# THE IMPACT OF TROPICAL FOREST DISTURBANCE AND CONVERSION ON INSECT DIVERSITY IN COSTA RICA, CENTRAL AMERICA

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*The unsolved mysteries of the rain forest are formless and seductive. They are like unnamed islands hidden in the blank spaces of old maps, like dark shapes glimpsed descending the far wall of a reef into the abyss. They draw us forward and stir strange apprehensions. The unknown and prodigious are drugs to the scientific imagination stirring insatiable hunger with a single taste. In our hearts we hope we will never discover everything. We pray there will always be a world like this one at whose edge I sat in darkness. The rain forest in its richness is one of the last repositories on earth of that timeless dream.*

E.O. Wilson 'Storm over the Amazon' The Diversity of Life 1992

# DECLARATION

I am responsible for composing this thesis. It represents my own work and where the work of others has been used it is duly acknowledged.

Signed……. ….
Date……23.03.2001.……

# ABSTRACT

Costa Rica is internationally renowned for its rich diversity of flora and fauna. Whilst it has an effective protected areas system deforestation continues outside these areas. The landscape of northern Costa Rica has been greatly impacted by human activity. Pristine forest has been reduced to a mosaic of forest remnants, forest plantations, agriculture and pasture. Lack of information regarding the potential of this landscape to maintain biodiversity is a major barrier to conservation management.

The effects of anthropogenic forest disturbance on leaf litter invertebrates are investigated in a fragmented landscape in northern Costa Rica, Central America. Altogether, 16845 ants (Hymenoptera: Formicidae) representing 230 morphospecies and 1877 beetles (Coleoptera) representing 422 morphospecies were sampled from 500 pitfall traps. Samples were collected over a gradient of human disturbance with two field sites being located in each of the following land uses: primary forest (as a control), logged primary forest, secondary forest, *Gmelina arborea* plantation and cattle pasture. There were marked gradients in microclimate and vegetation structure over the gradient. A total of 1902 trees representing 102 tree species were recorded and their dbh measured. Analysis revealed the effects of human impact on tree species composition.

Ants were collected from five subfamilies and beetles from 26 families. Both ant and beetle species richness, abundance and composition changed with land use. Ants were significantly more abundant in pasture than in all other land uses, whereas beetle abundance was greatest in logged primary forest and primary forest and lower in all other land uses. Ant and beetle species richness was also significantly different between land uses, with the two invertebrate groups demonstrating similar patterns of change over the gradient. Examination of $\beta$ - diversity revealed lower similarity between control sites and sites of greater disturbance. Patterns of species composition were analysed for the ant and beetle assemblages, and cluster analyses using Morisita's Index showed clear groupings by land use and degree of human intervention. TWINSPAN analyses revealed the varying species responses to forest disturbance. Many species of ants and beetles were found to be specific to particular land uses or groups of land uses. These 'indicator species' may be useful in future assessments of forest disturbance.

Disturbance effects on species composition were mediated by seven important environmental and physical variables: tree species diversity, litter biomass, soil temperature, soil pH, soil organic matter, altitude and slope. Multivariate analyses revealed the importance of soil organic matter levels, tree species diversity and litter biomass in defining the primary and logged forest ant and beetle assemblages, while changes in soil temperature and soil pH were shown to be important factors in defining the plantation and pasture assemblages.

A reference collection of the ants and beetles collected during this study will be held in INBio, the National Institute of Biodiversity, in Costa Rica, Central America.

The results presented indicate the negative effects of forest disturbance and conversion to plantation and pasture on the leaf litter invertebrate assemblage. Ant and beetle species richness, composition and abundance is considerably altered. It appears that the mosaic of land uses present in this neotropical landscape may facilitate the conservation of leaf litter ant and beetle fauna. Nevertheless, it is evident that the remaining natural forest sites are especially important in their maintenance.

# RESUMEN

Costa Rica es reconocido internacionalmente por su riqueza y diversidad de flora y fauna. A pesar de que cuenta con un sistema efectivo de áreas protegidas, las deforestación continua afuera de estas áreas. El paisaje de la región norte de Costa Rica ha sido muy fragmentado por actividades humanas. Los bosques primarios se han reducido y han formado un mosaico de remanentes de bosque, plantaciones forestales, agricultura y potreros. La falta de información con respecto al potencial de este paisaje para mantener la biodiversidad es el mayor obstáculo para su conservación y manejo.

Los efectos de los disturbios antropogenicos del bosque en los invertebrados de la hojarasca fueron investigados en un paisaje fragmentado en el norte de Costa Rica, Centro América. Un total de 16845 hormigas (Hymenoptera: Formicidae) representaron 230 morfo-especies y 1877 escarabajos (Coleoptera) represntaron 422 morfo-especies fueron muestreados de un total de 500 trampas pitfall. Las muestras fueron colectadas sobre un gradiente de disturbio humano en dos sitios localizados en los siguientes usos de suelo: bosque primario (como control), bosque primario manejado, bosque secundario, plantación de *Gmelina arborea* y potreros. Los gradientes fueron marcados por el microclima y la estructura de la vegetación. Un total de 1902 arboles representaron 102 especies siendo registrados y medidos (dap). El análisis revelo que las especies de arboles muestraron patrones bien definidos sobre el gradiente de disturbio.

Las hormigas colectadas pertenecieron a 5 subfamilias y los escarabajos a 26 familias. La composición de especies y su abundancia de hormigas y escarabajos cambiaron dependiendo del uso del suelo. La riqueza de especies en hormigas fue significativamente más abundantes en el potrero que en los otros tipos de suelo, mientras que la abundancia de escarabajos fue mayor en el bosque primario conservado y manejado y menor en los otros usos de suelo. La riqueza de especies de hormigas y escarabajos resulto también ser significativamente diferente entre los usos del suelo, los dos grupos de invertebrados mostraron patrones similares de cambios sobre el gradiente. El análisis de la diversidad $\beta$- mostró baja similaridad entre el sitio control y los sitios con gran perturbación. Los patrones de la composición de especies fueron analizados para el ensamblaje de hormigas y escarabajos, y el análisis de cluster usando el índice de Morisita mostró un claro agrupamiento por el uso de tierra y el grado de perturbación humana. El análisis de TWINSPAN revelo la variación de especies en respuesta al disturbio del bosque. Se encontró que muchas especies de hormigas y escarabajos fueron especificas a un particular uso de suelo o grupos de uso de suelo. Estas 'especies indicadoras' pueden ser muy útiles en evaluaciones futuras de disturbios en bosques.

Los efectos del disturbo en la composición de especies fueron indicados por siete variables ambientales y físicas: diversidad de especies de arboles, biomasa de hojarasca, temperatura del suelo, pH del suelo, materia orgánica del suelo, altitud y pendiente. Los análisis multivariados mostraron la importancia de los niveles de materia orgánica, diversidad de especies de arboles y la biomasa de la hojarasca en la definición del ensamblaje de las hormigas y los escarabajos en bosques primarios primario y manejado mientras que los cambios en la temperatura del suelo y el pH fueron factores importantes en el ensamblaje en las plantaciones y potreros.

La colección de hormigas y escarabajos estará a cargo del Instituto Nacional de la Biodiversidad (INBio) en Heredia, Costa Rica, América Central.

Los resultados indican los efectos negativos del disturbio del bosque y su conversión de plantación a potrero en el ensamblaje de los invertebrados de la hojarasca. La riqueza de especies, composición y abundancia de hormigas y escarabajos es considerablemente alterada. Al parecer el uso de mosaicos de uso del suelo presente en este paisaje neotropical puede facilitar la conservación de la fauna de hormigas y escarabajos en la hojarasca. Sin embargo, es evidente que los sitios remanentes de bosque natural son especialmente importantes en su conservación.

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# CHAPTER 1

# NEOTROPICAL LANDSCAPES: TROPICAL FORESTS AND REALITY IN THE 21$^{ST}$ CENTURY

## 1.1 Research context and rationale

The impact of human activities on the environment is increasingly affecting natural landscapes. Throughout the humid tropics this is resulting in a significant alteration in the spatial distribution and composition of natural forest. Large areas of previously extensive forest are being rapidly changed into mosaics of forest fragments. This, inevitably, is leading to changes in the ecological processes that maintain biodiversity and ecosystem functioning.

It is estimated that by 1990, 24 percent of the world's lowland tropical forest had been cleared (Turner and Corlett 1996). The majority of this deforestation was carried out in order to provide agro-pastoral land and it is believed that the rate of forest removal is still accelerating (FAO 1999). Forest cover changed globally from 3,510,728 thousand hectares in 1990 to 3,454,382 thousand hectares in 1995, a loss of 56,346 thousand hectares. In Central and South America respectively, 4794 thousand hectares and 23,872 thousand hectares were lost during the same time period (FAO 1999).

With increasing population pressure the scale and intensity of impact is increasing. Forests are being cleared or disturbed for various reasons. In the developing world, small-scale agriculture is proving to be the principal tool of destruction, as landless peasants push the disturbance frontier ever further into the forest (Kaimovitz 1997). The other principal perpetrators of forest destruction in tropical regions are logging companies and cattle ranchers. The latter tend to clear-cut the forest, producing severe land degradation and lowering the viability and recovery rate of any further secondary forest regeneration; whilst the logging companies, depending upon their timber extraction methods and intensity of harvest, cause varying levels of damage but rarely complete forest removal. Their main impact is the opening of previously inaccessible forest land due to the construction of logging roads. Together with deliberate or lax national policies, this encourages colonist farmers to settle and clear land for crops.

This destruction of the forest has serious implications for forest biodiversity. Lowland tropical forests are known to have the richest species diversity of all the terrestrial ecosystems (INBio 2000), and as far as current research suggests, also of the aquatic ecosystems. Therefore, their destruction will cause the greatest threat to global biodiversity. These areas should be the first to be conserved; however, in many cases there are no remaining large undisturbed areas of such forests. A common landscape pattern in tropical areas is a pattern of remnant, often small and isolated forest fragments. As anthropogenic processes causing forest fragmentation become ever more widespread, these patches are becoming increasingly important in the conservation of ecosystems.

It is generally believed that changes in forest structure induced by isolation and fragmentation may cause disruption to the biological processes that maintain species diversity and ecosystem functioning. These processes, many of which are carried out by insects, include pollination, seed dispersal and nutrient cycling. As yet, very little is known about the effects of forest fragmentation, disturbance and conversion on invertebrates, although there is now little doubt that resulting changes in abundance and species richness in many insect groups does occur (Turner and Corlett 1996). The conservation value of forest fragments is believed to be high (Schelhas and Greenberg 1996), although an overall pattern of reduced species richness and simplification of community structure has been observed in various studies (Didham et al. 1996).

The rapid rate of forest loss in the neotropics over recent years, particularly in Central America, has prompted efforts to develop sustainable methods of forest management and conservation planning (e.g., MINAE-SINAC 1996, Maginnis et al. 1998). In Costa Rica the disturbed forest landscape is typical of the contemporary situation in many parts of the neotropics. It has been transformed into a mosaic of forest patches, forest plantations, smallholder agriculture, cattle ranching, and banana and other cash crop plantations. The region is renowned for its high species richness and endemism (Daily and Ehrlich 1995, Janzen 1987, Watson et al. 1998) and it is therefore critically important to determine the capacity of the remaining forest patches and converted forest to conserve the existing biodiversity. This thesis is concerned with examining the changes in forest biodiversity which occur as forest is converted into predominantly agrarian landscapes. It focuses on insect communities over a range of land uses which represent a gradient of human disturbance.

## 1.2 Forest fragmentation and disturbance

The advent of agribusiness, industrial forestry and colonisation has led to large-scale deforestation with clearings on the scale of $10^2$ to $10^5$ ha (Bierregaard et al. 1992). Some of the inevitable changes in the forest ecosystem are easy to predict. Population sizes of plants and animals will be reduced and this may cause an erosion of genetic diversity. Additionally the fact that many populations do not have a homogeneous spatial distribution will result in some species being absent from some remaining fragments simply because they were not in the patches of forest before fragmentation (Bierregaard et al. 1992). There are a multitude of mechanisms which should be considered when examining changes due to forest disturbance and isolation, and many are inter-related. For example, Terborgh (1992b) believes that the loss of large predators may have a destabilising effect on the populations of seed predators, which in turn may affect the tree species composition. Basic questions such as 'How large should a reserve be?' or 'What shape should a reserve be?' have been discussed at length (Bierregaard et al. 1992, Shafer 1990) but few answers have been provided by experimental data. It remains evident that small forest fragments may become the last refuges of many rain forest species. Their conservation in an ever expanding landscape of anthropogenic disturbance is imperative for this reason and in providing the 'seeds' from which to re-establish forest areas (Turner and Corlett 1996).

It is evident that only extensive tracts of forest can conserve a full complement of the indigenous biota of a region and, therefore, ensuring such areas remain intact must be the conservationist's first priority (Turner 1996). Unfortunately this is not always possible and the conservation value of the remaining forest mosaic, within the context of the socio-economic and cultural constraints present in each individual case, should be recognised. As Turner and Corlett (1996) assert 'fragments are better than nothing' and their presence in the landscape will, at the very least, provide a habitat for the persistence of some of the indigenous biota. In the absence of extensive forest areas, conservation planners must evaluate these areas both as potential species reserves and as possible sources for forest regeneration.

## 1.3 Introducing the research topic and approaches

The research presented here considers the effects of anthropogenic forest disturbance on the forest ecosystem in northern Costa Rica, Central America, focusing on leaf-litter invertebrates, a vital component in ecosystem functioning. It examines ten field sites, which ranged over a gradient of disturbance from pristine forest to pasture. Costa Rica is a country which harbours an incredibly rich biodiversity, but which has also been extensively impacted upon by humans. The north of Costa Rica is no exception and, in fact, unlike most regions of Costa Rica, this impact is intensified, as the area does not benefit from any significant protected areas. As a result, there exists no buffer against disturbance, giving urgent point to this research in assessing changes to the ecosystem in a disturbed landscape.

### 1.3.1 Aim

The aim of this study is to investigate human impact on a neotropical forest ecosystem. It employs the analysis of leaf-litter invertebrates to monitor disturbance in logged and converted forest, using primary forest as a control. Such investigation requires an assessment of patterns of species composition, richness, abundance and diversity. Two groups of invertebrates (Coleoptera and Hymenoptera: Formicidae) have been selected in order to achieve this. Ecological and environmental variables of the forest and converted forest are also examined in an attempt to explain the patterns and changes occurring in forest patches and converted forest after anthropogenic fragmentation, disturbance and conversion.

### 1.3.2 Objectives

The study has three major research objectives. These are outlined below:

1. To enhance knowledge of the consequences of human activities on natural ecosystems.

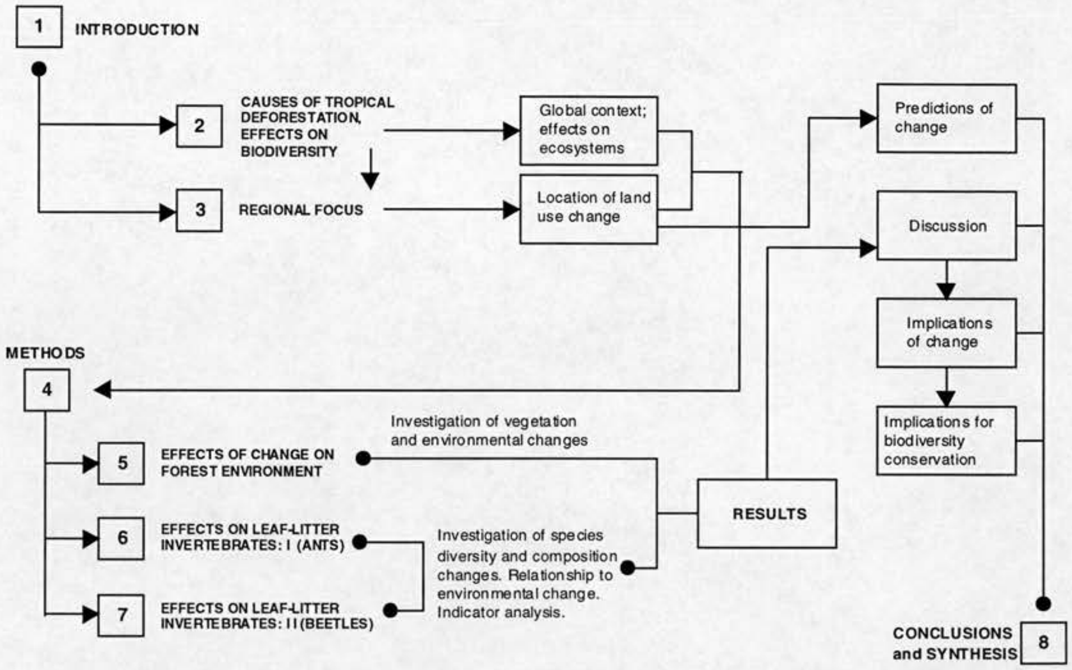
2. To examine how forest disturbance and clearance affect invertebrate diversity and composition. This is achieved by rapid inventory of leaf-litter invertebrates, principally ants (Hymenoptera: Formicidae) and beetles (Coleoptera), over a landscape gradient of human disturbance, allowing the following three issues to be addressed:

    - Ascertaining whether the change caused by human impact causes statistically significant differences in invertebrate communities.
    - Investigating the nature of these differences; identifying which invertebrates are important indicators of change.
    - Investigating changes in tree species composition after disturbance, and the corresponding effects on aspects of the forest environment.

3. To consider the implications that the results have for improved biodiversity conservation in forest and converted forest.

In order to meet these aims the research is divided into three parts: introductory chapters assessing the context and the contribution of earlier research, the fieldwork chapters, results and conclusions, and the final synthesis and discussion. This research format is detailed in Figure 1.1 below.

**Figure 1.1 A schematic view of the research structure**



This figure shows the research structure by chapter (indicated by numbered boxes). They are arranged to highlight the linkages between them and to illustrate the development of the argument. Chapter 1 introduces the research project and its context. Chapters 2 and 3 provide information to understand the nature of the problem and develop hypotheses. Chapter 4 describes the fieldwork strategy and the methods employed while chapters 5, 6 and 7 present the results obtained. Chapter 8 summarises the conclusions drawn from this work and considers the implications that the results have for improved conservation management.

## 1.4 Thesis outline

As summarised in Figure 1.1, this thesis is organised into eight chapters. The present introductory chapter provides a general context and explains briefly the rationale behind the study. Issues raised here are explored in more detail in chapters 2 and 3. In Chapter 2 the context of biodiversity and tropical forest is analysed further, their importance is highlighted, and insects are introduced as an important component of forest biodiversity. The relevant literature is also reviewed. Chapter 3 provides a detailed background to the study area, discussing pertinent issues in forestry and the area's importance for conservation.

In Chapter 4, the methodology and techniques used in this study are outlined. Field methods are presented along with laboratory analysis techniques. An examination is made of 'rapid biodiversity assessment' (RBA), the main methodological technique employed in this research.

Chapter 5 presents the environmental data collected. Tree species data are also presented, and discussed, along with an analysis of the impact of forest disturbance and conversion on a variety of environmental variables. Chapter 6 and 7 present the invertebrate data, examining the changes in species diversity, composition and abundance caused by human impact. The effects of environmental changes on the insect fauna are also assessed.

In conclusion, Chapter 8 draws together the study, linking the results presented into the context of tropical deforestation and forest conversion. It considers the implications that the results have for improved forest biodiversity conservation in lowland neotropical landscapes of disturbance.

# CHAPTER 2

# TROPICAL BIODIVERSITY AND CONSERVATION

## 2.1 THE CONCEPT OF BIODIVERSITY: its importance and conservation

The concept of biodiversity can be traced back as far as Aristotle, however it is perhaps the realisation that it is disappearing rapidly which has, in recent years, resulted in it becoming a much debated issue in ecological and popular literature (Wilson 1997). This focus is largely a result of the attention given to the increasing rate of species extinctions caused by deforestation and other human activities such as hunting, the introduction of exotics and habitat fragmentation (Lugo 1995). Many agencies are concentrating their attentions on the preservation of individual, often 'charismatic', species and in the public domain this is producing an increased desire for policies to reverse current trends of natural resource degradation. However, it is also important that this often biased attention to the more 'cuddly' members of the animal kingdom, be balanced by an awareness that species preservation can only be successful if a holistic approach to ecosystem management is applied. This chapter will consider the meaning of the term biodiversity and its importance as a concept, examine the reasons for its conservation and assess the usefulness of its monitoring in the planning of ecosystem conservation. It will also focus on invertebrate diversity as an example of monitoring biodiversity loss in landscapes of human disturbance.

### 2.1.1 The meaning of biodiversity

'Biodiversity' is commonly known as a synonym for the 'variety of life' (Gaston 1996). The Convention on Biological Diversity (1992) defines biological diversity as 'the variability among living organisms from all sources'. Glowka et al. (1994) extrapolates this to mean the variability of life in all its forms, levels and combinations. He divides it into three sections:

- ecosystem diversity - the variety and frequency of different ecosystems,
- species diversity - the frequency and diversity of different species, and
- genetic diversity - the frequency and diversity of different genes and/or genomes, i.e. the genetic diversity within each species Glowka et al. (1994).

DFID (1997) define it, more simply, as 'the diversity of all species of plant and animal; to the genetic variety within each individual species; and to the variety of the habitats that support them' whilst Gaston et al. (1991) define it as 'the variety, distribution and structure of plant and animal communities, including all vegetative stages, arranged in space over time that support self-sustaining populations of all natural and desirable naturalised plants and wild animals'. It is recognised that the variety and variability of genes, species, populations and ecosystems form a large part of our planet's essential natural resources.

The United Nations Conference on Environment and Development (UNCED), held in Rio de Janiero in 1992, established a basis for the global development of a more sustainable future. As a part of this the Convention on Biological Diversity was drawn up. This sets out actions for each signatory to ensure the sustainable use of species and habitats and to ensure an equitable sharing of the benefits arising from the utilisation of genetic resources (Ratcliffe 1995). The articles of the Convention consider identification and monitoring, in-situ and ex-situ conservation, sustainable use of the components of biological diversity, research and training, public education and awareness, impact assessment, technical and scientific co-operation, and financial mechanisms and resources (Ratcliffe 1995). Each of the signatories has agreed to develop a national plan for the conservation and sustainable use of biodiversity. The convention has been ratified by 114 States and by 1993 was international law (Glowka et al. 1994). However, in many areas the Convention provides guidance but lacks firm policies. For example, it requires the setting up of protected areas but does not specify how many. It has also been observed that its emphasis on action at a national level and its backing by widespread political momentum may result in the Convention being more useful as a political manifesto than as a guide to action (Glowka et al. 1994).

### 2.1.2 Does biodiversity matter?

The majority of the products which humans use in everyday life ultimately depend upon the planet's biological resources (Myers 1984, Ratcliffe 1995). This argument may be used to convince anthropocentric policymakers that the conservation of biodiversity is a global priority, however, there are many other factors which must be taken into account in its valuation.

'What is a species worth?' ask Kunin and Lawton (1996). Obviously it is a simple task to assign a value to a kilo of potatoes and extrapolate this valuation to the species as a whole. However, as biodiversity is a human construct its valuation becomes more complex when it is applied to species or ecosystems which are not directly used by humans. The valuation of biodiversity is concerned largely with unpriced goods and services (Kunin and Lawton 1996). It must also tackle the appropriate discounting of future developments and consider such concepts as the sustainability of human actions. Traditional economics and the calculation of such figures as cost-benefit analysis become increasingly complicated when considering such uncertain products. The case for the conservation of species can be divided into several sections, these include:

- the moral, ethical, cultural and religious considerations that humans have for the stewardship of life on earth,
- the fact that many organisms (e.g. flowers, butterflies) enrich the lives of many people,
- the 'existence value' of a species or habitat, demonstrated by people's willingness to contribute to conservation organisations which focus on 'charismatic' vertebrate species that they may never see,
- the usefulness of species, for example, in the search for new drugs, foods etc.,
- the provision by organisms of many 'ecosystem services' in the maintenance of the planet's life support systems, and

- the use of species diversity as a monitor of our use or abuse of the earth; thus a loss in species may indicate the unsustainability of our actions.
  (Kunin and Lawton 1996, Ehrlich and Ehrlich 1992)

Many of these justifications for the conservation of biodiversity can be easily refuted by sceptics and such global actors as economists and accountants. After all, it is unlikely that the relatively few species which are utilised by humans will become extinct. The pressing issue is the survival of the other species which fulfil no currently known or proven function for humans. It is this ignorance which we must consider. The majority of the earth's species have not been named let alone studied (Wilson 1988). The lack of knowledge surrounding the functioning of our own planet coupled with our inability to predict future needs necessitates an end to the anthropogenic indifference to species preservation and conservation which is permeating most of the world's cultures. Present knowledge does not provide us with the ability to rule out any habitat or species as unimportant. The issue is not whether species ought to be conserved but whether we, as the current tool of global change and degradation, have the sense and willpower to prevent further species loss in 'the face of ... collective global madness' (Kunin and Lawton 1996).

### 2.1.3 Tropical forest biodiversity and its conservation

The biodiversity of forested regions today is a result of complex historical interactions between physical, biological and social forces. Virtually all of the planet's forests have been anthropogenically altered at some point in history and the resulting landscape is a mosaic of unmanaged and managed habitats which vary in size, shape and arrangement (McNeely 1994). As yet only a very general characterisation of the types and varieties of ecosystems and organisms that exist in forests is possible (WCMC 1992).

Tropical forests contain the best known concentration of biodiversity on the planet (Huston 1994). The demand for the products and services of these tropical forests is continually increasing and solutions which conserve biodiversity whilst providing for human needs are urgently required. It is generally believed that remaining primary forest covers less than 9 million square kilometres out of the approximately 15 million or so that may once have existed according to bioclimatic data (Myers 1988). Myers (1988) also estimates that 1% of the biome is being deforested each year and that more than that is being seriously degraded. It is this destruction and degradation of the forest biome which is the main cause of species extinction. Tropical forest is home to at least two-thirds of the world's organisms, a number which probably exceeds 3 million species and that may even be 10 or more times greater than this (Raven 1988). To illustrate this Gentry (1986) quotes the example of the forested tracts of western Ecuador. This area is reputed to have once contained between 8,000 and 10,000 plant species with an endemism rate between 40 and 60%. Since 1960 95% of this area has been destroyed in order to establish banana plantations and various human settlements, and to exploit oil. By drawing upon the much debated theory of island biogeography Myers (1988) estimates that when a habitat has lost 90% of its extent it will eventually lose half its species. The accuracy of this may be doubtful however it is inevitable that a large number of species will be lost when such an extent of habitat is destroyed. The challenge to both science and land managers is the conservation of species within a framework which also provides the resources that the human population need and increasingly demand.

Lugo (1995) advocates a 'practical and sound approach to the conservation of tropical biodiversity' which he then defines as a type of 'ecosystem management' considering all organisms including people. This would focus on the whole ecosystem and emphasise the landscape and long-term phenomena. It would also advocate a balance between the strict exclusion zones of many nature preserves and the unrestricted development approaches that some areas have adopted for their tropical forest. Lugo (1995) focuses on the need for a paradigm shift from the view of tropical forests as fragile ecosystems to one which offers a more pro-active management. It can be argued that this shift has already occurred. Many systems and projects attempting various forms of tropical forest management already exist. These range from large scale timber operations, where carefully controlled management plans are utilised and extraction processes carried out to minimise disturbance to the remaining forest, to small scale extraction of non-timber forest products (NTPFs). Some areas should undoubtedly be left as pristine reserves but increasingly these can be allocated as core areas surrounded by buffer zones for sustained use by local people. The exclusion of local communities will never produce a spirit of forest stewardship in areas with no tradition of forest management and may well reduce it in those where it exists. Full participation of communities in the management of their forest resources is essential in order to ensure the future of both their landscape and their livelihood.

## 2.2 The impact of forest disturbance on biodiversity

### 2.2.1 Biodiversity loss in tropical forest fragments and converted forest

There have been numerous studies of biological diversity in fragments of tropical forest and in converted forest areas (Table 2.1). Factors such as fragment size, degree of isolation, and time since isolation from continuous forest may directly influence the biodiversity of a fragment while the method of land clearance when converting forest to agro-pastoral land has also been related to the degree of change in biodiversity after disturbance (Turner 1996).

**Table 2.1 Species richness studies in the disturbed tropical forest landscape**

| *STUDY* | *LOCALITY* | *TAXONOMIC GROUP* | *LANDSCAPE/ FRAGMENT SIZE* | *TIME SINCE FRAGMENTATION/ CONVERSION* |
|---|---|---|---|---|
| Bierregaard and Lovejoy 1989 | Manaus, Brasil | Forest birds | 3x1ha, 3x10ha and continuous | 0-3 years |
| Malcolm 1988 | Manaus, Brazil | Small mammals | 1x100ha, 3x10ha isolated;3x10ha, 3x100ha non-isolated | 2 months-3 years |
| Zimmerman and Bierregaard 1986 | Manaus, Brazil | Forest frogs | 1ha, 10ha and continuous | ? |
| Powell and Powell 1987, Becker et al. 1991 | Manaus, Brazil | Euglossine bees | 1ha, 10ha, 100ha, continuous forest | <2 years, 8 years |
| Klein 1989 | Manaus, Brazil | Dung and carrion beetles | 1ha, 10ha, continuous forest | 2-6 years |
| Fonseca de Souza and Brown 1984 | Manaus, Brazil | Termites | 1ha, 10ha, continuous forest | Isolated in 1980 |
| Willis, 1979 | Sao Paulo, Brazil | Forest birds | 21ha, <250ha, 1400ha | >100 years |
| Da Fonseca and Robinson 1990 | Atlantic forest, Brazil | Small mammals | 2x60-80ha, 3600 ha | 20 years |
| Kattan et al. 1994 | San Antonio, Colombia | Forest birds | Fragments totalling 700ha | 40-90 years |

| | | | | |
|---|---|---|---|---|
| Leck 1979 | Rio Palenque, Ecuador | Forest birds | 87ha | ? |
| Jullien and Thiollay 1996 | French Guiana | Raptors | Forest fragments and converted forest | various |
| Willis 1974; Karr 1982a | Barro Colorado Island, Panama | Forest birds | 1500ha | 60-70 years |
| Leigh et al. 1993 | Gatun Lake, Panama | Trees | 6x<1ha islands, continuous forest | 70-80 years |
| Daily and Ehrlich 1995 | Las Cruces, Costa Rica | Butterflies | 7 at 3-30ha, 1 of 227 ha | 18-33 years |
| Gallina et al. 1996 | Central Veracruz, Mexico | Mammals | Coffee plantations | >20 years |
| Estrada et al. 1993a,b 1994 | Las Tuxtlas, Mexico | Frugivorous mammals and birds, bats, non-flying mammals | 35 fragments of 1-2000 ha | 5-35 years |
| Askins et al. 1992 | St. Thomas and St. John, US Virgin Islands | Winter resident migratory birds | 2 islands compared, $71km^2$ (38% forested) vs. $50km^2$ (88% forested) | >100years |
| Brash 1987 | Puerto Rico | Land birds | $8628km^2$, 99.6% primary forest cleared, 32.7% forest cover | >100 years mostly |
| Newmark 1989 | Eastern Usambara Mountains, Tanzania | Forest birds | 0.1-30ha, 1520ha | 50-100 years |
| Corlett 1992, Turner et al. 1994 | Singapore | Vertebrates, plants | $620km^2$, 99.8%% primary forest clearance, c.5% forest cover | 100-150 years |
| Thiollay and Meyburg 1988 | Java | Forest falcons | 530, 15000, 25000, 36000 and 50000ha | Several centuries |
| Diamond et al. 1987 | Bogor Botanic Garden, Indonesia | Breeding birds | 86ha | 50 years |
| Pahl et al. 1988 | Queensland, Australia | Arboreal marsupials | 2.4-74ha | 2->28 years |
| Laurance 1990, 1994 | Queensland, Australia | Arboreal marsupials, small mammals | Continuous forest: 10 fragments of 1.4-590ha | 50-80 years |
| Dunstan and Fox 1996 | New South Wales, Australia | Small mammals | 0.3-29ha | Up to 175 years |

(adapted from Turner, 1996)

Table 2.1 demonstrates the strong bias of research towards birds and also the number of studies to come from one field area, the Biological Dynamics of Forest Fragments Project, Manaus, Brazil. There has been little work on invertebrates and, surprisingly, data regarding the effects of fragmentation on tropical forest plants also remain scarce. Some authors have begun to redress this imbalance (e.g. Didham 1997). This reliance on studies of one area (Manaus) and on one taxonomic group (birds) regarding the effects of fragmentation and disturbance on the biodiversity of tropical forest excludes many of the variables which may determine ecosystem changes. This is particularly true in the Manaus project that examined forest patches which have only been recently isolated. Obviously, the long-term changes that may occur in populations will not be reflected in these data and this enhances the need for monitoring.

Biodiversity loss was recorded in the majority of the studies listed in Table 2.1. For example, Leck (1979) reported a loss of 25 species of bird from an isolated 87ha forest fragment in just 5 years, whilst nearly a third of the species have been lost in 80 years from a fragmented area of montane forest at San Antonio in the Colombian Andes (Kattan et al. 1994). Barro Colorado Island, Panama lost 45 breeding bird species in the first 50 years of isolation. Other studies have demonstrated that diversity in small fragments is less than in larger ones although few studies have been entirely rigorous in their methodology (Turner, 1996). Turner (1996) also believes that more than just records of species numbers are required. A change in emphasis in order to decipher the underlying mechanisms of species loss in forest fragments is needed. Additionally, the identification of the species which will be most at risk of extinction should also be a priority.

### 2.2.2 Mechanisms of species loss

It is accepted that logging, forest fragmentation and forest conversion to plantation and pasture will, in almost all cases, cause a reduction in species diversity. There are many mechanisms of species loss in tropical forest some of which will be discussed below:

- **Deforestation-related disturbance**; due to the heterogeneous distribution of most forest species, the destruction of a certain area of forest may result in the loss of certain species from the remaining fragment. It is often assumed that remaining forest patches form a matrix of undisturbed fragments, however, the reality is more complex (Turner 1996). Factors such as tree felling, hunting and other anthropogenic influences will affect the structure of the fragment and ultimately its biodiversity.

- **Viability of fragment sizes**; it is assumed that as a fragment becomes smaller the population size will be restricted. Eventually it will fall below viable levels and extinction within the fragment will ensue. Genetic drift and in-breeding reducing genetic variation may also become a problem by causing increased homozygosity and eventually reduced population fitness (Caughley 1994).

- **Reduced immigration**; if the deforested matrix is inhospitable to forest species little or no immigration of individuals will occur to colonise fragments after isolation (Turner, 1996). The ability to move between fragments is species dependant. Klein (1989) shows that forest beetles are markedly affected by a break of 100m in forest cover. This is reinforced by the work of Bierregaard et al. (1992) who found that forest birds were similarly restricted. The distance between forest patches has also been shown to affect migration and therefore species richness. Some studies have examined the possibility that the viability of fragments may be increased by improving their connectedness through the utilisation of corridors of trees between patches (Laurance 1990, Daily and Ehrlich 1995). This has also been implied by results from work showing the paucity of mammalian rain forest specialists in unconnected monsoon forest fragments in Australia (Bowman and Woinarski 1994). Another important effect may be caused by changes in tree composition. Many tree species are widely distributed and therefore rare over small distances. In isolated fragments their pollination dynamics may be affected therefore reducing reproduction and imminently reducing population numbers. As plants are related mutualistically to the other components of the environment, it is probable that this change in forest structure will affect the ecosystem as a whole.

- **Edge effects**; the edges of fragments, particularly where they meet non-forest vegetation, represent major transition zones. The forest microclimate is usually hotter, drier and brighter nearer the edge (Kapos 1989). This may cause increased mortality of tree species although as the edge develops the impact lessens as both the understorey vegetation and trees form a barrier of increasing density between the forest and non-forest landscape (pers. observ.). The importance of an edge becomes greater as the fragment decreases in size and in small fragments the edge effects become highly influential (Murcia 1995). Where edge effects are substantial tree mortality, microclimate changes and other factors, such as, windthrow may combine to cause further erosion of the fragment size.

### 2.2.3 Species conservation within the disturbed forest landscape

Given the enormous biodiversity of tropical rain forest it is evident that ex-situ conservation methods alone will not be sufficient in the struggle to conserve species (Turner and Corlett 1996). This necessitates the use of existing forest and increasingly existing forest fragments as species reserves. Forest fragments within a mosaic of other land uses can provide a safety net for many species and perhaps a 'breathing space for conservationists to plan strategies for preventing the loss of the species concerned' (Turner and Corlett 1996).

It is safe to conclude that forest fragmentation and conversion pose a significant threat to biodiversity. The degree of the threat will however depend upon numerous biological and environmental factors which need to be understood in order to generalise for any one case study. The mechanisms producing local species extinctions are little known whilst the quantification of the factors which affect biodiversity, such as, the restriction of population size, forest edge effects, the negative effects of an inhospitable environment caused by forest conversion and invasion by exotic species is not yet possible. Turner (1996) concludes that rare and patchily distributed species, and those with large range or specialist habitats are more at risk from the effects of forest fragmentation and conversion.

