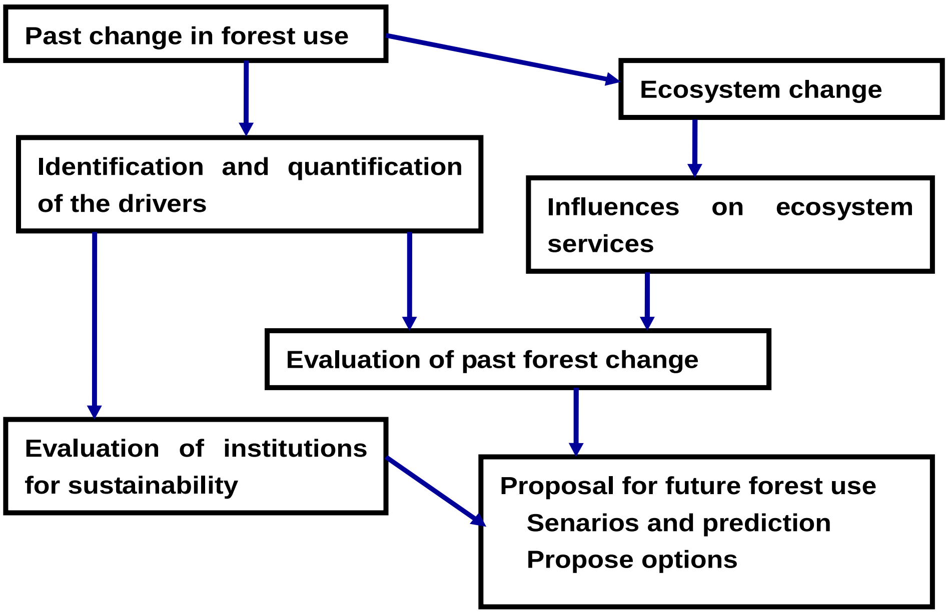

Figure 1. The process of the integrated assessment for sustainable use of forest ecosystems and biodiversity.

6.2.3. Identification and quantification of the driving forces

The drivers that caused the changes in forest and land use were identified by analyzing published literature, statistics, and historical records (Chapter 2). Some cells in the transition matrices were attributed to particular drivers. It may be possible to assign more transition probabilities to identified drivers if we subdivide the matrices into those of different land owners, actors, and so on. Using transition matrices with identified drivers, we were able to project the future land use (see below). These changes were also visualized as maps, which are useful decision-making tools.

6.2.4. Ecosystem and biodiversity changes

As shown in Chapter 3, we can evaluate the diversity of various taxa using classified forest types. Some species or taxa respond very sensitively to forest type, whereas others do not. Although an analysis of the biological responses is still in progress, several species and taxa seem to be very promising as reliable indicators of ecosystem function. These detailed analyses will provide information about index species or taxa for particular forest types, ecosystem functions, and ecosystem services.

It is possible to visualize the biodiversity of particular species or taxa by using maps that combine a diversity index and forest type. If we know that a species is a very good indicator of some ecosystem function, we can also show the spatial distribution of a particular ecosystem function. An example is shown in Figure 2. In this case, the diversity of wood-destroying fungi declined between 1962 and 1997.

6.2.5. Evaluation of ecosystem services

The ecosystem services provided by biodiversity are very difficult to evaluate. Few of them are economically appreciated, and the causal associations between biodiversity and ecosystem services are sometimes very weak. However, some ecosystem functions are closely related to biodiversity, such as pollination and pest control. If we can detect the relationships between forest type and diversity or between forest type and abundance of species or taxa, we can map the ecosystem services. An example is shown in Figure 3. In this case, the abundance of braconid parasitoids that control harmful insects decreased between 1962 and 1997.

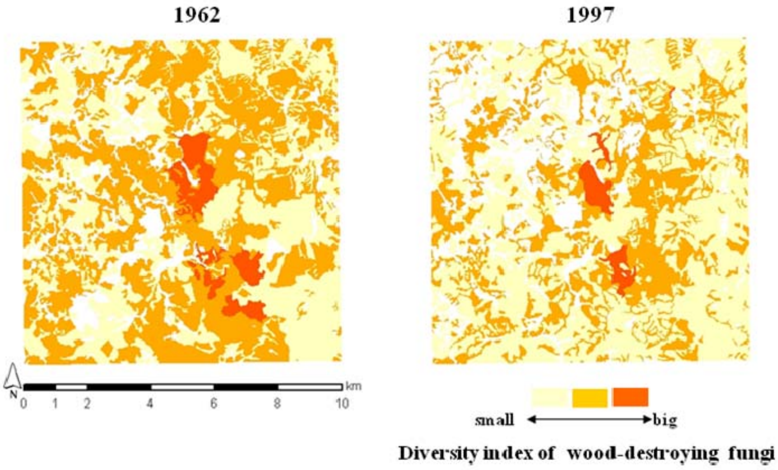

Figure 2 Ecological function map of wood-destroying fungi at Abukuma (Miyamoto et al. unpubl.).

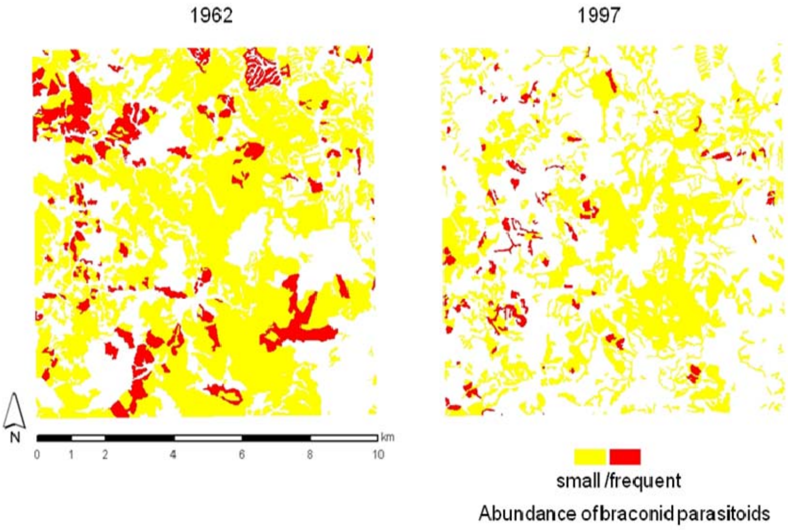

Figure 3 An ecological service map of braconid parasitoids at Abukuma. (Miyamoto et al. unpubl.).

6.2.6. Evaluation of past forest use as a whole

Following the procedures listed above, we were better able to understand how forests in a target region changed, how these changes affected the biodiversity and ecosystem, and how such changes in biodiversity affected ecosystem services. We were able to quantitatively analyze a change and its drivers through the use of a transition matrix and also able to visualize the changes in forest use, biodiversity, ecosystem functions, and ecosystem services on maps.

To increase the practical applicability of this assessment, we sometimes needed to create scenarios of future changes and then show the consequences of the changes. Examples of such projections are shown for land use (Fig. 4) and ecological function (Fig. 5) and services (Fig. 6) in Abukuma. The scenarios used in these examples are as follows: (1) continuation of present trends; (2) restoration of Satoyama—20% of coniferous forests are converted to broadleaf forests, no broadleaf forests are converted to coniferous forests, and 20% of broadleaf forests are converted to grassland; and (3) logging is conducted with a long period between cutting—10% of coniferous forests and broadleaf forests are not logged to help create old forests, and the cutting periods are 100 years for broadleaf forests and 80 years for coniferous forests.

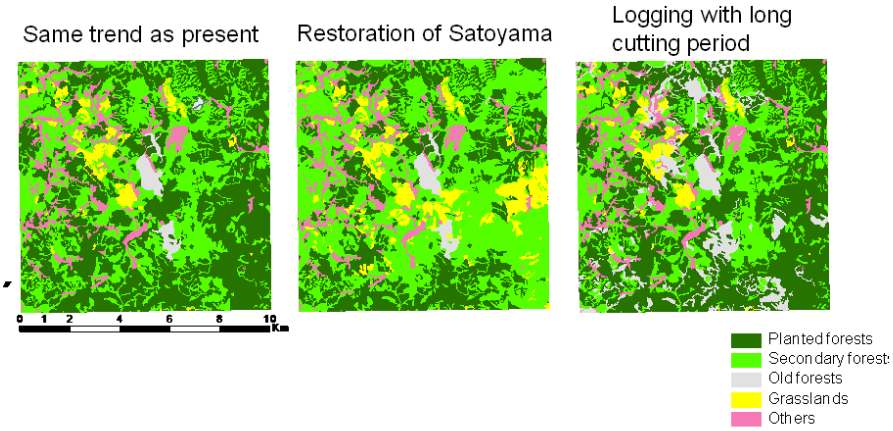

Figure 4 Projections of land use in 2017 under three scenarios in Abukuma (Miyamoto et al. unpubl.).

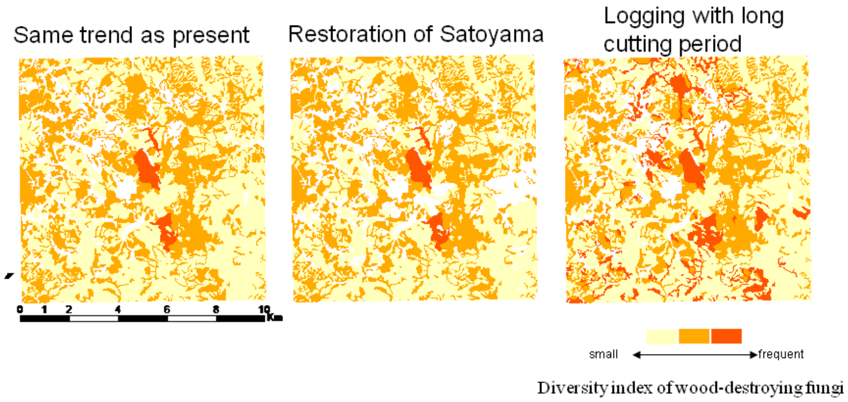

Figure 5 Projections of an ecological function in 2017 under three scenarios in Abukuma (Miyamoto et al. unpubl.).

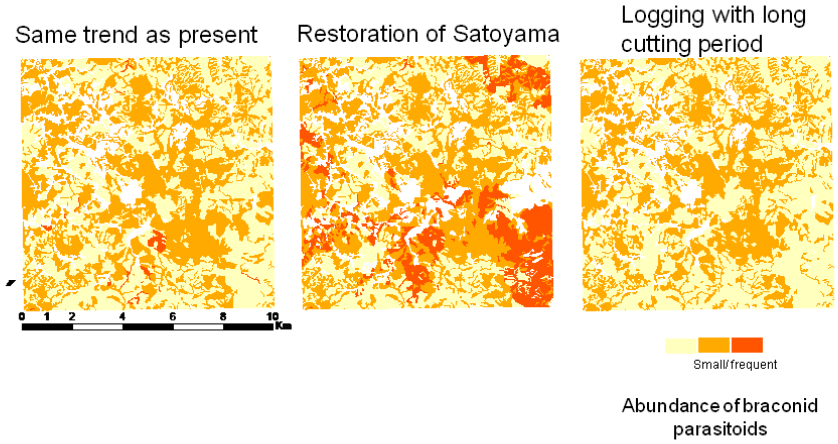

Figure 6 Projections of an ecological service in 2017 under three scenarios in Abukuma (Miyamoto et al. unpubl.).

6.3. Evaluation of institutions for sustainable use

In the rest of the chapter, we describe the final two steps of the assessment. It is necessary to evaluate existing institutions to understand a region’s sustainable use of forests. As we use it, the word “institution” covers a wide range, from local to global. Institutions, in this sense, include unwritten and written rules of local communities, regional or national laws, trading mechanisms, international conventions, and ways of thinking.

Our evaluation of the institutions had two stages: one was to evaluate an institution’s goals and expected effects, and the other was to evaluate its effectiveness in reaching those outcomes.

6.3.1. The aims of the institutions

The definitions of sustainability vary greatly, sometimes depending on what kinds of ecosystem services the stakeholders want to maximize. Considering both past published research and that presented in this volume, we used the following criteria to evaluate the aims or expected effects of institutions. Because the types of ecosystem services are sometimes not consistently described within an institution, we classified the ecosystem services into roughly three types (timber, food, and Non-Timber Forest Products (NTFPs)), according to the Millennium Ecosystem Assessment (2005). Each institution was first evaluated on the basis of whether it includes the following aims.

1. *Provisioning services*: Does the institution aim to sustain provisioning services, such as timber, foods, and NTFPs?
2. *Regulating services*: Does the institution aim to preserve regulating services, such as water quality, soil conservation, pest control, and pollination?
3. *Cultural services*: Does the institution aim to preserve cultural services, such as spiritual, educational, and artistic benefits from the ecosystem?
4. *Un-substitutable resource conservation*: Does the institution aim to avoid the exhaustion of resources for which there is no substitute (i.e., strong sustainability and pre-cautious principle)?
5. *Geographical evenness*: Does the institution aim to share the benefits in a geographically “even”, that is, fair way (e.g., benefits are not biased towards only developed countries)?
6. *Evenness beyond generations*: Does the institution aim to keep an even share of benefits for future generations (*sensu* G.H. Brundtland)?

From the perspectives of sustainable use and conservation of biodiversity, we also propose the following criteria.

7. *Genetic diversity*: Does the institution aim to preserve genetic diversity of the resource species or target ecosystem?
8. *Stable species composition*: Does the institution aim to preserve a stable species composition?
9. *Stable ecosystem*: Does the institution aim to preserve stable ecosystem functions (even if the species composition does change)?
10. *Biological uniqueness and rarity*: Does the institution aim to conserve rare or regionally unique species or ecosystems?

6.3.2. Effectiveness of institutions

Some institutions operate more effectively than others, irrespective of their aims. We had intensive discussions among the project members about the effectiveness of institutions and what factors actually determine effectiveness. Based on these discussions, we first evaluated whether an institution worked effectively or not. We then examined the institutions to identify the key criteria for effectiveness. These criteria are summarized below:

1. *Distinctiveness of rights*: Resource sustainability can be lost if the rights to use the resources are not clearly defined. For example, a governor may sell the right to log a tropical forest to an outside entity even though local residents insist on their traditional right to use the forest.
2. *Incentives for governors or managers*: Some institutions are not effective because the people who run the institutions do not have appropriate incentives to maintain the institutions.
3. *Incentives for users*: Some institutions do not work effectively because the users—the people who receive the ecosystem services—do not have any incentive to maintain sustainability.
4. *Punishment*: It is likely that some institutions operate more effectively because they punish people who do not follow the rules.
5. *Mismatched scales*: In some cases, the ecosystem service users are local in scale, whereas those who create the rules or manage the system are from a larger-scale institution (e.g., a government or international agency). Sometimes, the people who pay for the ecosystem services are not exactly the same as users. Ecosystem services may be received globally, but only local residents pay the social costs to keep the ecosystems functioning in a sustainable manner. Such mismatches in spatial scale among the users, managers, and payers lead to ineffective institutions.

6.3.3. Evaluation of the existing institutions

We evaluated 64 existing institutions (Table 1), which were classified as public institutions and policies; international aids; activities by citizens, enterprises, or NPOs; ranking; and thought. Each institution was evaluated based on the 10 criteria of aims and 5 criteria of effectiveness, as well as based on effectiveness itself.