## 2.3 The assessment of biodiversity

There has been much concern expressed regarding the effects of forest disturbance and clearance on biodiversity (Lawton et al. 1998). However, scientific data regarding its impact remain scarce. General data on global diversity exists in greater volumes for the plant world and groups such as the vertebrates, particularly mammals. There has been less work carried out in order to investigate effects on invertebrates (Lawton et al. 1998). On the whole, standardised methods used to document population changes are not widespread and where they do exist are often little known (Heyer et al. 1994).

As discussed, it is generally agreed that a reduction in biodiversity will occur with increasing disturbance of natural ecosystems and that this change will ultimately affect the ways in which ecosystems continue to function. This impact provides an urgency for scientists to understand what exactly is being lost and how this will affect the planet before it is too late. Studies of the abundance and distribution of species have already provided a wealth of basic knowledge and resulted in the development of ecological and evolutionary theory. Knowledge of which species occur, and where, is essential to an understanding of the intricacies of biological diversity (Heyer et al. 1994). Species lists of some organisms (e.g. butterflies, monkeys, birds and trees) exist for many sites, most of these in the developed world, but comparable data for the majority of the world's biota are lacking. This, coupled with a probable global species decline due to anthropogenic disturbance provide ever more impetus for monitoring species status, particularly little studied groups, such as insects, in the various biomes of the world.

### 2.3.1 Purpose of biodiversity assessment

The simple need for knowledge of the world's biological diversity provides sufficient impetus to carry out studies into biodiversity. However, as ecosystems are increasingly disturbed the urgency of this task increases. Recent work by the UK's Department for International Development recommends that biodiversity assessments should be carried out to fulfil certain specific purposes at various research levels (Watt et al. 1998). These are described below:

| ***Purpose of biodiversity assessment:*** | ***Level of assessment:*** |
|---|---|
| • conservation, | • international, |
| • development, | • national, |
| • commercial, and | • regional, |
| • social. | • local, |
| | • community, and |
| | • household. |

Before any assessment of biodiversity it is essential that both the purpose and the level of assessment be decided and that relevant user groups and stakeholders be identified. The specific biodiversity information needs (BINs) should also be pin-pointed and the relevant approaches to the assessment be outlined. The main purposes for biodiversity assessment are identified by Watt et al. (1998) as:

- to identify areas for management or protection,
- to define how to manage these areas,
- to assess the impacts of management or external factors (monitoring), and
- to increase global knowledge of biological diversity for its own sake.

These points can be applied at all the research levels mentioned above. At the regional scale and above biodiversity information is needed for policy making whereas at the local level and down biodiversity information is needed more for making practical management decisions. The major BINs can be summarised as:

- distribution and status of species and ecosystems,
- abundance and population structure of species, and
- distinctiveness and functioning of ecosystems. (Watt et al. 1998)

This study focuses on the conservation of biodiversity. The data are useful at an international level to assess priorities such as the focusing of conservation effort/pressure. They are also useful at a national level, in the host country, in order to fulfil the information needs required as, for example, signatories to the Biodiversity Convention (UNCED 1992) and in the certification of timber as being from a sustainably managed forest (FSC 2000). In addition, the information can be used in planning the location of national parks and in deciding what protection status, if any, the area of study affords. However, it is hoped that ultimately the data will be most useful as a local tool for forest management planning, effective resource use and resource base maintenance. Management needs, in terms of determining the methods and levels of utilisation that maintain biodiversity, are provided.

### 2.3.2 Monitoring the biodiversity of invertebrates

The components of biodiversity are being disrupted through human utilisation and management. This section provides a brief overview of existing work examining the effects such actions are having on insect diversity.

The monitoring and conservation of tropical insect faunas has received less attention than many other groups (Janzen 1987, Didham 1997). Fortunately conservation efforts focused upon entire ecosystems or vertebrate populations have implicitly conserved the insects present in those areas. Tropical wildlands contain a wealth of components from repositories of genes, seeds and interactions to watershed protection and recreation (Janzen 1987). However, insects have rarely been mentioned explicitly in such lists of conservation reasons. Attractive images such as towering rainforest and 'charismatic' large mammals are repeatedly promoted whilst the 'bugs' of the world are ignored. The assumption that insects will look after themselves within any conservation area may be short-sighted and it should be realised that in any habitat insects are an essential component in ecosystem function. Janzen (1987) describes a few of the essential functions that would be lost without the ecological services that invertebrates provide. These are summarised below:

- a removal of insects that are pollinators would, obviously, result in an altered and diminished flora. Their removal would also have a devastating effect on important crops,
- a loss of insects would result in a loss of insectivorous birds and other small carnivores,

- a loss of particular insect species would cause an imbalance in population dynamics and may result in increased seed predation or pest infestations by insects who no longer have their own predator,
- the untapped information possessed by insects would be lost as insect diversity decreases.

Invertebrate responses to forest fragmentation and conversion have been documented in various global habitats (e.g. Hopkins and Webb 1984, Webb 1984, Main 1987, Bauer 1989, Klein 1989, Becker et al. 1991, Verhaag 1991, Aizen and Feinsinger 1994, Daily and Ehrlich 1995, Gallina et al. 1996, Jullien et al. 1996, Brown and Hutchings 1997, Didham 1997, Malcolm 1997, Kotze and Samways 1999, Bolger et al. 2000). In fragmented and disturbed habitats many factors other than area come into effect. Habitat availability and suitability is particularly important for invertebrate populations in small fragments. Bach (1988) showed that three closely related species of chrysomelid beetles which feed on the same host plant had different population densities in habitat patches of different sizes which indicates some form of spatial-temporal interaction. Additionally, distance to nearest source population may be a better determinant of population size than habitat area, habitat heterogeneity or plant species richness (e.g. Launer and Murphy 1994).

Species richness and abundance are also affected by forest fragmentation and conversion. Termites show a significant and positive species-area relationship in forest fragments (Souza and Brown, 1994). Harper (1989) found that army ants had disappeared from some small forest fragments in Amazonia as did the leaf-cutter ant *Atta cephalotes* (Vasconcelos 1988). However, another species of leaf cutter ant, *A. sexdens*, showed no change in colony density in small fragments (Vasconcelos 1988). It appears that pollinating insects are greatly affected by forest fragmentation (Didham 1997). The abundance and species richness of native flower pollinators in Argentina was significantly lower in small forest fragments (<1ha) than in large fragments (>2ha)( Aizen and Feinsinger, 1994).

Didham (1997) concludes that scale is the most important factor in the study of invertebrate diversity and reponses to forest fragmentation. The scale of fragmentation, fragment area, edge, isolation, shape and connectivity all affect ecosystem impact and the diversity of the fragment components. Further results documenting the effects of forest disturbance on invertebrates also demonstrate changes in invertebrate diversity (e.g. Holloway et al. 1992, Roth et al. 1994, Watt et al. 1997, Lawton et al. 1998, Vasconcelos et al. 2000). These data can provide essential information in the study of human impacts on ecosystems and can also be used in the development of conservation strategies for mosaics of different land uses and for individual habitats, which contain varying levels of anthropogenic disturbance (Roth et al. 1994).

## 2.4 Island biogeography and biodiversity

In many parts of the tropics a forest landscape of patches of various sizes surrounded by anthropogenically altered land is becoming a common scenario and is increasing in its conservation importance. As this pattern becomes the rule rather than the exception it is essential that its conservation value is assessed and monitored. In the near future this landscape type may be the only one conservationists have for the preservation of the many species that rely on the forest for survival. With this in mind there have been various studies regarding the design of nature reserves and the viability of different sizes of forest fragments for species conservation (e.g. Pickett and Thompson 1978, Simberloff and Abele 1976 and 1982, Zimmerman and Bierregaard 1986). The ideas and theories developed to tackle the problems posed by the fragmentation of natural landscapes have frequently focused upon the tenets of the equilibrium theory of island biogeography (MacArthur and Wilson 1967). The relevance of the equilibrium theory of island biogeography and species-area relations to conservation planning and the maintenance of biodiversity, its subsequent modifications and extensions, and the arguments presented by its critics will be outlined below.

### 2.4.1 The equilibrium theory

The equilibrium theory of island biogeography was advanced to explain the observation that the number of species on an island generally increases with the increasing area of the island (Zimmerman and Bierregaard 1986). The theory proposes that an island's biota is determined by a dynamic balance between the immigration of new species to the island and the extinction of the species already present. An upper limit is set by the area of the island and the probability of species extinction will increase with smaller population sizes (Wilcox 1980). This implies that species turnover rates on smaller islands will be greater and that colonisation success will be reduced depending on the isolation of the island. The biota of more isolated islands will equilibrate at lower species richness levels than those of less isolated islands (Zimmerman and Bierregaard 1986). The theory relates the species richness of islands mathematically to area using the equation: $S = kAz$, where $S$ = species number; $A$ = area; and $k$ and $z$ are constants.

### 2.4.2 The design of nature reserves

Biogeographical theory is generally considered to be useful in the design of nature reserves. The MacArthur and Wilson equilibrium theory of island biogeography (1967) was seen as particularly suitable for reserve design due to the similarity between oceanic islands and areas of natural landscape surrounded by expanses of culturally modified habitat (Pickett and Thompson 1978). Various authors (e.g. Diamond 1976, Diamond and May 1981) advocated the production of guidelines for reserve design based upon this theory. The aim was to find a relationship that was more predictive and answered more complex questions than the simple assertion that large areas will hold more species than small areas. Diamond and May (1981) were seeking answers to such questions as:

- What fraction of its initial biota will a reserve eventually save and how rapidly will the remainder become extinct?
- How many species will survive in a reserve of a particular size?

Ecologists promoted species-area relationships derived from the equilibrium theory as tools for conservationists to maintain species diversity. There has been extensive mathematical modification of the theory and species-area regressions have been applied to recommend reserve size and predict their efficiency in species diversity maintenance after fragmentation (Zimmerman and Bierregaard 1986). The theory was soon promoted and both quoted regularly in the literature and readily used by conservationists and ecologists. Indeed Zimmerman and Bierregaard (1986) believe that it received 'paradigm status'. However ideas are now changing and many field ecologists are demanding a return to reality and a move away from theoretical manipulations

(Simberloff 1985). Simberloff and Abele (1976) point out that the equilibrium theory of biogeography was rarely properly tested. Margules et al. (1982) add that to demonstrate the applicability of the model it would be necessary to show a close correlation between island area and species richness, a constant species number over time, and an appreciable species turnover. Gilbert (1980) asserts that no one has, as yet, shown this.

### 2.4.3 The SLOSS concept

In much of the literature suggesting the application of the equilibrium theory of biogeography to the design of nature reserves, a frequent recommendation is that a single large refuges will maintain more species than two or more small ones with total area equal to that of the single large one (Diamond and May 1976, Prance 1982). The question of a single large or several small refuges has become represented by the acronym SLOSS. May (1975) states 'in cases where one large area is unfeasible, it must be realised that several small areas, adding up to the same total area as the single large area, are not biogeographically equivalent to it: they will tend to support a smaller species total'. However, this is quickly refuted by Simberloff and Abele (1976) who conclude that the theory of biogeography is neutral with respect to SLOSS. Depending upon the gradient of colonising abilities among species in the available pool the theory can predict that several small refuges will maintain more species than will one large one of equal area, or vice versa. However, Cole (1981) quotes them as having asserted that several small islands do in fact maintain greater species diversity and lists the following to illustrate that several small reserves are not necessarily the best conservation strategy:

- a system of small refuges may not preserve those species which require a minimum area or population size for survival,
- small refuges will be less likely to preserve all trophic levels,
- extinction would proceed more rapidly in the set of small refuges, and
- fragmentation of available refuge area is an irreversible strategy.

Simberloff and Abele (1982) conclude that not a single case which directly addresses SLOSS demonstrates an example where one large site unequivocally excels several small ones, but that many do exist showing that several small ones contain more species than one large one. Cole (1981) concludes the opposite, that larger refuges or islands will preserve more species. The debate becomes somewhat alarming when Simberloff and Abele (1982) quote Cole (1981) as stating that 'fragmentation of a potential refuge', presumably with the aim of enhancing species diversity and abundance maintenance, 'might be the wrong management strategy'. Simberloff and Abele (1982) are unequivocal by stating that indeed fragmentation may be incorrect but that equally it may be correct and that a firm conclusion cannot be drawn from the existing data. This assertion made within an argument which, on all sides, has better nature reserve planning and management as its focus should be regarded with caution. When can habitat destruction ever be sanctioned in the name of better conservation practises?

A consensus that both the equilibrium theory and the species-area relationship cannot be used as ecological justification for the preservation of large areas over several small areas of total equivalent area or vice versa has been reached by many (e.g. Higgs 1981 and Mader 1984). Haila (1983) concluded that 'the relation between *S* and *A* is indirect and is mediated by a chain of interrelated factors that comprise habitat composition differences in species-specific colonisation probabilities and species abundance relations'. The most recent island and habitat fragment biogeographic studies now consider the more specific autoecological factors of the species involved rather than simply area (Zimmerman and Bierregaard 1986). As Williamson (1989) concludes 'the MacArthur and Wilson theory today: true but trivial'. Biogeography must continue with its search for a simple set of explanations for the patterns of species but factors such as habitat heterogeneity and population dynamics must also be taken into account.

### 2.4.4 Relevance today

Zimmerman and Bierregaard (1986) have demonstrated the unreliability of simplistic species-area data in their study predicting the area needed to conserve species of Amazonian frogs. They believe their results lack relevance but, when combined with autecological information such as critical breeding habitat and high quality habitat, can provide a more accurate prediction for the design of nature reserves. They do not negate the value of the minimum area requirement but acknowledge the need for the consideration of a greater range of factors. One illustration of this *neo-biogeography* is given by Lynch and Whigham (1984) who used point surveys to examine the abundance and diversity of forest birds in relation to size, degree of isolation, floristics, physiognomy, and successional maturity of various forest patches. They consider structural and floristic characteristics as more important in determining species composition and the local abundance of individual species than patch area. They conclude that in many cases the most successful conservation strategy is to preserve the maximum total amount of breeding habitat rather than placing the emphasis on the area of each individual forest fragment. This conclusion obviously directly relates to their study of birds, perhaps with a less mobile fauna individual fragments again become more critical. From a biological point of view the simplest explanation for the distribution of species is that they occur 'in those habitats where the ecological conditions allow them to live and reproduce successfully, and that their distribution reflects the distribution of the preferred habitats' (Tuomisto and Ruokolainen 1997). Tuomisto and Ruokolainen (1997) believe that both biogeographical and biodiversity studies in the neotropics would benefit from a more rigorous analysis of present ecological conditions and their corresponding influence on the biota. It is becoming increasingly evident that biogeographical conclusions regarding species distribution patterns cannot be made without more detailed consideration of the ecological heterogeneity of a landscape.

## 2.5 Synopsis

This chapter has presented an overview of the main issues surrounding the theme of this thesis. Human impact, particularly on forests, may seriously compromise biodiversity. Various theories have been provided to explain species loss after disturbance and also to provide predictions for the biodiversity conservation potential of disturbed and fragmented habitats. A review of these reveals that none has provided a satisfactory solution to the dilemma of biodiversity conservation in a world of human intervention. It is concluded that a more rigorous analysis of present ecological conditions and their corresponding influence on the biota would benefit both biogeographical and biodiversity studies.

In order to assess the impact of disturbance on forest biodiversity, this study has carried out an analysis of present ecological conditions over a series of land uses, including forest and converted forest, and measured their corresponding influence on the biota, in this case, insect communities. It has employed a simple, repeatable, rapid biodiversity assessment methodology to provide baseline data in order to document the effects of disturbance on forest invertebrates and to assess their usefulness in monitoring human impact. The following chapter presents a detailed background of the mosaic of land uses present in the study area, discussing pertinent issues in forestry and the area's importance for conservation.

# CHAPTER 3

# BIODIVERSITY CONSERVATION IN COSTA RICAN FOREST AND CONVERTED FOREST: BACKGROUND AND STUDY SITES

## 3.1 Introduction

Costa Rica lies to the south of the Central American isthmus, the narrow strip of land which links the biogeographically distinct land areas of North and South America. This position, coupled with its varied physical environment, has resulted in a rich and diverse flora and fauna. Costa Rica is well known for its system of protected forest areas but less generally known is its dramatic rate of deforestation outwith these protected areas. The present endangerment of Costa Rica's natural wealth due to human intervention makes it essential that action be taken both to measure and monitor its biodiversity in order to document impact and encourage better resource management. This chapter examines the importance of Costa Rica, not only within the context of the global struggle to preserve forest biodiversity, but also from a national perspective in order to examine the history and reasons behind the development model adopted. It discusses the physical, environmental and social landscape, focussing on the forest resource and the policies which surround it. The area of study chosen for this research is introduced and discussed within this context.

## 3.2 The physical environment of Costa Rica

Costa Rica has a total land area of 51,000 km² and a population of 3.5 million (Rachowski 1997). It is bordered to the north by Nicaragua and to the east by Panama and has both a Caribbean and a Pacific coast (Figure 3.1). Geographic co-ordinates are 8°03' to 11°13' N latitude and 82°32' to 85°57'W longitude. Costa Rica's greatest length

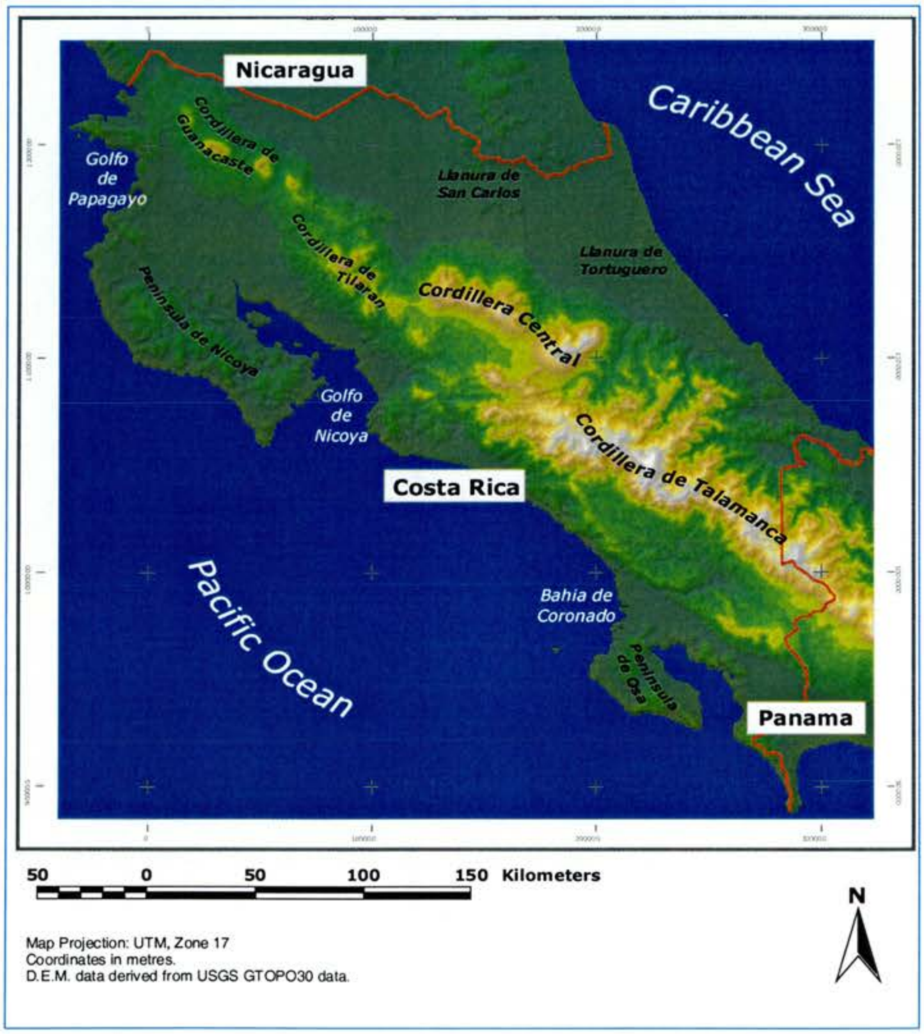
**Figure 3.1 Map of Costa Rica**

Source: Magellan Geographix 1992

is 480 km on a north-west to south-east axis while the shortest distance between the Pacific and Caribbean coasts is only 188 km (Hartshorn et al. 1982)(Figure 3.1). A series of volcanic mountain chains runs from the Nicaraguan border in the north-west to the

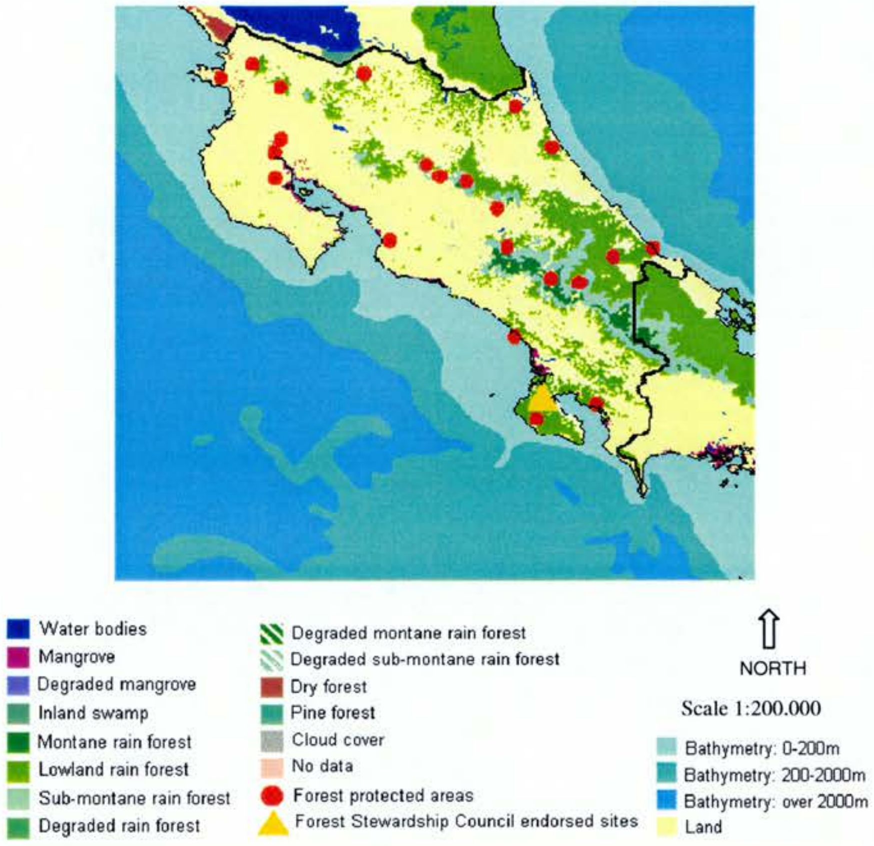
Panamanian border in the south-east, dividing the country in two. The highest peak being Volcan Chirripó (3818 m) within the Talamanca range towards the south of the country. In the centre of these ranges is a high-altitude 'inter-montane' valley where more than 60 percent of the population lives (Watson et al. 1998). This is situated between 1000 and 1400 metres above sea level and consists of fertile volcanic soils. Extensive lowlands occur in northern Costa Rica, extending from the Cordillera de Guanacaste foothills to the Caribbean coast (Figure 3.2). These extensive lowlands cover about 20 percent of the country (Hartshorn et al. 1982). The current forest area reflects the determining constraints of the physical environment, together with the expansion of human disturbance from the core areas of initial colonisation (Figure 3.3).

## Figure 3.2 Topographic map of Costa Rica



Map Projection: UTM, Zone 17
Coordinates in metres.
D.E.M. data derived from USGS GTOPO30 data.

**Figure 3.3 Forest cover in Costa Rica**



Adapted from: Ministerio de Recursos Naturales, Energía y Minas, Dirección General Forestal, Costa Rica (1988) *Mapa de Cobertura Boscosa de Costa Rica (+60% densidad)*; including additional data from *Mapa Ecológico -República de Costa Rica* based on Holdridge Life Zones.

Source: WCMC 1996

### 3.2.1 Climate

Costa Rica is situated entirely within the tropical latitudinal region although it possesses great climatic diversity. Variations in altitude and climate have created 12 'life zones' (Holdridge 1971), and at least three rainfall patterns (Watson et al. 1998). The national average annual rainfall is 3,300 mm, one of the highest in the world (Watson et al. 1998). Costa Rican mean annual temperatures range from about 26°C on the Caribbean coast and 27.8°C on the warmer Pacific coast to about 4.5°C at the highest elevation on Volcan Chirripó (3818m). Annual ranges of mean monthly temperatures are as little as

1°C in the Central Valley to as much as 3.7°C in the northern Pacific lowlands (Hartshorn et al. 1982).

As Costa Rica is so narrow the climate is strongly influenced by marine air masses. When including the large freshwater Lake Nicaragua, no point in the country is less than 80 km from a major water body. This results in marine tropical rainfall conditions over the entire country (Hartshorn et al. 1982). No point in the country averages less than 1350 mm of annual rainfall while high rainfall areas can record more than 5000 mm per year. There are two rainfall regimes, the Atlantic and the Pacific, but both are founded on a single, predictable pattern. The Pacific regime, which is modified by rain shadow and valley effects, has a predictable pattern of extended periods of heavy rains between late April or early May and mid-November (Hartshorn et al. 1982). In the Atlantic regime, this pattern is overlain by a secondary pattern involving warm temperate climatic influences. From mid-November to early May the Subtropical high-pressure belt of the northern hemisphere is drawn southwards over Costa Rica. This results in periods of lower air temperatures and stronger winds which result in heavier rains over the Caribbean coastal plain, foothills and eastern mountain exposures.

Wherever fogs and mists occur frequently, such as on windward and upper mountain slopes in the condensation or 'cloud belt', they provide a significant source of moisture not recorded by standard rainfall measures. This moisture condenses on foliage and drips to the ground providing an important addition to rainfall in upper watershed regions (Plate 3.1). Cloud forest condensation is believed to maintain a base flow in rivers during dry season months when little rainfall occurs but cloud and mist are abundant (Hartshorn et al. 1982). This climate has dictated the vegetation formations of Costa Rica from the dry forests of Guanacaste to the cloud forests of Monteverde, as the 'Holdridge Life Zone' vegetation classification system has outlined. The system is based on climatic data and was developed in Costa Rica.

### 3.2.2 Geological landscape

The formation of the Costa Rican portion of the Central American isthmus began in the late Jurassic (approximately 150 million years ago). Massive geological folding created islands in the oceanic gap between the Panamanian tip of South America and Central America which was north of present day Costa Rica. This chain of islands now makes up part of the Santa Elena, Nicoya, Osa and Burica peninsulas (Weyl, 1980). Costa Rica's oldest igneous rocks and sedimentary deposits date to these islands, known as the Western Archipelago, and although not yet forming a continuous land mass they probably served in the first mixing of Neartic and Neotropical biota by 'island-hopping' flora and fauna (Hartshorn et al. 1982).

**Plate 3.1 Monteverde Cloud Forest.** View of upper montane forest showing plant formations typical of this altitude and climate.

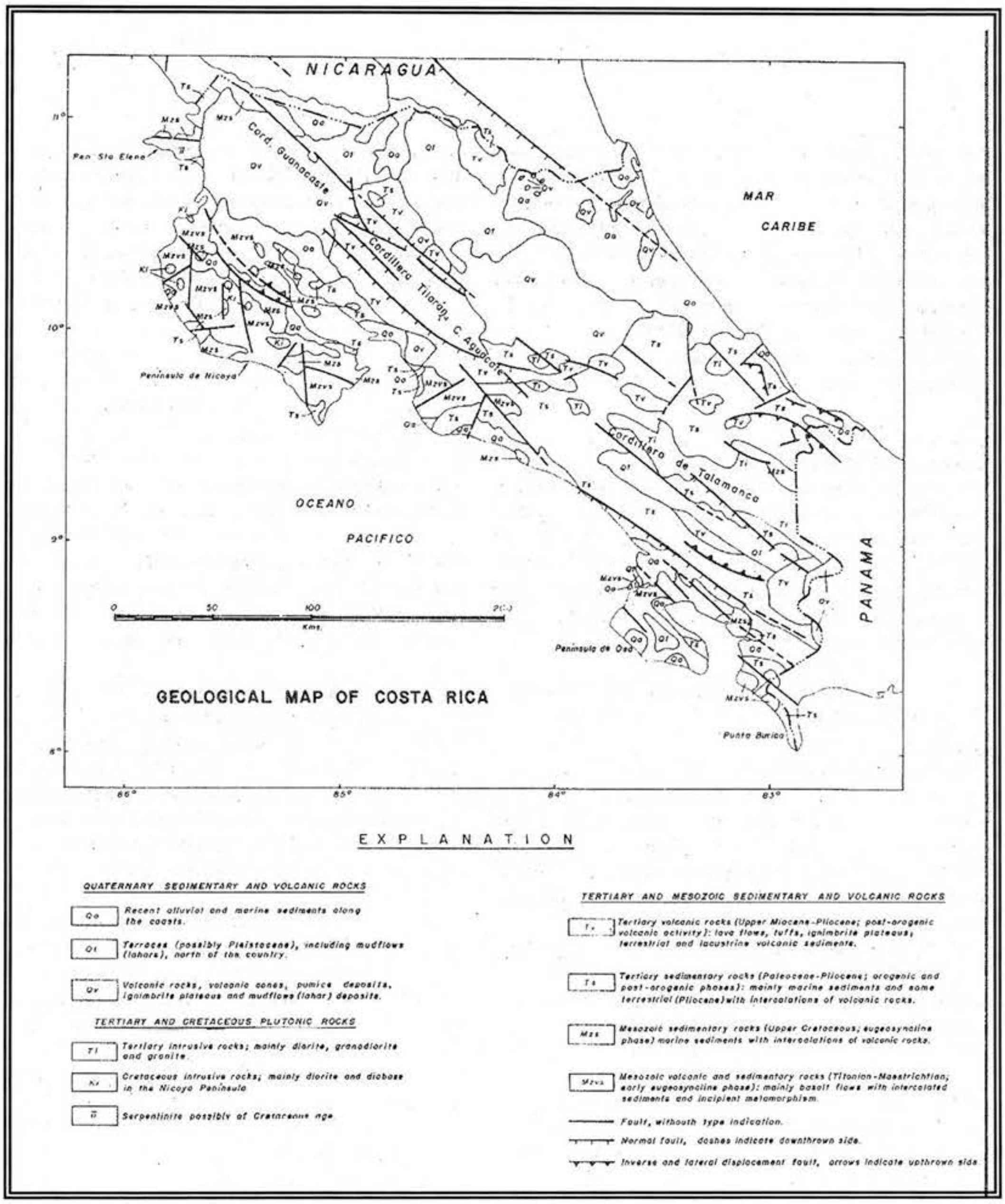
Several distinctive geological phases followed the establishment of the central American land link. South-eastern Costa Rica underwent major land building during the late Cretaceous to mid-Tertiary (approximately 70-15 million years ago) (Hartshorn et al. 1982). Eocene volcanic activity formed the igneous rocks of the Cordillera de Talamanca while marine sedimentation continued through the Oligocene and Miocene in the Térraba and Limón basins. Figure 3.4 illustrates the location of these geological formations.

The third major phase of land building occurred during the Quaternary. Volcanic activity in the Cordillera Central and Cordillera de Guanacaste, continued sedimentation in the Térraba and Limón basins and general uplifting all contributed to this. Quaternary vulcanism resulted in extensive depositions of pyroclastics around the two cordilleras. Rhyolitic ash and tuff are prevalent around the Cordillera de Guanacaste, whereas andesitic ash is more common around the Cordillera Central (Hartshorn et al. 1982).

In summary, the principal geological units constituting the territory of Costa Rica range in age from Jurassic to Quaternary. They can be grouped by lithology and age: Mesozoic volcanic and sedimentary rocks (Jurassic to Cretaceous); Tertiary sedimentary and volcanic rocks; Cretaceous and Tertiary plutonic rocks; Quaternary sedimentary and volcanic rocks (Janzen 1983). The geological history of Costa Rica has had a significant effect on the formation of the present day landscape and the resulting vegetation cover. In addition, a contemporary issue has arisen as mineral deposits are being mined and increasing the pressure on the remaining forest areas.

Costa Rica is not abundant in mineral resources. Some gold and silver deposits are mined in the Cordillera de Tilarán and on the Osa peninsula but mining contributed only 2 percent to the GDP in the 1970's (Kurian 1978). There has, however, been more recent mining activity in the frontier region with Nicaragua. Mining companies have been given permission to prospect for gold in an area of pristine forest. The economic and environmental outcome of this activity is, as yet, unknown although perhaps in future studies of land use change and biodiversity the environmental impact of mining will also have to be examined.

## Figure 3.4 Geological Map of Costa Rica



Source: Dengo et al. 1969

### 3.2.3 Soils and land use

The principal Costa Rican soil groups relate closely to geology and topography which forms the basis of the soil classification presented below. The fertile Central Valley of Costa Rica has some excellent agricultural soils; however, their high productivity and fertility coupled with their low erodibility and resilience to degradation have misled many into the assumption that the majority of the country has fertile soils. In fact, the country's soil resources are seriously threatened by erosion due to deforestation and agricultural overuse, to the point that the sustaining of agricultural productivity may be compromised (Hartshorn et al. 1982). The map reproduced in Figure 3.5 was constructed by Vasquez (1979) and shows the general distribution of soils in Costa Rica. The soil types are divided into four major categories based on relief:

1. soils on flat relief; i) soils of alluvial origin and ii) soils of fluviolacustrine origin,
2. soils on undulating relief,
3. soils on undulating to hilly relief, and
4. soils on steeply dissected to mountainous relief (Janzen, 1983).

These have then been divided into 18 distinctive site-category subdivisions based upon physiography, parent material, landforms and surface geology, using diagnostic horizons, according to U.S. soil taxonomy (Soil Survey Staff 1975). It is generally recognised that the classification used and the map produced by Vasquez (1979) is just the first step in developing an accurate national soils map. The map has non-uniform levels of cartographic generalisation; in some areas the data are very approximate and in others the data merely interpolated without field studies. This is typical of many areas of the tropics where surveys have, up to now, been at a reconnaissance scale (usually about 1:250,000) and with most information being available for specific, usually favourable, areas. The areal distribution of the soils detailed in Figure 3.5 is given in Table 3.1. This table demonstrates that of the soils classified on 'flat relief' both A-1 and A-2 consist of fertile sub-orders. These comprise 51 percent of the soils on this relief type and indicate the suitability of this land for agricultural activities. It is also noteworthy that 42.3 percent of Costa Rica has steeply dissected to mountainous relief and generally less fertile soil sub-orders.

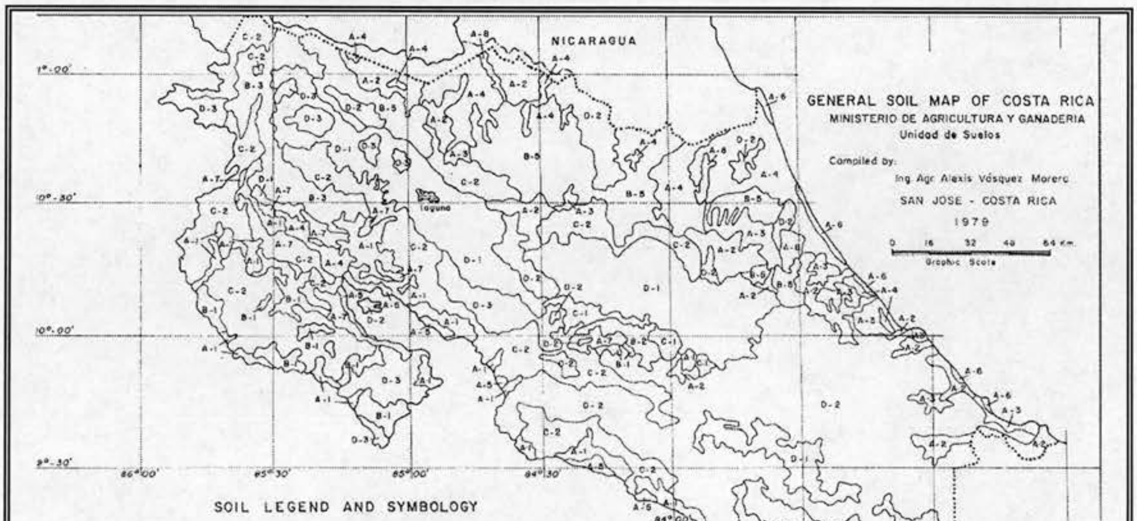
As agriculture and cattle rearing are the mainstays of the national economy, soils have a great importance and influence on land use potential. A common feature of Costa Rica's development has been the conversion of forestland to other uses, particularly agriculture. Hartshorn et al. (1982) have divided the country into three broad soil use classifications illustrating which land is suitable for agriculture, forest or protection. The following three sections provide an overview of these classifications.

### AGRICULTURAL SOILS

Five major land use capability classes are postulated (Tosi 1985); clean tillage is the most stringent in it requirements for soils quality followed by pasture, permanent crops, forestry, and absolute protection (Hartshorn et al. 1982). According to Figure 3.5 only 9,437 km$^2$ (19 percent) of the national soil cover is suitable for permanent production of clean-tilled field crops. These lands include most of the currently cropped and pastured lands on both the Pacific and Caribbean coastal plains together with the Central Valley. Lands in the next lower class have soils that can support permanent productive grazing of livestock without unacceptable soil degradation if properly managed (Hartshorn et al. 1982). This second category occupies 4,656 km$^2$. The land can also be used for permanent crops as an economic alternative to pasture but not for clean tillage due to moderate to high erosion risk or poor drainage. Pasture lands occupied close to 19,000 km$^2$ in 1980. This is 37 percent of Costa Rica's land area. In addition, 2,250 km$^2$ (4 percent) were devoted to clean-tilled crops, including plantations of banana and sugar cane. It is estimated by Hartshorn (1982) that as much as 7,187 km$^2$, which amounts to 76 percent of the best land, was under pasture for livestock in 1980. This land could provide an opportunity to increase crop production, which will be necessary if population continues to increase, without converting natural forest.

Intermediate quality soils suitable for permanent crops such as coffee, cacao, citrus, macadamia, pejibaye, harvested forage or timber plantations cover 8,158 km$^2$, which is 16 percent of the land area (Hartshorn et al. 1982). These lands are often situated in areas of high erosion risk due to high rainfall or steep topography. They may also be limited by poor or excessive drainage, low fertility combined with high levels of toxic aluminium, and/or a super-humid climate. Otherwise these soils have a good physical structure and can give good yields when cropped with climatically adapted plant species under careful management. These lands are not suitable for grazing or for agriculture where ground breaking instruments of cultivation are used. They are best suited to semi-subsistence small holder enterprises such as agroforestry. Unfortunately much of this land is used as extensive pasture and has suffered from a high level of erosion and degradation.

**Figure 3.5 General soil map of Costa Rica**



Source: Vásquez 1979

**Table 3.1 Areal distribution of Costa Rican soils.** (Soil sub-orders use the USDA Soil Taxonomy)

| Map Symbol | Major Site Features | Soil Sub-orders | Area in Km² | Percent |
|---|---|---|---|---|
| A | SOILS ON FLAT RELIEF | | 12,076 | 23.8 |
| A-1 | Well-drained alluvial soils | Udolls, Ustalls, Tropepts | 2,265 | 4.5 |
| A-2 | Moderately-drained alluvial soils | Tropepts, Aquepts | 3,884 | 7.6 |
| A-3 | Poorly-drained alluvial soils | Aquepts | 1,021 | 2.0 |
| A-4 | Very poorly-drained alluvial soils | Aquents | 2,955 | 5.8 |
| A-5 | Marshy soils | Aquents | 519 | 1.0 |
| A-6 | Excessively-drained alluvial soils | Psamments | 110 | 0.2 |
| A-7 | Heavy-textured soils of fluvio-lacustrine origin | Uderts, Usterts | 1,141 | 2.2 |
| A-8 | Organic soils, poorly-drained | Hemist, Saprists | 181 | 0.4 |
| B | SOILS ON UNDULATING RELIE | | 6,835 | 13.4 |
| B-1 | Coluvio-alluvial soils on slightly undulating terrain | Tropepts | 586 | 1.2 |
| B-2 | Volcanic ash-derived soils on gently-undulating terrain | Andepts | 219 | 0.4 |
| B-3 | Vocanic-tuff-derived soils on gently undulating terrain | Tropepts | 1,342 | 2.6 |
| B-4 | Coluvio-alluvial soils on gently-undulating terrain | Ustults, Tropepts | 859 | 1.7 |
| B-5 | Soils developed over ancient eroded terraces on gently-undulating terrain | Udults, Humults | 3,829 | 7.5 |
| C | SOILS ON UNDULATING-TO-HILLY RELIEF | | 10,427 | 20.5 |
| C-1 | Volcanic ash-derived soils on very undulating terrain | Andepts | 1,602 | 3.2 |
| C-2 | Residual soils, on hilly relief | Ustalfs, Tropepts | 8,825 | 17.3 |
| D | SOILS ON STEEPLY DISSECTED TO MOUNTAINOUS RELIEF | | 21,493 | 42.3 |
| D-1 | Volcanic ash-derived soils on mountainous relief | Andepts, Humods | 6,413 | 12.6 |
| D-2 | Residual soils on steeply-dissected relief | Humults, Ustults, Tropepts | 13,156 | 25.9 |
| D-3 | Deeply eroded and/or shallow soils on mountainous relief | Orthents | 1,924 | 3.8 |

Source: Vásquez 1979

In general, for all agricultural pursuits, including grazing and tree plantations, about 22,251 km² (44 percent) are available. Of this area, 19,000 km² of pasture already exists, taking up 85 percent of the available land. Site degradation is causing the reduction of productive capacity of many soils and following present trends productive land availability will decrease while population pressure continues to increase.

### FOREST SOILS

16,088 km², or 32 percent, of Costa Rica consists of lands deemed suitable, from an agricultural perspective, for only the permanent production of timber and other forest products. The land may also be important for other reasons such as conservation, wildlife and ecotourism ventures. It includes a range of land conditions from poorly drained lowland plains in high rainfall areas to mid and upper plateau regions (Hartshorn et al. 1982). These areas are characterised by inherently low fertility soils, which are often highly acidic and contain aluminium toxicity, high to very high rainfall and steep topography. There is a high risk of erosion, particularly during and after conversion to other land uses. This is the major reason for limiting this type of land to natural forests where timber exploitation can be carried out if techniques to avoid an unacceptable degree of soil erosion and stream sedimentation are applied.

Despite this high risk of degradation much of this land type has been deforested and converted into pasture in the last three decades. Sustainable forest management techniques are being increasingly advocated and if implemented in these areas of natural forest could provide a lasting contribution to development. Unfortunately the area of forest outwith protected areas is still decreasing and with it the potential for forest management. Grazing on converted forest areas on this class of land is highly destructive, impacting upon soil and vegetation resources and causing rapid site degradation. The soil organic matter layer is soon lost and the remaining soil becomes rapidly infertile and unsuitable for grazing or commercial forestry. It is evident that retaining of forest cover in this land type is a priority. More sustainable ventures, such as forest management or ecotourism, would need to be considered to ensure soil conservation and reduce forest conversion to other land uses.

SOILS REQUIRING PROTECTION

It is often difficult to distinguish between areas which could be utilised for sustainable management of natural forest and areas which should be protected. Land within the protected category consists of areas which have a high risk of soil erosion due to high rainfall on steep and often shallow mountain soils. Most of these are within the 'rain forest' life zones of Holdridge (1971), smaller areas consist of swamp and marsh land, rock outcrops and beach sands. The total area of th is land class covers 24 percent of the country (12,491 km$^2$)(Hartshorn et al. 1982). In the majority of cases this protection class is only represented in small areas and the recent forestry law (Government of Costs Rica 1996) accounts for this in its regulation that areas with slopes greater than 60 percent cannot be logged. Given the increasing rarity of timber in higher-use land classes there is increasing interest in and logging on this lower quality forest land although recent forest policy is beginning to address these issues.

As the areas in this land type are naturally hostile to development and particularly vulnerable to degradation, increasing pressure to extract timber should be resisted and other activities encouraged. In reality, this land use type is rarely found in large contiguous areas, often being combined with land in the forest land type. This may enable easier management for ecotourism or other functions such as providing environmental services.

A natural progression in this section, which has documented the climate, geology and soils of Costa Rica, would be a discussion of vegetation. However, as the natural vegetation types of Costa Rica consist predominantly of a variety of forest types, these have been discussed in Section 3.4, which addresses forests and biodiversity. In addition, the specific forest types present in the study area are addressed in more detail in Chapter 5.

## 3.3 Agricultural and cattle rearing activities

The conversion of forest to support agriculture and cattle grazing has been the major agent of change in Costa Rica's environment. The following sections provide a summary of these activities in order to demonstrate their importance for the Costa Rican economy and to outline the main factors which have produced the landscape examined in this study.

### 3.3.1 Agriculture

Agriculture is the largest employer in Costa Rica accounting for 28 percent of total employment (Estado de la Nación 1998, Hartshorn et al. 1982). The agricultural sector accounts for approximately 19 percent of the Gross National Product (GDP) and agricultural exports accounted for 74 percent of the total value of exports in 1979 (Estado de la Nación 1998, Hartshorn et al. 1982). The principal agricultural products for export are coffee, bananas, beef and cacao.

Approximately 42 percent of farms are less than 5 hectares but they only account for 2 percent of the area under cultivation. These smallholders who own or lease these farms of 5 to 10 hectares cultivate a diverse range of food crops and often produce the majority of their own food (Janzen 1983). In contrast, more than three quarters of agricultural land is held by only 13 percent of the largest farms (World Bank 1993). Table 3.2 details land distribution in Costa Rica. This predominance of large farms influences not only the crops produced but also the quality of land management. These larger farms, often owned by multinational companies, tend to farm more intensively and utilise more artificial inputs. This impacts on the general state of the environment and may have a negative impact on the biodiversity of adjoining forest areas.

Permanent crops such as coffee, cacao and fruit trees combined with corn, beans, pejibaye palm and various root crops, particularly yuca, are the principal source of income for small farmers. Large farms are generally dedicated to bananas, sugar cane, coffee and beef cattle. Many of these farms, particularly banana and sugar cane plantations, are owned by large multinational companies. In 1998, Costa Rica exported almost 4 million tonnes of bananas (FAO 1999), however, the social and environmental costs of such yields, 50 to 80 tonnes per hectare compared to 15 to 25 tonnes in the Windward Islands, are often very high. External inputs of fertilisers and pesticides are high while worker's wages are low and the effects of chemical inputs on their health deleterious. The average use of pesticides in the banana plantations of Costa Rica is 44 kg/ha/year compared to 2.7 kg/ha/year for crops in industrialised countries (IUCN 1995).

It is evident that agriculture is essential to Costa Rica's development. It produces the majority of the country's exports and provides a large proportion of the population with employment not to mention food. It has also necessitated the clearing of huge areas of forest and the input of large amounts of chemical fertilisers and pesticides. Although an essential part of Costa Rica's economy, improved farming methods could provide sustained production and reduce the need to convert more undisturbed natural areas.

**Table 3.2 Agricultural land distribution in Costa Rica**

| *Size class* Ha | *Holdings* number | *Holdings* (%) | *Area* Ha | *Area* % |
|---|---|---|---|---|
| 0 to 3.9 | 40,745 | 42.2 | 57,138 | 1.9 |
| 4 to 9.9 | 17,082 | 17.7 | 108,179 | 3.5 |
| 10 to 49.9 | 26,197 | 27.1 | 584,987 | 19.1 |
| 50 to 199.9 | 9,685 | 10.0 | 875,012 | 28.5 |
| 200+ | 2,833 | 2.9 | 1,445024 | 47.0 |
| **TOTAL** | 96,542 | 100.0 | 3,070,340 | 100.0 |

Source: World Bank 1993 - citing agricultural census from 1984.

### 3.3.2 Cattle production

One of the most widespread and drastic forms of forest conversion, which results in extensive fragmentation, is clearance for pasture. Cattle farming, for both beef and dairy produce, is one of the most prevalent land uses in Costa Rica. Hartshorn et al. (1982) show that over a 25-year period to 1973 the percentage of agricultural land used as pasture went up from 34 percent to nearly 50 percent. The area in planted pasture increased by 62 percent over 10 years to 1972 (Janzen, 1983). This acceleration in cattle production occurred almost solely to supply the export market. Many cattle farmers use a rotational system of grazing within a system of fenced areas. Although the beef market is still good, the profitability of pastureland decreases rapidly over time and requires constant inputs. The continuous use of pasture in the wet lowlands has affected soil structure, nutrient status and mycorrhizal associations (Janzen 1983). Indeed, cattle ranching has been documented as one of the least sustainable land uses in the tropics (Fearnside 1989, Schelhas 1994). In many areas of Costa Rica pastureland is currently being abandoned as farmers decide the venture is no longer lucrative. Unfortunately, the regeneration of forest and the recovery of soil fertility in these areas may take many years.

As with agriculture, cattle ranching is still an important economic source in Costa Rica. Unfortunately, it has a high impact on the natural environment and, even with substantial artificial inputs, is not sustainable. There are many alternatives to ranching and landowners could diversify into other ventures. The landscape produced by clearance for pasture and agriculture does not promote the rich biodiversity present in Costa Rica and perhaps concerted efforts by land owners to nurture forest regeneration could reap benefits in the form of payments for environmental services, sustainable timber extraction and ecotourism. The following section discusses forests and forestry in Costa Rica, and outlines the present resource base.

## 3.4 Forests and biodiversity

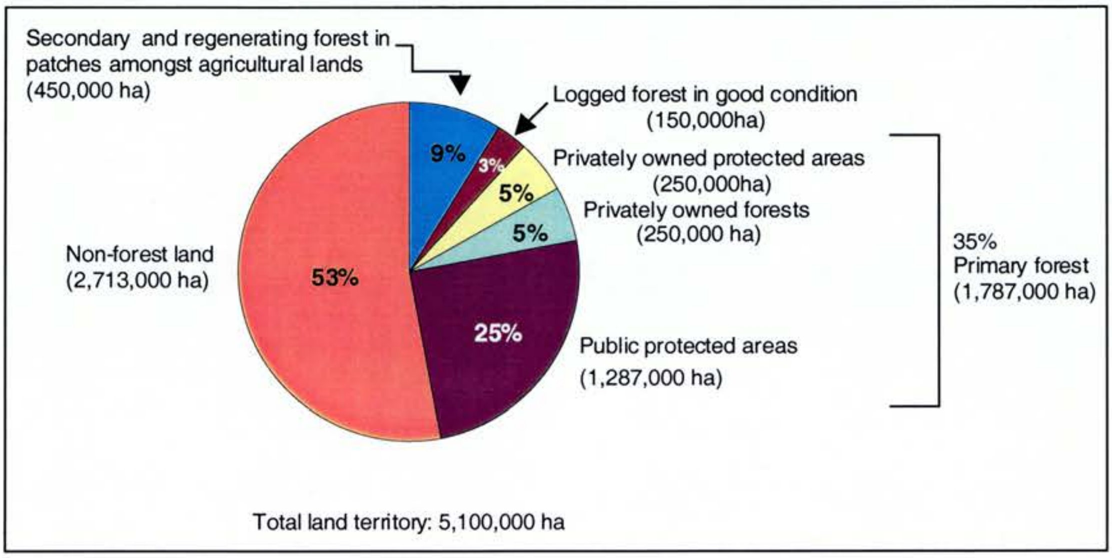
### 3.4.1 Forest classification, extent and management

The forests of Costa Rica cover 12 Holdridge Life Zones (Appendices 1 and 2). The zones covered by the field sites of this study are discussed in greater detail in Chapter 5. The Holdridge classification system uses temperature and rainfall combined with the seasonal variation and distribution of these two climatic parameters as the primary determinants of world vegetation (Janzen 1983). Each Holdridge Life Zone has a distinctive vegetation physiognomy and structure that occurs wherever similar bioclimatic conditions exist. In Latin America, Holdridge's classification system has been extensively used to prepare ecological maps (Appendix 2) and as a basis for detailed studies of land use capability, natural resource management, and environmental impact assessment (Janzen 1983).

Natural forests originally covered 99.8 percent of Costa Rica (Holdridge et al. 1982). According to FAO (1999) figures, today only 1,248,000 ha, a quarter of the original cover, remains. This figure includes forest plantations which account for 28,000 ha. FAO figures show that in the last five years Costa Rica has lost 207,000 ha of forest, a deforestation rate of 3 percent per year. This rate of deforestation is the second highest in Central and South America, only exceeded by El Salvador which has a deforestation rate of 3.3 percent (FAO 1999). These figures from the UN Food and Agriculture Organisation (1999) are the most recently available. However, in a recent forestry report co-ordinated by the Centro Cientifico Tropical (CCT) the figures for natural forest cover vary greatly being given as 1,787,000 ha in 1996 (Watson et al. 1998)(Figure 3.6). This area accounts for 35 percent of national territory of which 25 percent is protected, with the remaining 10 percent under private ownership (MINAE 1996). In addition, another 5 percent of national territory is protected as part of the National Network of Private Reserves (Bien 1997).

In comparing the conflictory forest statistics available, it is not clear which are the most accurate. The FAO figures indicate that less than 25 percent of the country remains under forest whilst the Ministry of Environment and Energy (MINAE) figures state that 25 percent of Costa Rica's forests are protected. The FAO figure therefore suggests that no forest remains outwith reserves. The author's personal observation can verify that this is not the case, although reserves may be being encroached upon, and, as such, it can only be concluded that the real figures for forest cover lie somewhere in the region of the figures given. Watson et al. (1998) calculate that when combining primary and logged primary forest in privately owned lands the total area of natural forest still available with the potential for management (timber extraction) is estimated to be 400,000 hectares (Alpizar et al. 1997)(Figure 3.6). This forest is distributed mainly in three regions: the Northern Zone, especially along the San Juan river; the lower area of the Talamanca Cordillera on the Atlantic coast; and the Osa peninsula in the south of the country (Watson et al. 1998). The climate in these areas is very hot and humid and stimulates tropical wet forest development. They are also located far from the principal timber market in the Central Valley although many local saw mills have been set up to process the timber more locally. In the Northern Zone the average potential timber volume for natural forest is 146 m³/ha, 104 m³/ha for managed forest and 45 m³/ha for secondary forest (Klein and Pelz 1994). In addition, patches of secondary forest growth on abandoned pasture, an increasingly common land cover type, present potential forest management areas (Watson 1995). The present estimate of the extent of these secondary forest areas is 450,000 ha, although this land cover type is growing, particularly in the Northern Zone. The following section examines the Northern Zone of Costa Rica in greater detail to provide a greater insight into the causes of land use change that has occurred there and on which this study is focused.

**Figure 3.6 Forest land in Costa Rica**



Source: Watson et al. 1998

### 3.4.2 Forests of the Northern and Atlantic zone

The forests of the Northern and Atlantic zone are situated on the plains bordering Nicaragua and on the northern sections of the Central Volcanic mountain range. Much of the land in these regions is now used for cattle farming on forested pasture (Plate 3.2). Some of these pasture areas have stands of valuable hardwood species such as laurel (*Cordia alliodora*). There may also be stands of cedar (*Cedrela odorata*), gavilan (*Pentaclethra macroloba*) and chancho (*Vochysia hondurensis*) amongst others (Watson et al, 1998). In areas where ranching has been discontinued in recent years due to a decrease in profits there is strong natural regeneration of secondary forests. These forests have a high potential for future productivity. There are also significant forest patches which have good natural forest management potential. Export crops such as pejibaye palm heart and ornamental plants are an attractive option for farmers. It may be possible to promote the establishment of these crops in already converted lands in order to minimise further land use change. Many agricultural and pasture areas are surrounded by living fences usually of madero negro (*Gliricidia sepium*) and poro (*Erythryna berterana and E. fusca*).

**Plate 3.2 Pasture area in San Carlos, Northern Zone.** This photo demonstrates a typical scene in the north of Costa Rica. Forest has been cleared to pasture on the more accessible land while the steep mountains, in the background, retain forest cover.

### 3.4.3 Forest plantations of commercial species

The reforestation incentives available between 1986 and 1995 resulted in a total of about 170,000 ha of new commercial plantations (MINAE-SINAC 1996). It is estimated that of these plantations 62 percent are in 'fair condition', 21 percent in 'poor condition' and only 17 percent in good condition (Watson et al. 1998). There are various reasons for this, the incentive system has had problems with poor seed quality, inadequate technical assistance and delays in funding, although there are many non-governmental organisations working to improve this (Martinez et al. 1994). There are also problems with pests, such as leaf cutter ants, and fungal disease which occurs particularly in the more humid areas. In addition, maintenance of these plantations, including weeding and thinning, is often not carried out due to lack of funds. In some areas this is confounded by the geographical location of these sites in remote areas where land owners are not present. The main aim in establishing these plantations is the production of sawmill grade timber however Torres et al. (1995) believes that only about 50 percent of the existing plantation timber resource is of industrial quality. Other commercial plantation projects have focussed on pulp production. The main plantation species for both timber and pulp are melina (*Gmelina arborea*), teak (*Tectona grandis*), and acacia (*Acacia sp.*). In addition to these exotic species some native species have been established in plantations. These species include chancho (*Vochysia sp.*), roble coral (*Terminalia amazonia*), pilón (*Hieronyma oblonga*) and almendro (*Dipteryx panamensis*). At the present time a new system of incentives exists and reforestation is continuing particularly on abandoned pasture.

**Plate 3.3 Pejibaye plantation with adjoining primary forest.** This photo illustrates the cultivation of pejibaye, an export crop, in a clearing within natural forest. It is hoped that further land use change for this type of activity can be minimised by use of already converted.

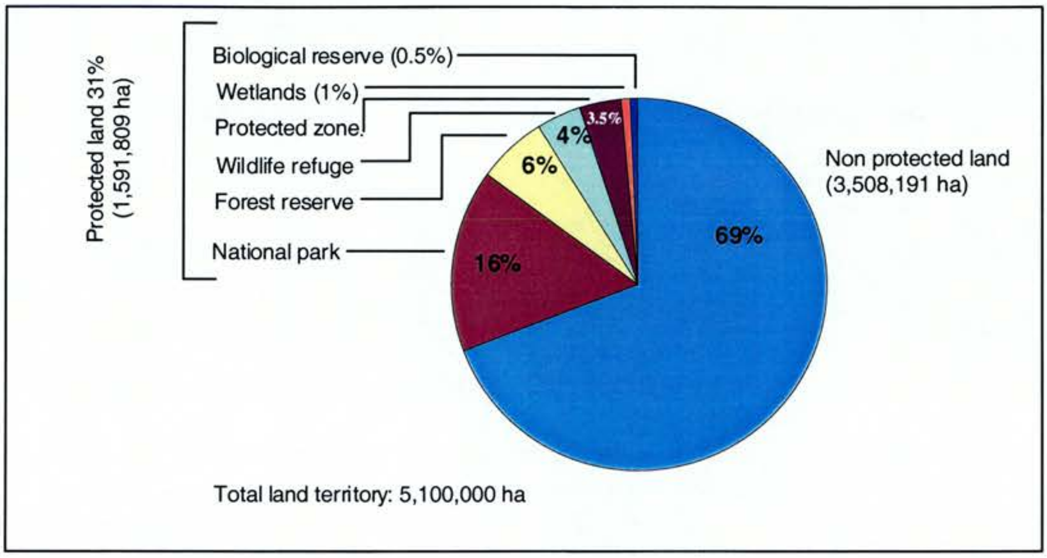
### 3.4.4 Protected areas of Costa Rica

Costa Rica has achieved an impressive system of protected areas. About 1.6 million hectares or the equivalent of 31.15 percent of the country's total land area is under some formal category of protection, including Forest Reserves, although this latter category does not ensure protection (Watson et al. 1998)(Figure 3.7). Forest reserves account for 5.7 percent of the national territory (Figure 3.7). The various areas of protection found in Costa Rica fall into eight categories which are detailed in Table 3.3 below.

Costa Rica has a substantial history of concern over natural resources. The first national park was declared in 1945 and the first biological reserve (Cabo Blanco) and forest reserve (Río Macho) were established in 1963 and 1964 respectively (Hartshorn 1982). By 1995 when the National System of Conservation Areas (SINAC) was established there existed 72 protected areas covering 21 percent of the country (Watson et al. 1998). Under SINAC (National System of Conservation Areas) Costa Rica has been divided into 11 conservation areas which are managed under the auspices of the Ministry of the Environment and Energy (MINAE). This development represents the efforts of the government to shift to a more integrated natural resource plan where people's needs are considered by implementing buffer zones. This replaces the former paradigm which emphasised absolute protection from human interference. Although often promoted as a model in nature conservation, conflict is still endemic to the Costa Rican protected areas system.

Despite the real success achieved in conserving a large proportion of Costa Rica's wildlands, there remain many issues, such as, land tenure, the administration of protected areas, restricted financial resources, and opposition from other government agencies, which have not yet been fully resolved. It is essential, in the present landscape of change, that conflict is resolved for the benefit of people and protected areas. Costa Rica's wealth of natural resources can be managed to combine protected areas, sustainable forestry and biodiversity conservation. The next section demonstrates the importance and wealth of the region's biodiversity, with a focus on Costa Rica

## Figure 3.7 Protected areas of Costa Rica



Source: MINAE-SINAC 1996

## Table 3.3 Protected area categories in Costa Rica

| *Protection category* | *Number of reserves in category* | *Area (ha)* |
|---|---|---|
| National parks | 22 | 838,542 |
| Forest reserves | 12 | 291,191 |
| Wildlife refuges | 34 | 197,402 |
| Protection zones | 30 | 184,496 |
| Wetlands | 14 | 50,465 |
| Biological reserves | 10 | 29,495 |
| National monuments | 1 | 218 |
| **TOTALS** | **48** | **1,138,209** |
| Non-protected land | | 3,508,191 |
| Total land territory | | 5,100,000 |

Source: MINAE-SINAC 1996

### 3.4.5 Costa Rica's biodiversity

The Neotropics, the tropical zones of the American continent, contain more species than most other tropical regions of the world and many more species than the world's temperate zones (INBio 2000). Costa Rica is one of the most biologically diverse countries of the world. It is estimated that there are 500,000 species of flora and fauna, a figure which represents four percent of the world's biodiversity (INBio 2000). This includes over 12,000 species of plants (1200 of these are trees), 848 species of birds, 205 mammal species, and 218 reptile species. Over 79 percent of the total species richness is composed of arthropods. Of the 500,000 species found in Costa Rica approximately 17 percent (87,000 species) have been described (INBio 2000).

At present 98.8 percent of vertebrates (excluding fish) are known, almost 90 percent of plants and 60 percent of fish (INBio 2000). However, less than 20 percent of the arthropods, the most diverse group, has been described. Groups such as fungi, bacteria and viruses are almost unknown with more than 98 percent of species yet to be described (INBio 2000). Although it is a small country, Costa Rica's topography results in a diverse landscape within which all the main ecosystems of Central America and Mexico are represented (Watson et al. 1998). When comparing Costa Rica with large countries well known for their richness in natural resources, such as Columbia or Brazil, Costa Rica's wealth in biodiversity becomes evident. For every 10,000 km$^2$ Costa Rica has 295 tree species while Columbia has 35 species and Brazil 6 species (INBio 2000).

Costa Rica is one of the few countries in the world which has an institute entirely dedicated to biodiversity. It was established as a non-governmental research institute in 1989 with the following objectives:

a. to form an institution in charge of designing strategies and developing activities needed to carry out a national inventory of existing biodiversity,
b. to centralise present and future information regarding biodiversity,
c. to make this information easily accessible to those interested and encourage its use by the Costa Rican public (Watson et al. 1998).

The national biodiversity inventory is on going and its programme has trained young people from forest area communities, primarily those near national parks, to collect samples of flora and fauna. These 'parataxonomists' send the samples to INBio's central institute where they are sorted and classified (Plate 3.4). Expert taxonomists both from INBio and other institutions world-wide have the immense task of identifying the samples to genus and eventually species level. There are still large numbers of new species of plants and animals, particularly insects, being collected. INBio has agreements with museums and institutions to assist with this taxonomy (Aylward et al. 1993).

**Plate 3.4 Insect collection. INBio, Costa Rica**

Photo: Allan Watt

INBio also has a number of other commercial agreements with companies and institutions world-wide. In 1991 INBio signed the first major bioprospecting contract with US based company Merck and Co.. This contract provided Merck with chemical extracts from wild plants, insects and micro-organisms in return for a two year research budget of US$1.135 million and an undisclosed share in royalties on any resulting commercial products (Watson et al. 1998). Costa Rica's national parks are supposed to receive half of the royalties. INBio has been criticised for being a private institution working with a public resource, namely biodiversity. It remains to be seen whether bioprospecting will provide sufficient economic incentives for communities to conserve their forests but undoubtedly the institute is proving a wealth of species information that would not otherwise have been gathered. It provides an important education to parataxonomists and their communities which must be the first step in any conservation programme and, both nationally and internationally, provides an indispensable resource for research and learning.

A more recent development is the Biodiversity Bill which was drafted in 1996. This concerns biological resources ranging from seed banks and the extraction and use of germplasms, to species and biodiversity research (Watson et al. 1998). It also covers intellectual property rights on scientific research and discoveries made in this field. Much controversy has been generated particularly in the area of 'national biodiversity patrimony' which considers biodiversity as the property of the state. INBio has questioned this assertion as have community representatives who object to the notion that government permission may be required before they can harvest anything that comes under the heading of 'biodiversity'.

It is evident that biodiversity is a very important component in Costa Rica's natural wealth. Many measures are in place to both conserve and utilise it in a sustainable manner for the benefit of the present, and future, local population. The following section discusses the traditional and innovative functions that forests, and their biodiversity, have within Costa Rican society. It demonstrates the importance of the forest and its components to local people's livelihoods.

## 3.5 Forest resources within the social and economic landscape

The stakeholders linked to the forest in Costa Rica are diverse and abundant. The forest resource is an integral part of life in Costa Rica, particularly in rural areas. A case study reported by Schelhas et al. (1997) found that a community in southern Costa Rica had many reasons for conserving forest and for reforesting activities. They prioritised watershed management as the most important forest service, particularly around sources of household water. Security of subsistence products, particularly fuelwood and construction timber, and vines for basket-making were also listed. The forest as a 'bank account' was also important, as the timber present provided a financial contingency. This example illustrates the importance of the forest and its biodiversity to the diverse needs of a rural community. Smallholders, such as the farmers quoted in the above study, are just one of many forest stakeholders. This section outlines a variety of functions served by the forest. It also emphasises the continuing economic need for forests despite developments in agriculture and other income sources. Table 3.4 summarises the myriad of forest actors in Costa Rica.

Costa Rican forests have traditionally been used as a source of timber for building (Watson et al. 1998). Until 30 years ago most houses were made of wood and even today the majority of houses in rural areas are still constructed from local timber harvested nearby. The forest also provides fuelwood, various non-timber forest products (NTFPs) including palm heart (although the law now restricts harvesting from certain naturally grown palms), ornamental and medicinal plants, and materials which are used in traditional handicrafts such as basket weaving. Hunting is also common, and the most widely hunted species are tepezcuintle (*Agoutis paca*), saino (*Tajassu tajacu*), white-tailed deer (*Odocoileus virginianus)*, brocket deer (*Mazama americana*) and the green iguana (*Iguana iguana*)( Janzen 1983, Watson et al. 1998). Use of forest wildlife is legally prohibited in the protected areas and, theoretically, regulated by law outside these areas. Unfortunately, in many forest areas outwith reserves, hunting for 'bush meat' continues unabated despite an increasingly smaller number of possible prey.

It is estimated that the 'forestry sector' contributes 4.7 percent of GDP and employs almost 12,000 people (Watson et al. 1998). This figure has risen in recent years perhaps as a result of new sustainable development policies implemented by the government. Governmental support is now provided to encourage some major economic activities linked to natural resources, particularly tourism and eco-tourism, the forest industry, 'bio-prospecting', and forest environmental services (Watson et al. 1998).

**Table 3.4 Stakeholders linked to the forest resource in Costa Rica**

| ***Stakeholders*** | |
|---|---|
| **Governmental institutions:** | Legislative institutions<br>Executive institutions<br>Judicial institutions<br>Decentralised institutions |
| **Forest and tourism industry actors:** | Forest managers<br>Loggers<br>Timber industries<br>Forest industry associations<br>Foreign investors and speculators<br>Ecotourism industry |
| **Community level actors:** | Smallholders<br>Smallholder organisations<br>Indigenous communities<br>Community development organisations |
| **Academics, conservationists, donors and consumers:** | Individual (scientific) opinion leaders<br>Academic and research institutes<br>Forest technicians (consultants and NGOs)<br>Conservation groups<br>International donors<br>Consumers |

Adapted from Watson et al. 1998

### 3.5.1 Forest industry

The forest industry is still an important economic force in Costa Rica. In 1993, the forest industrial sub-sector consisted of 628 companies representing 13.25 percent of companies that form the industrial manufacturing and/or processing sector (Watson et al. 1998). The largest group in this sector is the 404 small businesses that make furniture and accessories for the home and office. Following from that the next most important group consists of the 185 sawmill businesses which employ a large labour force. These sawmills process timber from natural forests but are also beginning to process the plantation timber of smaller diameters that is beginning to be harvested following government incentives to establish forest plantations. The forest industry employed 6,869 people in 1996 and it is believed that this figure has remained fairly constant since. The Free-On-Board value of forest products exported in 1993 was US$ 28 million (MINAE-SINAC 1996). In addition to traditional forest activities other ventures are being developed in Costa Rica to benefit both local and global communities. The following two sections present a synopsis of these.

### 3.5.2 Environmental services

It has, at last, been recognised that natural forests provide more than just a timber resource. They provide environmental services that benefit and, in many cases, are essential to society. In Costa Rica new national initiatives are being developed to increase the public's awareness of these. Forestry legislation passed in 1996 established the concept of compensation for forest-derived environmental services to land owners through a Payment for Environmental Services (PSA)(Table 3.6). This legislation recognises environmental services and classifies them as follows:

a. recycling soil nutrients
b. protection against erosion and flooding
c. protection of watersheds
d. carbon sequestration, and
e. protection of biodiversity (Watson et al. 1998).

These compensation payments to forest owners for the provision of environmental services to society through protection of their forests are being covered by a new tax which has been levied on fossil fuels (Watson et al. 1998). Economists continue to attempt a quantitative valuation of these services (Solorzano et al. 1995, Carranza et al. 1996).

In combination with the recognition that countries and communities which conserve their forests should be compensated by the wider global community, an increase in foreign travel to tropical areas has occurred. Tourists want to experience this natural wealth in a responsible way. The next section summarises the growth of 'ecotourism' in Costa Rica.

### 3.5.3 Ecotourism

Costa Rica is an increasingly popular tourist destination. This boost in the tourist industry has given Costa Ricans a new perspective on conservation and resource management. It has been the country's highest source of revenue since 1992. The Costa Rican Tourism Institute's (ICT) Strategic Plan for 1995 estimated that 66,500 people were employed in hotels and other related areas. The ICT also estimated that during the 1996 tourist season, 57.4% of all tourists visited a national park or carried out some sort of activity for example, guided nature walks, white water rafting, or forest canopy tours, which relies on the existence of protected forests (ICT 1996).

The importance of forest and its biodiversity to the livelihoods of a wide variety of stakeholders is evident from the previous three sections. The mechanisms which have been developed to ensure its maintenance both in sustainable forest management and in the promotion of other ventures are discussed in the next section

### 3.5.4 Forest policy in Costa Rica: a brief history

The way people and forests have interacted in Costa Rica has changed greatly in recent history. Alongside these changes, or perhaps driving them, has been diverse forest policy. Past and present forest policy is outlined in this section to provide a summary of the processes which have influenced the way Costa Rica's forests and people have evolved (Tables 3.5 and 3.6).

It is evident from Table 3.5 that an initial policy of forest exploitation for agricultural purposes changed in the 1970s to a more 'forest friendly' approach with the beginning of the Protected Area system. This led to a series of forest-orientated laws and strategies, and in 1996 the existing Forest Law (Government of Costa Rica 1996) was approved. As outlined in Table 3.6, present forest policy covers four major areas: the management of forest production and industry, fiscal and financial forestry incentives, management of forest protected areas, and decentralisation and participation of communities in policy processes. The policies are forward looking and innovative, they attempt to use the forest resource sustainably, while involving local stakeholders, and ensuring a high level of conservation. If adhered to, they provide the mechanisms for a sustainable future for Costa Rica. The present day reality in Costa Rica reflects some of these mechanisms, however eroding of the forest resource continues.

The first part of this chapter has provided a summary of the forest environment, and a background to forest use, in Costa Rica as a whole. It has discussed the causes of land use change and presented the development of alternatives to forest destruction. It has also documented the enduring importance of the forest and its biodiversity to many stakeholders, and the efforts of government and other organisations in sustaining the forest resource.

The next part of the chapter presents the situation in the Northern Zone of Costa Rica, an area where forestry plays a major role in income production, but where continued exploitation has resulted in a landscape of forest patches within a mosaic of agriculture, pasture and forest plantations. These forest patches are important for their many services, and their importance for biodiversity is documented in later chapters. The landscape of the Northern Zone is typical of many neotropical areas which have suffered extensive land use change. Despite this, the mosaic of forest and other land uses still harbours a wealth of biodiversity. The present study examines the effects of this altered landscape on biodiversity, and the following sections of the chapter summarise forestry in the region, while also introducing the field areas selected for investigation.