Several general trends can be seen from our evaluation. Some international conventions related to biodiversity (e.g., Convention on Biological Diversity (CBD)) show rather comprehensive coverage of aims, but they are not very effective. Institutions for assigned geographic areas (e.g., national parks and forest reserves) tend to cover the biodiversity aims and many criteria of sustainable forest use, but not provisioning services. The institutions that have aims in sustainable provisioning services usually do not meet the biodiversity criteria. Many institutions at the community level do not include the biodiversity criteria.

In terms of effectiveness, general trends can also be seen. The effective institutions have clearly defined distinct rights. Many effective institutions have high incentives for governors and use punishment. The users, managers, and cost payers of effective institutions tend to be on the same scale, and most of the effective institutions are local or regional in scale. We did not find global institutions with high levels of effectiveness.

6.4. Assessment application

We applied our assessment to the four project sites. First, we summarized each area’s problems concerning sustainability of forest use and biodiversity and examined the natural, social, economic, and cultural environments at each site (Table 2). We then extracted the key issues for sustainable forest use for each site, and we evaluated the aims and effectiveness of the existing institutions at each site (Table 3). Finally, we made recommendations to solve the key problems.

6.4.1. Abukuma Mountains (Japan)

<History>

The site includes large National Forest areas. From the time of the Tokugawa administration until the 1960s, horses for military use were produced in grasslands in this area. National Forest policy then shifted, and coniferous plantations increased while grasslands and natural forests rapidly decreased. At the same time, the fragmented natural forest was designated as either a Forest Preservation Area or Protected Area of the Prefecture. Secondary forests around residential areas had been managed for fuel production with the collaboration of the local community and National Forest managers. As fuel demand decreased, the timber from secondary forests has been used for mushroom production. Common grasslands existed until the 1990s, but they have since been divided into privately owned plots.

<Key issues >

Protected natural forests play an important role as habitat for locally unique or rare plants and animals. The recent decrease in coniferous forests has made it difficult to manage plantation forestry in a sustainable way. Secondary forests are important for the conservation of local flora and fauna, but successful collaboration is required between the local community and National Forest managers.

<Evaluation >

Although the area has been extremely fragmented, the natural forests are well protected. Since the Natural Forest covers a large area, its policies have significant influence on forest management, including on private secondary forests. The present system, however, does not work effectively except for provisioning services (timber). The manager’s incentives are low. Cultural services and biodiversity conservation are generally not included or effectively managed in the traditional agroforestry management system (Satoyama). Traditional community management, which had been at least partly effective, is no longer used because there are few user incentives.

<Recommendations>

Increasing the sustainability and biodiversity conservation of coniferous plantations and secondary forests must be prioritized. The incentives of resource users in both the plantations and secondary forests must be increased. Recently, subsidies have been offered for sustainable forestry and environmentally conscious agriculture, but the effectiveness of these programs is not yet clear.

6.4.2. Yaku Island (Japan)

<History>

National Forest policies for Yaku Island have caused natural forests to decrease greatly while, at the same time (1960 to 1970), coniferous plantations increased rapidly. Secondary broadleaf forests, which had provided fuel, were commonly used by local communities with the consultation of the National Forest. These secondary forests were also converted into coniferous plantations, and such collaboration between the National Forest and the local communities diminished. During 1950s and 1960s, old *Cryptomeria* trees were designated as Natural Monuments and parts of the island was designated as a National Park. The people who immigrated to the island played an important role in the nature conservation movement. After Yaku Island was designated as a World Heritage Site in 1992, tourism (including ecotourism) became increasingly popular, but there has been some overuse of parts of the ecosystem. The amount of agricultural damage caused by wild monkeys and deer has recently become a serious problem.

<Key issues >

It is important to protect natural forests for their ecosystem services, as well as for ecotourism. *Cryptomeria* trees (including old-growth trees) should be managed in a sustainable way both for resources and for ecotourism. Secondary broadleaf forests play an important role in maintaining biodiversity around residential areas, although they seem to be unused. The agricultural damage caused by wild animals should be solved.

<Evaluation >

Because areas in the central part of the island are designated as either National Park or as a World Heritage Site, or are protected by other institutions, the forest ecosystems and biodiversity are sustainably used, primarily for tourism. However, overuse and an uneven distribution of the benefits from ecotourism have become problems in some areas. The local and social costs associated with regulation are increasing. A scale mismatch is one of the causes of these problems. Old-growth *Cryptomeria* wood is no longer available, and wood harvested from plantations does not have the same value. The timber value of the island's forests is lower than that of other regions in Japan, which reduces incentives for the plantation owners. The local community has also lost the incentive to manage the secondary broadleaf forests because the wood is no longer used as fuel, and many of these forests have been converted into plantations. This has led to a loss of biodiversity and local culture, but ecotourism has started to utilize some secondary forests. The rapid increase in plantations combined with the decrease in broadleaf forest seems to be one of the reasons for the increased amount of agricultural damage caused by wild mammals. Increasing the amount of broadleaf forest is considered to be a measure that could solve this problem, but effective institutions would have to promote this. Many scientific studies have been conducted on this island, and they have played roles in enhancing the recognition of ecosystem services and incentives for the sustainable use of forest ecosystems and biodiversity.

<Recommendations>

Institutions need to enhance incentives for managers and users of secondary forests and plantations. An example of a possible solution is promoting the use of forest products using World Heritage brands. Filling the scale gaps between users and cost payers, such as instituting an island entrance fee, could improve the overuse situation. Subsidies for sustainable forestry or environmentally conscious agricultural practices may increase the incentives of users, but their effectiveness has not yet been evaluated.

6.4.3. Kinabaru and Deramakot, Sabah (Malaysia)

<History>

The area around Kinabaru Mountain was protected as both a National Park and a World Heritage Site. Because of the cool climate, some areas have also been developed for intensive vegetable cultivation. In addition, golf course, sericulture, and tourism have also been developing in this area, all of which act to reduce the area of primary mountain forests near the border of the National Park.

In the Deramakot area, commercial logging has been intensively conducted since the 1970s, and few primary forests remain. A reduced-impact logging system was introduced in the late 1980s, and the area received certification from the Forest Stewardship Council (FSC) in 1997.

<Key issues >

The primeval mountain forest around Kinabaru is valuable for ecosystem services in this region, including ecotourism and local culture. The balance between natural forest conservation and agricultural development is the key issue. An evaluation of the reduced-impact logging system in terms of biodiversity is necessary in the Deramakot area.

<Evaluation >

The World Heritage Site and National Park have operated to maintain incentives for both local residents and the local government by providing benefits through ecotourism. Local environmental education has been effective in enhancing the recognition of the importance of ecosystem services and forest conservation. Overuse has recently become an issue. Agricultural development around Kinabaru National Park has been rapid, and there are few effective institutions to regulate the cultural ecosystem services and biodiversity.

The government leased the land for reduced-impact logging with a 90-year contract, and this long-term contract enhanced the users' incentives for sustainably using the forests. Certification by the FSC requires a dialog with local residents; thus, it has played a role in enhancing incentives for geographical evenness.

<Recommendations>

Economic and institutional regulations are necessary to avoid overuse in Kinabaru National Park. Incentives must be provided to local residents to avoid further development around the park. Bringing local culture and products into the ecotourism scheme is a possible way to provide incentives. Reduced-impact logging in Deramakot remains an issue that has local social impacts.

6.4.4. Lambir Hills, Sarawak (Malaysia)

<History>

The Lambir Hills area was covered by primeval forests until the early 1900s. When the Iban colonized the area, they began to convert the forested areas to agricultural production. Some economic activities, such as commercial logging, rubber production, and commercial rice production, have caused rapid changes in land use. The lands owned by the Sarawak State have been rapidly and intensively converted into oil palm plantations since the late 1970s. Commercial logging was started in 1960s and became rapid in 1970 and 1980s. A 7000-ha area was designated as National Park in 1974.

<Key issues >

The forest in the National Park is a valuable remnant of the natural forests in this region, but the area is too small for animals with large home ranges. Traditional land uses, which now depend on the natural recovery of secondary forests, have declined recently. Commercial logging is still conducted, but some sustainable management practices have been introduced. The increase in oil palm plantations has caused a rapid decrease in biodiversity.

<Evaluation >

Rights are relatively clearly defined through both National Park policy and land ownership in this region.

The National Park system lacks local incentives, but frequent patrols and punishment of violators of the rules ensures some protection. Illegal logging and hunting still occur in the park, but these activities are small in scale. The lack of incentives for local residents to continue the traditional agroforestry system has led to an increased amount of land being converted into oil palm plantations. This may lead to a rapid loss in sustainability and biodiversity. NGOs have worked to increase local incentives for provisioning NTFPs and cultural services.

<Recommendations>

Traditional land uses are not very effective in maintaining biodiversity, but they are much better than the large-scale development of oil palm plantations. A combination of traditional land uses and National Park management may be more effective. That, however, would require incentives for local people to keep traditional land uses. Eco- and/or cultural tourism, which have recently been introduced in other regions of Sarawak, may provide such incentives. Domestic certification of sustainable forest management has also been recently introduced, but it is not as effective in maintaining sustainability as the FSC system. The geographical evenness of oil palm plantations and commercial logging need to be regulated.

6.5. Further development of the assessment system

Our proposed assessment system has several implications. First, the historical analysis provides useful information for evaluating future options. It is necessary to identify and quantify the driving forces responsible for forest change to project the consequences of future changes under the given scenarios. An algorithm to detect the effect of such changes in forest use on biodiversity and ecosystem functions was also developed in this project. The maps that show historical changes in biodiversity allowed us to evaluate what past forest changes have meant in terms of biodiversity and sustainability.

The evaluation methods for ecosystem services associated with biodiversity are vague and difficult to include in the assessment. However, the methods used in this project have shown some promise, especially through the use of spatial maps. Thus, through the use of scenarios of future land use or forest policy, it will be possible to present options to decision- makers.

Some new institutions may need to be introduced to ensure sustainability and biodiversity. In this case, the system of evaluating existing institutions explained in this chapter could be a useful tool. In the discussion up to now, partly because of the variety in definitions of sustainability, ecosystem services and the aspects of sustainability that an institution aims to maintain have not been clear. The first step of the evaluation is to clearly define the ecosystem services and institutional aims.

We also evaluated the effectiveness of institutions. We may be able to improve the effectiveness of existing institutions by identifying current problems and discuss the possibility of introducing new institutions as needed. Our system enables us to identify what institutions fit a given situation in the target region.

However, there are still several issues that require further development. First, we need to develop methods of quantifying the driving forces that are responsible for forest change in more detail. Otherwise, the projections developed will not be useful enough. We also need to develop good indicators for some ecosystem functions or services. If we succeed in finding such indicators, the options presented in our projections will be more informative. In particular, the evaluation of ecosystem services requires intensive study. The present knowledge of the types of ecosystem services associating with biodiversity is still limited. The evaluation of institutions for sustainable use also remains under discussion. The effectiveness of these institutions varies among regions, natural conditions, traditional cultures, and schools of thought. Detecting the causes of such variation is another challenge.

The system we have proposed is a starting point to develop assessment methods, and there is still a rather long way to go for the practical application of such methods. However, we think that the framework to approach such an assessment method has been made clear.

Reference

Millennium Ecosystem Assessment (2005) Ecosystem & Human Well-being. Island Press: Washington D.C.

Table 1 Evaluation of existing institutions for forest uses and biodiversity

Classification	Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
								Biodiversity conservation												
		Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
public institutions and policies	Protected area		○	○	○		○	○	○	○	○	○	○	○	○	○	R/G	L/R/G	L/R	
public institutions and policies	MAB Plan		○	○	○		○	○	○	○	○	○					R	L/R/G	L/R	
public institutions and policies	National Parks in Japan		○	○	○		○	○	○	○	○	○	○	○		○	L/R	L/R/G	R	
public institutions and policies	National Parks in Thailand		○	○	○		○	○	○	○	○			○		○	L/R	L/R/G	L/R	
public institutions and policies	National Parks in Sabah		○	○	○		○	○	○	○	○	○		○	(○)	○	L/R	L/R/G	L/R	There are both successful and unsuccessful cases using incentives.
public institutions and policies	National Parks in Indonesia		○	○	○		○	○	○	○	○					(○)	L/R	L/R/G	L/R	
public institutions and policies	Protected forest by Forest Agency of Japan		○	○	○		○	○	○	○	○	○	○				R	L/R	R	
public institutions and policies	Ideal National Park						○					○	○	○	○	○		L/R/G	L/R/G	How incentives are given to forest managers and users should be examined.
public institutions and policies	World Heritage			○	○		○				○	○	(○)	○	(○)	○	L/R	L/R/G	L/R/ (G)	Management is done by each national law and regulation, so vary depending on nations
public institutions and policies	Ramsar Convention						○	○		○	○	(○)		○			L/R/G	L/R/G	L/R/G	The areas are designated where proper regulations are established.
public institutions and policies	Bonn Convention						○	○		○	○	(○)		○			L/R/G	L/R/G	L/R/G	
public institutions and policies	Natural Treasure (place)			○	○		○				○	○	○	○	(○)	○	L/R	L/R	L/R	Effectiveness varies depending on region.

Classification	Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
								Biodiversity conservation												
		Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
public institutions and policies	Satoyama conservation areas	○	○	○			○				○	?	○	○	○		L	L/R	L/R	Not effective without subsidies.
public institutions and policies	Subsidies to lower mountainous regions	○	○	○				○		○		?	○	○	○		L	L/R	L/R	Effectiveness is not yet known because the system has just started.
public institutions and policies	Prevention of intrusion of exotic species	○	○	○	○		○	○	○	○	○	○	—	○		○	L/R	L/R	L/R	Conflicts among users exist.
public institutions and policies	Urging natural rehabilitation		○	○			○			○	○	?	○	○	○		L/R	L/R	L/R	Effectiveness is not yet known because the system has just started.
public institutions and policies	Natural Treasure (species)			○	○		○		○		○	○	○	○		○	L/R	L/R	R	
public institutions and policies	Species protection				○		○	○	○		○	○	○	(○)		○	L/R	L/R	L/R	
public institutions and policies	Environmental impact assessment		○	○	○		○	○		○	○	○	○	○		○	L/R	L/R	L/R	
public institutions and policies	Washington Convention				○		○				○	(○)	○	○		○	R/G	G	L/R	Effectiveness varies depending on black markets and characteristics of species.
public institutions and policies	Gene bank	○			○		○		○			○		○			R/G	R/G	R/G	Not costly.
public institutions and policies	Seed bank	○			○		○	○	○		○	○		○			R/G	R/G	R/G	
public institutions and policies	Cartagena Protocol on Biosafety						○	○	○	○		○	○	○		○	R/G	R	R	Conflicts among users and managers exist.
public institutions and policies	Regulation of exceptions by the WTO												○				G	R/G	G	Effectiveness varies depending on the exceptions.
public institutions and policies	Environmental impact assessment (EIA) of FTA		○	○									○				R	R	R	Effectiveness varies depending on conditions.

Classification	Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
								Biodiversity conservation												
		Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
public institutions and policies	Kyoto Protocol		○			○	○					(○)	○	(○)	(○)	○	R/G	G	L/R/G	The U.S. has not ratified it. China and India are included in the group of developing countries. There is no consideration of the present forest
public institutions and policies	Biodiversity convention	○	○	○	○	○	○	○	○	○	○	?	○	○			L/R/G	L/R/G	R/G	
public institutions and policies	UN Forestry Forum	○	○	○	○	○	○	○	○	○	○						-	-	-	It has not become a treaty because of conflicts among nations.
public institutions and policies	Criteria and agreement on sustainable forest management	○	○	○	○	○	○	○	○	○	○		○	○			L/R/G	L/R/G	L/R	
public institutions and policies	Forest environmental tax (Japan)	○	○			○				○		(○)	○	○		(○)	L/R	L/R	L/R	The tax will be used to increase ecological services. People who do not manage forests will also gain benefits.
public institutions and policies	Regional environmental tax											○	○	○	(○)	○	L/R	L/R	L/R	The tax will be established at the local government level. Effectiveness varies depending on objects to use.
public institutions and policies	Subsidy for thinning forests	○	○									○	○	○	○		L/R	L/R	L/R	
public institutions and policies	Subsidy for local products and local consumption	○	○	○								○	○	○	○		L	L	L	Scale is small. Motivation of participants should be high. It aims for productive forests.
public institutions and policies	ISO 14001		○									○	○	○	○	○	L	L/R	L	Sustainable forest use and biodiversity conservation are out of scope.
public institutions and policies	Law on promoting green purchasing		○									○	○	○			L/R	L/R	L/R	Sustainable forest use and biodiversity conservation are out of scope.
public institutions and policies	Green owner system	○	○			○						(○)	○	○	○		L/R	L/R	L/R	Not effective after the price of wood declined.
public institutions and policies	Environmental achievement awards											○	—	○	○		-	-	-	Effectiveness varies depending on the award.
public institutions and policies	Environmental education											○	—	○	○		-	-	-	Incentives of users should be increased.

Classification	Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
		Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Biodiversity conservation					Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
								Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity									
public institutions and policies	Carbon fund for community development		○			○	○						○	○	○		L/R	G	R/G	It must consider biodiversity. Leakage is possible.
	Academic research											(○)	—	○	○		-	-	-	Effectiveness varies depending on user's incentive.
activities by citizens	Eco-tourism			○	○	○	○				○	(○)	○	○	○		L	L/R/G	L/R/G	The number of users varies depending on the location and facilities.
activities by citizens	Green tourism	○		○		○						(○)	○	○	○		L	L/R	L/R	Cultural resources and facilities are important for success.
activities by citizens	National trust		○	○	○		○	○		○	○	(○)	○	○	○		L	L/R	L/R	Successful collection of funds depends on the site.
activities by citizens	Community forestry, CBM	○	○	○		○	○					(○)	○	○	○	(○)	L/R	L/R/G	L/R/G	Social capital of communities is important.
activities by citizens	Iriai forest management	○	○	○			○					(○)	○	○	○	○	L	L	L	This is the strictest institution, including punishments, in CBM.
activities by citizens	Local objections to forest development	○	○	○	○	○	○	○				(○)		○	○		L	L	L	It is not clear who has the initiative of the objection movement.
activities by citizens	Regional monetary											(○)	○	○	(○)		L	L	L	Effectiveness varies depending on monetary. Product distribution is important to increase users' motivation.
activities by enterprises	CSR																			Companies must be motivated (e.g., by an increased bank rating or improved stock price) as a result of the CSR.
international aid	Establishment of national parks		○	○	○			○	○	○	○	(○)	—	(○)	(○)		R/G	R	R/G	Although incentives for the aid exist, there is little incentive for environmental conservation. Incentives for users are important. Effectiveness varies depending on social conditions. Period of
international aid	Afforestation	○	○									(○)	—	(○)	(○)		R/G	L/R	R/G	
international aid	Assistance for CBM	○	○	○		○						(○)	—	(○)	(○)		L/R/G	L/R	L/R/G	

Classification	Institution	Sustainable forest use										Factors relevant to effectiveness								Comments
								Biodiversity conservation												
		Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity	Effectiveness of institutions	Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
international aid	Academic cooperation	○	○	○	○			○	○	○	○	(○)	—	(○)	(○)		R/G	R	R/G	implementation is usually short.
international aid	Cooperation for sustainable forest management	○	○	○	○	○		○	○	○	○	(○)	—	(○)	(○)		L/R/G	L/R/G	L/R/G	
NPOs	Fair trade	○		○		○						○	○	○	○		L	L	L	This institution works effectively only at a small scale.
NPOs	Forest certification	○	○	○	○	○	○	○	○	○	○	○	○	○	(○)	○	L/R	L/R/G	L/R	
NPOs	Objections to loss of forest	○	○	○	○	○	○	○	○	○	○	(○)		○			R/G	L/R/G	R/G	Effectiveness depends on the NPO's capacity
ranking	RDB (Red Data Book)				○		○				○			(○)						Managers are motivated to conserve the area.
ranking	Biodiversity hot spot				○		○				○									Managers are motivated to conserve the area.
thought	Precautionary principal				○		○				○									
thought	Adaptive management	○	○							○										
thought	Social capital	○	○																	
thought	Deep ecology			○			○	○			○									
thought	Access to and sharing the benefits of gene resources	○				○	○													

Remarks） L: village or town level; R: district, state, or national level; G: global level.

2. (○) indicates that the level of effectiveness varies depending on local conditions

Table 2 Characteristics of natural, social, and cultural conditions at the four study sites

Characteristics	Abukuma	Yakushima	Lambir	Sabah	
				Kinabaru	Deramacot
Problems concerning sustainable use of forest and biodiversity	In the Edo era, forests decreased and grassland increased. In the past 100 years, planted coniferous forests have increased drastically.	Loss of primary forests and increase of coniferous forests during the 1960s and 1970s. Nature protection movement in the 1970s. Overuse of natural resources as ecotourism prospers. Agricultural damage by monkeys and deer.	Primary forests have decreased in the past 100 years. Commercial logging from the 1960s and oil palm plantation development from the 1980s have had large effects on the forests. Indigenous people have cut primary forests and created a mosaic landscape with swidden rice fields and fallow forests.	Forests have been conserved since the establishment of the state park in 1964. Farmland near the park has been developed. Golf courses and tourism development have also progressed. Primary forests near the park are facing development pressure.	Since the 1970s, especially in the 1980s, commercial logging was active and most primary forests have disappeared. In the late 1980s, logging was banned and the forest was managed with international aid from GTZ. In 1997, the area was certificated by the FCS.
1. Natural Environment and Land Use					
Climate and vegetation	Temperate deciduous forest.	Warm-temperate rain forest.	Tropical rain forest.	Tropical mountain forest.	Tropical rain forest.
Forest and land use	Reserved forest, “Satoyama” system, natural regeneration practices, man-made forest, and pasture.	Reserved forests, ecotourism, common forests, and man-made forest.	Reserved forests, ecotourism, commercial logging, traditional and modern shifting cultivation, and oil palm plantations.	Reserved forests, ecotourism, commercial logging, man-made forest, and vegetable cultivation.	Commercial logging, forest certification, and low-impact logging.
Characteristics of biodiversity	Logged area up to primary forest. There are no bears and deer.	Relatively high in primary and secondary forests.	Very high in primary forests.	Very high. Fauna and flora varies with altitude.	Same fauna and flora as in mixed dipterocarp forests.
Land use changes	Primary forests, secondary forests, grassland, and man-made forest	See the changes listed in (1).	Primary forests have been converted to swidden fields, logged areas, plantations, and urban areas.	See the changes listed in (1).	See the changes listed in (1).
2. Social Environment					
Effectiveness of regulations on forest conservation	Relatively high.	Relatively high.	Relatively high as compared with neighboring countries.	Relatively high as compared with neighboring countries.	Relatively high as compared with neighboring countries.
Government organizations concerning policy, forests, and land use	Government, Ministry of Agriculture, Forestry and Fishery, Forestry Agency, and national forest.	Forestry agency, ministry of environment, and cultural affairs agency.	State government (forestry department and ministry for land development).	State government (Sabah Park).	State government (forestry department).
Policy and institutions on forest development	Forest Law, Forestry Basic Law, and prefectural park.	Transferred to national forest category (1889), national forest management plan (1923), and large-scale afforestation (1960s).	Forestry regulations, commercial logging system, national park law, land calcifications and NRC, and a license required for plantation development.	Commercial logging can be practiced in the part of the forest designated as a Class II Commercial Forest Reserve.	Commercial logging can be practiced in the part of the forest designated as a Class II Commercial Forest Reserve.
Policy and institutions on forest conservation	Protected forests, conserved forests, and prefectural parks.	The Yaku-sugi primary forest was designated as a National Treasure (1924) and a National Park (1964), and was an original nature conservation area. Construction of the west forest road was stopped (1999).	National park, protection of indigenous territory, and no ecotourism.	State park and World Heritage Site (2001).	Forest certification (FSC).
Effectiveness of policies	High.	High.	Relatively high as compared with neighboring countries.	Relatively high as compared with neighboring countries.	Relatively high as compared with neighboring countries.
NPOs practice forest conservation	Not very active.	Important for forest conservation.	Not active as compared with neighboring countries.	No activity.	Forest certification (FSC).
Local forest uses	Employment, grazing, and NFTP use.	Iriai system and cooperative management in coniferous plantations were seen before.	On land with native rights, the land can be used freely. On state land, land use has drastically changed.	The protected area cannot be used. Indigenous people have the right to use land around the park. In a part of these areas, forests are protected for water conservation, and sustainable timber production is observed there.	For forest certification, local use of the forest must be monitored. Local people must be employed for forest management. Traditional land use is allowed in a part of the territory.

Characteristics	Abukuma	Yakushima	Lambir	Sabah	
				Kinabaru	Deramacot
Social problems in rural areas	Depopulation and aging.	Depopulation of villages accelerated in the 1960s, but it stopped during the 1990s.	Depopulation is progressing in the middle and upper parts of the river basin.	Agricultural land has decreased as the population has increased.	Logging is the only way to earn money.
3. Economic Environment					
Forest resources and global economy	Economic growth in Japan and increase of planted coniferous forests following afforestation policy.	Coniferous afforestation was a failure due a changing global economy after the 1970s.	Forest uses, such as commercial logging and plantation development, have drastically changed as the global economy has changed.	Land use out of the park has changed following global economic conditions.	Forest resources have largely decreased because of a large global demand for timber.
Forest resources and national economy	Low price of pulp and timber.	Same as above	Government drives forest development policies relating to the global economy.	Government drives forest development policies relating to the global economy.	Unbalanced government budget between federal and state. The state budget depends heavily on natural resources.
Forest resources and enterprises	Retreatment of pulp company, and then ingress of lumber company.	Pulp industry logged broadleaf forests.	Private companies developed forests for commercial logging and plantation development following global economic trends.	Private companies developed forests for commercial logging and plantation development following global economic trends.	Forests were logged by companies that had concessions with short periods.
Forest resources and regional economy	Forest uses have changed as follw: 1. grazing, 2. carbon making, 3 .pulp tip and 4. mushroom cultivation	The timber industry was previously the main industry, but tourism currently is.	Rubber and pepper are widely cultivated as cash crops.	Primary forests and biodiversity are observed as sustainable resources. A large amount of income is derived from park entrance fees.	About 70% of state government income was generated from the forest industry in the 1980s.
Forest resources and rural economy	Local people were previously employed as workers in national forests. Today, forest cooperation only works. Wood for mushroom	Same as above.	Wage work at logging camps. Rice production for workers in logging camps.	Many villagers are employed as rangers and workers for the park. Many villagers also work for the tourism industry.	Local people are employed for afforestation work in sustainable forestry management.
4. Cultural Environment					
Ethnicity	Japanese, who immigrated after World War II.	Original inhabitants and immigrants (such as for tourist guides).	Iban (indigenous people), Chinese, and mixed-race people (Malay and Iban) living in urban areas.	Dusun (indigenous people).	Orang Sungai (indigenous people).
Local forest uses	Collection of mushrooms, edible fungi, and fallen leaves as fertilizer. Wood for mushroom cultivation.	No current traditional uses. Current forest products are used for souvenirs and firewood for drying mackerel. Houses are built using Sugi wood.	Forest resources are still used, although it has declined. Swidden agriculture is still important. Hunting, fishing, and collecting forest products are important.	Forest uses are declining, although local people still practice hunting and collect forest products. Sawmills produce wood for construction of houses.	Collected forest products and fish from nearby rivers for self-consumption are still very important.
Spiritual relationship between local people and the forests	Almost none.	Local people still spiritually depend on the forests. There are rituals concerning forest spirits.	The existence of forests is connected with agricultural rituals and the value of life and death.	Kinabaru Mountain was formerly a sacred place. The influences of Christianity and modernism have reduced such recognition.	Forests were strongly connected to ritual practices and spiritual values.
Forest management at the community level	Wood for mushroom cultivation is from national forests. Thinning is practiced in parts of private forests. Grasslands were previously managed as common land, but they are now owned privately. Foresters formerly lived near villages, and opinions from villagers were given to the officers.	Forests were managed cooperatively in common forests and in private forests.	There are no strong institutions, but there are informal rules, which change depending on prevailing social and economic conditions.	There is a common forest, which serves as a water supply, and the timber is sustainably produced there.	There is a 15-ha community forest in the reserve, and traditional forest uses by five villages are allowed there. Forest uses in the other areas are not allowed.

Table 3 (1) Evaluation of institutions for sustainable forest use and biodiversity (Abukuma)

Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
	Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Biodiversity conservation					Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
							Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity									
Protected forest by Forest Agency of Japan		○	○	○		○	○	○	○	○	○	○		(○)	○	R	L/R	R	
National Forest Management Plan	○	○					(○)	(○)	(○)	(○)	(○)	○	(○)			L/R	L/R	R	Bureaucratic organization is not effective. Managers' incentives vary depending on whether the forest is productive or non-productive.
Community forestry, CBM	(○)	(○)	(○)		(○)	(○)					(○)	○	(○)	(○)	(○)	L	L	L	Management is loosely cooperative. Depopulation and aging in the community are serious problems.
Forest uses in the Satomi community	(○)	(○)	(○)		(○)						(○)	○	(○)	(○)		L	L	L	Villagers hope that some areas become artificial forests.
The prefectural park is designated as an RDB				○		○				○	(○)		○						
Iriai forest management	(○)					(○)					(○)	(○)			(○)	L	L	L	The area previously had commonly owned Iriai grasslands, but they have been divided into privately owned plots in the past 10 years.
Academic research	○	○		○			○	○	○	○	(○)	–	○	○		-	-	-	Effectiveness varies depending on users' needs.

Remarks) L: village or town level; R: district, state, or national level; G: global level.