## Table 3.5 A chronology of Costa Rican forestry legislation and policy statements

| Year | Legislation | Main Theme |
|---|---|---|
| 1775 | Proclamation of Spanish governor Juan Fernández de Bobadilla | To ban setting fire to fields in mountain areas - to protect large livestock ranches |
| 1883 | Decree of land concessions to San José, Cartago and Alajuela for agriculture, pastures and forests. | Reforestation of mountain lands by town councils, with native species - cedar, "guachipelin' - for building wood |
| 1846 | Lands are awarded to San José, Cartago, Alajuela and Heredia for fuelwood, pasture and agriculture | Securing lands for pasture and fuelwood |
| 1888 | The decree of an inalienable 2 km wide zone on either side of the Barva Volcano. | Civic duty to protect mountain as watersheds for Heredia and Alajuela water supplies |
| 1906 | Presidential decree for a special executive commission to formulate a Forestry Law | Excessive deforestation and deterioration of soil and water resources. Commercial exploitation of forest resources |
| 1919 | Executive Decree Pres. Alfredo González Flores | To reforest the highlands of the Northern Zone and Heredia for wind shelter and water production |
| 1934 | 'Family Providers' Law | Distribution of unused public lands to heads of family to encourage colonisation and settling of new regions |
| 1941 | Land Tenancy Information Law | Colonisation of forest areas for agricultural purposes |
| 1969 | Forest Law No. 4465 | Legislating activities linked to the forest |
| 1977 | National Parks Service Law No.6084 | The Protected Area system is consolidated |
| 1977 | Indian Reserve Law No.6172 | Regulate and protect Indian Reserve lands |
| 1979 | Regulations regarding the protection and use of Forest Reserves | Use and management of the Forest Reserves |
| 1979 | National Forestry Development Plan | First coherent plan for the sectoral agencies |
| 1986 | Amendments to Forest Law No.7032 | Allocates proportions of revenues from forest taxes to municipalities (10%) and regional organisations (10%) |
| 1988 | Executive decree No.18105 establishing the Forest Bond Certificates | Financial incentives for production forestry activities |
| 1989 | National Conservation Strategy for Sustainable Development (ECODES) finalised | A sustainable development framework for all sectors to develop cross-sectoral and participatory strategies |
| 1990 | Ministry of Industry and Mines becomes the Ministry of Natural Resources, Energy and Mines (MIRENEM) | Joins the General Forestry Directorate and the National Park Service under MIRENEM. Centralisation of the natural resource and energy sector. |
| 1990 | Amendments to Forest Law, No.7174 | MIRENEM codifies *regimen forestal* including rules for forest management plans and incentives. Forest Law 7032 annulled. |
| 1990 | Forest Action Plan for Costa Rica (PAF-CR) presented | First cross-sectoral strategy for forests |
| 1992 | Wildlife Law No.7317 | Regulating and protection of wildlife |
| 1994 | Forest Policy for Costa Rica approved by MIRENEM | Policy statement developed by national-level professionals within the forestry sector |
| 1995 | Organic Environmental Law No.7554. | Creation of the Regional Environmental Councils |
| 1996 | Forest Law 7572. | Approval of Regional Agreement for the Management and Conservation of Natural Forest Ecosystems and the Development of Forest Plantations. |
| 1996 | Forest Law No. 7575. | Overrides former forest laws. Decentralises state forest management and provides guidelines for the management of National System of Conservation Areas - SINAC |

Source: Watson et al. 1998.

## Table 3.6 A summary of current government forest policy in Costa Rica

**Management of forest production and industry**

- Land use change forbidden for land which has trees on it (or is forest)
- Contracts between government and landowners to regulate: reforestation, prevention of land invasion, and land tax exemption
- EIAs required prior to forestry development (since 1996)
- Log export ban (since 1987)
- Timber taxes levied on volume at point of primary processing
- Technology development promoted - to reduce impact and wastage etc.
- Partial liberalisation of large-scale commercial forestry (since 1996)
- Register of private professional foresters - 'forest regents' - to provide technical assistance and provide and monitor timber harvesting and transportation permits

**Fiscal and financial forestry incentives**

- National Forestry Finance Fund (FONAFIFO) for smallholder forestry (since 1996). (In the 1997 national budget FONAFIFO was allocated about $7 million)
- Subsidised plantation development and some forest management (until 1997): income tax deductions, soft credit, transferable bonds (CAFs), municipal forest funds and forest development fund
- Credits, mainly through FONAFIFO, to replace above incentives (from 1998). Some credits for farmers to be sourced from carbon sequestration deals, packaged and sold on the international market
- Payments for protection (CCBs) and supply of environmental services (PSAs), prioritising buffer zones and biological corridors connecting protected areas (since 1996)

**Management of forest protected areas**

- Conservation areas system (SINAC) - core protection areas and buffer zones
- Approval of private sector/NGO land buy-outs and management for forest protection
- Arrangements with NGOs to manage some public protected areas where government unable to finance

**Decentralisation and participation in policy processes**

- Partial regional autonomy through SINAC
- Incorporation of some communities neighbouring protected areas in area patrol and protection
- Limited participation space for other actors since 1996: Regional Environmental Councils, National Forestry Office and FONAFIFO

Source: Watson et al. 1998

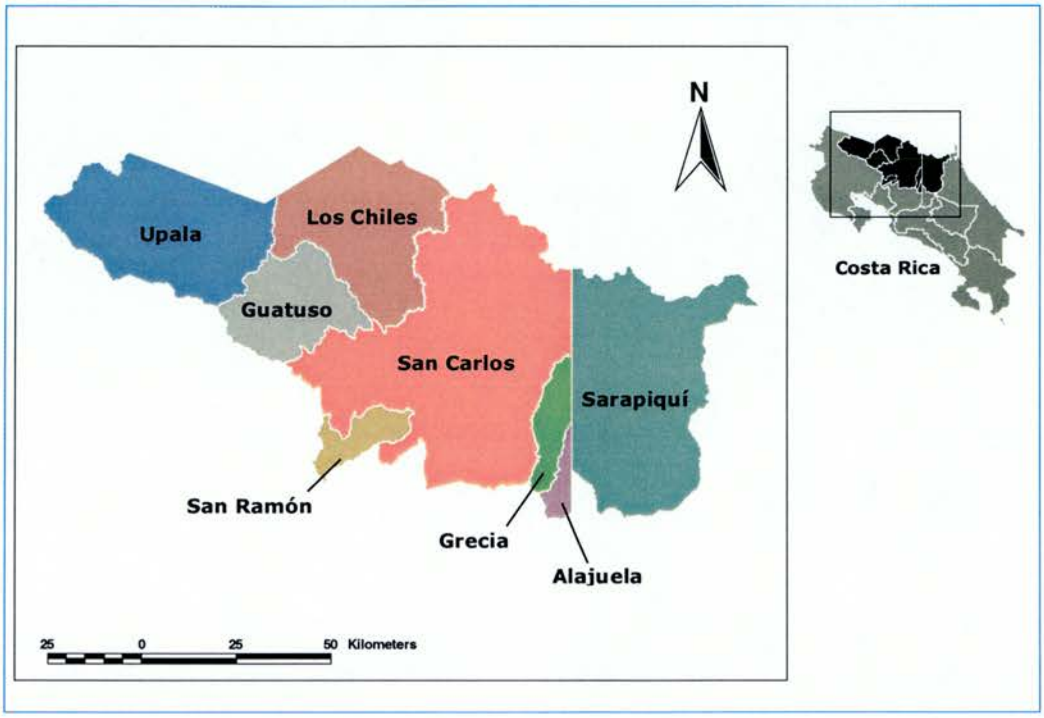
## 3.6 Forestry in the Northern Zone of Costa Rica

The Northern Zone of Costa Rica is characterised by plains which rise slowly from the Atlantic coast to the central mountains. As is obvious from its name, it is the northernmost zone and borders Nicaragua (Figure 3.8). The population is predominantly rural (85 percent of the total) and Ciudad Quesada, a small market town, is the only urban centre (UNEP/OAS 1997). Throughout the region 'quality of life' indicators are lower than national averages. The Northern Zone has undergone extensive land use change with natural forest being removed for cattle pasture and agricultural activities. Primary forest has been reduced to small fragments, while logged forests receive ever more pressure from selective logging (COSEFORMA 1995). Human activity is threatening both the biodiversity and the forest reproductive potential of this area (COSEFORMA 1995). According to a forest inventory carried out over two thirds of the Northern Zone in 1995, 26.8 percent of the area surveyed remains forested (COSEFORMA 1995). This is divided into the following categories of forest type:

| | |
|---|---|
| a. primary forest | 22.9% |
| b. logged over forest | 50.4% |
| c. secondary forest | 13.3%, and |
| d. forest plantations | 13.4% (COSEFORMA 1995). |

In 1992, 20,165 ha were reforested (COSEFORMA 1995). The species used in this reforestation were: 47% gmelina (*Gmelina arborea*); 32.8% laurel (*Cordia alliodora*); 10.8% eucalypt (*Eucalyptus sp.*); 3.3% teak (*Tectona grandis*); 2% pine (*Pinus caribea*); 1.4% terminalia (*Terminalia sp.*); 1.2 % pochote (*Bombacopsis quinata*) and 1.5% other species (COSEFORMA 1995).

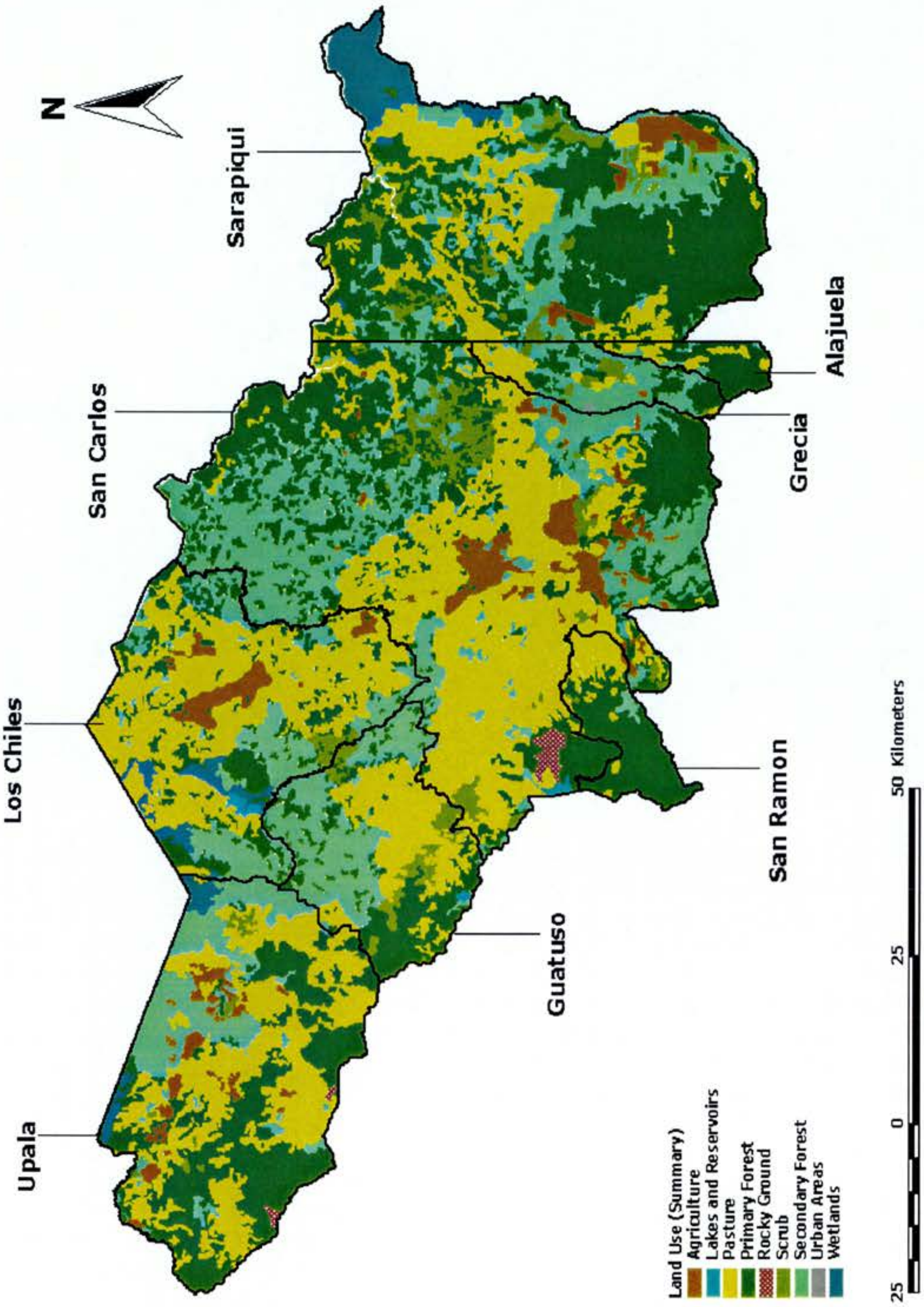
## Figure 3.8 The Northern Zone of Costa Rica



### 3.6.1 The San Carlos and Sarapiqui regions of the Northern Zone, Costa Rica

The area of the Northern Zone investigated in this study falls primarily within the San Carlos region, with one of the field sites just over the regional border into Sarapiqui (Figure 3.8). These regions follow the general trends of the Northern Zone. Pasture and agriculture are common, although the area of study still maintains significant forest cover (Figure 3.9). In the past 20 years, San Carlos and the adjoining part of Sarapiqui have changed from being on the agricultural frontier to the present situation where some of the more remote areas which had previously been cleared for pasture are now being abandoned. These pasture lands deteriorate rapidly without forest cover and cattle ranching has become uneconomical. Secondary forest is now becoming a more common land use in the area as abandoned pastures regenerate. The resulting secondary successions are valuable to land owners as many of the long-lived pioneer species are commercial or utilisable trees (Finegan 1992). The landscape of lowland San Carlos and Sarapiqui is typical of the type of land use mosaic developed by colonist

## Figure 3.9 Land use in the Northern Zone of Costa Rica



farmers in tropical regions. The challenge now is to develop sustainable land use practices, which incorporate the existing diverse land uses of the area while also considering the social, economic and environmental landscape.

### 3.6.2 The Commission for Forestry Development of San Carlos (CODEFORSA)

There are many organisations working in Costa Rica to promote and manage forests. Within the region discussed here there are various non-governmental organisations involved in natural resource management. One of these, the Commission for Forestry Development of San Carlos (CODEFORSA), is involved in natural forest management, reforestation and conservation, and was instrumental in this study (CODEFORSA 1999).

CODEFORSA was established in 1983 to represent the interests of loggers, transporters and processors but today has become a forest service organisation for the whole region, with both a technical and political role. CODEFORSA now has approximately 700 associates including small, medium and large farmers, timber companies and transporters, and forestry professionals (Watson et al. 1998). Its main objective is the management and conservation of the regions forest resources. To finance these activities CODEFORSA has received government funding from forest revenue, and recently various government forestry incentives have been managed by them and channelled to their associates. Funding and technical assistance has also been provided by various institutions, such as: CATIE; the UK's Department for International Development (formerly the ODA); the Costa Rican Institute of Technology (ITCR); and the Forestry and Logging Sector's Co-operation programme (COSEFORMA), run jointly by MINAE and GTZ.

Reforestation programmes began with smallholders in 1989 under the Forest Development Fund and the Forest Bond Certificates programme (CAF), while natural forest management projects were elaborated under the forest management bond (CAFMA) scheme. This latter programme provided a payment as an incentive to forest owners to manage their natural forest. Through this scheme CODEFORSA successfully implemented sustainable forest management on 130 properties amounting to approximately 14,500 hectares (Maginnis et al. 1998). CODEFORSA's reforestation programme is supported by their tree nursery, which produces up to a million seedlings of quick growing species per year (Watson et al. 1998). They also operate a forest extension programme in order to promote both good forest management and their related activities.

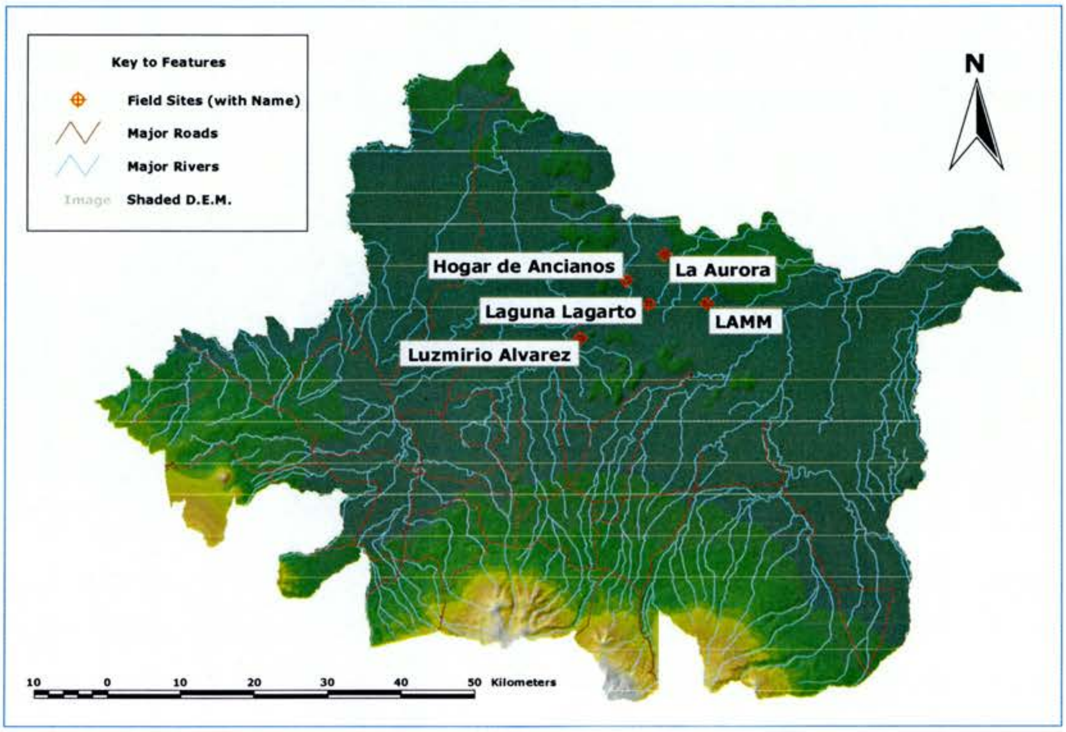
CODEFORSA has been instrumental in developing the 'forest regents' scheme through which professional foresters are licensed to inspect properties where natural forest management is taking place to ensure compliance with the technical conditions linked to incentives and regulations according to the 1996 Forestry Law (Richards et al. 1996). CODEFORSA is not, however, without its problems. As a public-private collaboration conflicts often exist between their strict implementation of forest controls and the agendas of some private sector actors. In recent years the incentive schemes have changed and CODEFORSA is now extending its expertise into implementation of the environmental services payments programme (PSA) (CODEFORSA 1999).

CODEFORSA's vision also includes research into forests and forest biodiversity, and they actively assisted the implementation of the study presented in this thesis. They were instrumental in identifying field sites, providing field assistance, and office resources. The following section introduces the study area and documents the specific field sites chosen.

## 3.7 The study area

The study area is located in the northern zone of Costa Rica, Central America (Figure 3.8). The sites are located within the regions of San Carlos and Sarapiqui, in the northernmost areas of these regions (between 10°37' to 10°45' N and 84°05' to 84°15 W)(Figure 3.10). This area is a part of the San Juan River Basin, which is the largest river basin in Central America, covering an area larger than the Salvadoran territory (Rizo et al. 2000). The river itself forms a natural border between Costa Rica and Nicaragua. It is an area rich in natural resources but remains economically undeveloped and politically isolated due to its position far from administrative centres. As already mentioned, this area of Costa Rica has been heavily impacted in very recent history by colonist farmers and ranchers, resulting in a landscape of agriculture and cattle ranching interspersed with areas of the original vegetation cover of tropical wet forest (Figure 3.11). More recently, abandoned pasture is being reforested with plantations of exotic and some native tree species.

**Figure 3.10 Map of study area with the Northern Zone of Costa Rica**



Study sites were identified by consultation of aerial photographs, preliminary field visits and from recent natural forest and forest plantation management plan maps. They lie between sea level and 400m above sea level. Rainfall averages >2500mm per year with most of the year being wet and a short dry season occurring between December and March. The average monthly temperature fluctuates between 22°C and 30°C. This area falls within the tropical wet forest (T-wf) and the premontane wet forest (P-wf) life zones (Holdridge 1971)(Appendices 1 and 2). Soils are generally infertile and acidic (pH 5.0 to 3.5) and fall into B-5, A-4 and D-2 categories according to Vásquez (1979)(Figure

3.5)(Table 3.7). Their accessibility and similarity to other sites (in terms of elevation, level of disturbance, surrounding habitat etc.) was investigated and every effort was made to minimise differences. The records of a local forestry non-governmental organisation (NGO), which produce the management plans and forest maps for this area, provided a comprehensive history of many forest and converted forest areas within the zone.

**Figure 3.11 Land use in San Carlos and Sarapiqui**

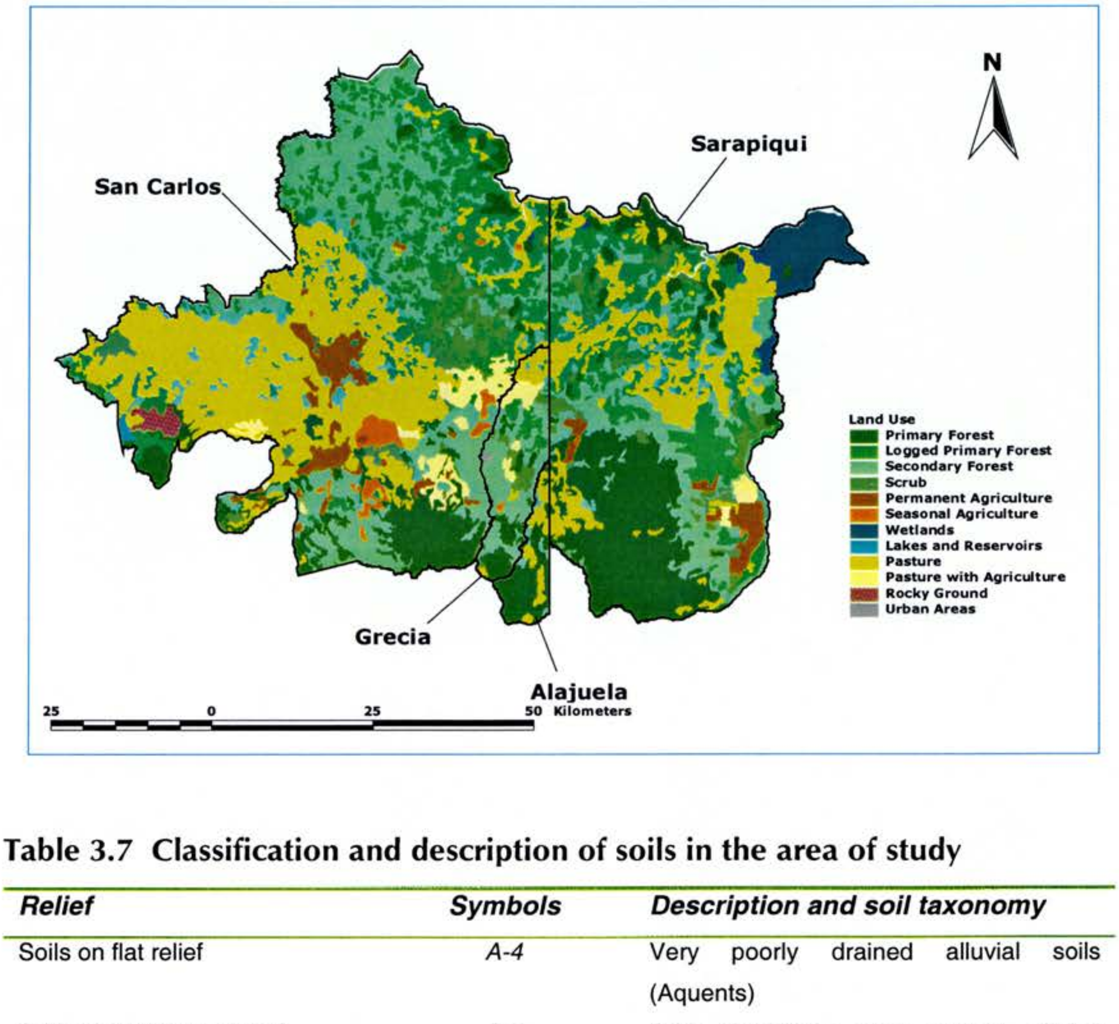


**Table 3.7 Classification and description of soils in the area of study**

| *Relief* | *Symbols* | *Description and soil taxonomy* |
|---|---|---|
| Soils on flat relief | *A-4* | Very poorly drained alluvial soils (Aquents) |
| Soils on undulating relief | *B-5* | Soils developed over ancient eroded terraces on gently undulating terrain (Humults, Tropepts) |
| Soils on deeply dissected to mountainous relief | *D-2* | Residual soils, on steeply dissected relief (Udults, Ustults, Tropepts) |

Source: Vásquez 1979

### 3.7.1 Field sites

Ten field sites were selected. The sites range along a gradient of disturbance and consist of two sites of each of the following habitats: primary forest, primary logged-over forest, secondary forest, forest plantations (*Gmelina arborea*), and heavily disturbed pasture area (Figure 3.11 and 3.12). Figures 3.10 and 3.13 to 3.15 illustrate the locations of the ranches (or *fincas*). The following sections outline in which ranch the various field sites are found. Five randomly located transects were laid in all ten field sites. The transects were oriented to 40° and their start coordinates are detailed in Figure 3.13. The sites were accessible by dirt road (requiring 4-wheel drive) and/or hiking. They were all of approximately 100 hectares.

**Figure 3.12 The gradient of anthropogenic disturbances examined in this study**

*Primary forest ⇒* *Primary logged over ⇒ forest* *Secondary forest ⇒* *Forest plantation ⇒* *Cattle pasture*

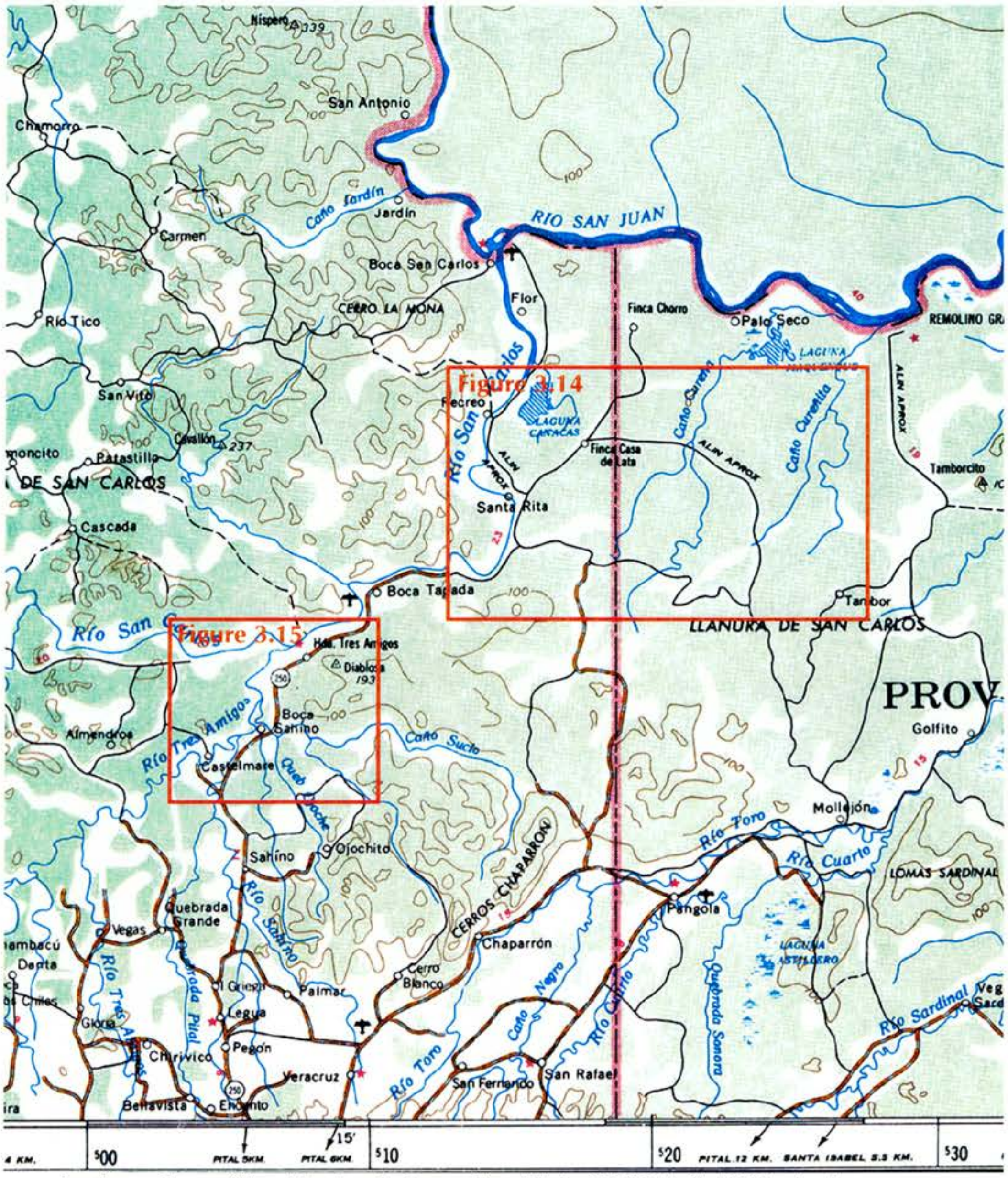
→ Increasing disturbance level →

### Primary forest

The two primary forest sites proved difficult to locate due to most forest areas being logged at some time. The first site, *Laguna Lagarto*, was located in a ranch owned by German conservationists who use the forest as a site for bird watching and ecotourism (Plate 3.5). The area selected for the site has not been logged and is located near a tourist lodge and used for forest walks. It has an undulating topography, with few steep slopes and averages about 30m above sea level (a.s.l.). The area sampled covered approximately 100 hectares.

The second site, *Hogar de Ancianos Primario*, was located in the middle of a forest which had been selectively logged in 1997 but due to steep slopes along a ridge through the middle of the area, a large proportion had not been affected by the operation. This area was about 80 hectares, with an altitudinal range from approximately 30m to 110m a.s.l.. It consists of a gently undulating area which drops off into very steep slopes on each side of the ridge.

## Figure 3.13 Map of general study area

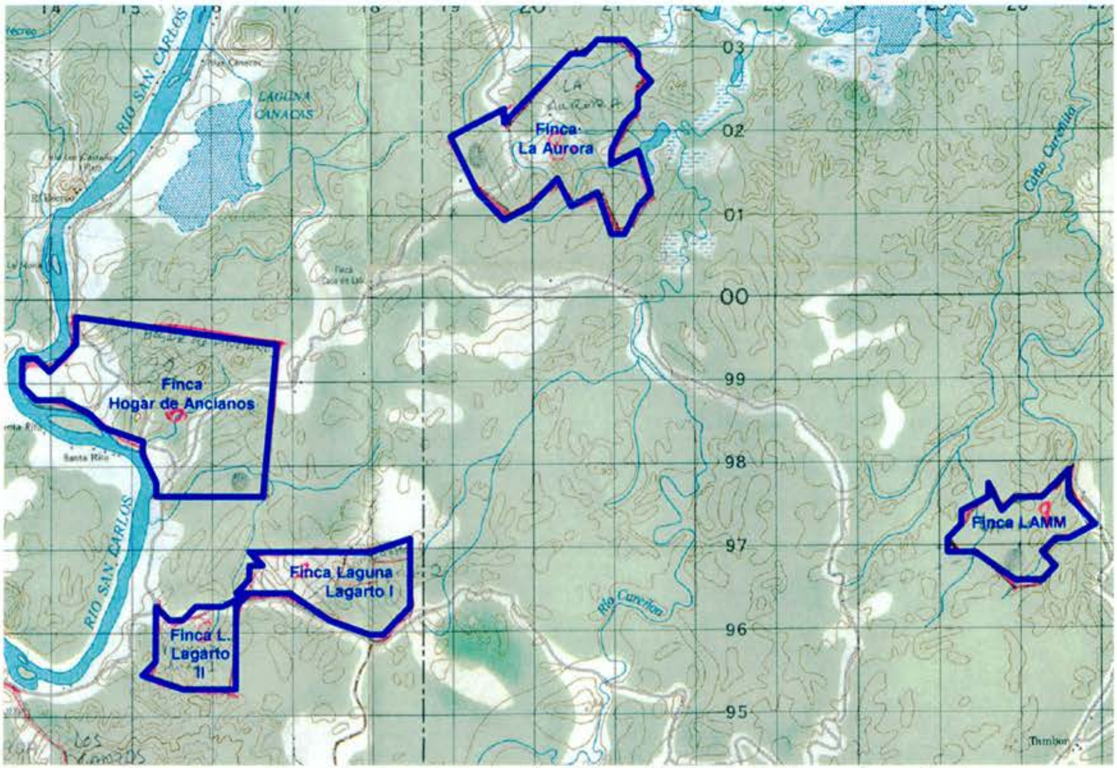


Source: Instituto Geográfico Nacional, Costa Rica (Hoja CR2CM-2) 1988. Scale:

NORTH ⇧ 0 1km

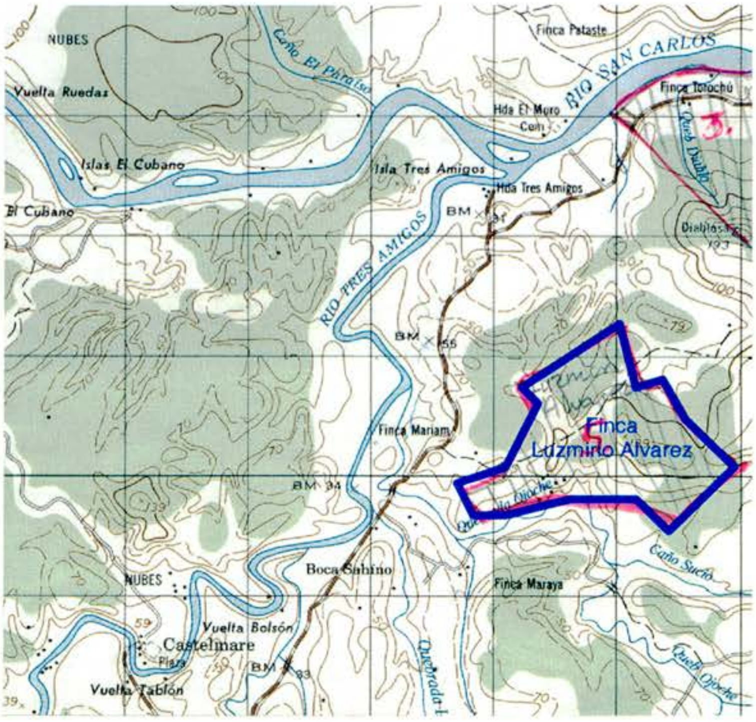
| SITE | FINCA | TRANSECT START COORDINATES (metres East, metres North): | | | | |
|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 |
| PrimFor1 | L. Lagarto II | 515500 296100 | 516100 296100 | 515600 295500 | 516100 295700 | 516100 296100 |
| PrimFor2 | H. de Ancianos | 514800 298900 | 515500 299200 | 515500 298800 | 515600 299400 | 516300 299400 |
| LogFor1 | L. Alvarez | 508300 290100 | 508200 290200 | 508200 289800 | 508800 290300 | 508800 289700 |
| LogFor2 | H. de Ancianos | 515900 298200 | 516300 298300 | 516300 298100 | 516100 298300 | 516700 298700 |
| 2ndFor1 | L. Lagarto I | 518100 296800 | 518100 296500 | 518300 296300 | 518800 296800 | 517800 296500 |
| 2ndFor2 | L. Alvarez | 507000 290900 | 507500 290900 | 507900 290200 | 508100 290600 | 506900 290800 |
| Plantat1 | La Aurora | 519500 301600 | 519800 301800 | 520100 302200 | 520400 302500 | 520800 301900 |
| Plantat2 | LAMM | 525800 296900 | 525300 297300 | 525900 297200 | 525800 297700 | 526200 297200 |
| Pastur1 | H. de Ancianos | 514200 300000 | 514200 299200 | 513900 298900 | 514800 298800 | 515000 298200 |
| Pastur2 | L. Alvarez | 507100 289900 | 507700 289800 | 507300 290200 | 507400 290600 | 507900 289700 |

**Figure 3.14 Location map of study areas (*fincas*): I**



Source: Instituto Geográfico Nacional, Costa Rica (Hoja 3348 II) 1986

**Figure 3.15 Location map of study areas (*fincas*): II**



Source: Instituto Geográfico Nacional, Costa Rica (Hoja 3347 IV) 1986

**Plate 3.5 Primary forest site (Site: *Laguna Lagarto Primario*).** This site demonstrates characteristic features of primary forest vegetation types, including high canopy and a ground layer of herbs and poles (of natural regeneration).

## Primary logged-over forest

As already discussed, much of Central America's forests have been reduced to scattered fragments, few of which are pristine. Given the political and socio-economic trends in the region one of the few realistic options to attempt their conservation is to make them economically productive through natural forest management (Stanley and Gretzinger 1996). Gómez-Pompa and Kaus (1990) demonstrate that some Central American traditional societies successfully manage their forest patches over a long period of time and at varying intensity, although this is less relevant in Costa Rica as there are few traditional societies remaining. In the area of this study the communities are, generally, recent incomers who practise more destructive forms of land management. Despite the degradation of the logged natural forest sites in these areas many rural dwellers are still dependent on them for various products. The sites often possess substantial timber and non-timber resources. They also provide a useful buffer in reducing impacts on critical protected areas (Terborgh 1992). It is widely recognised that forest patches, including those which have been selectively logged have a high conservation value. Many studies have demonstrated their importance ecologically and for wildlife protection and conservation (e.g. Nepstad et al. 1996, Lyon and Horwich 1996).

The first logged-over primary forest site, *Luzmirio Alvarez Intervenido*, was located in a ranch at approximately 400m a.s.l.. It has approximately 150 trees (over 10cm dbh) per hectare and a basal area of commercial species of 12 $m^2ha^{-1}$. The forest was logged in 1994 and 116 cubic metres of wood removed. Logging roads are still visible but regeneration is beginning. Tree felling gaps have recovered and new growth is taking place. It has an undulating topography with few steep slopes. The forest area covers 94.5 hectares and it is surrounded by a mix of exotic plantations, pasture and secondary forest. It is an ecologically important site and is nationally recognised as a refuge for the endangered Green Macaw (*Ara macao*).

The second logged-over site, *Hogar de Ancianos Intervenido*, is located in the same forest as the primary forest site, *Hogar de Ancianos Primario*. It was logged in 1992 and still has obvious logging roads although these are beginning to develop understorey regeneration and some small trees on these roads already have a diameter at breast height (dbh) greater than 10cm. It has a very gently undulating topography and is approximately 20m a.s.l..

### Secondary forest

A relatively common situation in northern Costa Rica, particularly in the San Carlos region of this study, is the abandonment of agriculture and pasture land which has previously been cleared from primary forest. The land is abandoned mostly for economic reasons. In this region the soils are poor and following forest removal lose their rich organic layer very rapidly, the majority of nutrients are also lost within a short time period. This loss necessitates additional inputs of fertiliser to maintain the land as a viable resource. There also appears to be a great need to reduce invertebrate pests and common practise involves huge inputs of pesticides (pers. observ.). The recent economic situation in the region has resulted in the cost of these inputs being uneconomic compared to the low returns from crops or livestock. The large human effort required to clear recolonising forest and weed invasion also becomes less viable as the land becomes more degraded. Therefore, although agriculture and cattle ranching is still widely practised in the region, it is decreasing and many areas have been abandoned and left to regenerate naturally. Depending upon the duration and degree of human impact the land regenerates at different rates. In this region it appears that regeneration is prolific and that forest species are re-established readily. This success may be due to an existing soil seed bank or to the still common fragments of natural forest nearby providing a seed source. The regenerating areas pass through typical successional stages beginning with rough impenetrable scrub which graduates to areas of pioneer species, such as *Cecropia sp.*, which then provide sufficient shade and organic matter to allow forest species to return. Within five to ten years the regeneration has evolved into an area of new forest which provides many of the services provided by natural forest. Although not as diverse or multi-layered as the original forest cover, the forest provides shade and a suitable habitat for many plants and animals.

In this study secondary forest is defined as forest which has regenerated on land which had been previously completely deforested (Maginnis et al. 1998). The first secondary forest site, *Laguna Lagarto Secundario*, is located within the same ranch as the *Laguna Lagarto* primary forest site (Plate 3.6). It is a mix of cattle pasture and some remaining forest trees which has been left to regenerate naturally for approximately 5 years. It has a undulating topography and is surrounded by a mixture of cattle pasture, agriculture (cassava and *pejibaye* palm) and a small remaining patch of natural forest.

The second secondary forest site, *Luzmirio Alvarez Secundario*, is located in the same ranch as the Luzmirio Alvarez logged-over forest site. It consists of an area which had been left to regenerate naturally after being used as cattle pasture, a few forest trees had been left for shade and regeneration has occurred primarily as a natural monoculture of *Vochysia ferruginea*. The topography is very gently undulating and is approximately 250m a.s.l..

**Plate 3.6 Secondary forest (Site: *Laguna Lagarto Secundario*).** This site demonstrates the characteristic vegetational features of regenerating secondary forest, including a predominance of small saplings and a few larger pioneer species.

## Plantation

*Gmelina arborea* is a common plantation tree in the neotropics. It is an exotic, fast-growing species which tolerates poor soils and can be harvested on a ten year rotation. Both sites are surrounded by natural forest or areas of cattle pasture. They are situated around 20m above sea level.

The first plantation site, *La Aurora*, is a plantation of the exotic fast growing species *Gmelina arborea* (Plate 3.7). It was established on abandoned cattle pasture in 1994 and 1995 and covers an area of 179 hectares. Areas of natural forest and pasture surround it. It is approximately 70m a.s.l. and has a gently undulating topography.

The second plantation site, *LAMM*, is also a plantation of *Gmelina arborea*. It was established in 1993 and 1994 again on abandoned cattle pasture and covers an area of 98 hectares. It is surrounded by natural forest. The topography is gently undulating. There are swampy areas which are drained by a small river.

**Plate 3.7 Gmelina arborea plantation (Site: *La Aurora*).** The plantation demonstrates a reduced field layer and a relatively open canopy.

## Pasture

Forest clearing for pasture is a common activity in the neotropics and Costa Rica is no exception. The two pasture sites sampled in this study are typical of the landscape which result from forest removal. Clearing is carried out to enable the land to be used for cattle grazing. Although initially profitable this activity becomes less productive with time as the land becomes poorer. The land can only sustain very few cows per hectare.

The first pasture site is located in the *Hogar de Ancianos* ranch, *Hogar de Ancianos Repasto* (Plate 3.8). It is an extensive area of cattle grazing which is intensively used. The area of approximately 85 hectares is fenced into smaller areas and cattle are grazed in rotation throughout the area. It was originally seeded with improved pasture grass seed, is gently undulating and has a few remaining forest trees used for shade. It is surrounded on one side by natural forest and on the other by the San Carlos River.

The second pasture site is located in the *Luzmirio Alvarez* ranch, *Luzmirio Alvarez Repasto*. It is also an area of intensively used grazing land. It was originally cleared from natural forest and is still surrounded by natural forest and a small area of plantation. It is situated on a slope at approximately 350m a.s.l.. Many forest trees have been retained for shade including a number of Almendro (*Carapa guianensis*) which are important for the conservation of the Green Macaw, which feed on the fruits of this tree.

**Plate 3.8 Pasture (Site: *Hogar de Ancianos Repasto*)** clearly demonstrating the near complete removal of forest trees and the scarcity of any other vegetation. The remaining forest is evident in the background.

## 3.8 The importance of the study area for biodiversity conservation

This chapter has given an overview of Costa Rica as a country while focussing on its environment and natural resources and providing the context for the selected study areas. Due to its position in the Central American isthmus and its diverse landscapes, Costa Rica is one of the most biologically diverse countries in the world (INBio 2000). However, its rapid development and the geographical expansion of its population have resulted in a fragmented rural landscape where natural forest remains only as patches within the wider mosaic of ranching and agriculture. The remaining forests and their biodiversity are increasingly threatened. Studies of biodiversity, including species inventories, are being carried out by many organisations, not least the National Institute of Biodiversity (INBio 2000). However the majority of these studies take place within the protected areas of Costa Rica. Little work has been carried to investigate the effects of humans on natural resources outwith these areas (Guindon 1996). For this reason sites with a non-protected area status were selected for the field investigations.

The northern areas of the San Carlos and Sarapiqui regions in the Northern Zone of Costa Rica represent a landscape which has been heavily disturbed but which still contains important natural forest fragments. Investigation of the biodiversity of this area, incorporating studies over a gradient of human disturbance, provides knowledge regarding forests and biodiversity in a landscape which is increasingly representative of lowland humid tropical regions. It also provides valuable information for better biodiversity conservation management in areas outwith any formal category of protection.

# CHAPTER 4

# MEASURING BIODIVERSITY IN A LANDSCAPE OF HUMAN DISTURBANCE:

## RESEARCH APPROACH AND METHODOLOGY

### 4.1 Introduction

This chapter will describe the methods used in this study. It discusses rapid biodiversity assessment (RBA), which is the principal method employed. The usefulness of the approach is examined in the analysis of tropical forest biodiversity and in the evaluation of changes caused by human disturbance. The chapter presents an overview of existing methods and expands upon the techniques used throughout this research. It is divided into the following five sections: monitoring biodiversity, field methods, invertebrate identification, laboratory methods, and data analysis.

### 4.2 An overview of biodiversity research

Scientific data regarding the effects of forest disturbance and clearance on biodiversity remain scarce (Lawton et al. 1998). Standardised methods used to document population changes are not widespread and, where they do exist, are often little known (Heyer et al. 1994). Knowledge of which species occur, and where, is essential to an understanding of the intricacies of biological diversity (Heyer et al. 1994). Species lists of some organisms (e.g., butterflies, monkeys, birds and trees) exist for many sites, most of these in the developed world, but comparable data for the majority of the world's biota are lacking. This, coupled with a probable global species decline due to anthropogenic disturbance provides ever more impetus for monitoring species status, particularly little studied groups, such as, insects, in the various biomes of the world.

### 4.2.1 Monitoring the biodiversity of invertebrates

This section will review the monitoring methods utilised and discuss innovative techniques of rapid biodiversity assessment which are currently being developed (Watt et al. 1998).

The data gathered during inventory and monitoring studies form the basis for evaluating species status over broad geographical areas and for determining population changes. These data are utilised to compare species richness among assemblages, for evaluating the importance of specific habitats for species maintenance and for making conservation and management-related decisions (Heyer et al. 1994). As forest conservation becomes an increasing priority, it is evident that rapid methods of assessment are necessary. Traditional taxonomy and species inventories have produced lists of species for specific areas, however, this has proved to be time-consuming and the task has really only just begun. As natural habitats are destroyed, more appropriate and far quicker methods of monitoring and assessment are urgently required. Conservationists and scientists simply no longer have the time to rely on long-term studies. This change in focus has resulted in the development of methods of RBA which move away from traditional inventory methods. Often, for example, particular species are targeted, or species are identified only to morphospecies level, or a specific group is used as a surrogate for a larger section of biological diversity. An RBA may be used to (Watt et al. 1998):

- assess the status of a particular species,
- assess overall biodiversity, or
- assess the 'sustainability' or 'healthy functioning' of a particular ecosystem.

In many cases, particularly for invertebrates, RBA methods for sampling and analysis already exist. However, Watt et al. (1998) call for further consideration of the choice of taxa, particularly in relation to ecosystem sustainability, and for pilot studies of the methods to be applied alongside RBAs of vertebrates and higher plants. Many studies have focused on mammals, particularly ungulates, which can be surveyed from the air, or top carnivores. These are thought to provide good indicators of ecosystem health.

However, inventories of other ecosystem components, for example invertebrates, are likely to reveal more information regarding ecosystem functioning.

In recent years there has been an increase in studies investigating invertebrate diversity and, in particular, a growing interest in how this information can be used to monitor human impact on natural systems. Studies of insect diversity range from studies of Amazonian ant communities (Vasconcelos and Delabie 2000) to investigations of arachnids in the Highlands of Scotland (Dennis et al. 1998). A variety of sampling methods have been employed. Harris and Burns (2000) used Malaise traps to investigate beetle assemblages in New Zealand, while termites were sampled in Cameroon by using a rapid biodiversity assessment protocol which involved timed sampling effort by scientists along a transect (Jones and Eggleton 2000). In Tanzania, Kruger and McGavin (1998) used tree fogging to sample all tree canopy invertebrates, and Watt et al. (in press) utilised a suite of insect sampling methods to examine ant diversity. They employed tree canopy fogging with insecticide, and leaf litter extractions with samples separated by use of 'Winkler bags' (Davies and Stork 1996). Junker et al. (2000) sampled spiders in Germany using pitfall traps in order to examine the impacts of silvicultural practice. Thus the evidence of earlier research reveals a focus on group specific studies undertaken to investigate the effects of human impact in a variety of situations.

It was decided that the most appropriate method for the rapid assessment of biodiversity in this study would be a system of pitfall traps where leaf litter invertebrates could be compared across various land uses. This methodology is outlined in the next section, which also considers the selection of the focus insect groups.

## 4.3 Field methods

Many existing studies have focussed on individual insect orders, or selected indicator species. Such studies often focus on taxa which are not typical of the majority of invertebrates because they are large, functionally unique or specialised (e.g. dung beetles, Klein 1989; leaf cutter ants, Vasconcelos 1988). Although these studies are undoubtedly important, their relevance to larger invertebrate assemblages may be limited. The present study employs a multi-species RBA approach in order to examine the effects of human disturbance on leaf litter invertebrates and to provide an assessment of the effectiveness of natural forest patches and anthropogenic land uses in supporting invertebrate diversity. It focuses particularly on a numerically dominant group of insects (ants: Hymenoptera, Formicidae) and a taxonomically and trophically diverse group (beetles: Coleoptera) in order to produce results which may have greater applicability to other forest invertebrate assemblages. This section describes the field methods employed to carry out this study.

### 4.3.1 Pitfall trapping

For the purposes of this study, pitfall traps were arranged in transects over a range of sites of human impact. To achieve the aims of the study a complete inventory of invertebrates was not required. The objectives, to measure and monitor the impact of human disturbance on forest, are achieved by a sampling strategy which was consistent over all field sites and provided a rapid assessment of relative invertebrate diversity. This enabled a comparison to be made over sites and demonstrated the changes that disturbance causes.

Pitfall trapping, as a method of invertebrate sampling, is recommended by Sutherland (2000), New (1998), Agosti et al. (2000) and Southwood and Henderson (2000) among others. Specifically, pitfall traps have been used extensively for leaf-litter invertebrate studies (Bromham et al. 1999, King et al. 1998, Finn et al. 1999, Davies and Margules 1998 etc.). Some sampling strategies use baited traps (Perfecto and Sediles 1992). However, simple traps are generally to be preferred as they minimise further sources of error (Greenslade and Greenslade 1971). Preservatives are often used in traps but these may also affect the catches of species differentially (Greenslade and Greenslade 1971). Ethylene glycol has been found to work well for the Carabidae (Clark and Blom 1992) but causes catch differences when compared with traps holding just water (Holopainen 1992). Pitfall traps have many advantages; they are cheap, easy and quick to operate and a reasonable sampling effort can provide an impressive set of data (Southwood and Henderson 2000). Many studies have shown that a wide range of factors influence catch size (Niemela et al. 1990, Weeks and McIntyre 1997). However, when potential sources of variation are recognised, they provide valuable information (Southwood and Henderson 2000). Pitfall traps are frequently used in studies of community richness and for habitat assessment. Obviously such studies only sample the surface dwelling community, and sweep nets, suction sampling, fogging etc. will reveal a different species pattern (Samu and Sarospataki 1995). Jansen and Metz (1979) consider that the number of animals trapped depends on: 1) their population density, 2) their movement, assumed to be Brownian, 3) the boundary of the pitfall, and 4) the outer boundary of the area and the extent to which the animals penetrate it. Movement of invertebrates may be affected by temperature, moisture and other weather conditions (Mitchell 1963), food supply (Briggs 1961), the character of the habitat and the condition of the individual. In addition, the retaining efficiency of the trap may influence the catch, traps with smoother sides are preferable.

The factors discussed above were taken into account when planning the methodology for this study. It was decided that, in order to assess human impact on invertebrates over a gradient of disturbance, the data provided by a standardised pitfall trapping strategy would reveal the changes occurring in leaf-litter invertebrate diversity and composition.

### 4.3.2 Invertebrate field sampling

This section describes the sampling strategy employed in order to examine leaf-litter ant and beetle diversity in the sites detailed in Chapter 3.

#### ANTS

Ants were chosen as a representative component of leaf-litter insect diversity as they are frequently the most abundant insects in tropical forest (Wilson, 1987). In samples from a Peruvian rain forest, for example, ants comprised >70% of individual insects (Wilson, 1987). The wide distribution of ants throughout the world in diverse habitats makes them a strong indicator of biological diversity (Roth et al. 1994). Ant assemblages can also be used to indicate habitat disturbance (Mackay et al. 1991, Gadagkar et al. 2000). Ants play many important roles in structuring communities, from nutrient cycling and seed dispersal to influencing the flora and fauna (Janzen, 1983). They are also frequently involved in symbiotic relationships with other species of plant and animal. This study considers ground-foraging ants as a component of biodiversity with the potential to reflect patterns of loss of diversity of other species. The focus on ground-foraging ants is based on the uniqueness of this fauna and the specific tested methods by which it can be surveyed (Agosti et al. 2000). The number, heterogeneity and abundance of ant species will be investigated and compared between the different forest patches. Ant ecology is discussed further in Chapter 6.

### BEETLES

Ground dwelling beetles are also sampled in this study, using the same methodology as used for the ants. Coleoptera are the insect order with great taxonomic diversity (García-Villanueva et al. 1998). Ecologically, they occupy a wide range of niches and exploit many trophic resources through phytophagy, predation, necrophagy, detritus eating, coprophagy etc. (García-Villanueva et al., 1998). They have also been documented as good ecological indictors due to the influence that changes in environmental conditions have on their populations and communities. Coleoptera, particularly carabids, have been used to classify habitats in temperate regions (Luff et al. 1989). In addition, the taxonomy of the group is relatively stable, and identification, at least to family level, is simple. They are distributed over the total range of terrestrial habitats (Luff 1990) and can be sampled by standardised techniques (for example, pitfall trapping).

### TRAPPING ROUTINE AND SAMPLING

As it is normally impossible to count and identify all animals in a habitat, it is necessary to estimate the population by sampling (Krebs 1989, Southwood and Henderson 2000). There are three principal sampling designs used in ecology; random sampling, stratified random sampling and systematic sampling (Krebs 1989). Random sampling is the most common and the simplest design. Each possible sample unit has an equal chance of being selected. However, this design often results in a sampling strategy which has uneven spatial coverage (Southwood and Henderson 2000). It does, nevertheless, allow greatest statistical utility as all parametric tests are based on random sampling designs. In stratified random sampling, points are randomly located within user-defined areas (the stratification), while in systematic sampling, an even coverage of sample points is achieved by a pre-planned arrangement, for example, a grid system (Niemela et al. 1990). This may be easier to apply in the field than a random design but may produce biased estimates of means and confidence limits (Krebs 1989) while preventing the use of tests assuming a random distribution. All of the above sampling strategies have been used in invertebrate studies which utilise pitfall trapping as the principal collecting method.

Examples include the work of Niemela et al. (1990) which used a systematic design with 300 pitfall traps arranged in a grid of 12 x 25 traps. Vasconcelos and Delabie (2000) also employed a systematic design of plots with evenly distributed sampling points. Roth et al. (1994) employed a stratified random design by sampling over 11 sites, which represented a gradient of land use, using 10 parallel transects with pitfall traps arranged along their lengths. Buse and Good (1993) also employ a stratified random sample with pitfall traps arranged in transects over 21 sites, although transects were deliberately laid away from site edges. No studies that employed an entirely random sampling design were identified, possibly as a result of the reasons indicated above.

For the purposes of this study, consideration of the literature suggested that the most efficient sampling method would consist of a stratified random design. The ten sites, which are principally characterised by land use, were chosen to represent a gradient of disturbance from primary forest to pasture with each land use replicated once. In order to apply the random stratified design decided upon and avoid uneven spatial coverage, each site was divided approximately into five sections and a transect located randomly within each section. The transect locations were identified by overlaying forest management plan maps (produced by CODEFORSA, a local NGO) with a grid and then picking random x and y co-ordinates (Sutherland 2000). All transects were oriented to 40°. In order to prevent the sampling being biased by invertebrates moving from adjacent sites, transects were not located near the edge of sites. Specifically, if the randomly chosen transect end point lay within 20m of the site edge or, due to uneven boundaries, some point in the transect passed within 20m of the site edge the possible transect was excluded. Using this design, five randomly located 100 metre transects were laid, as close to the identified locations as possible, in all ten field sites. The design also resulted in a representative coverage of topographical features.

One pitfall trap was located every 20 metres along each transect including one at each end, five in total (Figure 4.1). The pitfall traps had a diameter of 100mm. Abenspergtraun and Steven (1995) demonstrated that up to an approximate diameter of 90mm, ant species catch is significantly improved; beyond that there is no significant improvement. Indeed, in their study, traps of 86mm diameter caught all species >10mm in length. They also showed that differences in catches between traps of different sizes were due primarily to different capture rates of rare species. Traps of 86mm caught 44 percent of rare species, traps with a diameter of 135mm caught 52 percent, while 18mm diameter traps only caught 25 percent of rare species.

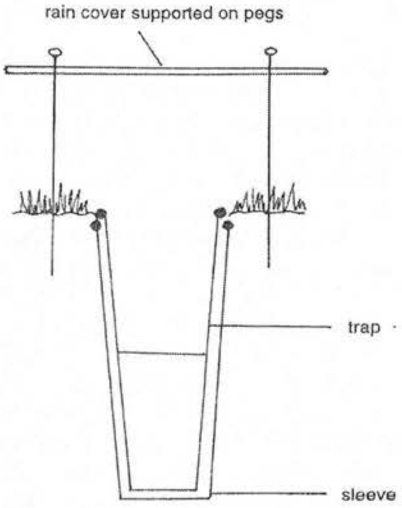


**Figure 4.1 Diagram of pitfall trap used in this study.** This model consisted of two plastic cups (diameter 100mm), the outer one maintaining the shape of the hole and the inner one being the trap, and removable for emptying. A roof is suspended above the trap to prevent flooding by rain. Source: New 1998.

Each site was sampled for a seven-day period, once during the wet season of 1998, in October to November, and once during the dry season of 1999, in February to March, to account for seasonal changes in species composition. The traps were filled with 2cm of an alcoholic preservative (Ethylene glycol) and a drop of detergent added as a wetting agent. They were placed in holes, dug with a minimum of soil and vegetation disturbance, with rims flush to the soil surface. A plastic cover was fixed over each trap to prevent flooding during heavy rain. The recommended time period to leave traps varies with the level of ant and beetle activity and in hotter regions sufficient samples can often be obtained after 24 hours (Andersen, 1990). In this study, the traps were left for one week in order to ensure an adequate sample was obtained.

### 4.3.3 Tree inventory and site characterisation using environmental variables

Environmental conditions in the field sites were monitored by taking measurements of a variety of environmental variables. A comprehensive tree inventory was also carried out. The methods employed to sample and measure these variables are presented below.

#### ENVIRONMENTAL VARIABLES

The range of influential variables is considerable and a selection was made based on relative ease of collection and rapidity of analyses whilst representing as closely as possible the most diagnostic parameters. The following environmental variables were measured in order to assess ecological and physical changes and differences between land uses and to characterise the sites:

- soil temperature (°C),
- soil moisture (kPa),
- soil pH,
- maximum and minimum temperature (°C),
- mean and range of canopy closure at trap locations (%),
- ground vegetation cover (%),
- leaf litter quality (kg/m$^2$),
- elevation (m),
- aspect of transect,
- mean and range of slope at trap locations (°),and
- timber volume removed (m$^3$) and harvesting date (month, year).

## MEASUREMENT OF ENVIRONMENTAL VARIABLES

### SOIL TEMPERATURE

Soil temperature was measured with a thermometer which was placed at 10cm depth in the soil, for 2 minutes, before recording a reading. The thermometer was located 1m from each trap. The ambient air temperature was also recorded in order to calibrate for any changes caused by time of sampling.

### SOIL MOISTURE AND PH

Soil samples (0-10cm) were taken at each trap location. These were used primarily to calculate soil moisture content but soil pH was also calculated. Soil moisture content was measured gravimetrically by weighing before and after both air and oven drying. Loss on ignition, used as an approximate measure of soil organic matter, as well as incorporated moisture held at tensions greater than air drying, was also calculated.

### MAXIMUM AND MINIMUM TEMPERATURE

The maximum and minimum temperature was recorded over the seven-day sampling period using a maximum/minimum thermometer at two points in each site. This measure provided a logistically simple approximation of temperature. It also provided an overall temperature estimation which was not provided by the instantaneous ambient temperature reading.

### CANOPY COVER

Hemispherical photographs were taken at trap one, three and five in each transect. Analysis of these provided a measure of canopy cover.

### GROUND VEGETATION COVER

Ground vegetation cover was estimated using a 10m x 10m quadrat at each trap site. The estimate was calculated in percentage cover.

### LEAF LITTER

Leaf litter samples were taken at trap one, three and five in each transect in each site. Leaf litter over an area of 0.25 x 0.25 metres was collected during the dry season. It was sealed and later measured before and after air drying to calculate the moisture content.

### ELEVATION

The elevation of each site was measured at each trap location on each transect using an altimeter (Stanton Hope no. 181300). This was calibrated regularly at a nearby Costa Rican Geographical Institute calibration point.

### ASPECT AND SLOPE

The mean and range of slopes in each transect was calculated by taking Suunto Clinometer readings every 20 metres in each transect. The aspect was recorded using a Suunto KB14 compass.

## TREE INVENTORY

A comprehensive tree species inventory was carried out in all of the field sites. Quadrats and strip transects are typically used to sample species which can be easily counted and are among the most common techniques for counting trees and plants (Gibbs et al. 1998, Kent and Coker 1992, Krebs 1989, and Sutherland 2000). Strip transects have the advantage that they are more likely to include a range of habitats and so reduce variation between quadrats and increase precision (Bormann 1953). They also account for a greater proportion of habitat heterogeneity. Indeed, Krebs (1989) states that 'nearly everyone has found that long thin quadrats are better than circular or square ones of the same area'. Bormann (1953) demonstrated that long thin quadrats reduce the standard deviation of basal area measurements of trees in North Carolina considerably. A plot of 4 x 4 metres had a standard deviation of 50.7 whilst a plot of 4 x 140 metres a standard deviation of 34.8. It is, however, also important to note that strip transects have a long perimeter which may increase inaccuracies due to decisions regarding whether an individual is inside the strip or not (Sutherland 2000).

Considering these findings and the logistics of the present study, it was decided to measure tree species diversity and basal area over strip transects. The transects established for the invertebrate survey were used as a basis for these vegetation strip transects, and trees that were located 5 metres either way from the original transect were measured. This resulted in five 10 x 100 metre strip transects being measured in each field site. All trees with a diameter at breast height (dbh) greater than 10cm were included in the inventory. They were identified to vernacular name, by a parataxonomist (INBio 2000), and their dbh recorded in order to calculate basal area.

## 4.4 Invertebrate identification

With the increasing recognition of the importance of invertebrates in ecosystem processes, there has been an improved effort to incorporate this component of biodiversity into biological surveys (Oliver and Beattie 1996). As discussed earlier, this often involves rapid collection techniques but in order to complete a RBA, data processing has also to be accelerated. Oliver and Beattie (1996) suggest five procedures which may achieve this:

- the use of surrogate, indicator taxa in place of all taxa,
- surrogate or restricted sampling in place of intensive sampling,
- the use of morphospecies identified by non-specialists,
- the use of taxonomic ranks other than species, and,
- extrapolation, for example, from species accumulation curves.

To utilise surrogate taxa, also known as priority taxa (New 1987), indicator taxa (Brown 1991, Warren and Key 1991, Kremen 1992, Pearson 1994, Sparrow et al. 1994, and Stork 1994, Reyers and van Jaarsveld 2000), focal groups (di Castri et al. 1992) predictor sets (Kitching 1993), or target taxa (Kremen 1994), the species chosen should have known relationships to the diversity of other taxa (Oliver and Beattie 1996). They may also respond in a predictable way to environmental parameters or disturbance or represent a range in a functional attribute such as trophic level (Hammond 1994).

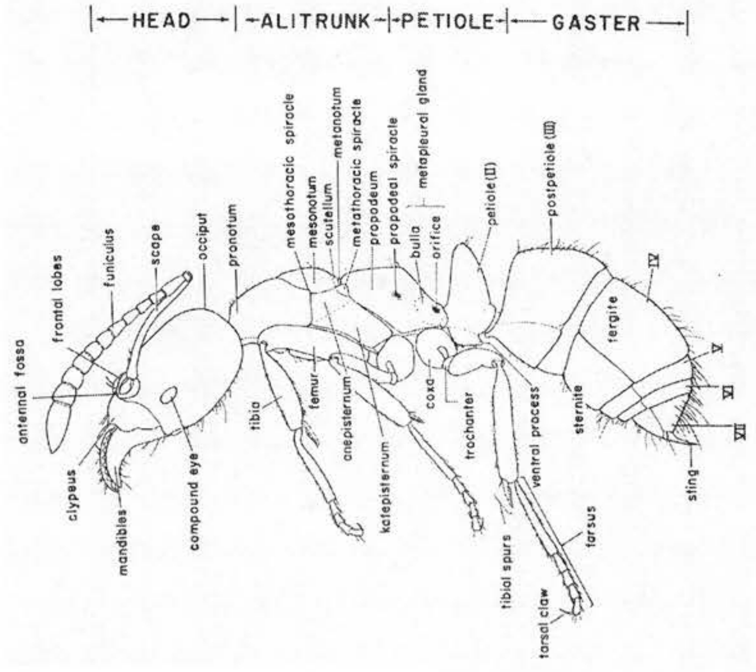
Surrogate sampling utilises a restricted sampling methodology to measure relative differences among diversities at different sites (Hammond 1994). The use of morphospecies identification to process invertebrate inventories is a relatively recent attempt to reveal species diversity and composition patterns in a cost effective and rapid methodology. Pik et al. (1999) found that morphospecies richness was highly correlated with actual species richness. They also found that ordination analyses revealed similar site separation for morphospecies, species, and genus data. This procedure of sorting invertebrate specimens to morphospecies, or to recognisable taxonomic units (RTUs) as they are called by some, has been widely employed (Gadagkar et al. 1990, Hutcheson 1990, Janzen 1991, Cranston and Hillman 1992, Oliver and Beattie 1993, Beattie and Oliver 1994, New 1996, Kruger and McGavin 1998). By consideration of this previous research, and regarding the lack of existing knowledge from the study area, it was decided to employ the same method of invertebrate sorting in this study. The utilising of surrogate taxa was not possible, as no previous work had been carried out on the ants and beetles in the area. As part of the research output, this study aims to identify some taxa which may be used as indicators in the future.

The invertebrates collected by the system of pitfall traps were sorted, and the ants and beetles separated. Both ants and beetles were then sorted by trap to morphospecies level. These insect groups have many obvious external morphological characteristics (Figure 4.2). The morphospecies were then identified to family, sub-family or, where possible, genus and/or species. In order to achieve this, a variety of invertebrate keys were consulted (e.g. Bolton 1994), and expert advice was sought from the National Institute of Biodiversity (INBio), Costa Rica and the Natural History Museum of the University of Oxford. All beetles were sorted to family level and all ants to sub-family. Experts from both the National Institute of Biodiversity in Costa Rica, and the Natural History Museum of the University of Oxford checked these classifications. Individual morphospecies were pointed and/or pinned. The number of individuals of each morphospecies from the two insect groups in each trap were also recorded and a list of all morphospecies and their abundances was tabulated for each trap in every transect, site, and land use so that the relative distribution of morphospecies could be determined. A complete list of morphospecies and their corresponding sub-family or family is presented in Appendix 3 and 6.

A reference collection of the ants and beetles collected during this study will be held in INBio, the National Institute of Biodiversity, in Costa Rica, Central America.

**Figure 4.2 The principal morphological features used in ant identification.**

(showing a worker of the Ponerinae, *Pachycondyla* sp.)



Source: Holldobler and Wilson 1990.

## 4.5 Laboratory methods to analyse environmental variables

Most of the environmental variables collected during this study did not need further processing (soil temperature, maximum and minimum temperature, ground vegetation cover, elevation, aspect and slope, and timber harvesting data). However, in order to calculate soil moisture, soil pH, and leaf litter quality some laboratory analysis was required.

### 4.5.1 Soil and leaf litter analyses

SOIL MOISTURE LOSS AND LOSS ON IGNITION

Soil samples were initially weighed and then oven dried at 105°C overnight. They were then weighed again and the moisture loss recorded. The soil samples were then ignited in an oven at 375°C for 15 hours and, afterwards, cooled in a dessicator (Rowell 1994). The samples were weighed before and after ignition and the loss in weight recorded. This measurement is known as loss on ignition and is largely equivalent to the burning off of organic matter. Although some of the weight loss may be due to water being released as the intense heat begins to break down the mineral lattice, this measurement provides a satisfactory initial estimate of soil organic matter.

SOIL PH

pH is a measure of the hydrogen ion (H+) concentration and as such is an indicator of the acidity or alkalinity of the soil (Hesse 1971). In order to calculate pH values a standard air dried, soil-deionised water suspension technique was used (Furley and Minty 1992, Ukpong and Areola 1995). A proportion of the soil samples was air-dried in the laboratory and then passed through a 2mm sieve; 25 mm of deionised water was added to 10 grams of this soil and placed on a mechanical shaker for 20 minutes. The samples were left to equilibrate for an hour and then the pH was taken with a carefully calibrated electronic pH meter.

In humid regions, where the leaching potential is high, there is a significant positive correlation between pH and the exchangeable cations available. Exchangeable calcium, magnesium and sodium ions are lost from soils by leaching leading to an increase in soil acidity. In low pH conditions, relatively large amounts of aluminium, iron and manganese ions are soluble, possibly resulting in toxic levels of these ions for some plants, whilst the presence of aluminium accelerates the exchange acidity (Brady 1984).

LEAF LITTER QUANTITY

Leaf litter was air dried for five days, weighed and expressed as weight of litter per square metre (kg/m$^2$). This provided an approximate measure of litter production.

## 4.6 Data analysis

Analysis of the data comprised various diversity indices (e.g. Shannon and Weaver; Krebs 1989), species richness and evenness calculations (Pielou, 1969), similarity indices, and multivariate analysis (Jongman et al. 1995) as described below.

### 4.6.1 Insect diversity

There are a variety of diversity indices with various strengths and weaknesses. No single index includes all the desirable properties of high discriminant ability, low sensitivity to sample size, and ease of calculation (Magurran 1988). As a result of this it is often appropriate to use a combination of indices. The indices chosen reflect a combination of richness, dominance, evenness, and relative abundance. Based on recommendations from Roth *et al.* (1994), Magurran (1988) and Krebs (1989), species richness ($S$), the Shannon ($H$) and the Simpson ($D$) indices of diversity, the Shannon evenness index ($E$) and the Berger-Parker dominance index ($d$) were calculated from the data in order to examine $\alpha$-diversity within all the sites and habitats. Both the Sorensen and Morisita indices of similarity were used to examine $\beta$-diversity among the forest patches. These indices are outlined below.

### ALPHA ($a$) DIVERSITY

**Species richness (*S*)** equals the total number of species in the community. As an index, $S$ is easily conceptualised and can be compared across different habitats. As all species in a community can rarely be enumerated (Krebs 1989) species accumulation relationships are also calculated using the Estimates program (Colwell 1999).

**Simpson's index of diversity (*D*)** was the first non-parametric measure of heterogeneity developed that makes no assumptions about the shape of species abundance curves (Simpson 1949). A non-parametric methodology was required due to the complexity of the logarithmic series and the lognormal distribution, and due to the lack of a theoretical justification for these approaches (Krebs 1989). Simpson's index measures the 'probability of picking two organisms at random that are different species (Krebs 1989). This study uses Simpson's index in the form developed by Pielou (1969) to take account of the sample being collected from a finite population. The estimator is:

$$1 - D = \sum_{i=1}^{S} [\, n_i (n_i - 1) / N (N - 1) \,],$$

where $1 - D$ is Simpson's index of diversity, $n_i$ is the number of individuals of species i in the sample, N is the total number of individuals in the sample ( $\sum n_i$ ), and S is the number of species in the sample.

**Shannon's index of diversity (*H*)** reflects both evenness and richness and is also commonly used in diversity studies (Magurran 1988, Krebs, 1989). If this index is calculated for a number of samples the resulting indices will be normally distributed making it possible to use parametric statistics to compare the sets of samples for which the diversity has been calculated (Taylor 1978, Magurran 1988). It is calculated by the equation:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where $p_i$ is the proportion of individuals of the $i^{\text{th}}$ species, and S is the total number of species.

Two categories of diversity indices exist (Peet 1974, Krebs 1989). *Type I* indices are most sensitive to changes in the rare species in the community sample. The Shannon index is an example of a type I index. *Type II* indices are the most sensitive to changes in the most abundant species. Simpson's index is an example of a type II index. Both types of index have been calculated in this study in order to examine heterogeneity focussing on both the rare and the dominant species in the communities examined.

**The Berger-Parker dominance measure (*d*)** expresses the proportional importance of the most abundant species (Magurran, 1988). Low values indicate lowered dominance by any one species in a system and are generally accompanied by increased evenness of species. The Berger-Parker index, *d*, equals $p_{imax}$, the proportion of the most abundant species.

**Shannon's evenness index (*E*)** indicates relative abundances of species in terms of evenness and is based on the Shannon index of diversity. Both the Berger-Parker dominance index and the Shannon evenness index are important measures of heterogeneity. The Shannon evenness index is calculated by the equation:

$$E = H/H_{\max} = H/\ln S,$$

where $H$ is Shannon's diversity index and ln $S$ is the natural logarithm of the number of species.

$\alpha$ - diversity was examined by using the data from all of the transects, pooled in order to calculate one value per site for each index ($S$, $H$, $D$, $d$, $E$).

### BETA ($\beta$) DIVERSITY

Beta ($\beta$) diversity is essentially a measure of how different (or how similar) a range of habitats, or samples, are in terms of the variety and abundances of species found in them (Magurran 1988). It can be applied to examine the degree of change in species diversity between habitats. $\beta$ - diversity can be calculated by examining the species compositions of different communities. $\beta$ - diversity is proportional to the inverse of similarity.

There are two broad classes of similarity measures. *Binary* similarity coefficients use only presence-absence data for the species in a community, while *quantitative* similarity coefficients require a measure of relative abundance for each species (Krebs 1989). Both the Sorensen's similarity coefficient ($S_s$), a binary measure, and the Morisita's similarity coefficient ($C_\lambda$), a quantitative measure, were calculated. Both types of similarity index were calculated in order to reveal whether the changes between communities are caused by variation in species presence or absence, or by variation in species abundance.