2. (○) indicates that the level of effectiveness varies depending on local conditions

Table 3 (2) Evaluation of institutions on sustainable forest uses and biodiversity (Yakushima)

Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
							Biodiversity conservation												
	Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
National park		○	○	○		○	○	○	○	○	○	○	○		○	L/R	L/R/G	R	
National Forest Management Plan		○	○	○		○	○	○	○	○	○	○				R	L/R	R	
World Heritage			○	○		○				○	○	(○)	○	○	○	L/R	L/R/G	L/R	
Ramsar Convention						○	○		○	○	(○)		○			L/R/G	L/R/G	L/R/G	
Natural Treasure (place)			○	○		○				○	○	○	○	(○)	○	L/R	L/R	L/R	
Biodiversity hot spot				○		○				○									
Prevention of intrusion of exotic species	○	○	○	○		○	○	○	○	○	○	–	○		○	L/R	L/R	L/R	
Natural Treasure (species)			○	○		○		○		○	○	○	○		○	L/R	L/R	R	
Act of species protection				○		○	○	○		○	○	○	(○)		○	L/R	L/R	L/R	
Eco-tourism			○	○	○	○				○	(○)	○	○	○		L	L/R/G	L/R/G	
Satoyama conservation areas	○	○	○			○				○	?	○	(○)	(○)		L	L/R	L/R	The effectiveness is not yet known because the system has just begun.
Subsidies to lower mountainous regions	○	○	○				○		○		?	○	(○)	(○)		L	L/R	L/R	The effectiveness is not yet known because the system has just begun.
NPO objection to forest loss	○	○	○	○	○	○	○	○	○	○	(○)		○	○		R/G	L/R/G	R/G	
Local objection to forest development	○	○	○	○	○	○	○				(○)		○	(○)		L	L	L	
Green tourism	○		○		○						(○)	○	○	○		L	L/R	L/R	
Iriai forest management	○	○	○			○					(○)	○	○	(○)	(○)	L	L	L	The frequency of forest uses has decreased.

Subsidies for thinning	○	○									○	○	○	(○)	(○)	L/R	L/R	L/R	
Subsidies for local products and local consumption	○	○	○								○	○	○	○		L	L	L	
Academic research											(○)	−	○	○		-	-	-	
Environmental education											○	−	○	○		-	-	-	

Remarks） L: village or town level; R: district, state, or national level; G: global level.

2. (○) indicates that the level of effectiveness varies depending on local conditions

Table 3 (3) Evaluation of institutions on sustainable forest uses and biodiversity (Sabah)

Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
							Biodiversity conservation												
	Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
Kinabaru Mountain																			
State park		○	○	○		○	○	○	○	○	○	○	○	○	○	L/R	L/R/G	L/R/G	
Environmental tax (fee for entrance and mountain climbing		○	○	○		○	○	○	○	○	○	○	○		○	L/R	L/R	L/R	The fees are used for park maintenance.
World Heritage			○	○		○	○	○	○	○	○	○	○	○	○	L/R	L/R/G	L/R/G	Since 2000, there has been an overuse problem.
Eco-tourism			○	○	○	○				○	(○)	○	○	○		L	L/R/G	L/R/G	Many tourists are only interested in mountain climbing.
Local environmental education											○	–	○	○		-	-	-	Since the 1980s, educators have stressed that forest protection is important for local residents' livelihood
Community forest management	○	○	○			○					(○)	○	(○)	(○)	○	L	L	L	It works for forest conservation outside of the park and is good for provisioning services
Academic research											○	–	○	○		-	-	-	Research contributed to the designation as a World Heritage Site.
Deramacot																			Productive forest area for timber.
Criteria and agreement for sustainable forest	○	○	○	○	○	○	○	○	○	○		○	○			L/R/G	L/R/G	L/R	
Forest certification (FSC)	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	L/R	L/R/G	L/R	The incentive for sustainable forest management increased as a result of the introduction of a 90-year concession
International aid for sustainable forest uses	○	○	○	○	○		○	○	○	○	○	–	(○)	○		L/R/G	L/R/G	L/R/G	
Local environmental education	○		○								○	–	○	○		-	-	-	It was required for FSC. Some communities do not reside in the productive forest area
Kyoto Protocol		○			○	○					(○)	○	(○)	(○)	○	R/G	L/R/G	L/R/G	FSC forests should be considered under the protoco.
Biodiversity convention	○	○	○	○	○	○	○	○	○	○	?	○	○			L/R/G	L/R/G	R/G	

Remarks） L: village or town level; R: district, state, or national level; G: global level.

2. (○) indicates that the level of effectiveness varies depending on local conditions

Table 3 (4) Evaluation of institutions on sustainable forest uses and biodiversity (Lambir, Sarawak)

Institution	Sustainable forest use										Effectiveness of institutions	Factors relevant to effectiveness							Comments
							Biodiversity conservation												
	Provisioning services	Regulationg services	Cultural services	Un-substitutable resource conservation	Geographilcal evenness	Evenness beyond generations	Genetic diversity	Stable species composition	Stable ecosystem	Biological uniqueness and rarity		Distinctiveness of the right	Incentives for governors and/or managers	Incentives for users	Punishment	Scale of managers	Scale of users	Scale of cost payer	
Lambir National Park		○		○		○	○	○	○	○	○	○	○	(○)	○	R	L/R/G	R	Well managed, although small-scale illegal logging is sometimes done.
Biodiversity hot spot				○		○				○									
Species conservation law				○		○	○	○		○	(○)	○	○		○	L/R	L/R	L/R	
Washington Convention				○		○				○	○	(○)	○		○	R/G	G	L/R	
Eco-tourism			○	○	○	○				○		○	○	(○)		L	L/R/G	L/R/G	Just in small scale. Little economic contribution to local communities
NPO objection to logging	○	○	○	○	○	○	○	○	○	○	(○)		○	(○)		R/G	L/R/G	R/G	Not significant around Lambir.
Local objection to logging	○	○	○	○	○	○	○				(○)		○	○		L	L	L	Oil palm plantations are developed around Lambir.
International cooperation for afforestation	○	○									(○)	—	○	(○)		R/G	L/R	R/G	Only a pilot project for small research level.
Environmental education											○	—	○			–	–	–	Small trial only in the park.
Land use by indigenous people	○	○	○		○	○					(○)	○	○	○	(○)	L/R	L/R/G	L/R	Land use is secondary-forest based and in transition.

Remarks） L: village or town level; R: district, state, or national level; G: global level.

2. (○) indicates that the level of effectiveness varies depending on local conditions

Appendix

LIST OF PUBLICATIONS

List of Publications

Original Articles

2002

Aiba S, Kitayama K (2002) Effects of the 1997-98 El Nino drought on rain forests of Mount Kinabalu, Borneo. Journal of Tropical Ecology 18: 215-230

Aiba S, Kitayama K, Repin R (2002) Species composition and species-area relationships of trees in nine permanent plots in altitudinal sequences on different geological substrates of Mount Kinabalu. Sabah Parks Nature Journal 5: 7-69

Fukamachi K, Oku K, Nakashizuka T (2002) The change of Satoyama landscape and its causality in Kamiseya District, Kyoto Prefecture, Japan, between 1970-1995. Landscape Ecology 16: 703-717

Hatada A, Itioka T, Yamaoka R, Itino T (2002) Carbon and nitrogen content of food bodies in three myrmecophytic species of *Macaranga*: implications for antiherbivore defense mechanisms. Journal of Plant Research 115: 179-184

Ichie T, Kitahashi Y, Matsuki S, Maruyama Y, Koike T (2002) The use of a portable non-destructive type nitrogen meter for leaves of woody plants in field studies. Photosynthetica 40: 289-292

Isagi Y, Kenta T, Nakashizuka T (2002) Microsatellite loci for a tropical emergent tree, *Dipterocarpus tempehens* V. Sl (Dipterocarpaceae). Molecular Ecology Notes 2: 12-13

Kitayama K, Aiba S (2002) Control of organic carbon density in vegetation and soil of tropical rain forest ecosystems on Mount Kinabalu. Sabah Parks Nature Journal 5: 71-90

Kitayama K, Aiba S (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. Journal of Ecology 90: 37-51

Matsumoto T, Itioka T, Nishida T (2002) Fitness cost of parasitoid avoidance behavior in the arrowhead scale, *Unaspis yanonensis* Kuwana. Entomologia Experimentalis et Applicata 105: 83-88

Momose K (2002) Environments and people of Sumatran peat swamp forests II: distribution of villages and interactions between people and forests. Southeast Asian Studies 40: 85-107

Momose K (2002) Ecological factors of the recently expanding style of shifting cultivation in Southeast Asian subtropical areas: why fallow periods could be shortened? Southeast Asian Studies 40: 190-199

Momose K, Shimamura T (2002) Environments and people of Sumatran peat swamp forests I: distribution and typology of vegetation. Southeast Asian Studies 40: 72-84

Murase K, Itioka T, Inui Y, Itino T (2002) Species specificity in settling-plant selection by foundress ant queens in *Macaranga–Crematogaster* myrmecophytism in a Bornean dipterocarp forest. Journal of Ethology 20(1): 19-24

Nomura M, Itioka T (2002) Effects of sysnthesized tannin on the growth and survival of a generalist herbivorous insect, the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae). Applied Entomology and Zoology 37: 285-289

Sakai S (2002) General flowering in lowland mixed dipterocarp forests of Southeast Asia. Biological Journal of Linnean Society 75: 233-248

Sakai S (2002) A review of brood-site pollination mutualism: plants providing breeding site for their pollinators. Journal of Plant Research 115: 161-168

Sultana F, Toda MJ, Yafuso M, Lakim MB, Mohamed MB, Cuong NM (2002) A new species-group of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae), with descriptions of two new species from eastern Malaysia and Vietnam. Entomological Science 5: 305-315

Takyu M, Aiba S, Kitayama K (2002) Beta-diversity and changes in population structure along topographical gradients

on different geological substrates in tropical montane forests on Mount Kinabalu. Sabah Parks Nature Journal 5: 165-218

Takyu M, Aiba S, Kitayama K (2002) Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. Plant Ecology 159: 35-49

Tanabe S, Toda MJ, Lakim MB, Mohamed MB (2002) Abundance, biomass, and composition of insect communities in various forests on Mt. Kinabalu. Sabah Parks Nature Journal 5: 219-237

北山兼弘・相場慎一郎・武生雅明（2002）炭素とミネラルのバランスから見た熱帯山地林生態系の長期動態－物質循環における種交代の重要性－．日本生態学会誌　52: 125-129

酒井章子（2002）花の上で繁殖する送粉者．日本生態学会誌　52: 177-187

2003

Agetsuma N, Sugiura H, Hill DA, Agetsuma-Yanagihara Y, Tanaka T (2003) Population density and group composition of Japanese sika deer (*Cervus nippon yakushimae*) in ever-green broad leaved forest of Yakushima, southern Japan. Ecological Research 18: 475-483

Akashi N, Kohyama T, Matsui K (2003) Lateral and vertical crown associations in mixed forests. Ecological Research 18: 455-461

Harrison RD, Hamid AA, Kenta T, LaFrankie J, Lee H-S, Nagamasu H, Nakashizuka T, Palmiotto P (2003) The diversity of hemi-epiphytic figs (*Ficus*; Moraceae) in a Bornean lowland rain forest. Biological Journal of Linnean Society 78: 439-455

Ichikawa M (2003) Shifting swamp rice cultivation with broadcast seeding in Insular Southeast Asia: a survey of its distribution and the natural and social factors influencing its use. Journal of Southeast Asian Studies 41: 239-261

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomological Science 6: 151-163

Itioka T, Yamauti M (2004) Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. Journal of Tropical Ecology 20: 479-482

Kenzo T, Ichie T, Ninomiya I, Koike T (2003) Photosynthetic activity in seed wings of Dipterocarpaceae in a masting year: Does wing photosynthesis contribute to reproduction? Photosynthetica 41: 551-557

Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. J Ecol 91:797-806

Kurokawa H, Yoshida T, Nakamura T, Lai J, Nakashizuka T (2003) The age of tropical rain-forest canopy species, Borneo ironwood (*Eusideroxylon zwageri*), determined by 14C dating. Journal of Tropical Ecology 19: 1-17

Murase K, Itioka T, Nomura M, Yamane Sk (2003) Intraspecific variation in the status of ant symbiosis on a myrmecophyte, *Macaranga bancana*, between primary and secondary forest in Borneo. Population Ecology 45: 221-226

Nagaike T (2003) Edge effects on stand structure and regeneration in a subalpine coniferous forest on Mt. Fuji, Japan, 30 years after road construction. Arctic, Antarctic, and Alpine Research 35: 454-459

Nagaike T, Hayashi A (2003) Bark-stripping by Sika deer (*Cervus nippon*) in *Larix kaempferi* plantations in central Japan. Forest Ecology and Management 175: 563-572

Nagaike T, Hayashi A, Abe M, Arai N (2003) Differences in plant species diversity in *Larix kaempferi* plantations of different ages in central Japan. Forest Ecology and Management 183: 177-193

Nagaike T, Kamitani T, Nakashizuka T (2003) Plant species diversity in abandoned coppice forests in a temperate deciduous forest area of central Japan. Plant Ecology 166: 63-74

Nakagawa M, Itioka T, Momose K, Yumoto T, Komai F, Morimoto K, Jordal BH, Kato M, Kaliang H, Hamid AA, Inoue T, Nakashizuka T (2003) Resource use of insect seed predators during general flowering and seeding

events in a Bornean dipterocarp rainforest. Bulletin of Entomological Research 93: 455-466

Nomiya H, Suzuki W, Kanazashi T, Shibata M, Tanaka H, Nakashizuka T (2003) The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest central Japan. Plant Ecology 164: 263-276

Ozanne CMP, Anhuf D, Boulter SL, Keller M, Kitching RL, Korner C, Meinzer FC, Mitchell AW, Nakashizuka T, Silve Dias PL, Stork NE, Wright SJ, Yoshimura M (2003) Biodiversity meets the atmosphere: a global view of forest canopies. Science 310: 13-186

Sakai S, Nagamasu H (2003) A significant range extension for the monotypic Tamijioideae (Zingiberaceae). Acta Phytotaxonomica et Geobotanica 54: 81-83

Sakai S, Nagamasu H (2003) Systematic studies of Bornean Zingiberaceae IV. Alpinioideae of Lambir Hills, Sarawak. Edinburgh Journal of Botany 60: 181-216

Sato J (2003) Public land for the people: Institutional basis of community forestry in Thailand. Journal of Southeast Asian Studies 32: 329-346

Shinohara W, Takamiya M, Murakami N (2003) Taxonomic study of Japanese *Deparia petersenii* complex (Woodsiaceae) based on cytological and moleculae information. Acta Phytotaxonomica et Geobotanica 54: 137-148

Slik JWF, Poulsen AD, Ashton PS, Cannon CH, Eichhorn KAO, Kartawinata K, Lanniari I, Nagamasu H, Nakagawa M, Nieuwstadt MGLvan, Payne J, Purwaningsih, Saridan A, Sidiyasa K, Verburg RW, Webb CO, Wilkie P (2003) A floristic analysis of the lowland dipterocarp forests of Borneo. Journal of Biogeography 30:1517-1531

Takyu M, Aiba S, Kitayama K (2003) Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. Oecologia 134: 397-404

市川昌広（2003）サラワク州イバン村落の世帯にみる生業選択．Tropics 12：201-219

王培英・百瀬邦泰（2003）太湖沿岸伝統型環境利用与沿岸農村社会的可持続発展．経済地理　2003 年 4 期：524-528

金沢謙太郎（2003）熱帯雨林と生態資源．神戸女学院大学 人間科学研究科紀要ヒューマンサイエンス　6：62-63

神谷大介・森野真理・萩原良巳・内藤正明（2003）屋久島における地域住民の生活の満足感と生息地保全に関する認識構造の分析．ランドスケープ研究 66：775-778