**Sorensen's similarity coefficient ($S_s$)** is a qualitative measure where a value of zero indicates no similarity and a value of 1 complete similarity, although it can be affected by sample size and by species richness. It is a binary co-efficient and only takes account of presence-absence data. Smith (1986, in Magurran 1988) tested qualitative and quantitative similarity measures and concluded that the Sorensen index was the best of the existing qualitative measures. It is also the most appropriate index to use if many species are present in a community but not present in a sample from that community (Krebs 1989). Considering the very high species diversity generally present in humid tropical forest areas, and specifically in the communities studied in this research, the Sorensen coefficient was employed here. It is calculated by:

$S_s = 2a / 2a + b + c$ ,

Where $S_s$ is Sorensen's similarity coefficient, *a* is the number of species in sample A and B (joint occurrences), *b* is the number of species in sample B but not in sample A, and *c* is the number of species in sample A but not in B (Magurran 1988).

**Morisita's similarity coefficient ($C_\lambda$)** is a quantitative similarity index. Wolda (1981) recommends it as the best overall measure of similarity for ecological use. It is independent of sample size but has a serious drawback in its high sensitivity to the abundance of the most abundant species (Magurran 1988). It is calculated by:

$C_\lambda = 2\ \Sigma^n X_{ij} X_{ik} / (\lambda_1 + \lambda_2) N_j N_{k,}$

where $C_\lambda$ is Morisita's index of similarity between sample j and k, $X_{ij}$ $X_{ik}$ are the number of individuals of species i in sample j and sample k, $N_j$ is the total number of individuals in sample j, and $N_k$ is the total number of individuals in sample k.

### 4.6.2 Analysis of variance

Analysis of variance (ANOVA) was used to test whether two or more sample means could have been obtained from populations with the same parametric mean. ANOVA tests the null hypothesis that the two sets of data are random samples from a common, normally distributed population, or two identical, normally distributed populations by comparing the value of the two sample variances. The differences between samples were checked by one way ANOVA tests (MINITAB 13), when the population distribution was normal.

Before statistical analyses were carried out the observed data were tested for normality. The departure of the observed data from expected distributions was tested using the Anderson - Darling normality test (MINITAB 13). In normal distributions it is assumed that the error terms, $\varepsilon_{ij}$, of the variable in each sample are also normally distributed

(Sokal and Rohlf 1995). Where data did not conform to the assumptions of normality, the Kruskal-Wallis test or the Mann-Whitney U-test were employed (MINITAB 13)(Krebs 1989, Wardlaw 1999).

### 4.6.3 Multivariate statistical analyses

Multivariate analysis methods can deal with complex data attributes relating biological communities to their environment (ter Braak and Smilauer 1998). The quantification of relationships between species and environmental variable can be used to model and/or predict species abundances from observed environmental data, or to predict values for environmental variables from observed species data (Jongman et al. 1995).

Multivariate classification (discrete) and ordination (continuous) techniques are important tools which can be used to describe community structure and reveal patterns in community data (Krebs 1989). Classification can be based on faunal characteristics such as species composition or dominance (Kent and Coker 1992, Webb et al. 1970). Ordination is a method which arranges species and samples along axes so that similar species or samples are close together and dissimilar species or samples far apart (Krebs 1989). It, therefore, allows analysis of species variation according to composition along continuous environmental gradients, independent of spatial contiguity (Greig-Smith 1983, Kent and Coker 1992). The study of spatial patterns of species is permitted in relation to environmental factors by reducing the multi-species data to a few relatively homogeneous clusters of both species and communities along a few axes representing environmental gradients (Ter Braak 1987). It can summarise the community data of many species and samples by representing the data on a single graph. Ordination results can then be combined with environmental information to gain a more complete description and understanding of the community (Krebs 1989).

There are four main classes of ordination methods described by Ter Braak and Smilauer (1998):

1. Methods to describe the structure in a single data set. For example, the structure of a biological community or the correlation structure of a set of environmental variables (ordination, indirect gradient analysis).

2. Methods to explain one data set by another data set. For example, to explain or predict species abundances from environmental data (canonical ordination, direct gradient analysis).
3. Methods to explain one data set by another data set, after accounting for variation explained by a third data set (covariable data)(partial canonical ordination).
4. Methods to describe the structure in a single data set after accounting for variation explained by a second data set (covariable data)(partial ordination).

This study employs ordination methods from the first two classes described above; namely, ordination in the form of detrended correspondence analysis (DCA), and canonical ordination, which has an environmental basis, in the form of canonical correspondence analysis (CCA)(Ter Braak and Smilauer 1998).

**Detrended correspondence analysis (DCA)** was developed by Hill and Gauch (1980) as a heuristic modification of correspondence analysis (CA). It was designed to correct the two main faults in CA: 1) that the ends of the axes are often compressed relative to the axes middle; 2) that the second axis frequently shows a systematic, often quadratic relation with the first axis, principally resulting in an arch effect (Jongman et al. 1995). The arch effect is a 'mathematical artefact, corresponding to no real structure in the data' (Hill and Gauch 1980), and it has been eliminated in DCA by 'detrending'.

In this study, DCA was used to analyse absolute species abundance data using the CANOCO program, version 4 (Ter Braak and Smilauer 1998). DCA produces a set of ordinations for samples and for species, represented by different axes. Samples are arranged on these axes so that those that are close together are found in a similar range of field sites. Each of the axes is associated with an eigenvalue, which measures the importance of the axes (Ter Braak 1995). As in other indirect methods of ordination analyses, the DCA method 'extracts' the ordination axes from the species data alone. The axes denote the deviation of sample sites due to the differences in species composition between them.

**Canonical correspondence analysis (CCA)** investigates the effects that a particular set of environmental variables has on species composition. Canonical ordination techniques are designed to detect the patterns of variation in the species data that can be explained 'best' by the observed environmental variables (Jongman et al. 1995). The resulting ordination diagram illustrates not only the pattern of variation in species composition but also the main relations between the species and each of the environmental variables. Canonical ordination therefore combines aspects of regression and ordination (Jongman et al. 1995).

Canonical correspondence analysis is another eigenvector technique that combines aspects of regular ordination with aspects of direct gradient analysis (Ter Braak, 1996). It too is considered an extension of correspondence analysis (CA). The ordination diagram it produces illustrates the main pattern of variation in community as accounted for by the environmental variables and an approximate representation of the distribution of each species along each environmental variable (Ter Braak 1988). In this study, CCA is used to analyse species and site data in relation to the environmental variables described in section 4.3.2, again using CANOCO, version 4 (Ter Braak and Smilauer 1998). These analyses test for differences between habitats and for correlation between diversity, biotic and abiotic factors (Torres 1984).

**Two Way INdicator SPecies ANalysis (TWINSPAN)** is the final multivariate method used in this study. The TWINSPAN program was developed by Hill (1979), and it not only classifies sites but also constructs an ordered two-way table from a sites-by-species matrix (Jongman et al. 1995). It is a method of numerical classification which, like ordination methods, can be used in data reduction and exploration and has become one of the most widely used programs in community ecology (Kent and Coker 1992, Jongman et al. 1996). It is used in this study to look for patterns in invertebrate species.

Indicator Species Analysis is a divisive polythetic method that uses reciprocal averaging ordination to reflect the most important species gradient in the first axis (Hill et al. 1975). Sites or samples are divided into two groups at the centroid, the mean value of the stand scores. Species whose occurrences are most nearly confined to stands on one side or the other of the division are identified as 'differential species' or 'pseudo-species'. These species are then used to refine the initial ordination of the sites, dividing them into two groups. The procedure is repeated again for each subgroup (Van Tongeren 1995).

The TWINSPAN program, written in Fortran, makes use of pseudo-species with differential indicator value at different levels of abundance (Hill 1979). It is used to classify a set of species within a set of samples. The most significant feature is that the program first constructs a classification of the samples, and then utilises this classification to obtain a further classification of the species according to their perceived ecological preferences. The two classifications are then used together to produce a two-way table (a site by species matrix) that expresses the species' synecological relations as succinctly as possible (Hill 1979). The data in this table are ordered to make sample plot and species dendrograms. The species classification best describe the species association in sample, or site, groups identified by the sample classification.

The approach and methods described in this chapter were selected in order to achieve the objectives presented in Chapter 1. They provide the means to represent clearly the trends found in the data collected, and have the ability to demonstrate the diversity and composition of leaf litter invertebrates in a northern Costa Rican landscape. The impact of disturbance, on the vegetation and forest environment, in this landscape is the subject of the next chapter, while the effects of these changes on leaf litter ants and beetles are examined in the two following chapters.

# CHAPTER 5

# THE VEGETATION OF NORTHERN COSTA RICA: IMPACT OF DISTURBANCE ON THE FOREST AND ITS ENVIRONMENT

## 5.1 Introduction

A mosaic of land uses covers the San Carlos region of northern Costa Rica. This mosaic has been caused by human intervention, the majority of which has occurred over the last 20 years. The original land cover consisted of extensive lowland evergreen rain forest. This forest is still present in patches over the region (Figure 3.11). Personal observation indicates that forest cover may be increasing, and this may be explained by changing socio-economic and environmental conditions over the past 10 years. In many areas, cattle raising and crop growing have been abandoned due to increasing costs and low soil fertility. This abandonment results in the land recovering some of its previous forest vegetation although the time for complete recovery is not known. Finegan (1996) suggests that the succession process may last for centuries, although a structural resemblance may be achieved in a few decades. Despite this change in farmer's practices, timber exploitation, and encroachment by agriculture and cattle continues to threaten existing forest patches.

Features such as access and slope appear to have an important role in forest clearance for agricultural land use (Bohrer, 1998). Marginal land in steeply sloping and inaccessible areas is less likely to be cleared or disturbed. This fact is clearly demonstrated in northern Costa Rica where much of the remaining forest lies on steeply sloping land or on the sides of river gorges.

This chapter examines the vegetation of the study area and investigates the effects of changing land use on a variety of environmental variables. Disturbance effects, caused by forest conversion, are mediated by a number of important environmental variables including tree species diversity, litter biomass, soil temperature, physical properties and chemical attributes, and maximum and minimum air temperature. These variables provide an overview of changes in microclimate, soil condition, and tree species diversity and composition. The observed changes are the inevitable results of conversion from primary forest, and the data will be drawn upon in further chapters in order to examine the relationship between these aspects of the ecosystem and resulting insect communities.

## 5.2 Objectives

The aims of this chapter are to:

- present a brief overview of neotropical forest ecology and physiognomy in order to provide a background to the forests found in the study sites;
- document the tree species diversity and composition of the study sites which contain forest (primary, logged and secondary forest sites), and discuss the changes that have occurred as a result of human disturbance;
- present data on a number of environmental variables, for all the study sites, in order to reveal the changes in microclimate and soil condition after forest disturbance and conversion; and
- provide an initial assessment of change to the forest environment (tree species composition and diversity, microclimate, and soil condition) after human intervention, in order to relate this to observed changes in insect communities in later chapters.

## 5.3 Forest ecology

Although the majority of studies on neotropical forest ecology have been carried out in the forests of South America, a significant research effort has also been undertaken in the smaller forest areas of Central America. Notable centres for research in Central America include CATIE (Tropical Agronomy and Teaching and Research Centre) and La Selva Biological Station, both in Costa Rica.

### 5.3.1 Forest dynamics and ecosystem processes

Studies on the dynamics of the neotropical rain forest ecosystem relate the production of organic matter to the local environment and also to the successional stage of the forest (Bohrer 1998, Clark and Clark 2000). In order to understand the forest ecosystem and its processes these interrelationships between the vegetation and the physical environment must be examined (Clark and Clark 1992, Medina 1995, Clark et al. 1999). Many studies have focussed on nutrient fluxes through the forest litter (Johnson and Wedin 1997) while others have also identified the importance of atmospheric nutrient inputs into the forest ecosystem (Clark et al. 1998). The insect component of the ecosystem is also vital in many functions, and the decomposition of forest litter is strongly mediated by leaf litter invertebrates (Didham 1996).

Epiphytes form a further important contributor to the nutrient cycling process. Some epiphytes trap nutrients by collecting falling detritus amongst their leaf bases or by aerial root absorbance (Whitmore 1992). These plants are more common in montane, particularly cloud forest, areas where they also provide an important habitat for several animal species (Terborgh 1992).

Topography and soil type have strong effects on stem size, stand density and the spatial heterogeneity of stems in tropical forest (Clark and Clark 2000). There have been recent studies which examined neotropical forest at the landscape and ecosystem scale in order to reveal the reasons for variations in their structure (Clark and Clark 2000). Indeed it has been suggested that such studies over environmentally similar areas could be used to develop models of forest ecosystem dynamics. Such models could be used to analyse and predict the impact of climatic changes or human intervention (Helmer 2000).

### 5.3.2 Forest disturbance and diversity

The world's forests are being increasingly disturbed and according to latest figures this disturbance and destruction is continuing at a frightening rate (FAO 1999). There are many theories which consider first, the natural dynamics of tropical forest and second, the recovery of these forests after human intervention. The **intermediate disturbance hypothesis** considers that most tropical forests are maintained naturally in a condition of perpetual disequilibrium, which prevents the occurrence of dominant species

(Terborgh 1992, Givrish 1998). Both seasonal and annual variability affect seed germination responses from different tree species. Different regeneration strategies are demonstrated by different species (Fredericksen and Mostacedo 2000, Guariguata 2000). Seed germination physiology and the response of different tree species to disturbance and light availability affect the succession process in tropical forest (Whitmore 1989, Attiwill 1994, Perera 1997, Fredericksen and Mostacedo 2000, Guariguata 2000, Svenning 2000). There has been widespread research into gap-phase dynamics in tropical forest. A study of seed and seedling ecology in Costa Rica demonstrated that seed longevity in the soil differed markedly among species, and that seedling survival was uniformly low between species, averaging about 10 percent after 1 year. Regeneration also required nearly complete canopy opening, as the species studied (common timber species in the area) showed limited capacity either to germinate or to survive as seedlings in the understorey (Guariguata 2000). Indeed, Frederickson and Mostacedo (2000) show that the regeneration of some commercial species in Bolivian forest respond more favourably to disturbances that exceed those provided by a single tree fall gap, or a single tree selection logging. Another important factor in the current overall structure of forest communities is the occurrence of past extreme events, such as, fire, hurricanes, floods, and droughts (Goldhammer 1992). Within the context of northern Costa Rica the above points have serious implications. The limited longevity of the seed bank may reduce the regeneration potential of many abandoned agricultural or pasture areas, while regeneration of high value timber within the remaining forest patches may also be poor.

The **equilibrium hypothesis** considers that species avoid competition through distance dependent strategies with regular population fluctuations within a constant long-term population size (Bohrer 1998). This strategy could also help avoid or reduce seed predation (Terborgh 1992a). Spatial heterogeneity in tropical forest may be explained by recruitment pattern variations due to gap size, or location within the gap, also between gaps and shaded areas, and due to distance from seed trees (Hartshorn 1989). This heterogeneity may be compromised in small forest areas, such as in the landscape examined in this study, although in a mosaic landscape of forest patches and other land uses, metapopulation dynamics may allow a form of species heterogeneity to develop over a number of patches.

Forest fragmentation is now a major factor in tropical forest disturbance (Laurance and Bierregaard 1997, Schelhas and Greenberg 1996). Factors such as the shape, size, connectivity and edge characteristics of forest fragments could affect forest structure and dynamics. These have been discussed in greater detail in Chapter 2. It is important to note that human impact can mimic, to some extent, natural disturbance processes. Both gap-phase dynamics and the structure and dynamics of logged and secondary forests are important for sustainable natural forest management methodologies (Whitmore 1990, Attiwill 1994, Helmer 2000, Fredericksen and Mostacedo 2000).

## 5.4 Forest physiognomy

One of the major considerations in analysing the impact of forest fragmentation and conversion is to set the forest in its regional context. Twelve of Holdridge's Life Zones (Holdridge et al. 1971) occur in Costa Rica and are clearly distinguishable. The vegetation of the area of the San Carlos region, northern Costa Rica, studied here lies within the tropical wet forest (T-wf) and premontane wet forest (P-wf) life zones (Appendix 1 and 2).

### 5.4.1 Tropical wet forest

The tropical wet forest life zone (T-wf) is the second most extensive life zone in Costa Rica (Appendix 1). Tropical wet forest is a tall, multistratal, evergreen forest (Janzen, 1983). A few emergent canopy species are briefly deciduous but this is not sufficient to change the overall evergreen state of the forest. In general, canopy trees are 45-55 m tall, with round to umbrella-shaped crowns, and have clear boles to 30 m and attain 100-200 cm dbh (Janzen, 1983). Bark is often smooth, thin and of a light colour, and high buttresses are common. Sub-canopy trees are 30-40 m tall, with round crowns and slender trunks, generally lacking buttresses. Understory trees are 10-25 m tall, with narrow conical crowns and slender boles usually with smooth, dark bark, and sometimes cauliflorous (Janzen, 1983). Stilt-rooted palms are often abundant. The shrub layer is 1.5-2.5 m tall with abundant dwarf palms, and giant broad-leaved herbs are sometimes present. The ground layer is sparse with a few ferns. Tropical wet forest is the most species-rich 'life zone' in Costa Rica (Janzen 1983).

### 5.4.2 Tropical premontane wet forest

This life zone occupies a large part of the San Carlos lowlands (Janzen, 1983). The forest is medium to tall, semi-evergreen with two or three strata. A few of the canopy species are dry season deciduous. The canopy trees are about 30-40 m tall, with mostly round to spreading crowns and relatively short clear boles. Buttresses are common but small. Bark is generally brown or grey, moderately thick and flaky or fissured (Janzen, 1983). Understorey trees are 10-20 m tall with deep crowns and smooth, often dark bark. Stilt roots are common and tree ferns are occasionally found (Janzen, 1983). The shrub layer is 2-3 m tall and often dense. The ground layer is generally bare except for ferns. Epiphytes are present but not abundant, while climbing herbaceous vines are more common. Many trees have a layer of moss.

### 5.4.3. Physiognomic features and patterns of tropical trees

Tropical forest trees demonstrate many distinctive features such as buttresses, crown shapes, epiphytes and lianas. In this section the most prominent physiognomic features are briefly reviewed in order to provide a background to the characteristics of the forest found in the study area.

#### BUTTRESSES AND STILT ROOTS

Within Costa Rica buttressing is largely restricted to the tropical basal belt and is best developed in tropical Moist and Wet Life Zones (Janzen 1983). Buttress height correlates well with trunk diameter (Holdridge et al. 1971), but not all canopy trees develop buttresses. In general, buttressing is more prevalent on poorly drained soils although some trees characteristic of well-drained areas do develop buttresses, for example, *Dussia macroprophyllata* (Janzen 1983). It may be that buttressing develops in an area of instability from which individuals have dispersed to habitats no longer requiring mechanical support. The height, thickness, form and degree of bifurcation of buttresses can be very useful in species identification. The growth of buttresses is strongly epinastic, that is, the anatomical centre of the buttress is at or near ground level and growth is strongly skewed to the upper edge of the buttress (Richards 1952). An analysis of buttresses using engineering models indicates that they are excellent support structures (Henwood 1973). In addition a strong negative correlation is found between buttressing and bark thickness, which may be one of the reasons that thick-barked temperate trees do not demonstrate buttressing (Smith 1979).

Stilt roots differ from buttresses in that the former are adventitious, that is, growing from the stem (Janzen 1983). Some stilt roots elongate in a vertical plane sometimes appearing as raised buttresses. Stilt roots occur in various dicot trees such as *Protium* spp. and *Virola* spp.. Numerous palms, including *Iriartea* and *Socratea* species, also have stilt roots. In the *Socratea* species the original stem below the stilt roots dies, resulting in all support and translocation occurring through the adventitious stilt roots. Stilt rooted palms are shade intolerant and must grow quickly to take advantage of canopy openings.

### BARK

Bark colour, thickness and texture along with odour and sap are sufficiently varied yet species-specific that they are useful diagnostic characters for species identification (Janzen 1983). Costa Rican bark colours are predominantly dark. Bark thickness ranges between, in general, 5 and 10 mm with some species having thinner bark but few having thicker. Janzen (1983) believes that Smith's (1979) observation that thick barked trees do not have buttresses is valid for Costa Rican species.

### LEAVES

In general, tropical tree leaves are mesophylls, that is, between 20 to 182cm$^2$ in upper surface area (Greig-Smith 1952). Many compound leaves have leaflets of mesophyll size. There has been some debate but it is generally believed that simple and compound leaves occur in the same proportion in tropical montane areas as in the lowlands (Grubb et al. 1963, Tasaico 1959).

With increasing altitude, average leaf length decreases at a rate of about 0.5 cm per 100m (Tasaico 1959). Entire leaf margins, drip tips and thin leaves are most common in wet lowland forest. Drip tips result in more rapid water run off and leaf surface drying (Dean and Smith 1978).

### CROWN SHAPE

Canopy or emergent tree crowns are wider than they are deep and often umbrella-shaped; subcanopy tree crowns are deeper than wide or are equal; and understorey tree crowns are conical and much deeper than wide (Richards 1952). Holdridge et al. (1971), in their analyses of useful physiognomic and structural features, report that the largest crown volumes occur in Tropical Moist and in poorly drained alluvial associations in Tropical Wet Life Zones. Tropical wet (well-drained associations) and Premontane Wet are intermediate in crown volume.

### STRATIFICATION

The discussion of the presence or absence of strata of trees, shrubs, and herbs has resulted in considerable controversy (Janzen 1983). Tropical forest is commonly described as being layered or stratified and this is a useful aid to description or analysis (Whitmore 1990). However, as the forest is dynamic and has patches at all stages of the growth cycle, stratification is a simplification and abstraction. The differentiation of a forest into abstract canopy (and/or emergent), subcanopy and understorey strata, without necessarily defining height limits, is an ecologically meaningful positioning of the hundreds of tree species in a tropical forest (Janzen 1983).

The next section will examine the forest structure of the field sites, focussing on the primary, logged and secondary forest sites, in order to characterise the sites and land uses, and reveal the tree species composition and diversity.

## 5.5 The vegetation structure of northern Costa Rican forest sites

The first stage of the field study, following the reconnaissance surveys, was an analysis of the forest structure of the field sites. Tree inventories were carried out in five 100 x 10 m$^2$ plots per site. The results of these surveys are summarised in Table 5.1 and set out fully in Appendix 3. A total of 1902 trees with dbh (diameter at breast height) □ 10cm were measured in the ten sites which ranged from primary forest to pasture (see Table 5.1 for site types). These trees represented a total of 102 species. The trees were identified in the field to common name by a parataxonomist (a skilled local person with a knowledge of local tree species). Of these common names, 89 were then converted to species names and family using a species list produced by a local NGO, CODEFORSA, in collaboration with INBio (the Costa Rican National Biodiversity Institute). This species list is used in the elaboration of natural forest management plans, which are then presented to the government Forestry Department.

The number of individuals within the sampled area of each site varied from 297 trees in one of the secondary forest sites to only 1 tree in one of the pasture sites. The primary forest sites had 239 and 280 trees respectively. The average tree density sampled per land use was 259.5 individuals in primary forest, 225.5 individuals in logged forest, 195 individuals in secondary forest, 266 individuals in plantation and 8 in pasture (Figure 5.1). The average dbh was 24.6 cm with a range from 16.6 cm to 49.1 cm. The largest tree ( a specimen of *Dipteryx panamensis*, Leguminosae) reached a dbh of 205.0 cm. The average basal area per hectare was 32.2 m$^2$ in primary forest, 21.7 m$^2$ in logged forest, 24.3 m$^2$ in secondary forest, 12.4 m$^2$ in plantation and 1.3 m$^2$ in pasture (Figure 5.2).

As described in Chapter 4, the logged forest sites have had a percentage of their larger commercial tree species removed. This is reflected in the average basal area figure (Figure 5.2). Also noteworthy is the figure for the average basal area of the plantation sites. Although the plantation site had the greatest number of trees per hectare it had the lowest basal area, with the exception of pasture. This can be explained by the relatively recent establishment of these plantations and the resulting small dbh measurements.

**Figure 5.1 Average number of trees >10cm dbh per hectare by land use**

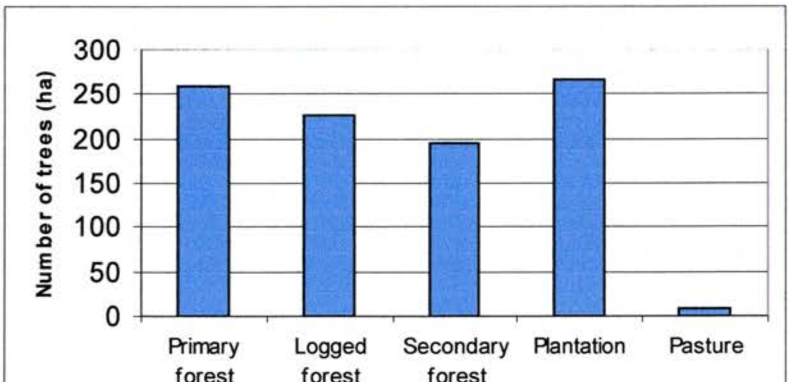


**Figure 5.2 Average basal area of trees per hectare by land use**

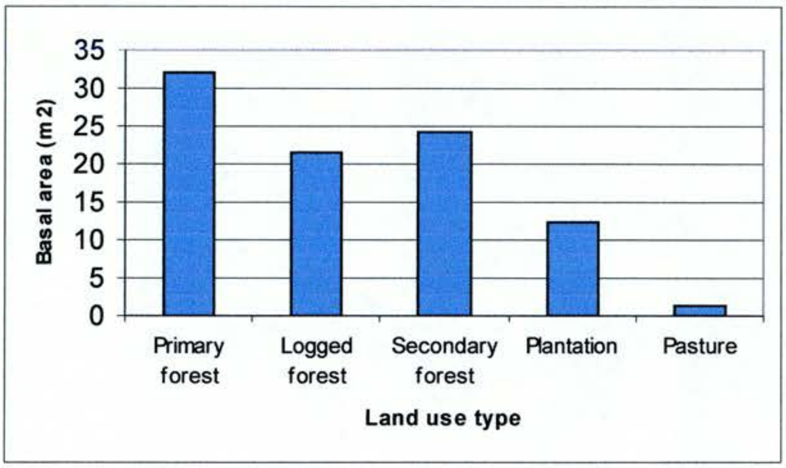


**Table 5.1 Summary of tree measurements**

| Habitat | Site | Site no | Tree density | Trees /ha | dbh (cm) | BA ($m^2$). | BA/ha ($m^2$). | Species richness |
|---|---|---|---|---|---|---|---|---|
| Primary | PrimFor1 | 1 | 239 | 478 | 26.2 | 20.48 | 40.964 | 53 |
| forest: | PrimFor2 | 2 | 280 | 560 | 19.91 | 11.76 | 23.52 | 52 |
| Logged | LogFor1 | 3 | 243 | 486 | 19.29 | 9.55 | 19.104 | 50 |
| forest: | LogFor2 | 4 | 208 | 416 | 22.52 | 12.15 | 24.294 | 58 |
| Secondary | 2ndFor1 | 5 | 93 | 186 | 23.72 | 5.73 | 11.452 | 34 |
| forest: | 2ndFor2 | 6 | 297 | 594 | 23.04 | 18.56 | 37.11 | 44 |
| Plantation: | Plantat1 | 7 | 274 | 548 | 16.84 | 6.46 | 12.92 | 2 |
|  | Plantat2 | 8 | 258 | 516 | 16.59 | 5.89 | 11.78 | 1 |
| Pasture: | Pastur1 | 9 | 15 | 30 | 29.05 | 1.09 | 2.184 | 8 |
|  | Pastur2 | 10 | 1 | 2 | 49.1 | 0.19 | 0.378 | 1 |
| ***Total*** |  |  | 1908 trees |  |  | 91.85 $m^2$ |  | 102 species |
| ***Average*** |  |  | 190.80 | 381.60 | 24.63 | 9.19 | 18.37 | 30.30 |
| ***Std. Dev.*** |  |  | 111.80 | 223.62 | 9.456 | 6.729 | 13.460 | 24.400 |
| ***Variance*** |  |  | 12501.3 | 50005.2 | 89.412 | 45.29 | 181.17 | 595.34 |

The values are given per site (sum of the five plot values) except where otherwise indicated. Values of diameter (dbh, cm) are site averages. BA = basal area ($m^2$).

### 5.5.1 Size class distribution

The forest structure size distribution was estimated according to the diameter distribution (number of trees for each dbh class). The result for all samples sites is shown in Figure 5.3 while Figure 5.4 shows the size distribution for each forest plot. The diameter distribution for the two primary forest sites suggest a well-balanced forest structure in a state of dynamic equilibrium, with a high percentage of natural regeneration characterised by the high number of trees belonging to the first diameter class. These factors were also reflected in the logged forest sites. The secondary forest sites also demonstrated a high level of regeneration shown by the first two size classes. The second secondary forest site (2ndFor2) was characterised by the high percentage of Vochysia ferruginea (86%) found there. This near monotypic form is naturally occurring and characteristic of this species. The majority of these trees fell within the first two size classes as regeneration began at the same point in time when the land was allowed to begin to return to natural forest.

**Figure 5.3 Tree diameter distribution (all sites).** The first diameter class (10-20cm) is subdivided into two classes (10-15cm, 15-20cm) to illustrate the dominance of small trees.

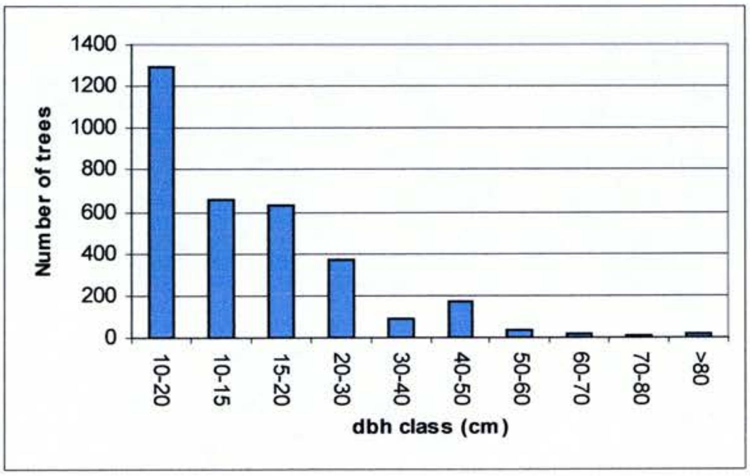
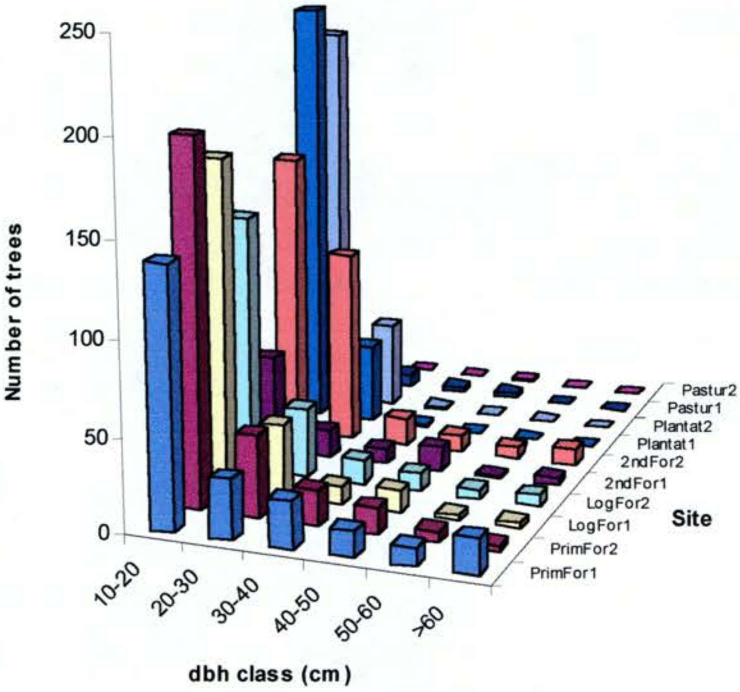


**Figure 5.4 Tree diameter distribution by site.** Illustrating the predominance of smaller classes in both the natural forest sites and the plantations.



The two plantation sites had all their trees within the first two size classes obviously reflecting the time of plantation establishment. The pasture sites have been cleared of nearly all trees and the specimens that do remain have been left for shade purposes.

### 5.5.2 Floristic composition

The total list of species recorded in the sites sampled in shown in Table 5.2. As already mentioned, it was possible to convert 89 of the 102 species collected to family and species by use of the CODEFORSA/INBio tree species list for northern Costa Rica. Initial species identifications were made by a local parataxonomist to common name only. Many studies have demonstrated the wealth of indigenous knowledge and its usefulness in tree identification (Wilkie and Saridan 1999). Most societies have common names for the trees they find in their environment. However, there are uncertainties and local common names are not always classified by the same criteria as scientific names. As a result of this, inaccuracies may occur in the direct translation of common name to species name. However, with regard to the aims of this study, the species identification was sufficient to characterise the vegetation of the sites, and to distinguish, both clearly and easily, between the communities sampled.

At the floristic level, the sites studied in northern Costa Rica showed a high diversity in terms of both species (102) and families (42), especially considering the total sample area of 5 hectares and the inclusion criteria (dbh ≥ 10cm). The Leguminosae had the greatest number of species (11), followed by the Lauraceae (6) and then the Sapotaceae (5) and the Myrsinaceae (5). The Bombacaceae, Euphorbiaceae, Meliaceae, Palmae, Rubiaceae, and Tiliaceae all had three species each.