佐藤仁（2003）開発研究における事例分析の意義と特徴．国際開発研究 12：1-15

中静透・斎藤宗勝・松井淳・蒔田明史・神林友広・正木隆・長池卓男・杉田久志・金指達郎・関剛・太田敬之・櫃間岳・八木貴信・橋本徹・酒井暁子・壁谷大介・高田克彦・星崎和彦・丑丸敦史・阿部みどり・大場信太郎・福田貴文・新井伸昌・上迫正人・中健太・市栄智明・鈴木まほろ・乾陽子・中川弥智子・黒川紘子・藤森直美・鮫島弘光・畑田彩・堀真人・沢田信一（2003）白神山地における異なった構造をもつブナ林の動態モニタリング．東北森林学会誌 8：67-74

正木隆・杉田久志・金指達郎・長池卓男・太田敬之・櫃間岳・酒井暁子・新井伸昌・市栄智明・上迫正人・神林友広・畑田彩・松井淳・沢田信一・中静透（2003）東北地方のブナ林天然更新施業地の現状－二つの事例と生態プロセス－．日本林学会誌 85：259-264

百瀬邦泰（2003）雲南の棚田地帯を涵養する雲霧帯の土地利用の変遷と竜山の消長．アジア・アフリカ地域研究　3：87-102

森野真理・萩原良巳・坂本麻衣子（2003）地域社会における生息地の保全インセンティブに関する分析．環境システム研究論文集　31：9-17

2004

Aiba S, Kitayama K, Takyu M (2004) Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. Plant Ecology 174: 147-161

Eguchi K, Bui TV, Yamane Sk (2004) A preliminary study on foraging distance and nesting sites of ants in Indo-Chinese lowland vegetation (Insecta, Hymenoptera, Formicidae). Sociobiology 43: 445-457

Hall S, Asner GP, Kitayama K (2004) Substrate, climate, and land use controls over soil N dynamics and N-oxide emissions in Borneo. Biogeochemistry 70: 27-58

Ichie T, Hiromi T, Yoneda R, Kamiya K, Kohira M, Ninomiya I, Ogino K (2004) Short-term drought causes synchronous leaf shedding and flushing in a lowland mixed dipterocarp forest, Sarawak, Malaysia. Journal of Tropical Ecology 20: 697-700

Ichikawa M (2004) Relationships among secondary forests and resource use and agriculture, as practiced by the Iban of Sarawak, East Malaysia. Tropics 12: 269-286

Irino KO, Iba Y, Ishizuka S, Kenzo T, Ripot S. Kendawang JJ, Miyashita N, Nara K, Hogetsu T, Ninomiya I, Iwasaki K, Sakurai K (2004) Effects of controlled-release fertilizer on growth and ectomycorrhizal colonization of pot-grown seedlings of the dipterocarp *Dryobalanops lanceolata* in a tropical nursery. Soil Science and Plant Nutrition 50: 747-753

Isagi Y, Kanazashi T, Suzuki W, Tanaka H, Abe T (2004) Highly variable pollination patterns in *Magnolia obovata* revealed by microsatellite paternity analysis. International Journal of Plant Sciences 165: 1047-1053

Ishii H, Tanabe S, Hiura T (2004) Exploring the relationships among canopy structure, stand productivity and biodiversity of temperate forest ecosystems. Forest Science 50: 342-355

Itioka T, Yamauti M (2004) Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. Journal of Tropical Ecology 20: 479-482

Kato H, Yamane Sk, Phengklai C (2004) Ant-colonized domatia on fruits of *Mucuna interrrupta* (Leguminosae). Journal of Plant Research 117: 319-321

Kenta T, Isagi Y, Nakagawa M, Yamashita M, Nakashizuka T (2004) Variation in pollen dispersal between years with different pollination conditions in a tropical emergent tree. Molecular Ecology 13: 3575-3584

Kenzo T, Ichie T, Yoneda R, Kitahashi Y, Watanabe Y, Ninomiya I, Koike T (2004) Interspecific variation of photosynthesis and leaf characteristics in five canopy trees of Dipterocarpaceae in tropical rain forest. Tree Physiology 24:1187-1192

Kitayama K, Aiba S, Takyu M, Majalap N, Wagai R (2004) Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podozolization. Ecosystems 7: 259-274

Kitayama K, Suzuki S, Hori M, Takyu M, Aiba S, Majalap-Lee N, Kikuzawa K (2004) On the relationships between leaf-litter lignin and net primary productivity in tropical rain forests. Oecologia 140: 335-339

Kurokawa H, Kitahashi Y, Koike T, Lai J, Nakashizuka T (2004) Allocation to defense or growth in dipterocarp forest seedlings in Borneo. Oecologia 140: 261-270

Manfroi OJ, Kuraji K, Tanaka N, Suzuki M, Nakagawa M, Nakashizuka T, Chong L (2004) The stem flow of trees in a Bornean lowland tropical forest. Hydrological Process 18: 2455-2474

Masaki T, Ohta T, Sugita H, Oohara H, Otani T, Nagaike T, Nakamura S (2004) Structure and dynamics of tree populations within unsuccessful conifer plantations near the Shirakami Mountains, a snowy region of Japan. Forest Ecology and Management 194: 389-401

Momose K (2004) Plant reproductive interval and population density in aseasonal tropics. Ecological Research 19: 245-253

Nagaike T, Hayashi A (2004) Effects of extending rotation period on plant species diversity in *Larix kaempferi*

plantations in central Japan. Annals of Forest Science 61: 197-202

Nakagawa M, Nakashizuka T (2004) Relationships between physical and chemical characteristics of dipterocarp seeds. Seed Science Research 14: 363-369

Nakashizuka T (2004) The role of biodiversity in Asian forests. Journal of Forest Research 9: 293-298

Otani T (2004) Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. Ecological Research 19: 495-501

Tsujino R, Yumoto T (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecological Research 19: 291-300

Tsujino R, Noma N, Yumoto T (2004) Growth in sika deer (*Cervus nippon yakushimae*) population in the western lowland forest on Yakushima Island, Japan. Mammal Study 29: 105-111

Ushimaru A, Fukui A, Imamura A (2004) Effect of floral organ sizes on female reproductive success in *Erythronium japonicum* (Liliaceae). Journal of Plant Biology 46: 245-249

井鷺裕司　（2004）マイクロサテライトマーカーで明らかになった低頻度出現種の更新プロセス．日本林学会誌 86：169-176

市川昌広（2004）マレーシア　サラワク州の焼畑農業における化学的適応化．熱帯農業　48 Extra issue 1；111-112

森野真理・萩原良巳・神谷大介・坂本麻衣子（2004）屋久島における地域住民の自然に対する保全意識－森林の非利用価値に注目して－．地域学研究　34：311-324

2005

Abe M, Miguchi H, Honda A, Makita A, Nakashizuka T (2005) Short-term changes affecting regeneration of *Fagus crenata* after simultaneous death of *Sasa kurilensis*. Journal of Vegetation Science 16: 49-56

Aiba M, Nakashizuka T (2005) Sapling structure and regeneration strategy in 18 *Shorea* species co-occuring in a tropical rainforest. Annals of Botany 96: 313-321

Aiba S, Takyu M, Kitayama K (2005) Dynamics, productivity and species richness of tropical rainforests along elevational and edaphic gradients on Mount Kinabalu, Borneo. Ecological Research 20: 279-286

Chen H-w, Toda MJ, Gao J-j (2005) The *Phortica* (s.str.) *foliiseta* species-complex (Diptera, Drosophilidae) from China and its adjacent countries. Acta Zootaxonomica Sinica 30: 198-209

Chen H-w, Toda MJ, Wang B-c. (2005) A taxonomic revision of the genus *Pseudostegana* Okada, 1978 (Diptera, Drosophilidae). Insect Systematics & Evolution 36: 407-442

Ebihara A, Ishikawa H, Matsumoto S, Lin S-J, Iwatsuki K, Takamiya M, Watano Y, Ito, M (2005) Nuclear DNA, chloroplast DNA, and ploidy analysis clarified biological complexity of the *Vandenboschia radicans* complex (Hymenophylaceae) in Japan and adjacent areas. American Journal of Botany 92: 1535-1547

Enoki T, Kawaguchi H, Nakashizuka T, Hamid AA (2005) Growth pattern and leaf morphology of *Shorea parvistipulata* saplings in a tropical rain forest of Sarawak, Malaysia. Journal of Tropical Ecology 21: 215-218

Hanya G (2005) Comparisons of dispersal success between the species fruiting prior to and those at the peak of migrant frugivore abundance. Plant Ecology 181: 167-177

Hanya G, Zamma K, Hayaishi S, Yoshihiro S, Tsuriya Y, Sugaya S, Kanaoka MM, Hayakawa S, Takahata Y (2005) Comparisons of food availability and density of Japanese macaques in primary, naturally regenerated and plantation forests. American Journal of Primatology 66: 245-262

Harrison RD, Momose K, Inoue T (2005) Pollination of *Dipterocarpus* by *Apis dorsata* during a general flowering. Malaysian Nature Journal 57: 67-80

Ichie T, Kenzo T, Kitahashi Y, Koike T, Nakashizuka T (2005) How does *Dryobalanops aromatica* supply carbohydrate resource for reproduction in a masting year? Trees 19: 703-710

Ichie T, Kenta T, Nakagawa M, Sato K, Nakashizuka T (2005) Resource allocation to reproductive organs during masting in the tropical emergent tree, *Dipterocarpus tempehes*. Journal of Tropical Ecology 21: 237-241

Isagi Y, Kudo M, Osumi K, Sato T, Sakio H (2005) Polymorphic microsatellite DNA markers for a relict angiosperm *Cercidiphyllum japonicum* Sieb. *et* Zucc and their utility for *C. magnificum*. Molecular Ecology Notes 5: 596-598

Iwata K, Eguchi K, Yamane Sk (2005) A case study on urban ant fauna of southern Kyushu, Japan, with notes on a new monitoring protocol (Insecta, Hymenoptera, Formicidae). Journal of Asia-Pacific Entomology 8: 263-272

Kohyama T (2005) Scaling up from shifting gap mosaic to geographic distribution in the modeling of forest dynamics. Ecological Research 20: 302-312

Kohyama T, Kubo T, Macklin E (2005) Effect of temporal autocorrelation on apparent growth rate variation in forest tree census data and an alternative distribution function of tree growth rate. Ecological Research 20: 11-15

Koizumi M (2005) Ethnobotany of the Penan Benalui of East Kalimantan, Indonesia: Difference of ethnobotanical knowledge between villagers of Long Belaka. African Study Monographs, supplement 29: 53-60

Koizumi M, Nagamasu H (2005) A new record of the monotypic *Harmandia* (Olacaceae) from East Kalimantan, Indonesia. Acta Phytotaxonomica et Geobotanica 56: 257-259

Kubo T, Kohyama T (2005) *Abies* population dynamics simulated by a functional-structural tree model. Ecological Research 20: 255-269

Nagaike T, Kamitani T, Nakashizuka T (2005) Effects of different forest management systems on plant species diversity in a *Fagus crenata* forested landscape of central Japan. Canadian Journal of Forest Research 35: 2832-2840

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Pre-dispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. Biotropica 37: 388-395

Nakashizuka T (2005) The role of biodiversity in Asian forests. Journal of Forest Research 9: 293-298

Shimamura T, Momose K (2005) Organic matter dynamics controls plant species coexistence in a tropical peat swamp forest. Proceeding of Royal Society of London Series B 272: 1503-1510

Takeuchi Y, Kenta T, Nakashizuka T (2005) Comparison of sapling demography of four dipterocarp species with different seed-dispersal strategies. Forest Ecology and Management 208: 237-248

Takyu M, Kubota Y, Aiba S, Seino T, Nishimura T (2005) Pattern of changes in species diversity, structure and dynamics of forest ecosystems along latitudinal gradients in East Asia. Ecological Research 20: 287-296

市岡孝朗（2005）アリ−オオバギ共生系の多様性: 生物群集への波及効果. 日本生態学会誌 55: 431-437

井上大成（2005）日本のチョウ類の衰亡理由．昆虫（ニューシリーズ）8(2)：43-64

佐藤仁（2005）スマトラ沖地震による津波被害の教訓と生活復興への方策：タイの事例．地域安全学会論文集　7：433-442

清野達之（2005）材の生態機能特性からみた熱帯林樹種の多様性. 日本生態学会誌 55: 301-305

正木隆・柴田銃江（2005）森林の広域・長期的な試験地から得られる成果と生き残りのための条件．日本生態学会誌　55：359-369

百瀬邦泰（2005）ニューエコロジーなる誤解：生態学と環境人類学の間の深い溝を埋めるために．アジア・アフリカ地域研究　3：72-84

2006

Aiba S, Suzuki E, Kitayama K (2006) Structural and floristic variation among small replicate plots of a tropical montane forest on Mount Kinabalu, Sabah, Malaysia. Tropics 15: 219-236

Akao K-I, Managi S (2006) Endogenous growth with material balance principle. International Journal of Global Environmental Issues 6: 4-28

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the

evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9: 1146-1156

Farzin YH, Akao K (2006) Non-pecuniary value of employment and natural resource extinction. Fondazine Eni Enrico Mattei Working Paper Series 24.06: 1-25

Fujimori N, Kenta T, Kondo T, Kameyama Y, Isagi Y, Nakashizuka T (2006) Microsatellite loci for a sparsely distributed species, *Kalopanax pictus* (Araliaceae) in Japanese temperate forests. Molecular Ecology Notes 6: 468-469

Fujimori N, Samejima H, Kenta T, Ichie T, Shibata M, Iida S, Nakashizuka T (2006) Reproductive success and distance to conspecific adults in the sparsely distributed tree *Kalopanax pictus*. Journal of Plant Research 119:195-203

Hasegawa M, Ito MT, Kitayama K (2006) Community structure of oribatid mites in relation to elevation and geology on the slope of Mount Kinabalu, Sabah, Malaysia. European journal of soil biology 42: s191-196

Hasegawa M, Fukuyama K, Makino S, Okochi I, Goto H, Mizoguchi T, Sakata T, Tanaka H (2006) Collembolan community dynamics during deciduous forests regeneration in Japan. Pedobiologia 50: 117-126

Hirao T, Murakami M, Kogi H, Kashizaki A, Hirai Y, Tanabe S, Inari N, Yorozuya H, Toda MJ (2006) International Biodiversity Observation Year in Western-Pacific and Asian Region (DIWPA-IBOY): A case report on species rarity and spatio-temporal variability of species composition in Lepidoptera and Coleoptera communities from a temperate forest of northern Japan. Ecological Research 21: 811-818

Kato Y (2006) The use of forest resources for food and income in a Borneo hunter-gatherer community. The Proceedings of Kyoto Symposium "Crossing Disciplinary Boundaries and Re-visioning Area Studies: Perspectives from Asia and Africa", 21st Century COE Program, ASAFAS& CSEAS, Kyoto University: 253-256.

Kenzo T, Ichie T, Yoneda R, Watanabe R, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with height from seedlings to mature canopy trees in five dipterocarp species in a tropical rain forest. Tree Physiology 26: 865-873

Kohyama T (2006) The effect of patch demography on the community structure of forest trees. Ecological Research 21: 346-355

Kumagai T, Ichie T, Yoshimura M, Yamashita M, Kenzo T, Saitoh TM, Ohashi M, Suzuki M, Koike T, Komatsu H (2006) Modeling CO_2 exchange over a Bornean tropical rainforest using the measured vertical and horizontal variations in leaf-level physiological parameters and leaf area densities. Journal of Geophysical Research 111: D10107

Kumano Y, Yamaoka R (2006) Synchronization between temporal variation in heat generation, floral scents and pollinator arrival in the beetle-pollinated tropical Araceae *Homalomena propinqua*. Plant Spec Biol 21:173-183

Makino S, Goto H, Inoue T, Sueyoshi M, Okabe K, Hasegawa M, Hamaguchi K, Tanaka H, Okochi I (2006) The monitoring of insects to maintain biodiversity in Ogawa forest reserve. Environmental Monitoring and Assessment 120: 477-485

Maleque MA, Ishii HT, Maeto K (2006) The use of arthropods as indicators of ecosystem integrity in forest management. Journal of Forestry 104: 113-117

Maleque MA, Ishii HT, Maeto K, Taniguchi S (2006) Management of insect biodiversity by line thinning in Japanese cedar (*Cryptomeria japonica* D. Don) plantations, central Japan. Urasian Journal of Forest Research 9: 29-36

Manfroi OJ, Kuraji K, Suzuki M, Tanaka N, Kume T, Nakagawa M, Kumagai T, Nakashizuka T (2006) Comparison of conventionally observed interception evaporation in a 100-m^2 subplot with that estimated in a 4-ha area of the same Bornean lowland tropical forest. Journal of Hydrology 329: 329-349

Matsubayashi H, Lagan P, Sukor JRA (2006) Utilization of *Macaranga* trees by Asian elephant (*Elephas maximus*) in Borneo. Mammal Study 31: 115-118

Nagaike T, Hayashi A, Kubo M, Abe M, Arai N (2006) Plant species diversity in a managed forest landscape composed of *Larix kaempferi* plantations and abandoned coppice forests in central Japan. Forest Science 52: 324-332

Nagaike T, Hayashi A, Kubo M, Takahashi K, Abe M, Arai N (2006) Changes in plant species diversity over 5 years in *Larix kaempferi* plantations and abandoned coppice forests in central Japan. Forest Ecology and Management 236: 278-285

Nagaike T, Kamitani T, Nakashizuka T (2006) Effects of different forest management systems on plant species diversity in a *Fagus crenata* forested landscape of central Japan. Canadian Journal of Forest Research 35: 2832-2840

Nagaike T, Masaki T, Ito S (2006) Special feature: ecology and management of conifer plantations in Japan: control of tree growth and maintenance of biodiversity. Journal of Forest Research 11: 215-216

Nakagawa M, Miguchi H, Nakashizuka T (2006) The effects of various forest uses on small mammal communities in Sarawak, Malaysia. Forest Ecology and Management 231: 55-62

Ohsawa M, Nagaike T (2006) Influence of forest types and effects of forestry activities on species richness and composition of Chrysomelidae in a central mountainous region of Japan. Biodiversity and Conservation 15: 1179-1191

Prigent SR, Toda MJ (2006) A revision of the *Zygothrica samoaensis* species group (Diptera, Drosophilidae), with its division into three species subgroups and descriptions of five new species. Entomological Science 9: 191-215

Raich JW, Russel A, Kitayama K, Parton W, Vitousek PM (2006) Temperature influences carbon accumulation in moist tropical forests. Ecology 87: 76-87

Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yasunari T, Chong L, Nakashizuka T (2006) Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. American Journal of Botany 93: 1134-1139

Sakai S, Nagamasu H (2006) Notes on inflorescence structure of *Boesenbergia* (Zingiberaceae). Acta Phytotaxonomica et Geobotanica 57: 107-111

Sato T, Isagi Y, Sakio H, Osumi K, Goto S (2006) Effect of gene flow on spatial genetic structure in the riparian canopy tree *Cercidiphyllum japonicum* revealed by microsatellite analysis. Heredity 96: 79-84

Sultana F, Hu Y-g, Toda MJ, Takenaka K, Yafuso M (2006) Phylogeny and classification of *Colocasiomyia* (Diptera, Drosophilidae), and its evolution of pollination mutualism with aroid plants. Systematic Entomology 31: 684-702

Terada Y, Takamiya M (2006) Cytological anf genetic study of two putative hybrids and their parents of *Athyrium* (Woodsiaceae; Pteridophyta) in Yakushima Island, southwestern Japan. Acta Phytotax. Geobot. 57: 95-406

Terakawa M, Kikuchi S, Kanetani S, Matsui K, Yumoto T, Yoshimaru H (2006) Characterization of 13 polymorphic microsatellite loci for an evergreen tree, *Myrica rubra*. Molecular Ecology Notes 6: 709-711

Tsujino R, Takafumi H, Agetsuma N, Yumoto T (2006) Variation in tree growth, mortality and recruitment among topographic positions in a warm-temperate forest. Journal of Vegetation Science 17: 281-290

Tuda M, Matsumoto T, Itioka T, Ishida N, Takanashi M, Ashihara W, Kohyama M, Takagi M (2006) Climatic and intertrophic effects detected in 10-year population dynamics of biological control of the arrowhead scale by two parasitoids in southwestern Japan. Population Ecology 48: 59-70

赤尾健一（2006）生物多様性の経済分析－多様性関数と不確実性に関する最近の研究－．環境経済・政策学会年報 11：136-147

阿部俊夫・坂本知己・田中浩・延廣竜彦・壁谷直記・萩野裕章（2006）モデルによる河畔域の落葉散布パターンの評価．応用生態工学 8：147-156

井上大成（2006）草地・森林の変遷とチョウ類の保全．日本草地学会誌　53: 40-46

大沼あゆみ（2006）絶滅のおそれのある野生生物保全の経済学．環境科学会誌 19：573-585.

北山兼弘（2006）土壌栄養と陸上生態系の関係．土と基礎の生態学３．土と基礎 54：39-46

田中憲蔵・小田あゆみ・増田寛子・二宮生夫・王林和・吉川賢（2006）中国内蒙古自治区に生育する臭柏（*Sabina vulgaris* Ant.）の個体サイズにともなう光合成能力と葉の特性の変化. 日本緑化工学会誌 31：436-440

辻野亮・揚妻-柳原芳美（2006）鹿児島県屋久島の森林で発見された外来哺乳類～タヌキ・ノイヌ・ノネコ・ヤギ. 保全生態学研究 11：167-171

長谷川弘（2006）開発プロジェクトにおける環境影響評価と経済評価の統合：特に農林業開発事業事例にみる実務的課題と提言. 日本評価研究 6：31-42

森野真理・小池文人（2006）猿害の空間パターンによるリスク評価. 保全生態学研究 11：43-52

安田雅俊・川路則友・福井晶子・金井裕（2006）ファイ係数であきらかになった 20 世紀後半の日本の鳥類群集の変化傾向. 日本鳥学会誌 54：86-101

米田令仁・松本陽介・田中憲蔵・Mohamad Azani Alias・Nik Muhamad Majid（2005）全天条件下における植栽直後の *Dyera costulata* のガス交換および光阻害におよぼす人工遮光物の初期効果. 森林立地 47：113-118

米田令仁・松本陽介・田中憲蔵・Mohamad Azani Alias・Nik Muhamad Majid（2005）裸地植栽における脆弱な熱帯樹種のための人工遮光物の試作. 森林立地 47：119-123

2007

Agetsuma N (2007) Minimum area required for local populations of Japanese macaques estimated from the relationship between habitat area and population extinction. International Journal of Primatology 28: 97-106

Agetsuma N (2007) Ecological function losses caused by monotonous land use induce crop raiding by wildlife on the island of Yakushima, southern Japan. Ecological Research 22: 390-402

Aiba M, Nakashizuka T (2007) Differences in the dry-mass cost of sapling vertical growth among 56 woody species co-occurring in a Bornean tropical rain forest. Functional Ecology 21: 41-49

Aiba S, Hanya G, Tsujino R, Takyu M, Seino T, Kimura K, Kitayama K (2007) Comparative study of additive basal area of conifers in forest ecosystems along elevational gradients. Ecological Research 22: 439-450

Akao K-I (2007) Tax schemes in a class of differential games. Economic Theory, Available Online (DOI 10.1007/s00199-007-232-9)

Akao K-I, Farzin YH (2007) When is it optimal to exhaust a resource in a finite time? Ecological Research 22: 422--430

Akao K-I, Managi S (2007) Feasibility and optimality of sustainable growth under materials balance. Journal of Economic Dynamics and Control, Available Online (DOI: 10.1016/j.jedc.2007.01.013)

Akutsu K, Chey VK, Toda MJ (2007) Assessment of higher insect taxa as bioindicators for different logging-disturbance regimes in lowland tropical rain forest in Sabah, Malaysia. Ecological Research: 22: 542-550

Chen H-w, Toda MJ, Lakim MB, Mohamed MB (2007) *Amiota sinuata* species group from eastern Malaysia (Diptera, Drosophilidae). Entomological Science 10: 73-80

Chen H-w, Toda MJ, Lakim MB, Mohamed MB (2007) The *Phortica* sensu stricto (Insecta: Diptera: Drosophilidae) from Malaysia. The Raffles Bulletin of Zoology 55: 23-41

Dounias, Edmond, Selzner A, Koizumi M, Levang P (2007) From sago to rice, from forest to town: The consequences of sedentarization on the nutritional ecology of Punan former hunter-gatherers of Borneo. Food and Nutrition Bulletin, special issue 28: 294-302

Hamaguchi K, Matsumoto T, Maruyama M, Hashimoto Y, Yamane S, Itioka T (2007) Isolation and characterization of eight microsatellite loci in two morphotypes of the Southeast Asian army ant, *Aenictus laeviceps*. Molecular Ecology Notes 7: 984-986

Hanya G, Kiyono M, Takafumi H, Tsujino R, Agetsuma N (2007) Mature leaf selection of Japanese macaques: effects of availability and chemical content. Journal of Zoology 273:140-147

Ichikawa M (2007) Degardation and loss of forest land and land-use changes in Sarawak, East Malaysia: a study of native land use by the Iban. Ecological Researach 22: 403-413

Isagi Y, Saito D, Kawaguchi H, Tateno R, Watanabe S (2007) Effective pollen dispersal is enhanced by the genetic structure of an Aesculus turbinate population. Journal of Ecology 95: 983-990

Kendawang JJ, Ninomiya I, Kenzo T, Ozawa T, Hattori D, Tanaka S, Sakurai S (2007) Effects of burning strength in shifting cultivation on the early stage of secondary succession in Sarawak, Malaysia. Tropics 16: 309-321

Kenzo T, Ichie T, Watanabe Y, Hiromi T (2007) Ecological distribution of homobaric and heterobaric leaves in tree species of Malaysian lowland tropical rainforest. American Journal of Botany 94: 764-775

Koizumi M, Momose K (2007) Penan Benalui wild-plant use, classification, and nomenclature. Current Anthropology 48: 454–459

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forest by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Ecological Research 22: 414-421

Makino S, Goto H, Hasegawa M, Okabe K, Tanaka H, Inoue T, Okochi I (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan. Ecological Research 22: 372-381

Matsubayashi H, Lagan P, Majalap N, Tangah J, Rafiah JRA, Kitayama K (2007) Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecological Research 22: 742-748

Matsuki Y, Isagi Y, Suyama Y (2007) The determination of multiple microsatellite genotypes and DNA sequences from a single pollen grain. Molecular Ecology Notes 7: 194-198

Nakagawa M, Hyodo F, Nakashizuka T (2007) Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes. Canadian Journal of Zoology 85:472-478

Nakagawa M, Miguchi H, Sato K, Nakashizuka T (2007) A preliminary study of sympatric two Maxomys rats in Sarawak, Malaysia: spacing patterns and population dynamics. The Raffles Bulletin of Zoology 55:381-387

Nakagawa M, Miguchi H, Sato K, Sakai S, Nakashizuka T (2007) Population dynamics of arboreal and terrestrial small mammals in a tropical rainforest, Sarawak, Malaysia. The Raffles Bulletin of Zoology 55:389-395

Takeuchi Y, Nakashizuka T (2007) Effect of distance and density on seed/seedling fate of two dipterocarp species. Forest Ecology and Management 247: 167-174

Ushimaru A, Kikuchi S, Yonekura R, Maruyama A, Yanagisawa N, Kagami M, Nakagawa M, Mahoro S, Kohmatsu Y, Hatada A, Kitamura S, Nakata K (2007) The influence of floral symmetry and pollination systems on flower size variation. Nordic J Botany 24:593-598

大沼あゆみ・山本雅資 2007　「プレミアムつきのカーボンクレジットについて　－WWF のゴールド・スタンダードとカーボンマーケット」,『環境情報科学』36 巻 3 号, 55-60

佐藤仁（2007）財は人を選ぶか：タイ津波被災地にみる稀少財の配分と分配．国際開発研究 16：83-96

In Press

Abe S, Motai H, Tanaka H, Shibata M, Kominami Y, Nakashizuka T (in press) Population maintenance of the short-lived gap-dependent shrub *Sambucus racemosa* ssp. Sieboldiana in an old-growth deciduous forest.. Ecology.

Kamoi T, Kenzo T, Kuraji K, Momose K (in press) Abortion of reproductive organs as an adaptation to fluctuating daily carbohydrate production. Oecologia.

Kenzo T, Ichie T, Ozawa T, Kashimura S, Hattori D, Irino K, Kendawang JJ, Sakurai K, Ninomiya I (2007) Leaf physiological and morphological responses of seven dipterocarp seedlings to degraded forest environments in Sarawak, Malaysia：A case study of forest rehabilitation practice. Tropics (in press).

Kitahashi Y, Ichie T, Maruyama Y, Kenzo T, Kitaoka S, Matsuki S, Chong L, Nakashizuka T, Koike T (in press) Photosynthetic water use efficency in tree crowns of *Shorea beccariana* and *Dryobalanops aomatica* in a tropical rain forest in Sarawak, East Malaysia. Photosynthetica.

Matsubayashi H, Lagan, P, Sukor, JRA (in press) Herbal seed dispersal by the banteng (*Bos javanicus*) in a Bornean tropical forest. Malayan Nature Journal.

Matsubayashi H, Lagan P, Sukor JRA, Kitayama K (in press) Seasonal and daily use of natural licks by sambar deer (*Cervus unicolor*) in a Bornean tropical rain forest. Tropics.

Sakai S, Nagamasu H (2006) Systematic studies of Bornean Zingiberaceae V. Zingiberoideae of Lambir Hills, Sarawak. Blumea (in press).

Sato J (2007) Formation of resource concept in Japan: Post-war efforts in knowledge integration. *Sustainability Science* 2 (in press).

Tanaka H, Shibata M, Masaki T, Iida S, Niiyama K, Abe S, Kominami Y, Nakashizuka T (2007) Comparative demography of three coexisting maples in gaps and under closed canopy. Journal of Vegetation Science (in press).

Toda MJ, Lakim MB, Mohamed MB (2007) The genus *Colocasiomyia* (Drosophilidae: Diptera) in Sabah: High species-diversity and utilization of host aroid inflorescences. Sabah Parks Nature Journal (in press).

Tsujino R, Yumoto T (in press) Spatial distribution patterns of trees at different life stages in a warm temperate forest. Journal of Plant Research.

Wagai R, Mayer LM (in press) Significance of hydrous iron oxides for sorptive stabilization of organic carbon in a range of soils. Geochimica et Cosmochimica Acta.