## Table 5.2 List of tree species measured in sample sites

| ***Species*** | ***Family*** | ***Common name*** |
|---|---|---|
| *Annona sp.* | Annonaceae | Anono |
| *Apeiba membranacea* | Tiliaceae | Botijo |
| *Ardisia sp.1* | Myrsinaceae | Piedra de uva |
| *Ardisia sp.2* | Myrsinaceae | Piedrilla |
| *Aspidosperma megalocarpon* | Apocynaceae | Amargo |
| *Bactris sp.* | Chrysobalanaceae | Pejivaye |
| *Billia colombiana* | Hippocastanaceae | Cucaracho |
| *Brosimum alicastrum* | Moraceae | Ojoche |
| *Brosimum utile* | Moraceae | Lechoso |
| *Carapa guianensis* | Meliaceae | Caobilla |
| *Cecropia insignis* | Cecropiaceae | Guarumo |
| *Cedrela odorata* | Meliaceae | Cedro maria |
| *Ceiba pentandra* | Bombacaceae | Ceiba |
| *Cespedesia macrophylla* | Ochnaceae | Tabacon |
| *Chimarrhis parviflora* | Rubiaceae | Yema huevo |
| *Chrysophyllum cainito* | Sapotaceae | Caimito |
| *Chrysophyllum sp.* | Sapotaceae | Zapotillo |
| *Coccoloba tuerckheimii* | Polygonaceae | Piedra |
| *Conceveiba pleiostemona* | Euphorbiaceae | Algodón |
| *Conocarpus erecta* | Combretaceae | Mangle |
| *Cordia alliodora* | Boraginaceae | Laurel |
| *Couma macrocarpa* | Apocynaceae | Baco |
| *Croton schiedeanus* | Euphorbiaceae | Colpachi |
| *Croton tonduzii* | Euphorbiaceae | Amarguito |
| *Cupania glabra* | Sapindaceae | Bejuco |
| *Cupania sp.* | Sapindaceae | Huesillo |
| *Dendropanax arboreus* | Araliaceae | Fosforillo |
| *Dialium guianense* | Leguminosae-caes | Tamarindo |
| *Didymopanax morototoni* | Araliaceae | Pava |
| *Dipteryx panamensis* | Leguminosae-pap | Almendro |
| *Dussia macroprophyllata* | Leguminosae-pap | Paleta |

| **Species** | **Family** | **Common name** |
|---|---|---|
| *Elaeoluma glabrescens* | Sapotaceae | Carey |
| *Enterolobium cyclocarpum* | Leguminosae-mim | Guanacaste |
| *Eschweilera costaricensis* | Lecythidaceae | Repollito |
| *Faramea sp.* | Rubiaceae | Cafecillo |
| *Genipa americana* | Rubiaceae | Guaitil |
| *Gmelina arborea* | Verbenaceae | Melina |
| *Guarea bullata* | Meliaceae | Cocora |
| *Heliocarpus appendiculatus* | Tiliaceae | Burio |
| *Inga sp.1* | Leguminosae-mim | Guabilla |
| *Inga sp.2* | Leguminosae-mim | Guabo |
| *Iriartea deltoidea* | Palmae | Palmito dulce |
| *Laetia procera* | Flacourtiaceae | Manga larga |
| *Lecythis ampla* | Lecythidaceae | Jicaro |
| *Licania affinis* | Chrysobalanaceae | Cuero de sapo |
| *Manilkara zapota* | Sapotaceae | Nispero |
| *Manilkara zapota* | Sapotaceae | Zapote |
| *Miconia argentea* | Melastomataceae | Lengua de vaca |
| *Minquartia guianensis* | Olacaceae | Manu |
| *Muntingia calabura* | Tiliaceae | Capulin |
| *Ochroma pyramidale* | Bombacaceae | Balsamo |
| *Ocotea ira* | Lauraceae | Aguacaton |
| *Ocotea sp.* | Lauraceae | Ira |
| *Ocotea stenoneura* | Lauraceae | Aguacatillo |
| *Ocotea stenoneura* | Lauraceae | Tostado |
| *Ormosia macrocalyx* | Leguminosae-pap | Nene |
| *Otoba novogranatensis* | Myristicaceae | Frutilla |
| *Pachira aquatica* | Bombacaceae | Ponponjoche |
| *Pentaclethra macroloba* | Leguminosae-mim | Gavilan |
| *Persea americana* | Lauraceae | Aguacate |
| *Phoebe valeriana* | Lauraceae | Quizarra |
| *Podocarpus guatemalensis* | Podocarpaceae | Cipresillo |
| *Pourouma minor* | Cecropiaceae | Lija |
| *Prestoea decurrens* | Palmae | Palmito mantequilla |
| *Protium panamense* | Burseraceae | Alcanfor |
| *Psidium sp.* | Myrtaceae | Guayabillo montaña |
| *Qualea paraensis* | Vochysiaceae | Areno |
| *Rehdera trinervis* | Verbenaceae | Melon |
| *Rollinia pittieri* | Annonaceae | Anonillo |
| *Roupala sp.* | Proteaceae | Danto |
| *Sacoglottis trichogyna* | Humiriaceae | Titor |
| *Schyzolobium parahyba* | Leguminosae-caes | Gallinazo |
| *Simarouba amara* | Simaroubaceae | Aceituno |
| *Sloanea sp.* | Elaeocarpaceae | Alma negro |
| *Socratea exorrhiza* | Palmae | Maquenque |
| *Sterculia apetala* | Sterculiaceae | Panama |
| *Stryphondendron microstachyum* | Leguminosae-mim | Vainillo |
| *Tabebuia ochracea* | Bignoniaceae | Corteza |
| *Talauma gloriensis* | Magnoliaceae | Magnolia |
| *Tapirira guianensis* | Anacardiaceae | Manteco |
| *Terminalia amazonia* | Combretaceae | Roble coral |

| **Species** | **Family** | **Common name** |
|---|---|---|
| *Tetragastris panamensis* | Burseraceae | Querosene |
| *Vatairea lundelli* | Leguminosae-pap | Cocobolo |
| *Virola guatemalensis* | Myristicaceae | Fruta |
| *Virola koschnyi* | Myristicaceae | Fruta dorada |
| *Vismia ferruginea* | Guttiferae | Achiotillo |
| *Vochysia ferruginea* | Vochysiaceae | Botarrama |
| *Xylopia sericophylla* | Annonaceae | Vara alta |
| *Zanthoxylum ekmanii* | Rutaceae | Lagarto |

### 5.5.3 Forest species composition and abundance patterns

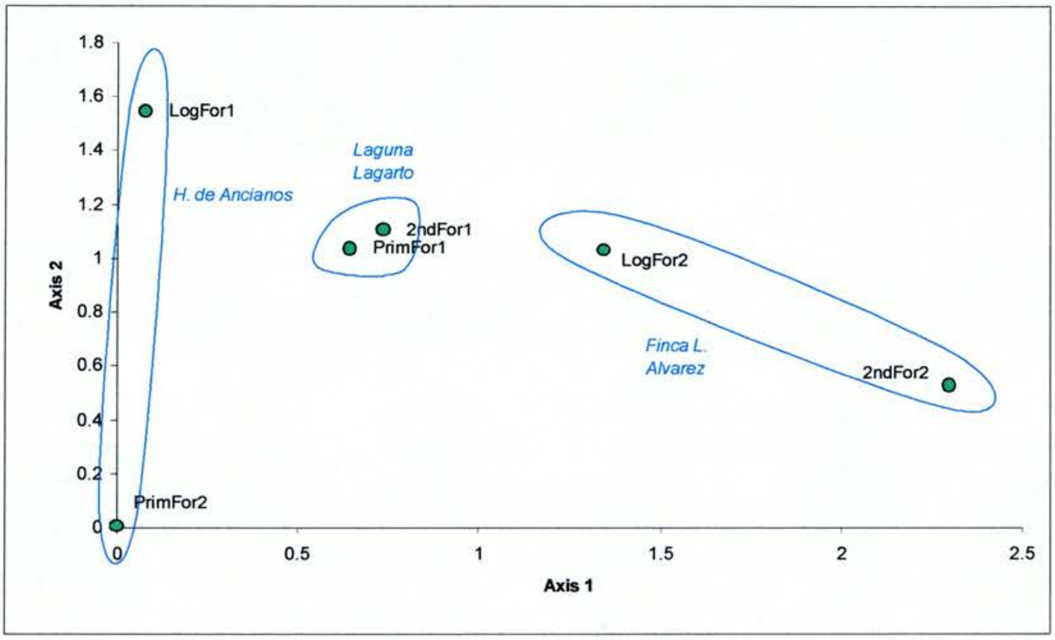
INDIRECT ORDINATION

The absolute tree species abundance data (trees >10cm dbh) for the primary (PrimFor1 and PrimFor2), logged (LogFor1 and LogFor2) and secondary forest (2ndFor1, 2ndFor2) sites was used in ordination analyses. Detrended Correspondence Analysis (DCA) examined tree species composition over the forest sites. DCA produces a set of ordination axes which differentiate between the species and samples in terms of perceived environmental gradients, allowing groups to be distinguished from each other. The measure of importance of each axis in explaining variance is represented by eigenvalues. These are equal to the maximised dispersion of the species scores on the ordination axes. The first ordination axis has the largest value and thus individually explains the greatest proportion of the variation in the set. Values lie between 0 and 1 and a value around 0.5 is regarded as denoting a good separation of the species along the axis. Table 5.3 shows that the first axis, which appears to demonstrate disturbance level, explains 35 percent of the variance, with 54 percent being explained by axes 1 to 3. Figure 5.5 and Figure 5.6 show plots of the first two axes for site and species scores.

**Table 5.3 Eigenvalues and percentage variance for forest site tree species data**

| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.467 | 0.193 | 0.057 | 0 | 1.321 |
| Cumulative percentage variance of species data | 35.4 | 50 | 54.3 | 0 | |
| Sum of all unconstrained eigenvalues | | | | | 1.321 |

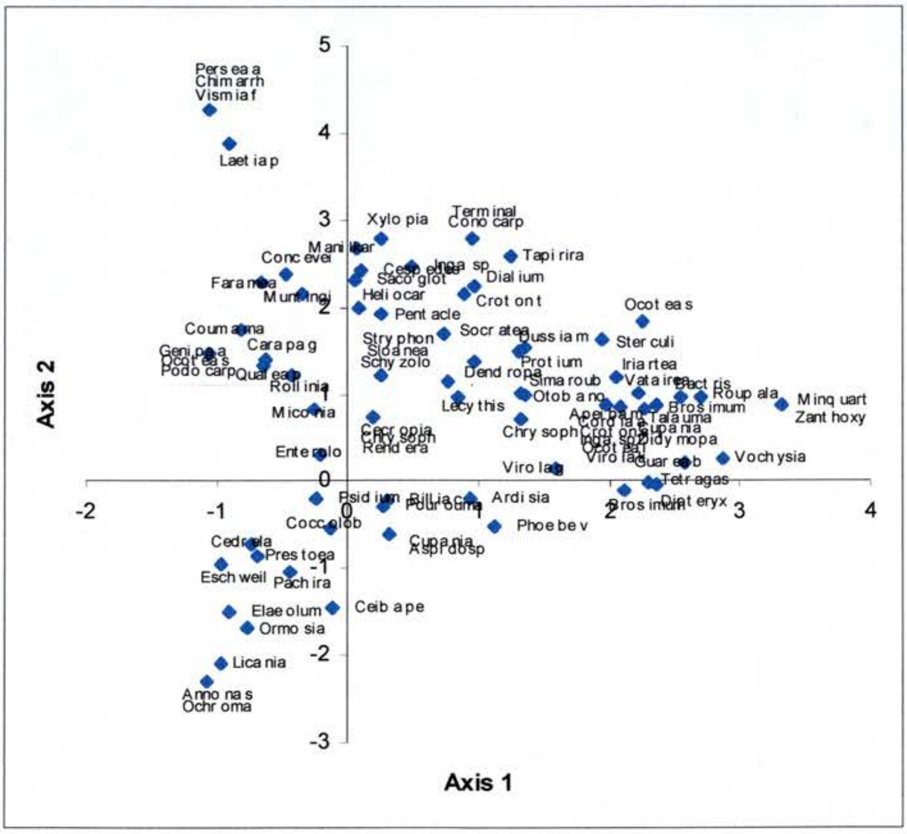
**Figure 5.5 Sample score plot diagram produced by DCA of 87 species and 6 forest sites in northern Costa Rican,** showing a gradient from left to right which corresponds, to some extent, with degree of human intervention. A geographical grouping by site proximity, exclusive of land use, is also demonstrated. PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest. The numbers denote sites 1 and 2 of each land use. The names in blue denote the *finca,* or estate, where the sites are located; i.e. the sites found in the same *finca* are geographically close to each other.



These diagrams demonstrate whether any significant site groupings have occurred and also examine species distribution. The circling superimposed on Figure 5.5 denotes the site location within each estate, or field area (*H. de Ancianos, Laguna Lagarto* etc.). This demonstrates a degree of grouping and shows that general site characteristics may have an effect on species distribution. However, there is also evidence for a gradient along Axis 1 which may indicate the degree of disturbance. Both primary forest sites and one of the logged primary forest sites (PrimFor1, PrimFor2 and LogFor1) fall closer to zero than the other 3 sites. The tree species scores (Figure 5.6) also show evidence of a gradient which relates to disturbance, although there may also be some grouping by field area again perhaps reflecting site characteristics. This is particularly evident for the species grouped around the *Finca Hogar de Ancianos* sites and the *Finca Luzmirio Alvarez* sites. The latter sites have a higher altitude (around 150 metres above sea level (a.s.l.)) than the other sites (which are all between 40-80 metres a.s.l.) and this may cause the species similarity revealed between the logged primary forest and the secondary forest found there. Species found grouped around the 2ndFor2 include *Bactris sp. Vatairea lundelli* and *Vochysia ferruginea*, amongst others. By comparing Figures 5.5 and 5.6 species relations with individual sites can be revealed.

In summary, the species scatterplot from the DCA analysis (Figure 5.6) shows that, although generally all species are grouped together, a gradient from left to right in the diagram is evident. This demonstrates the changes occurring over the gradient of disturbance implied by the land uses in the sites studied. Figure 5.5 also demonstrates this gradient, while showing evidence of site similarities in general field areas or estates. These may represent similar site characteristics due to the geographical proximity of the sites examined.

**Figure 5.6 Species score diagram produced by DCA of 87 species and 6 forest sites in northern Costa Rican,** showing a gradient from bottom left to upper right which corresponds with human intervention. A degree of clustering of tree species, which corresponds to the sites shown in Figure 5.5, is also evident. A key to the tree species codes is given in Appendix 4.



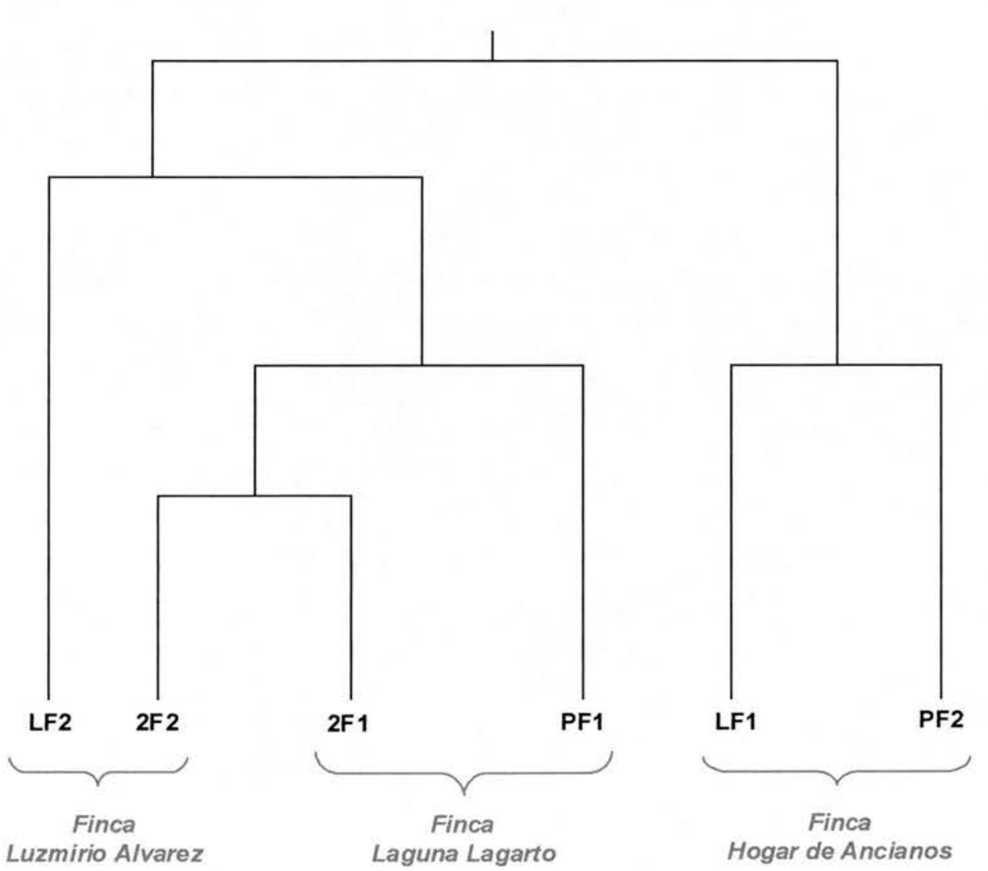
### TWINSPAN ANALYSIS

Further analysis of the tree species abundance data was carried out using the TWINSPAN program (Hill 1979)(see Section 4.6.3). TWINSPAN produces two main outputs. The first is a table, which details the species and sample groups with the species abundance in terms of pseudospecies. The second is the detailed output of the actual analysis, which has created the species and sample groups. In this second output depth divisions are created on the basis of two main groups which are known as negative and positive. Often the distribution of pseudospecies reveals that some species are only found on one side of the division. These species are identified as good indicator species (Kent and Coker 1992). More commonly species are found on both sides of the division but with a greater concentration on one side than the other. From this information TWINSPAN calculates an indicator value for the species. When a pseudospecies occurs in every depth on the positive side but none on the negative side the indictor value allocated is –1. Pseudospecies with this value are perfect indicators while species that occur in every depth will have an indicator value of 0 (Kent and Coker 1992). In the TWINSPAN analysis of the tree species data 5 pseudospecies have been identified.

The results from this analysis are shown in Figure 5.7. The first division revealed two distinct groups, with sites PF1, LF2, 2F1 and 2F2 in one group and PF2 and LF1 in the other. A second division further divides the first group, with site LF2 separated from PF1, 2F1 and 2F2, and a third division of the left group separates PF1 from 2F1 and 2F2, which are grouped together. On the right side of the classification a second division segregates LF1 from PF2.

The results from the classification demonstrate two main groups, which may illustrate that both geographical location and forest type affect species composition. Sites PF1, LF2, 2F1 and 2F2, represent the first group. These sites include primary forest, logged forest and naturally regenerated secondary forest. This group of sites divides into two of the field areas sampled, *Finca Luzmirio Alvarez* and *Finca Laguna Lagarto*. It appears that, despite the differences in land use between these sites, tree species data are grouped together by the TWINSPAN analysis. Species composition in primary forest may not be greatly changed by the low intensity logging which occurred in the logged forest site, LF2, explaining the presence of both primary and logged forest on this side of the diagram. The grouping of the two secondary forest sites within the left-hand group may also be due to the natural regeneration that has occurred there. It is likely that most regeneration resulted from the seed bank of the previous primary forest and remaining adjoining primary, or logged primary, forest, therefore maintaining a similar species composition. PF1 is located next to 2F1 geographically, and LF2 adjoins 2F2.

**Figure 5.7 Dendrogram of the TWINSPAN classification of forest sites in northern Costa Rican**



**KEY TO FIELD SITES:** PF1: Primary forest 1; PF2: Primary forest 2; LF1: Logged forest 1; LF2: Logged forest 2; 2F1: Second. forest 1; 2F2: Second. forest 2.

It is noteworthy that the right hand section of the first group has been further divided, grouping the two secondary forest sites together despite their geographical distance (see Figures 3.11 to 3.13). This is probably due to similarities in tree species regeneration composition and may be a result of a greater number of pioneer species being present in both sites. According to the analysis, shown in Appendix 4, *Apeiba membranacea, Cordia alliodora*, *Croton schiedeanus*, *Didymopanax morototoni*, *Iriartea deltoidea*, and *Vochysia ferruginea* are found exclusively in LF2. *Cecropia insignis*, *Chrysophyllum cainito* and *Rollinia pittieri* are found only in PF1, while *Muntingia calabura*, *Simarouba amara*, *Socratea exorrhiza* and *Talauma gloriensis* are found only in the secondary forest sites. Species that are found exclusively in the left group of the TWINSPAN classification, and therefore are not present in the plots measured in LF1 and PF2, the second group, include those mentioned above together with *Brosimum utile*, *Cupania glabra*, *Bactris sp.*, *Sacoglottis trichogyna*, *Sloanea sp.*, *Licania affinis*, and *Terminalia amazonia.*

The second group of the first division of the TWINSPAN analysis has grouped LF1 and PF2 together. These two sites are both located within the *Finca Hogar de Ancianos* field area and are geographically very close. PF2 is an area of primary forest within the larger primary logged forest where LF1 is located. It is therefore probable that species composition in these two sites will be very similar thus explaining the TWINSPAN grouping. Species found exclusively in this field area include *Genipa americana*, *Ocotea stenoneura*, *Ocotea ira*, *Pourouma minor*, *Chimarrhis parviflora*, *Phoebe valeriana, Xylopia sericophylla*, and *Annona sp.*.

In summary, the TWINSPAN classification divides the 6 forest sites into two main groups, which appear to be based principally upon field area. These show that grouping by tree species composition in the field sites sampled is primarily influenced by the tree composition of the original forest of the area. However, underlying this pattern of geographical proximity, the analysis has also identified that the two secondary forest sites, despite being located at a significant distance from each other, had similar species associations. The analysis reinforces the pattern revealed by axis 1 of the DCA ordination in the previous section.

It is evident that there were distinctions between the land uses examined, although the analysis has also shown the importance of geographical proximity in tree species composition between sites. Inevitably, many of the changes demonstrated are mediated by human actions. Humans have not altered the tree species composition of the primary forest but the logged forest has suffered the removal of timber species. The secondary forests are regenerating naturally although the seed source may also have been influenced by human actions. In general, the existing patterns of tree composition and diversity are primarily a result of **direct** human action, such as selective logging and land clearing methods before abandonment of pasture to allow secondary growth. Further chapters will examine the **indirect** effects of human intervention on insect communities. They will investigate whether, like the tree species, geographical proximity and previous vegetation history affects species composition, or whether the impacts of changing land use overshadow these effects.

## 5.6 The forest environment

This section examines the physical environment of the forest as a basis for the RBA work to follow. Various statistical techniques are utilised to identify changes in environmental variables over the field sites of increasing human impact, and also to examine their relationship to forest site heterogeneity. The main objective is to determine the influence of land use change due to human impact on the forest environment. To achieve this, the structure and floristic composition of the forest is also examined.

### 5.6.1 The forest and its physical environment

As discussed, geology, relief and soil characteristics are the principal factors in determining forest physiognomy and floristic composition within any given climate category (Schnell 1987, Clark and Clark 2000). Specific research conducted in Costa Rica has demonstrated the relationship between current forest structure and environmental factors, and shown the importance of the local physical environment in nutrient cycling, plant community structure and phenologic processes (Clark and Clark 2000, Clark et al. 1999, Johnson and Wedin 1997). Clark et al. (1999) have demonstrated that the relation between edaphic factors and spatial distributions of tree species in old growth tropical rain forest may dictate the high species diversity found there. They suggest that edaphically linked processes lead to differential recruitment.

In addition, various researchers have reported altitude, total annual rainfall and dry season length as the main environmental determinants of tropical forest physiognomy (Beard 1955, Leigh 1999). A change in altitude implies changes in many other variables including temperature, moisture, light and soil types (Austin and Smith 1989, Whitmore 1992). This complexity makes it difficult to identify which variables are the main determinants of each specific situation. Holdridge (1967) uses temperature and rainfall and the seasonal variation and distribution of these two climatic parameters as primary determinants of vegetation type. The relevance of his classification, which was developed in Costa Rica, has been discussed in section 5.3.

Tropical forests play an essential role in the hydrological cycle, and in the prevention of soil erosion, particularly on steep slopes and in very wet areas (Whitmore 1990, Bruenig 1996, Leigh 1999). The forest influences the hydrological process through rainfall interception, moisture storage by the soil and leaf litter, water absorption by tree roots and consequent transpiration (Salati and Vose 1984, Fearnside 1995, Leigh 1999). Forests also have a mechanical role in maintaining soil structure (Lal 1983).

In the present study, the relationship between forest composition and aspects of the physical environment was investigated by examination of selected environmental parameters. These parameters are also employed in later chapters to investigate environmental relationships with invertebrate diversity. There exists a body of research relating the environment to tropical forest structure and composition (Whitmore 1990, Breunig, 1996, Richards 1996, Whitmore 1998, Leigh 1999, Clark et al. 1999, Clark and Clark 2000, etc.). Such past research helped to determine the most appropriate and logistically feasible environmental measures for this study.

### 5.6.2 Soils in a northern Costa Rica landscape

Soils are one of the primary factors that affect which plant species grow in a particular location (Richards 1996, Whitmore 1998, Leigh 1999) and are therefore examined in greater detail for the ten field sites in this research. There have been considerable advances in the study of processes and interactions between tropical soils and forests (Jordan 1985, Parker 1994, Guggenberger and Zech 1999, Montagnini 2000, Clark and Clark 2000), although the relationships between soil parameters and Costa Rican forest structure and composition are still poorly understood (Clark et al. 1999). It is noteworthy that one study has investigated the effects of the nutrient rich organic material produced by leaf cutting ant colonies. They conclude that the relative abundance of *Atta spp.* may influence the structure and/or composition of tropical forests (Farji-Brener and Medina 2000). Most recent studies of Costa Rican forest soils have focussed on the changes in soil properties after disturbance and/or their recovery when abandoned (Guggenberger and Zech 1999, Deuchars et al. 1999, Caldwell et al. 1999, Herrera et al. 1999, Holl 1999, and Montagnini 2000).

In order to investigate soil characteristics over the land uses examined in this study, samples were collected from all sites as described in Section 4.3.2. The relationships between these soil characteristics and forest structure are also related to invertebrate diversity in further chapters. The parameters estimated in the soil analyses were pH (in water) and soil organic matter (estimated from loss on ignition). The methods of soil analysis are presented in Chapter 4. Soil temperature was also measured in the field. The results are summarised in Table 5.4 below.

The mean results of the soil analyses revealed a common pattern of low pH with a narrow range from 3.8 to 4.5, characteristic of very acid soils. Soil organic matter varied from 1.6 percent to 3.2 percent, while the soil temperature measurements ranged from approximately 24°C to 34°C. The lowest pH was found in one of the primary forest sites and one of the secondary forest sites. It is probable that a higher organic matter level in these sites has resulted in a higher production of organic acids which have in turn lowered the pH. This could be expected from the primary forest but it is interesting to note an equal result from secondary forest. Guggenberger and Zech (1999) have documented that soil carbon in secondary forest recovers to a pre-clearance level within 18 years. The secondary forests examined in this study were much younger than this and such a high level of soil organic matter may be due to the number of forest trees left when the original forest was cleared for pasture. The actual figures for soil organic matter show average levels for tropical forest soils. Both the lowest and the highest levels were found in natural forest sites, one unlogged and one logged (PrimFor2 and LogFor1, respectively). Both these sites were located within the same forest area but PrimFor2 was located along a ridge with steeply sloping sides, which may explain the lower organic matter content due to increased runoff and erosion.

**Table 5.4 Summary of soil characteristics (soil temperature, soil pH, and soil organic matter) for each site.** Values indicated are means for each site ± 1 standard deviation.

| *Habitat* | *Site* | *Soil temp (°C)* | *Soil pH* | *Soil organic matter (loss on ignition %)* |
|---|---|---|---|---|
| *Primary forest* | PrimFor1 | 23.8 ± 0.33 | 3.8 ± 0.46 | 2.1 ± 2.47 |
| | PrimFor2 | 28.1 ± 1.51 | 4.0 ± 0.26 | 1.6 ± 0.65 |
| *Logged forest* | LogFor1 | 26.8 ± 1.55 | 3.9 ± 0.28 | 3.2 ± 1.10 |
| | LogFor2 | 26.0 ± 1.62 | 4.2 ± 0.42 | 2.3 ± 1.09 |
| *Secondary forest* | 2ndFor1 | 29.2 ± 2.04 | 3.8 ± 0.42 | 1.7 ± 0.74 |
| | 2ndFor2 | 29.8 ± 1.47 | 4.2 ± 0.36 | 1.7 ± 0.72 |
| *Plantation* | Plantat1 | 31.6 ± 1.96 | 4.0 ± 0.26 | 1.8 ± 0.84 |
| | Plantat2 | 34.4 ± 2.53 | 4.0 ± 0.42 | 1.7 ± 0.71 |
| *Pasture* | Pastur1 | 33.9 ± 1.36 | 4.5 ± 0.39 | 1.9 ± 0.94 |
| | Pastur2 | 32.2 ± 2.75 | 4.4 ± 0.57 | 1.7 ± 0.86 |

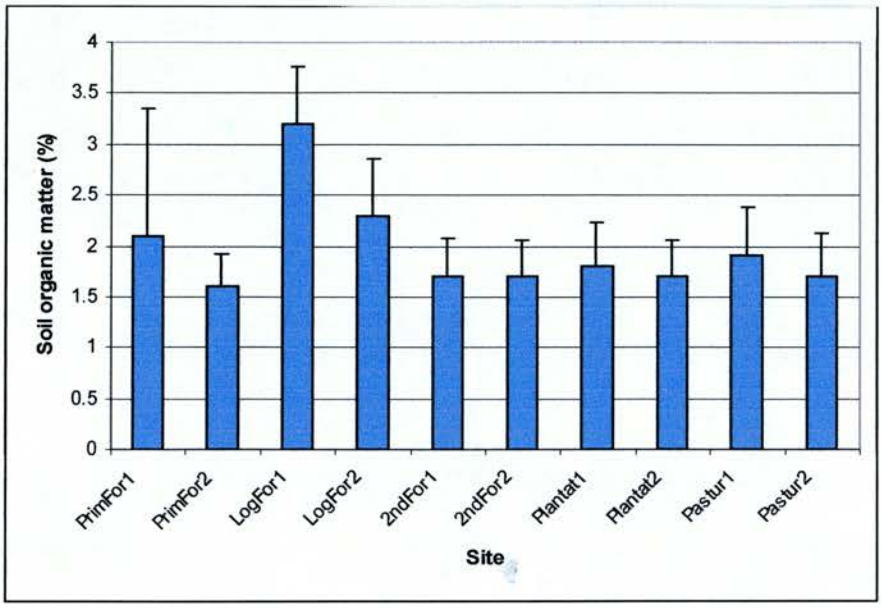
### SOIL ORGANIC MATTER

The analysis of soil organic matter percentages revealed a significant effect of land use type (One-way ANOVA, F = 2.70, $p$ = 0.006; Table A1 in Appendix 5). Soil organic matter was greatest in the two logged forest sites (LogFor1 and LogFor2), and also in one of the primary forest sites (PrimFor1)(Figure 5.8). Further examination of the data using Tukey's multiple comparison test ($p<0.05$) reveals that the ANOVA output is a result of significant differences between LogFor1 and all other sites except LogFor2, and Pastur1 (Table A2, Appendix 5). Soil organic matter between the remaining sites was not significantly different.

### SOIL TEMPERATURE

Figure 5.9 shows that the mean soil temperature per field site was significantly higher in the more disturbed sites (One-way ANOVA, F = 90.98, $p < 0.001$; Table A3 in Appendix 5). Indeed, the temperature increases over the gradient of disturbance. Further investigation of the soil temperature data using Tukey's multiple comparison test ($p<0.05$) reveals that the ANOVA output is a result of significant differences between almost all the sites. Table A4 (Appendix 5) details which sites did not show a significant difference. These sites are illustrated in Figure 5.9.

**Figure 5.8 Soil organic matter in field sites sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits.



SOIL PH

Figure 5.10 illustrates that soil pH was significantly higher in the sites of greater human impact (One-way ANOVA, F = 5.76, $p < 0.001$, Table A5 in Appendix 5). The field sites 2ndFor2, Plantat1, Plantat2, Pastur1 and Pastur2 appear to show higher soil pH levels. These sites represent secondary forest, plantation and pasture sites and are therefore the sites of greatest human intervention. It is possible that the loss of a leaf litter layer, resulting from clearance or grazing, has reduced the organic matter present in the soil resulting in a less acidic surface soil layer. Theoretically, soil pH would increase as more organic litter was decomposed through greater oxidation and/or through fire, a common method of forest and scrub clearance in this area. This increases nutrient elements in the remaining ash and would reduce the acidifying radicals of hydrogen and aluminium.

Further examination of soil pH data using Tukey's multiple comparison test ($p<0.05$) reveals that the ANOVA output is a result of significant differences between the soil pH in Pastur1 and Pastur2 and almost all other sites. Table A6 (Appendix 5) details which sites show significant differences. Despite apparent visual differences between soil pH in the plantation sites and in one of the secondary forest sites in Figure 5.10, these were shown not to be significantly different from the other sites by Tukey's multiple comparison test.

**Figure 5.9 Soil temperature (°C) in field sites sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits. And means with the same letter do not differ significantly from each other (Tukey multiple comparison test, $p < 0.05$).

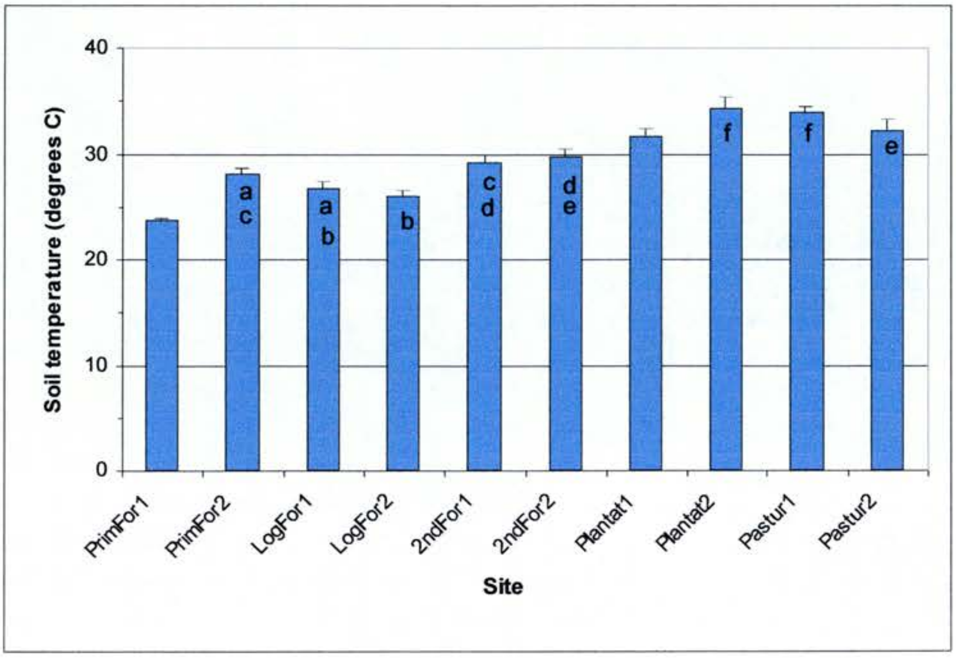
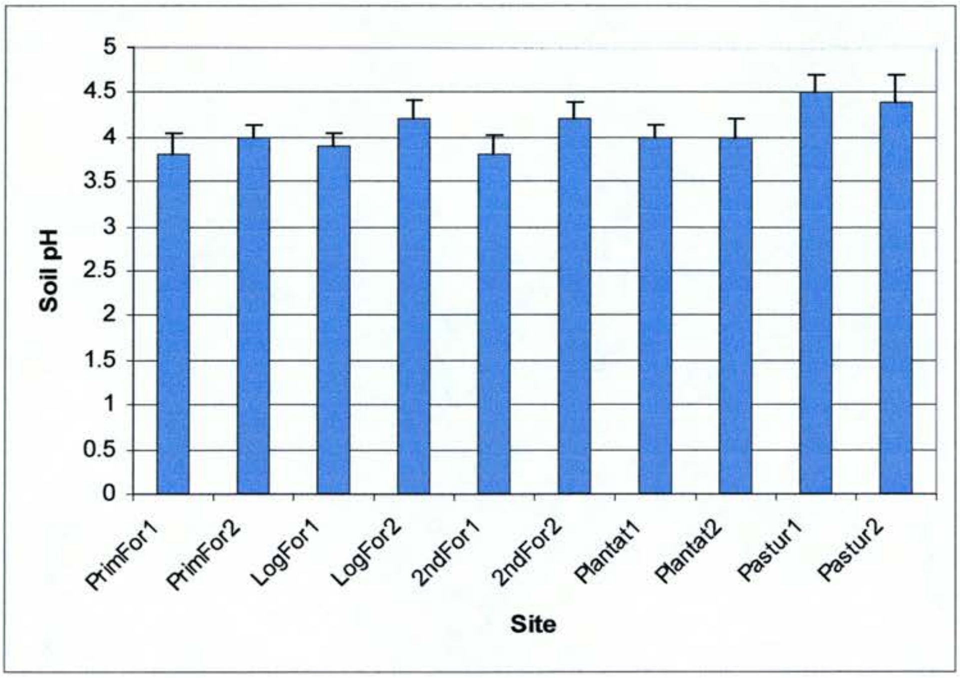


**Figure 5.10 Soil pH in field sites sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits.



SUMMARY AND DISCUSSION

As predicted, soil characteristics have changed over the gradient of disturbance examined in the field sites. Soil organic matter was higher in three out of four of the primary and logged primary forest sites than in the other sites of greater human impact. These results indicate that human intervention causes a loss in organic matter. This may be due to increased soil erosion, particularly in pasture sites, to a reduction in leaf litter input, which would replenish the level of soil organic matter, and an enhanced decomposition rate with insolation and exposure. Guggenberger and Zech (1999) have indicated that in secondary forest succession, soil organic matter increases from that present in pasture. The results presented here do not support their conclusion although the secondary forests studied were at an earlier stage of succession. The findings of Foth and Schafer (1996) may help to explain why the pasture sites have a higher soil organic matter level than the plantation sites. They illustrate that root biomass and therefore soil organic matter can be higher in soils under grassland vegetation than in some forest soils. The loss in organic matter after disturbance shown in this study could, conceivably, affect forest regeneration and composition but personal observation has indicated that forest recovery in abandoned pasture in the region of the study area is vigorous.

Soil temperature was higher in sites of greater human intervention, such as, plantation and pasture sites. This is a result of changes in microclimate caused by the removal of natural forest. The forest canopy is less dense in secondary forest and in plantation forest which leaves it more exposed to direct sunlight. The pasture sites are obviously almost entirely exposed to solar radiation, with the exception of the small areas protected by remnant forest trees left specifically for shade purposes. In the forest sites which have closed canopies the soil temperature is not greatly affected. The natural forest sites (including primary and logged primary forests) show similar soil temperatures, although these were significantly different from the secondary forest sites which have a more open canopy. Soil temperature under forest cover is largely controlled by air temperature, and soil temperature appears to be practically unaffected even by considerable differences in soil texture and in the amount of soil moisture (Schultz 1960).

Soil pH remained relatively unaffected by human intervention with the only sites showing significant differences being the pasture sites where the forest has been almost entirely removed. The pasture sites have a higher pH (mean pH=4.4) perhaps resulting from a decrease in the organic acids normally produced by the leaf litter layer. It is also possible that the use of fire as a clearing mechanism could increase soil pH by increasing ash nutrients levels which in turn would reduce the acidifying radicals of hydrogen and aluminium. Overall the soils are acidic with a narrow pH range from a little over pH3.5 to slightly over pH4.

### 5.6.3 Other environmental and physical parameters in a northern Costa Rica landscape

Table 5.5 presents a summary of the environmental and physical variables measured, excluding the soil data. Measurements of maximum and minimum air temperature, slope, altitude, and leaf litter quality were taken. The highest maximum temperature was recorded in Pastur1 and the lowest minimum in 2ndFor2. Slopes varied from 3.3 percent to 29.6 percent, the latter characterising very steep relief. The altitude ranged between 38.7 and 160.7 metres, covering most of the altitudinal range of the northern area of the San Carlos region. Leaf litter amount varied from 1.8 g in Pastur1 to 13.9g in PrimFor2.