Yamane Sk (2005) *Pachycondyla nigrita* and its related species (Hymenoptera: Formicidae) in Southeast Asia. Memoirs of the American Entomological Institute (in press).

Yamashita S, Hattori T, Momose K, Nakagawa M, Aiba M, Nakashizuka T (in press) Effects of forest use on aphyllophoraceous fungal community structure in Sarawak, Malaysia. Biotropica.

市川昌広（印刷中）マレーシア・サラワク州の焼畑栽培にみられる除草剤利用とその背景．農耕の技術と文化．

佐藤仁（2007）持たざる国の資源論：環境論との総合に向けて．環境社会学研究 13 号（印刷中）．

柴田銃江（2005）多くの樹種が一斉に結実する意味を考える：受粉効率説と捕食者飽食説．種生物学研究 29（印刷中）．

百瀬邦泰（2005）焼畑を行うための条件．農耕の技術と文化　27（印刷中）．

安田雅俊（印刷中）絶滅のおそれのある九州のニホンリス，ニホンモモンガ，ムササビー過去の生息記録および現状と課題ー．哺乳類科学．

安田雅俊（印刷中）九州地方のニホンリスについて．リスとムササビ, 18.

Book

2002

Nakashizuka T, Stork N (eds.) (2002) Protocols for Biodiversity Research. Kyoto University Press, Kyoto, and Trans Pacific Press, Melbourn. pp.209

Nakashizuka T, Matsumoto Y (eds.) (2002) Diversity and Interaction in a Temperate Forest Community. Ogawa Forest Reserve of Japan. Springer, Tokyo. pp.319

Toda MJ, Kitching RL (2002) Chapter 2: Forest ecosystems. In: Nakashizuka T, Stork N (eds.) Biodiversity Research Methods, IBOY In Western Pacific and Asia. 27-110. Kyoto University Press, Kyoto & Trans Pacific Press, Melbourne

半谷吾郎（2002）分布南限の島．大井徹・増井憲一編著　ニホンザルの自然誌　第十三章．229-250．東海大学出版会

佐藤仁（2002）稀少資源のポリティクス：タイ農村にみる開発と環境のはざま．東京大学出版会

佐藤仁（2002）ダン吉島の夢の後:発展途上国にみる不足と開発．岩波講座　アジア新世紀　市場．101-116. 岩波書店

佐藤仁（2002）問題を切り取る視点：環境問題とフレーミングの政治学．石弘之編　環境学の技法．41-75. 東京大学出版会

2003

Ichikawa M (2003) One hundred years of land-use changes: Political, social, and economic influences on an Iban village in Bakong River basin, Sarawak, East Malaysia. In: Tuck Po, L., de Jong W, Abe K (eds.) The Political Ecology of Tropical Forests in Southeast Asia: Historical Perspectives. 117-199. Kyoto University Press

Itioka T, Kato M, Kaliang H, Merdeck MB, Nagamitsu T, Sakai S, Mohamad SU, Yamane Sk, Hamid AA, Inoue T (2003) Insect responses to general flowering in Sarawak. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds.) Arthropods of Tropical Forests Spatio-temporal Dynamics and Resource Use In the Canopy. 126-134. Cambridge University Press, Cambridge

Kanazawa K (2003) Sabah and Sarawak States. In: Japan Environmental Council (ed.) The State of the Environment In Asia 2002/2003. 191-193.

Koike F, Nagamitsu T (2003) Canopy foliage structure and flight density of butterflies and birds in Sarawak. In: Basset Y, Novotny V, Miller SE, Kitching, RL (eds.) Arthropods of Tropical Forests Spatio-temporal Dynamics and Resource Use in the Canopy. 86-91. Cambridge University Press, Cambridge

Roubik DW, Sakai S, Gattesco F (2003) Canopy flowers and certainty: loose niches revisited. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds.) Arthropods of Tropical Forests: Spatio-temporal Dynamics and Eesource Use in the Canopy. Cambridge University Press, Cambridge

佐藤仁（2003）誰が何を管理するのか．鈴木和夫ほか編　森林の百科．朝倉書店

佐藤仁（2003）「貧困」,「持続可能な開発」．キーワードで読みとく世界の紛争．242-247．河出書房

田中浩（2003）樹木の生活史．鈴木和夫ほか編　森林の百科．朝倉書店

田中浩（2003）モニタリングの意義と実例．鈴木和夫ほか編　森林の百科．朝倉書店

中静透（2003）「森林とは」,「森林・樹木の構造と機能，はじめに」,「森林の遷移と動態」,「生物多様性と森林」．井上真・桜井尚武・鈴木和夫・富田文一郎・中静透編　森林の百科，pp. 2-7，33，110-117，677-681．朝倉書店．

中静透（2003）熱帯林の生態．不破敬一郎・森田昌敏編　地球環境ハンドブック第 2 版．562-566．朝倉書店,

百瀬邦泰（2003）熱帯雨林を観る．講談社選書メチエ

2004

Momose K, Shimamura T (2004) Malay riverbank community: environment, network and transformation. In: Furukawa H, Nishibuchi M, Kono Y, Kaida Y (eds.) Kyoto Area Studies on Asia Vol. 8: Ecological Destruction, Health, and Development -Advancing Asian Paradigms, Part 4, Chapter 28. 534-537. Kyoto University Press

Nakashizuka T, Sakai S, Chong L (2004) Lambir Hills National Park Canopy Crane, Malaysia. In: Basset Y, Horlyck V, Wright SJ (eds.) Studying Forest Canopies from Above: The International Canopy Crane Network, 120-125.

Toda MJ, Matsushita K, Mawatari SF (2004) Biological Classification and Identification System (BioCIS). In: Mawatari SF, Okada H (eds.) Neo-Science of Natural History: Integration of Geoscience and Biodiversity Studies, Proceedings of International Symposium on “Dawn of a New Natural History - Integration of Geoscience and Biodiversity Studies”. 41-44. Sapporo, Japan

Yamane Sk (2004) ANeT: Goals, development and perspective. In: Shimura J (ed.) Building Capacity in Biodiversity

Information Sharing. 31-38. NIES, Tsukuba

安部竜一郎・鳴原敦子・藤岡美恵子・伊藤美幸・平井朗・宮寺卓・大内穂・蓮井誠一郎・鶴田雅英・小川景子・竹峰誠一郎著（2004）脱「開発」へのサブシステンス論．郭洋春・戸崎純・横山正樹編．法律文化社

市栄智明（2004）物質の分配. 小池孝良編　樹木生理生態学．183-185．朝倉書店

甲山隆司（編著）（2004）植物生態学．朝倉書店

佐藤仁（2004）貧困と”資源の呪い”．　井村秀文他編　環境と開発．27-50．日本評論社

中静透（2004）生物の多様性の場としての森林. 鈴木和夫編著　森林保護学．7-15．朝倉書店

中静透（2004）森のスケッチ. 東海大学出版会，pp. 236

中静透（2004）森林の保全生態. 小池孝良編　樹木生理生態学　1-36．朝倉書店

2005

Itioka T (2005) Diversity of anti-herbivore defenses in *Macaranga*. In: Roubik DW, Sakai S, Karim AAH (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 158-171. Springer, New York

Momose K (2005) Beetle pollination in tropical rain forests. In: Roubik DW, Sakai S, Hamid AA (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 104-110. Springer-Verlag, New York, USA

Momose K, Hamid AA (2005) The plant-pollinator community in a lowland dipterocarp forest. In: Roubik DW, Sakai S, Hamid AA (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 65-72. Springer-Verlag, New York, USA

Nagaike T, Yoshida T, Miguchi H, Kamitani T, Nakashizuka T (2005) Rehabilitation for species enrichment in abandoned coppice forests in Japan. In: Stanturf JA, Madsen P (eds.) Restoration of Boreal and Temperate Forests. 371-381. CRC Press

Nakagawa M, Itioka T, Momose K, Nakashizuka T (2005) Insect predators of dipterocarp seeds. In: Roubik DW, Sakai S, Hamid AA (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 145-157. Springer-Verlag, New York, USA

Roubik DW, Sakai S, Hamid AA (eds.) (2005) Pollination Ecology and the Rain Forest: Sarawak studies. Springer, NY

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T, Inoue T (2005) Plant reproductive phenology and general flowering in a mixed dipterocarp forest. In: Roubik DW, Sakai S, Hamid AA (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 35-50. Springer, NY

Yumoto T, Nakashizuka T (2005) The canopy biology program in Sarawak: Scope, methods, and merit. In: Roubik DW, Sakai S, Hamid AA (eds.) Pollination Ecology and the Rain Forest: Sarawak studies. 13-21. Springer, New York

相場慎一郎（2005）なぜ傾いてねじれるの？－サクラツツジ．　ヤクスギ林の林床の主－ハイノキ．埣田宏（監修）森の花を楽しむ 101 のヒント．132-135．東京書籍

揚妻直樹（2005）食物網．中村太士・小池孝良編　森林の科学-森林生態系科学入門-．80-85．朝倉書店

市栄智明（2005）マスティング現象　－数年に一度の大勝負－．中村太・小池孝良編　森林の科学－森林生態系科学入門－．14-15．朝倉書店

井上大成（2005）森林の成長に伴うチョウ類群集の変化．日本自然保護協会編　生態学からみた里やまの自然と保護．36-39．講談社

金沢謙太郎（2005）サラワクの森林伐採と先住民プナンの現在. 池谷和信編　熱帯アジアの森の民. 273-301. 人文書院

佐藤仁（2005）開発はいかに学習するか―”意図せざる結果”を手がかりに．新崎盛輝ほか編　地域の自立，シマの力（上）．250-271．コモンズ

佐藤仁（2005）現状の奥行きをとらえる学問（解説）．川田他訳　レヴィストロース講義．247-259．平凡社ライブラリー

佐藤仁（2005）社会開発の制度と担い手. 日本福祉大学COE推進委員会編　福祉社会開発学の構築. 177-182. ミネルヴァ書房

佐藤仁（2005）日本における資源社会科学の創成と未発達．松原望・丸山真編　アジア太平洋環境の新視点．27-50．彩流社

中静透（2005）　生物多様性とはなんだろう？　日高敏隆編　生物多様性はなぜ大切か．1-40．昭和堂

2006

Koizumi M (2006) Ethnobotany of the Punan Benalui. In: Topp L, Eghenter C (eds.) Kayan Mentarang National Park: In the heart of Borneo. 66-67. WWF Denmark, Copenhagen / WWF Indonesia, Jakarta

相場慎一郎（2006）屋久島の森林の構造と機能．大澤雅彦・田川日出夫・山極寿一（編）世界遺産　屋久島．102-117. 朝倉書店.

相場慎一郎・岩川文寛（2006）春田浜の植生．大澤雅彦・田川日出夫・山極寿一（編）世界遺産屋久島. 96-101．朝倉書店.

赤尾健一（2006）環境と経済成長．環境経済・政策学会編 環境経済・政策学の基礎知識. 70-71．有斐閣.

揚妻直樹（2006）野生動物の管理と保護．北海道大学北方生物圏フィールド科学センター編　フィールド科学への招待．98-108．三共出版.

揚妻直樹・揚妻－柳原芳美（2006）ヤクシカの森林環境利用．大澤雅彦・田川日出夫・山極寿一（編）世界遺産　屋久島．143-149. 朝倉書店.

市川昌広（2006）ボルネオ・イバン人の｢里山｣利用の変化と日本とのかかわり．日高利隆・秋道智彌（編）森はだれのものか？　アジアの森と人の未来．61－83．昭和堂.

ウィリアム・アッシャー著・佐藤仁訳（2006）発展途上国の資源政治学：政府はなぜ資源を無駄にするのか. 東京大学出版会.

甲山隆司（2006）東アジアの陸域生態系の特性と環境応答．武田博清・占部城太郎（編）陸域生態系の科学：地球環境と生態系．244-253．共立出版.

酒井章子（2006）生物が創り出す熱帯雨林の季節．正木隆・田中浩・柴田銃江（編）森林の生態学－長期大規模研究からみえるもの．17-38．文一総合出版.

佐藤仁（2006）「貧困と環境破壊」章の解説，環境経済・政策学会編『環境経済・政策学の基礎知識』有斐閣.

柴田銃江（2006）多くの樹種が同時に結実する意味を考える．正木隆・田中浩・柴田銃江（編）森林の生態学-長期大規模研究からみえるもの．39-57．文一総合出版.

武生雅明・久保田康裕・相場慎一郎・清野達之・西村貴司（2006）気候の季節性は森林生態系にどう影響するのか. 正木隆・田中浩・柴田銃江（編）森林の生態学－長期大規模研究からみえるもの．247-266. 文一総合出版.

田中憲蔵・市栄智明（2006）葉を透かせば分かる違い－等圧葉と異圧葉－．甲斐昌一・森川弘道（編）プラントミメティックス～植物に学ぶ～．560-562．NTS出版.

田中浩（2006）カエデ属の生活史－近縁な種の共存はいかにして可能か－．107-130．文一総合出版.

中静透（2006）森林の長期（大面積）研究は続ける必要はあるだろうか？　正木隆・田中浩・柴田銃江（編）森林の生態学－長期大規模研究からみえるもの．291-297．文一総合出版.

中静透（2006）生態系にとっての「種の絶滅」と移入種．日高敏隆・総合地球環境額研究所（編）こどもたちに語る　これからの地球．129-142．講談社.

正木隆・田中浩・柴田銃江（2006）森林の生態を長く広く観てみよう．正木隆・田中浩・柴田銃江（編）森林の生態学－長期大規模研究からみえるもの．7-14．文一総合出版.

2007

Agetsuma N (2007) Ecological function losses caused by monotonous land use induce crop raiding by wildlife on the island of Yakushima, southern Japan. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 33-45. Springer.

Akao K, Farzin YH (2007) When is it optimal to exhaust a resource in a finite time? In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 69-77. Springer.

Ichikawa M (2007) Degradation and loss of forest land and land-use changes in Sarawak, East Malaysia: a study of native land use by the Iban. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 47-57. Springer.

Isagi Y, Tateno R, Matsuki Y, Hirao A, Watanabe S, Shibata M (2007)Genetic and reproductive consequences of forest fragmentation for populations of *Magnolia obovata*. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 25-32. Springer.

Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical forest by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 61-68. Springer.

Makino S, Goto H, Hasegawa M, Okabe K, Tanaka H, Inoue T, Okochi I (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. 15-24. Springer.

Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. Springer. pp86 (Reprinted from Ecological Research 22(3)).

Nakashizuka T (2007) An interdisciplinary approach to sustainability and biodiversity of forest ecosystems: an introduction. In: Nakashizuka T. (ed.) (2007) Sustainability and Diversity of Forest Ecosystem: An interdisciplinary approach. v-vi. Springer.

スプレイグ DS（2007）屋久島の獣被害農業地域の把握．秋山　侃・石塚直樹・内田論・岡本勝男・小川茂男・斎藤元也（編）農業リモートセンシング・ハンドブック．II79-II81．システム農学会．

山内健生・矢田脩（2007）シロチョウ科．矢田脩（編著）新訂原色昆虫大図鑑第 I 巻（蝶蛾篇）．13-32．北隆館．

In Press

秋道智彌・市川昌広（編）（2008）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院，京都（印刷中）

秋道智彌・市川昌広（2008）序論．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

市川昌広（2008）うつろいゆくサラワクの森の一〇〇年：多様な資源利用の単純化．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

市川昌広（2008）第 2 章　序文．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

加藤裕美（2008）サラワク・シハン人の森林産物利用――狩猟や採取にこだわる生計のたてかた．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

佐藤仁（2007）タイの環境政策と地方分権．寺尾・大塚（編）アジア諸国の分権化と環境政策．アジア経済研究所（印刷中）．

佐藤仁（2007）資源と民主主義：日本資源論の戦前と戦後．内堀基光（編）講座　資源人類学　第 1 巻　資源と人間．弘文堂（印刷中）．

佐藤仁（2007）津波被災地のモラルエコノミー．竹中千春ほか（編）市民社会．慶応大学出版会（印刷中）．

佐藤仁（2007）「国際援助」，「環境問題」，「資源管理」の各項．柳澤雅之ほか（編）新版　東南アジアを知る事典．平凡社（印刷中）．

鮫島弘光・小泉都（2008）ボルネオ熱帯林を利用するための「知識」と「技」．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

祖田亮次（2008）サラワクにおけるモノクロップ・プランテーションの拡大．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

藤田渡（2008）バリケード・裁判・森林認証――サラワクの原生林に刻みこまれたポリティクス．秋道智彌・市川昌広（編）東南アジアの森でなにがおきているか　－熱帯雨林とモンスーン林の諸相．人文書院（印刷中）．

Thesis

Doctoral degree

中川弥智子（2002 年度）マレーシア・サラワク州におけるフタバガキ科種子の対散布前種子捕食者戦略. pp 62．京都大学

田中憲蔵（2003 年度）サラワク熱帯雨林におけるフタバガキ科樹木の光合成に関する生態生理学的研究. pp200．愛媛大学

鮫島弘光（2005 年度）Interaction between migratory pollinator and forest trees in aseasonal tropical region. pp 87. 京都大学

竹内やよい（2005 年度）フタバガキ科 4 種における種子・花粉散布の生態的・遺伝的意義．pp 73．京都大学

饗庭正寛（2006 年度）Coexistence mechanisms of tropical tree species based on structural trade-offs 82p．京都大学

藤森直美（2006 年度）Mechanisms of population maintenance in sparsely distributed species, *Kalopanax pictus*．pp 94．京都大学

小泉都（2007 年度）Ethnobotany of the Penan Benalui of East Kalimantan, Indonesia．pp 126．京都大学

近藤（辻）祥子（2007 年度）Ecopysiological study on drought stress strategy of trees in humid and semi arid tropical ecosystems．pp 107．京都大学

Master's degree

田中洋（2004 年度）樹上性アリ類の共生系に及ぼす人為的撹乱の影響－ボルネオ低地林での研究－. pp 49. 名古屋大学

加藤裕美（2005 年度）熱帯雨林における定住狩猟採集民の生計戦略－ボルネオ・シハン社会における食物資源の獲得と消費．pp 120．京都大学

川口達也（2005 年度）マレーシア、キナバル山における陸生大型貧毛類の多様性と生活史．pp 44．横浜国立大学

土屋泰三（2005 年度）東南アジア熱帯産チョウ類にみられる警告色に関する生態学的研究．pp 53．京都大学

潮雅之（2006 年度）熱帯山地林における局所的土壌微生物群集の存在．pp 53．京都大学

半田千尋（2006 年度）東南アジア熱帯雨林におけるアリ-半翅目-植物相互作用系～森林ギャップの効果～. pp 62．京都大学

福田大介（2006 年度）ボルネオ島の植生モザイクに見られるコウモリと植物の相互作用．京都大学

松木悠（2006 年度）昆虫付着花粉の遺伝子型直接判別に基づく送粉者の送粉効率解析．広島大学

松本大吾（2006 年度）オオバギ *Macaranga*（トウダイグサ科）を餌資源として利用する植食性昆虫の種構成に関する研究．pp 42．京都大学

石田千香子（2007 年度）アリ植物オオバギ属（トウダイグサ科）における送粉様式の進化．京都大学

直江将司（2007 年度）森林の分断化は鳥散布樹木の更新に影響を及ぼすか？京都大学

Others

2002

市栄智明（2002）フタバガキ科巨大高木の資源利用．日本熱帯生態学会ニューズレター49：9-11

市岡孝朗（2002）地上 40m での昆虫調査: 熱帯低地フタバガキ林の林冠昆虫の生態．昆虫と自然 37：16-19

衣笠里美・藤吉正明・里村多香美・堀越孝雄（2002）山林火災後の植生回復における菌根菌の動態に関する研究（第 1 報）－緑化技術への応用を目指して－．環境科学総合研究所年報 21：73-84

佐藤仁（2002）資源・環境問題はなぜ放置されるのか．科学 2002 年 8 月号：787-791

佐藤仁（2002）資源管理の分権化を阻む「不足」意識．論座 2002 年 6 月号：108-115

戸田正憲（2002）IBOY（国際生物多様性観測年）．昆虫と自然 37：24-27

中静透（2002）これからの林業・林学と森林生態学．森林科学 36：39-42

2003

Inoue T (2003) Butterfly fauna in and near the Ogawa Forest Reserve. Bulletin of the Forestry and Forest Products research Institute 2: 237-246

衣笠里美・藤吉正明・里村多香美・堀越孝雄（2003）山林火災後の植生回復における菌根菌の動態に関する研究（第 2 報）－緑化技術への応用を目指して－．環境科学総合研究所年報 22：97-104

鮫島弘光（2003）ボルネオのオオミツバチ *Apis dorsata* F.と蜂蜜採集．熱帯生態学会ニューズレター　51

末吉昌宏・前藤薫・槇原寛・牧野俊一・祝輝男（2003）皆伐後の温帯落葉樹林の二次遷移に伴う双翅目昆虫群集の変化．森林総合研究所研究報告 2：171-191

中静透（2003）熱帯林の生物多様性−林冠という知られざる世界　「生物多様性の世界」人と自然の共生というパラダイムを目指して．第 17 回「大学と科学」公開シンポジウム講演収録集（株）クバプロ

半谷吾郎（2003）レッドリストの生き物たち 4「ヤクシマザル」．林業技術 733：38-39

2004

益守眞也・中静透・鈴木和夫（2004）第 12 回バイオリフォル・ジョグジャカルタ集会．熱帯林業 61: 69-72

2005

Akutsu K, Khen CV (2005) Assessment of the bioindicator values of flying insects at a higher taxonomic level for different logging schemes in the lowland tropical rain forests of Deramakot, Sabah, Malaysia. In: Lee YF, Chung AYC, Kitayama K (eds.) The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation In Tropical Rain Forests. 71-78. Forest Research Centre, Sandakan, Malaysia

Hasegawa M, Ito MT, Kitayama K, Seino T, Chung AYC (2005) Logging effects on soil macrofauna in the rain forests of Deramakot Forest Reserve, Sabah, Malaysia. In: Lee YF, Chung AYC, Kitayama K (eds.) The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation In Tropical Rain Forests. 53-60. Forest Research Centre, Sandakan, Malaysia

Inoue T (2005) Change in a butterfly community with forest growth in central Japan. Proceedings, 5th Asia-Pacific Congress of Entomology 19

Kitayama K, Nakazono E, Seino T, Matsubayashi H, Gobilik J, Ong R (2005) Landscape-level evaluation of carbon and biodiversity in the tropical rain forests of Deramakot Forest Reserve, Sabah, Malaysia. In: Lee YF, Chung AYC, Kitayama K (eds.) The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation In Tropical Rain Forests. 13-28. Forest Research Centre, Sandakan, Malaysia

Matsubayashi H, Lagan P, Majalap N, Tangah J, Sukor JRA, Kitayama K (2005) Diversity of mammalian species at natural licks in rain forest of Deramakot and their conservation. In: Lee YF, Chung AYC, Kitayama K (eds.)

The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation In Tropical Rain Forests. 61-70. Forest Research Centre, Sandakan, Malaysia

Seino T, Takyu M, Aiba S, Kitayama K, Ong RC (2005) Floristic composition, stand structure, and above-ground biomass of the tropical rain forests of Deramakot and Tangkulap Forest Reserve in Malaysia under different forest managements. In: Lee YF, Chung AYC, Kitayama K (eds.) The 2nd Workshop on Synergy between Carbon Management and Biodiversity Conservation In Tropical Rain Forests. 29-52. Forest Research Centre, Sandakan, Malaysia

揚妻直樹（2005）やくしかノート１（食物編）．生命の島 71：21-26

揚妻直樹（2005）やくしかノート２（遊動編）．生命の島 72：42-46

市栄智明（2005）環境ストレスと樹木の繁殖 －光合成産物の分配の視点から－．森林科学 45：18-24

大谷達也（2005）南限と北限のニホンザル．森林科学 45：58-62

中静透（2005）アジアの森林持続性と生物多様性．森林科学 43：68-72

長谷川弘・三谷和臣・岡野千裕（2005）開発途上国における農林業プロジェクトの環境経済評価手法と事例（国際協力機構客員研究報告書）．国際協力機構国際協力総合研修所

百瀬邦泰（2005）野生生物はどのような条件下で持続的に利用されているか：豊富な生物知識と生物多様性の効果．科学 75：542-546

2006

相場慎一郎（2006）熱帯林における樹木の幹肥大成長の季節性：デンドロメータによる研究．フェノロジー研究 41：28-31

赤尾健一（2006）環境と経済成長．環境経済・政策学会（編）環境経済・政策学の基礎知識．70-71．有斐閣

揚妻直樹（2006）やくしかノート３（あくび編）．生命の島 73：33-37

揚妻直樹（2006）やくしかノート４（お仕事編）．生命の島 74：59-63

揚妻直樹（2006）やくしかノート５（杉林編）．生命の島 75：87-92

揚妻直樹（2006）やくしかノート６（神様編）．生命の島 76：80-85

市川昌広（2006）地球研発．森に還る農地のモザイク．毎日新聞（京都版 7 月 1 日付）．

加藤裕美（2006）サラワクにおける定住狩猟採集民の生計戦略．JAMS News マレーシア研究会会報 35：13

加藤裕美（2006）森林資源の利用をめぐる狩猟採集民の市場経済への対応-ボルネオ・シハン社会の生存戦略．文化人類学研究 7：191

小泉都（2006）吹き矢：ボルネオのプナンの植物利用 1．植物の自然誌プランタ 104：55-58

小泉都（2006）軽建築：ボルネオのプナンの植物利用 2．植物の自然誌プランタ 105：53-56

小泉都（2006）食べ物：ボルネオのプナンの植物利用 3．植物の自然誌プランタ 106：53-58

柴田銃江・安井さち子（2006）小川群落保護林におけるコテングコウモリの樹冠部での偶発的捕獲． 東洋蝙蝠研究所紀要 5：23-25

中静透（2006）生態系長期モニタリングの意義と動向．生物多様性センターニューズレター20：3

中静透（2006）「生物多様性が減る」とはどういう問題なのか？関西自然保護機構会誌 28：3-7

松林尚志（2006）自動撮影カメラで動物の行動をはかる．森林科学 48：66

2007

大谷達也，揚妻直樹，揚妻－柳原芳美（2007）屋久島西部　世界自然遺産地域における森林利用の歴史．保全生態学研究 12：78-85

東條一史（2007）日本産森林依存性鳥類種数の推定．森林総合研究所研究報告 6(1)：9-26

山下　聡（2007）マレーシアでのキノコ調査を振り返って．日本菌学会ニュースレター2007 年 4 月号：11-12

In Press

赤尾健一・大沼あゆみ・長谷川弘・藤田渡・市川昌広・酒井章子・畑田彩（2008）どうすれば生物多様性を保全できるか？　－経済学編－．畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

揚妻直樹・井鷺裕司・丑丸敦史・北村俊平・酒井章子・清野達之・長池卓男・藤田渡・畑田彩（2008）生物多様性が減少すると何が起きるか？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．昭和堂.

市岡孝朗（印刷中）一斉開花するフタバガキ林の種子食昆虫．昆虫と自然 43（1）

市川昌広（印刷中）書評“History of the Borneo environment”(2005)Wadley R.L. edted. KITLV: Leiden.東南アジア研究.

市川昌広・小泉都・新山馨・中川弥智子・辻野亮・山下聡・畑田彩（2008）人間活動は生物多様性にどのような影響を与えるか？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版. 総合地球環境学研究所.

丑丸敦史（編集）地球研プロジェクト 2-2 作成　生物多様性写真集．CD-ROM.

丑丸敦史・山下聡・湯本貴和・馬場健・畑田彩（2008）生物多様性はなぜ減少しているのか？－生物の絶滅－．畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

加藤裕美（2007）ボルネオ島・シハンにおける資源へのアクセスと狩猟活動の変容．生態人類学ニュースレター13（印刷中）

加藤裕美（2007）ボルネオの豊かな動物世界．アジア・アフリカ地域研究 7（印刷中）

岸本圭子（印刷中）東南アジア熱帯林の林冠部における訪花性ハムシ類の餌資源利用様式．昆虫と自然 43

佐藤仁（2006）「サステイナビリティと資源の分配」（１）から（４）まで連載『サステナ』サステイナビリティ学連携研究機構.

佐藤仁（印刷中）タイ，シンガポール，マレーシアの援助政策．開発金融研究所報 35

中静透・相場慎一郎・井鷺裕司・畑田彩（2008）生物多様性とは何か？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

畑田彩・市岡孝朗・市川昌広（2008）地球上の生物はなぜ多種多様なのか？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

畑田彩・市川昌広・中静透（監修）（2008）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．全 11 章．総合地球環境学研究所.

畑田彩・市川昌広・山下聡・中静透（2008）生物多様性とどのように付き合っていくか　－まとめ－．畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

藤田渡・市川昌広・金沢謙太郎・畑田彩（2008）どうすれば生物多様性を保全できるか？　－社会制度編－．畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

百瀬邦泰・小泉都・嶋村鉄也・田中浩・湯本貴和・畑田彩（2008）生物多様性のもとでどのような文化が育まれてきたか？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－．CD-ROM　Windows & Mac ハイブリッド版．総合地球環境学研究所.

森野真理・清野達之・饗庭正寛・大沼あゆみ・畑田彩（2008）人間は生物多様性をどのように利用しているか？　畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレ

ゼン教材－. CD-ROM　Windows & Mac ハイブリッド版. 総合地球環境学研究所.

山下聡・揚妻直樹・柴田銃江・竹内やよい・武生雅明・金沢謙一郎・畑田彩（2008）どうすれば生物多様性を保全できるか？　－生態学編－. 畑田彩・市川昌広・中静透（監修）生物多様性の未来に向けて　－大学講義のためのプレゼン教材－. CD-ROM　Windows & Mac ハイブリッド版. 総合地球環境学研究所.

Prize

市川昌広（2004 年度）吉良賞　奨励賞. 日本熱帯生態学会
市川昌広（2005 年度）尾瀬賞. 財団法人尾瀬保護財団
百瀬邦安（2005 年度）吉良賞. 日本熱帯生態学会
潮雅之（2006 年度）奨励賞. 日本生態学会近畿地区会
小泉都（2006 年度）Student Paper Prize. 10th International Congress of Ethnobiology
藤田真梨子・松井淳・寺川眞理・駒井古実・湯本貴和. ポスター賞（優秀賞）.（2006 年度）日本生態学会
中静透（2007 年度）緑の学術賞. 内閣総理大臣

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