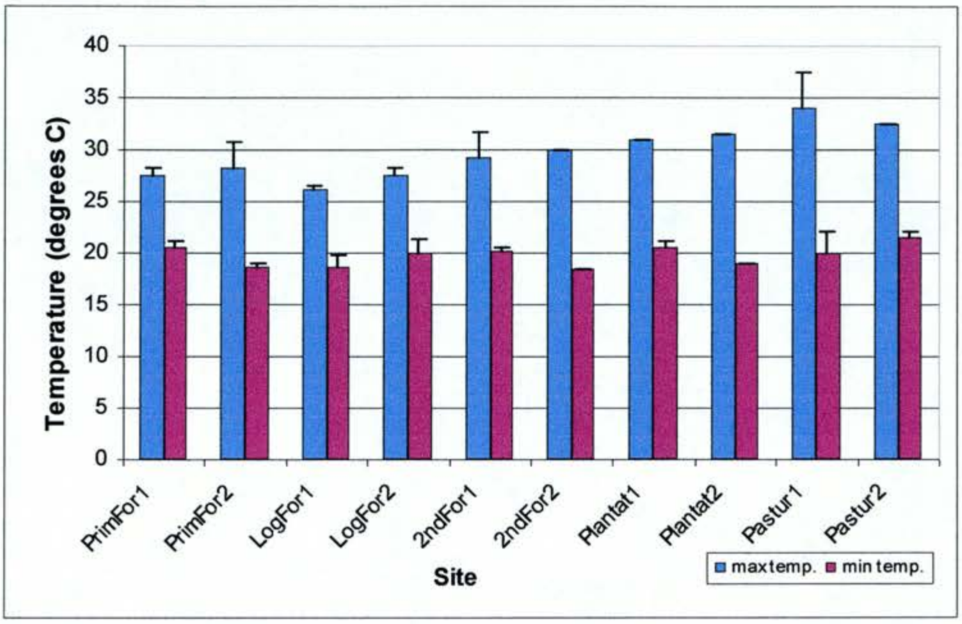
**Table 5.5 Environmental and physical site characteristics.** Values indicated are means for each site ± 1 standard deviation (Leaf litter units measure dry mass).

| *Habitat* | *Site* | *Max temp (°C)* | *Min temp (°C)* | *Slope (%)* | *Altitude (m)* | *Leaf litter(g)* |
|---|---|---|---|---|---|---|
| *Primary forest* | PrimFor1 | 27.5 ± 0.71 | 20.5 ± 0.71 | 5.2 ± 6.20 | 38.7 ± 4.17 | 13.0 ± 4.1 |
| | PrimFor2 | 28.3 ± 2.48 | 18.8 ± 0.35 | 29.6 ± 17.59 | 82.2 ± 10.88 | 13.9 ± 5.33 |
| *Logged forest* | LogFor1 | 26.3 ± 0.35 | 18.8 ± 1.06 | 13.6 ± 10.41 | 45.9 ± 9.60 | 8.2 ± 4.23 |
| | LogFor2 | 27.5 ± 0.71 | 20.0 ± 1.41 | 13.9 ± 9.96 | 160.7 ± 16.83 | 9.1 ± 3.19 |
| *Secondary forest* | 2ndFor1 | 29.3 ± 2.48 | 20.3 ± 0.35 | 12.1 ± 0.75 | 40.7 ± 4.91 | 8.5 ± 5.22 |
| | 2ndFor2 | 30.0 ± 0.00 | 18.5 ± 0.00 | 12.1 ± 7.48 | 79.4 ± 26.97 | 12.6 ± 7.41 |
| *Plantation* | Plantat1 | 31.0 ± 0.00 | 20.5 ± 0.71 | 8.7 ± 6.57 | 41.5 ± 5.36 | 8.5 ± 3.76 |
| | Plantat2 | 31.5 ± 0.00 | 19.0 ± 0.00 | 9.2 ± 8.74 | 43.8 ± 3.75 | 10.2 ± 4.25 |
| *Pasture* | Pastur1 | 34.0 ± 3.54 | 20.0 ± 2.12 | 18.6 ± 2.93 | 158.6 ± 12.14 | 1.8 ± 2.05 |
| | Pastur2 | 32.5 ± 0.00 | 21.5 ± 0.71 | 3.3 ± 4.27 | 48.2 ± 9.17 | 2.3 ± 2.82 |

### MAXIMUM AND MINIMUM AIR TEMPERATURE

Maximum air temperature readings increased over the gradient of human impact denoted by field site whilst minimum temperatures remained nearly constant (Figure 5.11). Analysis of the maximum temperature readings revealed a significant effect of land use type (One-way ANOVA, F = 4.14, $p$ = 0.023; Table A7 in Appendix 5). The same analysis of the minimum temperature readings did not show a significant effect of land use, indicating that minimum temperatures were not affected significantly by land use (One-way ANOVA, F = 1.78, $p$ = 0.201; Table A8 in Appendix 5).

**Figure 5.11 Maximum and minimum air temperatures in field sites sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits.



SLOPE AND ALTITUDE

Both slope and altitude were measured over the field sites studied. Average slope by site is shown in Figure 5.12. Analysis of the data reveals that slope varied significantly over the sites studied (Kruskal-Wallis, H = 60.64, $p < 0.001$; Table A9 in Appendix 5). As illustrated in Figure 5.12, the steepest slopes were found in PrimFor2 and Pastur1. The least sloping ground was found in PrimFor1 and Pastur2.

The average altitude of the field sites is illustrated in Figure 5.13. Both LogFor2 and Pastur1 were located in the field area *Finca Luzmirio Alvarez*, and it is therefore not surprising that they have similarly high altitudes. PrimFor2 was also situated at a higher altitude than the other sites. This site was located on a steeply sloping ridge explaining its high values for both slope and altitude. Analysis of the data shows that site altitudes were significantly different (Kruskal-Wallis, H = 193.48, $p < 0.001$, Table A10 in Appendix 5). This factor is addressed further in the multivariate analysis presented in Section 5.5.4.

**Figure 5.12 Average slope of field sites sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits.

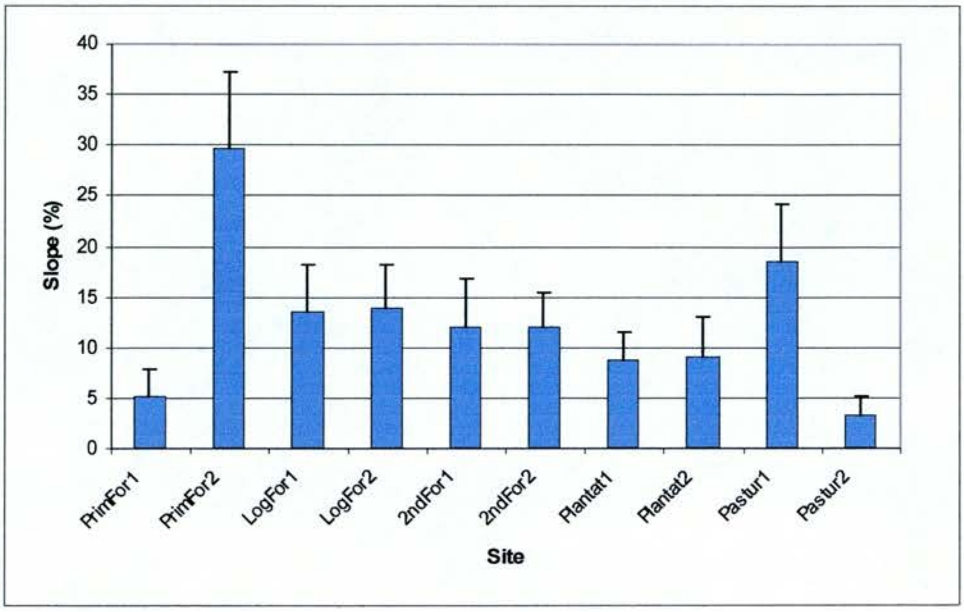
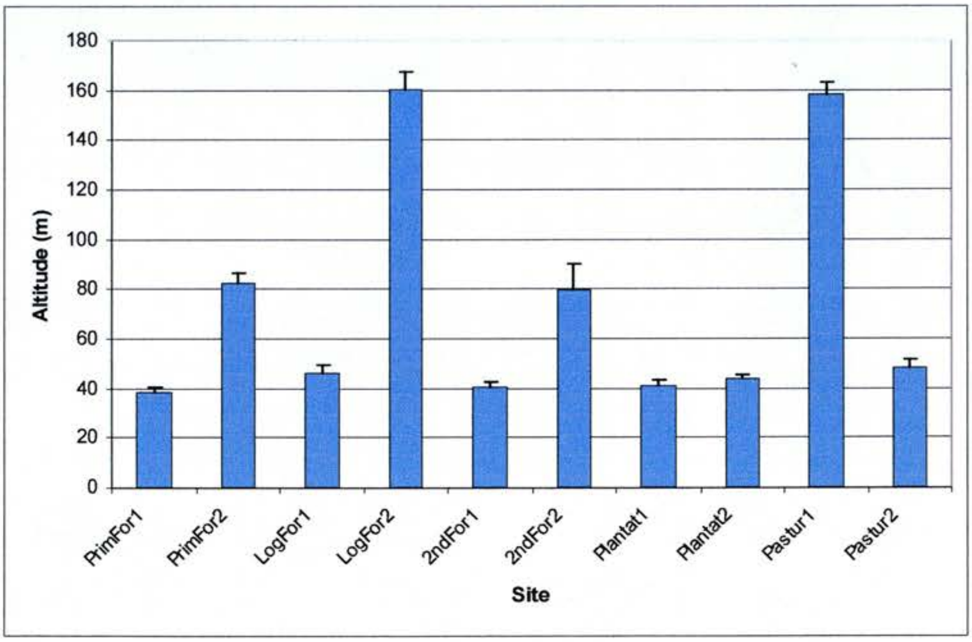


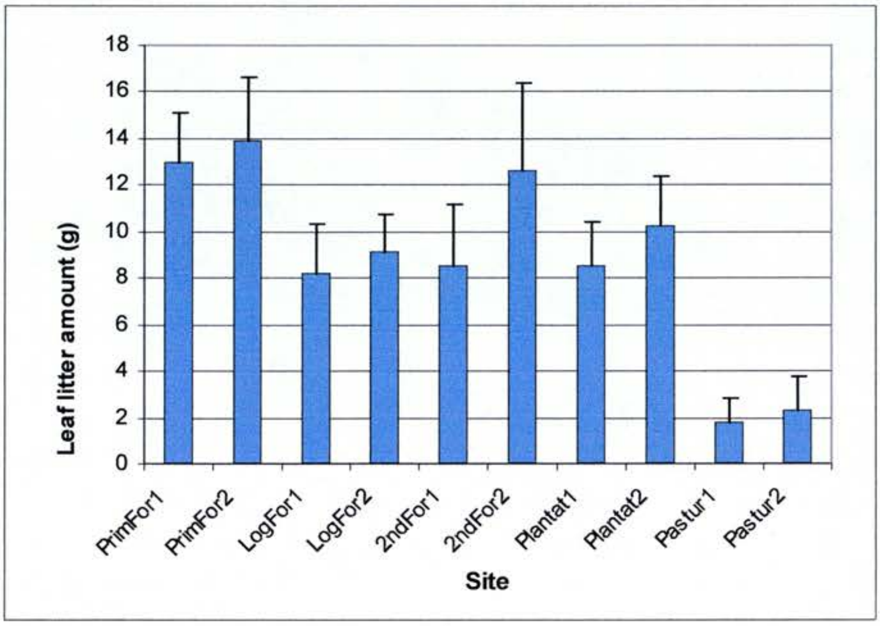
**Figure 5.13 Field site altitudes, northern Costa Rica.** Error bars denote 95% confidence limits.



### LEAF LITTER QUALITY

Figure 5.14 illustrates that the levels of leaf litter in each field site were significantly affected by land use (One-way ANOVA, F = 12.77, $p < 0.001$; Table A11 in Appendix 5). Further investigation of leaf litter levels using Tukey's multiple comparison test ($p < 0.05$) (Table A12 in Appendix 5) reveals that there are significantly different levels of leaf litter between the two pasture sites (Pastur1 and Pastur2) and all other sites. Figure 5.14 also shows that the primary forest sites (PrimFor1 and PrimFor2) have higher levels of leaf litter than all other sites, although Tukey's test reveals that only PrimFor2 has levels that are significantly different from the majority of the other sites (Table A12).

**Figure 5.14 Leaf litter amount sampled over a gradient of disturbance in northern Costa Rica.** Error bars denote 95% confidence limits.



### SUMMARY AND DISCUSSION

This section has illustrated the variation in field characteristics between study sites. The physical parameters of slope and altitude obviously do not change with human intervention but some of the differences between sites are shown to be significant. It is probable that such parameters affect both tree species composition and the related insect population.

Microclimatic changes in air temperature are caused primarily by changes in direct sunlight levels. The natural forest sites showed lower temperatures during the day as they have a closed canopy. The sites of human intervention, namely secondary forest, plantation forest and pasture, have reduced canopy closure, or, in the case of pasture, no canopy. This results in greater exposure to the sun which, logically, raises air temperatures. Minimum temperatures during the night are unaffected by this factor and therefore they remained almost constant over the study sites and did not change with land use. The differences revealed in daytime air temperatures between land use are important as they may affect tree seedling recruitment and regeneration. Temperature may also have an effect on the range of insect species present in each site. The next section will examine the parameters discussed here, along with the soil characteristics, in order to investigate possible environmental relationships with forest structure. In later chapters these data will be further examined in order to investigate the possibility of relationships with insect species composition and diversity.

### 5.6.4 Environmental relationships with the forest

The forest sites, namely primary forest (PrimFor1 and PrimFor2), logged primary forest (LogFor1 and LogFor2) and secondary forest (2ndFor1 and 2ndFor2), were examined alongside the associated environmental and physical variables using Canonical Correspondence Analysis (CCA)(Ter Braak and Smilauer 1998). Within this analysis, both sample and species plots were produced, together with biplots of the environmental variables. The CCA output was used to investigate the correlations between variables. It also identified which variables carry the most relevant information and are therefore responsible for the largest part of any environmental heterogeneity. These variables were then examined to identify possible relationships with forest structure.

#### CANONICAL CORRESPONDENCE ANALYSIS (CCA) OF TREE SPECIES AND ENVIRONMENTAL VARIABLES

A CCA analysis was performed on tree species and environmental variables. The correlation matrix for the environmental data is shown in Table 5.6. All coefficients with a value higher than 0.6 are shown in red. The highest coefficients, except clear auto-correlation such as between soil temperature, and minimum and maximum air temperatures, and between leaf litter and soil organic matter, were between maximum temperature and soil organic matter ($r^2 = -0.84$) and, altitude and soil pH ($r^2 = 0.75$). These appear to reveal an influence of altitude on soil parameters, and also of maximum temperature on soil organic matter. It is probable that the correlation between maximum temperature and soil organic matter is not a direct causal relationship but a result of differences in forest cover. Highest temperatures occur in forests with reduced canopy closure which are exposed to more direct sunlight. The canopy of these forests, for example the secondary forest sites, produces less organic matter to add to the soil. It is therefore evident that, despite an apparent influence on each other, these two parameters are both independently related to forest canopy density and, therefore, also to forest type.

**Table 5.6 Correlation coefficients among environmental variables.** CCA weighted correlation matrix output.

| | *leaf litter* | *soil OM* | *soil pH* | *soil T* | *max T* | *min T* | *slope* | *altitude* |
|---|---|---|---|---|---|---|---|---|
| *leaf litter* | 1.0000 | | | | | | | |
| *soil OM* | -0.7425 | 1.0000 | | | | | | |
| *soil pH* | -0.0010 | -0.2496 | 1.0000 | | | | | |
| *soil T* | 0.0907 | -0.4447 | 0.5510 | 1.0000 | | | | |
| *max T* | 0.4999 | -0.8374 | 0.4798 | 0.7093 | 1.0000 | | | |
| *min T* | -0.1446 | 0.0564 | -0.4918 | -0.7558 | -0.2785 | 1.0000 | | |
| *slope* | 0.3114 | -0.3505 | 0.1619 | 0.4216 | 0.0626 | -0.5265 | 1.0000 | |
| *altitude* | -0.1287 | -0.1794 | 0.7466 | 0.0817 | 0.0983 | 0.0184 | 0.2543 | 1.0000 |

The existence of relationships between forest structure and composition, and the selected environmental variables was also investigated using CCA analysis. The results of the direct ordination are shown in a biplot of site and environmental variables (Figure 5.15) and in a biplot of species and environmental variables (Figure 5.16). The correlation coefficients of the environmental variables with the CCA ordination axes are detailed in Table 5.7. In Figures 5.15 and 5.16 the environmental data are represented by arrows which are plotted in the direction of the maximum change. The length of the arrows is proportional to the magnitude of that change. The longest arrows illustrate variables that are more closely correlated in the ordination than those illustrated by short arrows. They are therefore more important in influencing community variation.

Species can be related to arrows by their relative positions. Those found close to the arrow tip are strongly correlated with the variable in question. The further down the arrow from the tip the less affected are species found there (Kent and Coker 1992).

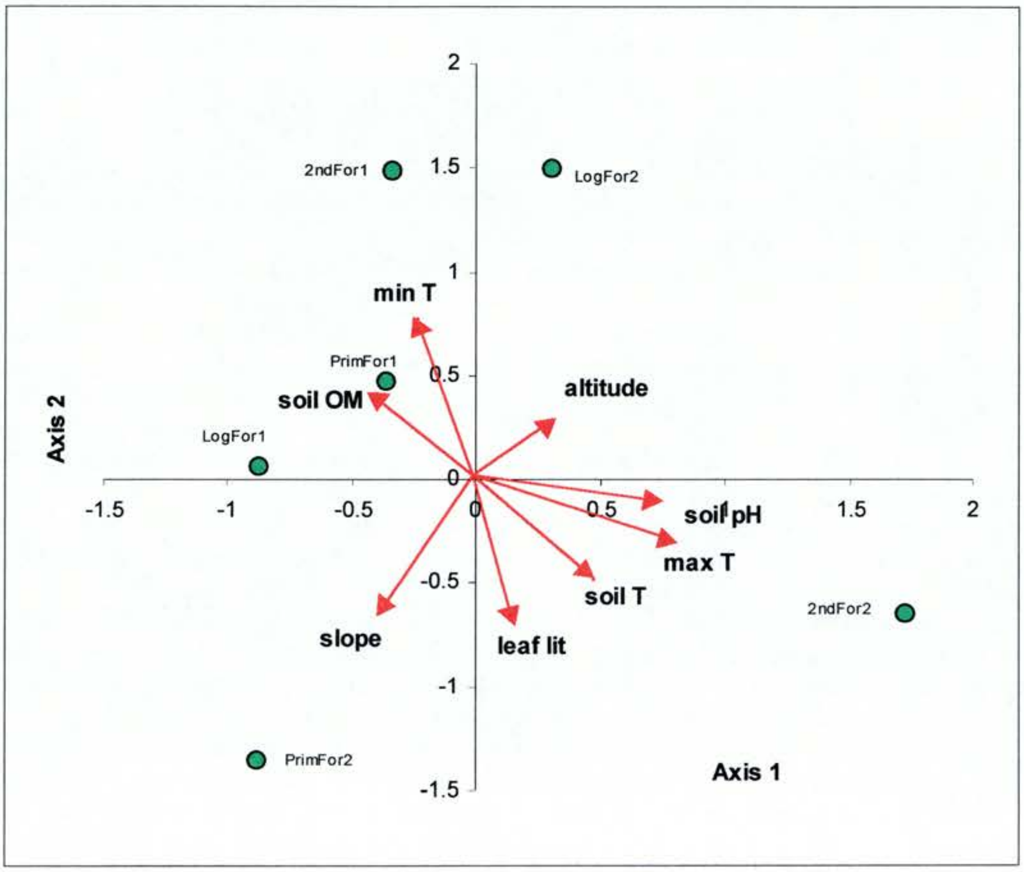
The ordination biplot of the first two axes of site and environmental variables (Figure 5.15) reveals the existence of a correlation between soil pH and the first ordination axis ($r^2$ = 0.74)(Table 5.7), maximum temperature also showed a positive correlation ($r^2$ = 0.76). Of the other variables, leaf litter ($r^2$ = -0.69), minimum temperature ($r^2$ = 0.77) and slope ($r^2$ = -0.63) correlate with Axis 2 (Figure 5.15 and Table 5.7). The ordination diagram separates both the primary and one of the logged primary forest sites to the left of the diagram. PrimFor1 is plotted next to the tip of the soil organic matter arrow indicating a strong correlation (Kent and Coker 1992). A correlation with this site and minimum temperature is also indicated. PrimFor2 is correlated with slope and, at the opposite side of the diagram, LogFor2 is more strongly correlated to altitude than any other variable. 2ndFor2 appears to be correlated to temperature, as both the maximum and the soil temperature arrows are directed towards it.

**Table 5.7 Correlation coefficients of environmental variables with the CCA ordination axes.** CCA weighted correlation matrix output.

| | *SPEC Axis 1* | *SPEC Axis 2* | *SPEC Axis 3* | *SPEC Axis 4* | *ENVI Axis 1* | *ENVI Axis 2* | *ENVI Axis 3* | *ENVI Axis 4* |
|---|---|---|---|---|---|---|---|---|
| ***leaf litter*** | 0.1600 | -0.6866 | 0.1125 | 0.1479 | 0.1600 | -0.6866 | 0.1125 | 0.1479 |
| ***soil OM*** | -0.3934 | 0.3783 | -0.2103 | -0.6876 | -0.3934 | 0.3783 | -0.2103 | -0.6876 |
| ***soil pH*** | 0.7362 | -0.1166 | -0.5872 | 0.2065 | 0.7362 | -0.1166 | -0.5872 | 0.2065 |
| ***soil T*** | 0.4795 | -0.4825 | 0.1437 | 0.4255 | 0.4795 | -0.4825 | 0.1437 | 0.4255 |
| ***max T*** | 0.7607 | -0.3151 | 0.3257 | 0.4569 | 0.7607 | -0.3151 | 0.3257 | 0.4569 |
| ***min T*** | -0.2266 | 0.7665 | 0.1905 | 0.0562 | -0.2266 | 0.7665 | 0.1905 | 0.0562 |
| ***slope*** | -0.3623 | -0.6319 | -0.3363 | 0.5742 | -0.3623 | -0.6319 | -0.3363 | 0.5742 |
| ***altitude*** | 0.3003 | 0.2552 | -0.7983 | 0.4544 | 0.3003 | 0.2552 | -0.7983 | 0.4544 |

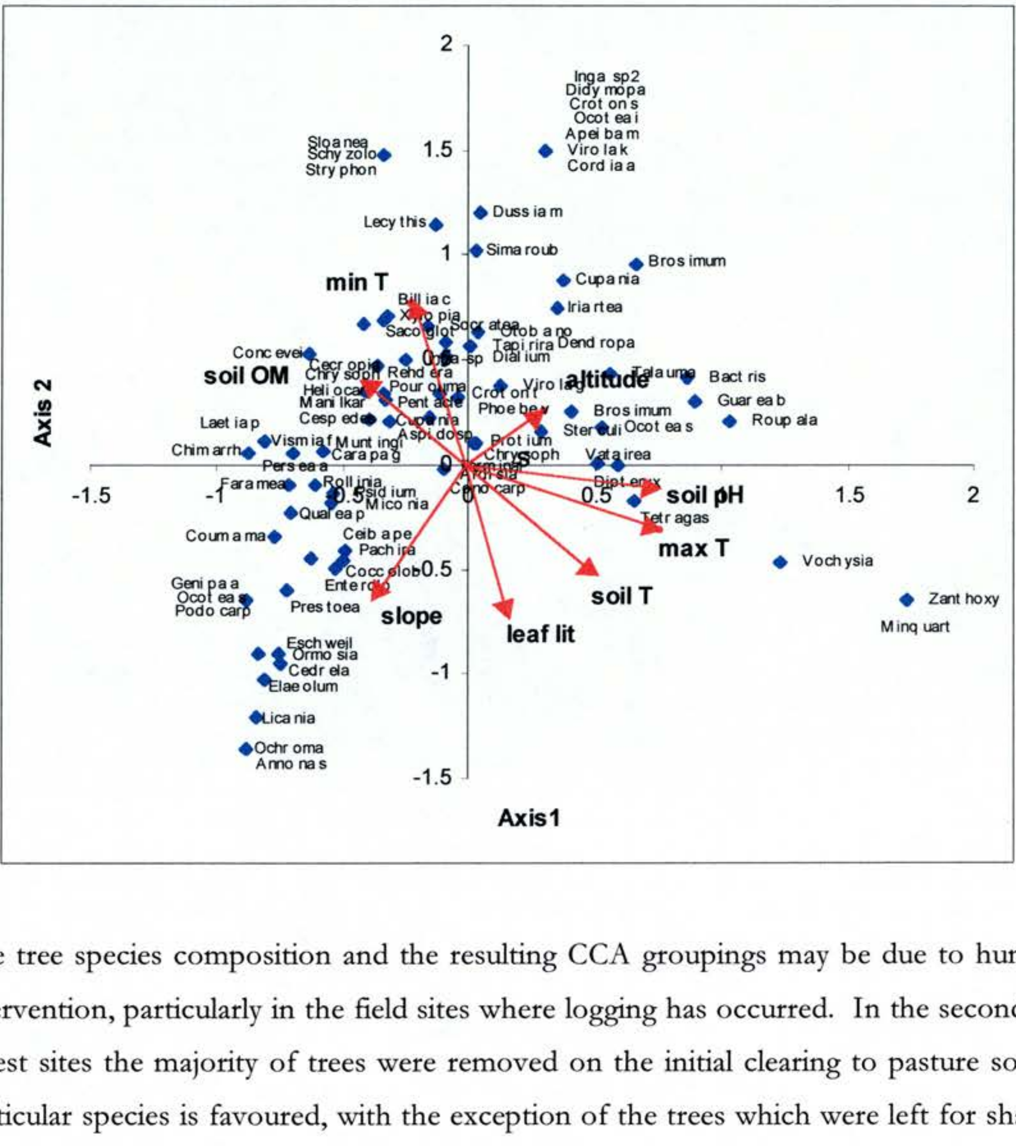
**Figure 5.15 CCA ordination of the forest plots and environmental variables.**

The ordination biplot of the first two axes of site and environmental variables reveals varying degrees of correlation of environmental variables with field sites (e.g. PrimFor 1 is highly correlated with soil organic matter).



Consideration of Figure 5.16 reveals tree species associations with the environmental and physical variables. Some of the species are clearly distinguished as only being found on one of the field sites. By examination of both Figures 5.15 and 5.16, it is evident that *Sloanea sp.*, *Schyzolobium parahyba* and *Stryphondendron microstachyum* are characteristic of 2ndFor1. There is also a clear group of species which are found in LogFor2; *Inga sp.2, Didymopanax morototoni, Croton sp., Ocotea sp., Apeiba membranacea, Virola koschnyi, and Cordia alliodora.* It is also evident that PrimFor2 has a small number of site specific species (*Eschweilera costaricensis, Ormosia macrocalyx, Cedrela odorata, Elaeoluma glabrescens, Licania affinis, Ochroma pyramidale*, and *Annona sp.*), and that 2ndFor2 has a limited range of species found there, primarily *Vochysia ferruginea, Zanthoxylum ekmanii* and *Minquartia guianensis.* The principal factor in grouping the above species appears be land use type.

**Figure 5.16 CCA ordination of tree species and environmental variables.** The ordination biplot of the first two axes of site and environmental variables reveals varying degrees of correlation of environmental variables with tree species. Groupings of tree species by field site are also evident if this diagram is compared to Figure 5.15.



The tree species composition and the resulting CCA groupings may be due to human intervention, particularly in the field sites where logging has occurred. In the secondary forest sites the majority of trees were removed on the initial clearing to pasture so no particular species is favoured, with the exception of the trees which were left for shade. However, in the logged primary forest sites selective removal of valuable timber species will have changed the tree species composition. This may have caused both the DCA and CCA outputs to group sites separately.

In addition to tree species that have an obviously link to field site, some grouping by environmental gradients is revealed. Principally slope and soil organic matter content influence species on the left side of the diagram. Minimum temperature is also important in defining the species to the left upper area of the graph. Altitude is an important parameter, and is correlated with the tree species found on the top right side of the diagram, while soil pH, soil temperature, maximum temperature and leaf litter quality appear to drive only a small percentage of tree species.

### FOREST ENVIRONMENT RELATIONSHIPS

The CCA ordination of vegetation and environmental data indicate a relatively similar pattern to that of the TWINSPAN classification and DCA ordination in Section 5.4 of this chapter, particularly with respect to tree species distributions. The CCA has shown that variations in forest structure and composition are related to environmental factors particularly soil organic matter and minimum temperature, and to the physical variables of altitude and slope. It also reveals that some environmental factors are more important in particular sites, for example soil organic matter is highly correlated to PrimFor1 and LogFor1, while maximum temperature is negatively correlated with these sites and positively correlated with 2ndFor2.

In general the results of the CCA appear to demonstrate that forest composition can be related to site characteristics. The changes in forest cover found in the study are mainly a result of direct human impact, and the corresponding changes in environment can be related to the land use type present. Despite the overshadowing of natural processes by human intervention, the relationship between forest species, and slope and altitude is still evident.

## 5.7 Overall summary and conclusions

### FOREST STRUCTURE AND COMPOSITION

A total of 1902 trees with dbh $\geq$ 10cm were measured in the ten sites which ranged from primary forest to pasture. These trees represented a total of 102 species. The trees were identified in the field to common name by a parataxonomist, and of these common names, 89 were then converted to species names and family. The number of individuals per site varied from 297 trees in one of the secondary forest sites to only 1 tree in one of the pasture sites. The primary forest sites had 239 and 280 trees respectively. The average tree density sampled per land use was 259.5 individuals in primary forest, 225.5 individuals in logged forest, 195 individuals in secondary forest, 266 individuals in plantation and 8 in pasture. The average dbh was 24.6 cm with a range from 16.6 cm to 49.1 cm. The largest tree (*Dipteryx panamensis*, Leguminosae) reached a dbh of 205.0 cm. The average basal area per hectare was 32.2 $m^2$ in primary forest, 21.7 $m^2$ in logged forest, 24.3 $m^2$ in secondary forest, 12.4 $m^2$ in plantation and 1.3 $m^2$ in pasture.

At the floristic level, the sites studied in northern Costa Rica showed a high diversity in terms of both species (102) and families (42). The Leguminosae had the greatest number of species (11), followed by the Lauraceae (6) and then the Sapotaceae (5) and the Myrsinaceae (5). The Bombacaceae, Euphorbiaceae, Meliaceae, Palmae, Rubiaceae, and Tiliaceae all had three species.

A Detrended Correspondence Analysis (DCA) examined tree species composition over the forest sites. Although in general all species were grouped together a gradient from left to right in the DCA diagram was evident. This demonstrated the changes which have occurred over the gradient of disturbance implied by the land uses in the sites studied. There was also evidence of site similarities in general field areas or estates, which may represent similar site characteristics due to geographical proximity

A TWINSPAN classification divided the 6 forest sites into two main groups, which appeared to be based principally upon field area. This appeared to demonstrate that the clustering of sites according to tree species composition was primarily influenced by the original forest cover. However, underlying this pattern, the analysis also revealed that the two secondary forest sites, despite being located at a significant distance from each other, had similar species associations. The analysis reinforces the pattern revealed by axis 1 of the DCA ordination. In summary, distinctions between the land uses were demonstrated, but the analysis also illustrated the importance of geographical proximity in tree species composition.

### THE FOREST ENVIRONMENT

The forest environment was examined using a CCA ordination of vegetation and environmental data. It indicated a similar pattern, with respect to tree species distributions, as the TWINSPAN classification and the DCA ordination. The CCA revealed the greater importance of some environmental factors in forest composition at specific sites but also demonstrated that forest composition can be related to site characteristics despite the changes in forest cover being mainly a result of direct human impact. Notwithstanding the overshadowing of natural processes by human intervention, the relationship between forest species, and slope and altitude was still evident.

This chapter has provided a background to the ecology of the study sites containing forest (the primary, logged and secondary forest sites), as well as documenting the tree species diversity and composition of these sites. It has presented data on a number of environmental variables, for all the study sites, in order to reveal the changes in microclimate and soil condition, and provide an initial assessment of change to the forest environment (tree species composition and diversity, microclimate, and soil condition) after human intervention. It is evident that environmental conditions do vary by land use, but that tree species composition is also strongly related to geographical location and, probably, to the original forest cover. In general, the existing patterns of tree species composition and diversity are primarily a result of **direct** human action. The **indirect** effects of human intervention on insect communities will be investigated in the following two chapters. They will examine whether geographical proximity and previous vegetational history influence insect species communities, or whether the impacts of changing land use are the predominant factors determining the population structure.

# CHAPTER 6

# THE RESPONSE OF LEAF LITTER INVERTEBRATES TO TROPICAL FOREST DISTURBANCE AND CONVERSION:

# I. THE ANTS

## 6.1 Introduction

'Ants run much of the terrestrial world as the premier soil turners {and} channelers of energy. {They are} dominatrices of the insect fauna {and} represent the culmination of insect evolution' (Holldobler and Wilson 1990).

Ants are the most important group of insects in tropical rainforest with regard to their biomass, number of individuals and ecological impact (Fittkau and Klinge 1973, Stork 1988, Hölldobler and Wilson 1990, Watt et al. in press). Ants play an important role in structuring communities, from nutrient cycling in the soil (Lal 1988) and roles in seed dispersal (Beattie 1985, Majer 1990), to influencing floral and faunal communities (Roth et al. 1994). They perform many significant functional roles, for example as predators of other arthropods and tenders of leaf sucking insects (Hölldobler and Wilson 1990, Watt et al. in press). They are also involved in several, often symbiotic, interactions with other species of plants and animals (Roth et al. 1994). The soil and litter inhabiting ants, in particular, are of great importance to nutrient cycling because of their soil turning activity. Hölldobler and Wilson (1990) quote recent measurements suggesting that one-third of the entire animal biomass of the Amazonian *terra firme* rain forest is composed of ants and termites, with each hectare of soil containing in excess of 8 million ants.

This chapter examines the leaf litter ant fauna of a northern Costa Rican forest landscape, and its response to disturbance over a gradient of human impact. It investigates the consequences of land use change on ant species diversity, abundance and composition. In addition, it incorporates an analysis of the effects of environmental change on this group of ant fauna. The knowledge presented here is essential in understanding the changes that occur in insect diversity after logging and clearing of lowland tropical forest. Improved biodiversity conservation management can only be applied when such information is available.

## 6.2 Objectives

The aims of this chapter are to:

- provide an overview of the neotropical ant fauna and discuss its importance within the forest ecosystem (Section 6.3);
- describe the changes that occur in the species composition, diversity and abundance of leaf litter ants over a landscape of human disturbance (Section 6.4, 6.5, 6.6);
- relate changes in species composition to environmental changes in forest and converted forest (Sections 6.7 and 6.8); and
- assess the overall effects of logging and forest conversion to other land uses, on the ant fauna (Section 6.9).

## 6.3 The ants

Ants are dominant in both the tropical forest canopy and ground fauna (e.g. Erwin 1983, Adis et al. 1984, Stork and Brendell 1990, Belshaw and Bolton 1993, Floren and Linsenmaier 1997, Watt et al. 1997a, b and c). Other more speciose groups than ants exist, such as Coleoptera, Hymenoptera (Parasitica) and Diptera (Watt et al. in press); however ants demonstrate a significant local species richness. For example, Wilson (1987) recorded 43 species from a single tree in Peru, Floren and Linsenmaier (1997) recorded 192 species from 19 trees in Sabah, Malaysia, Stork (1991) recorded 82 species from ten trees in Borneo, and Harada and Adis (1997) recorded 82 species on a single tree in Brazil. This richness and abundance translates into ecological dominance (SIWeb 1998).

Ants are an extensively studied group and are well known taxonomically (Bolton 1994 and 1995). Their biology has been as well recorded as any other invertebrate group (Hölldobler and Wilson 1990). Ants also have a symbiotic relationship with many species of tropical plants due to the protection that they provide the plants from attack by other insects and perhaps also from pathogens.

These factors suggest a central role for social insects, particularly ants, in biodiversity inventory. Social insects, by virtue of their great abundance, are the easiest of all animals to sample. They can be collected in all seasons as their colonies are perennial and continuously active, and it is not necessary to wait for the occasional emergence of adult forms.

An overview of the neotropical ant fauna is outlined first and discussed in terms of its importance to the ecosystem. It documents ant colony structure, ant function in the ecosystem and lastly focuses on the leaf litter ants, the target group of ants investigated in this research. It provides an up to date summary of neotropical leaf litter ant guilds, in order to illustrate their many roles in ecosystem function.

### 6.3.1 The ant colony

All ants are social insects and therefore live in colonies. Most of these colonies contain three castes: queens, males and workers. The queens are larger than the members of the other castes and are usually winged, though the wings are shed after the mating flight. The queen usually initiates a colony and does the majority of the egg laying (Borror et al. 1981). Males are also winged and are generally smaller than the queen; they are short-lived and die soon after mating. The workers are wingless females and make up the bulk of the colony. In smaller ant colonies there are usually just three types of individual, but in larger colonies there may be two or three types within each caste.

Ant colonies vary in size, from a dozen or more individuals to many thousands. Ants nest in a variety of locations; some nest in various types of cavities in plants (in stems, in nuts, in galls etc.), some, such as the carpenter ants, excavate galleries in wood, but probably the majority of ants nest in the ground (Borror et al. 1981). The ground nests of ants may be small and relatively simple, or they may be quite large and elaborate, consisting of a maze of tunnels and galleries. Some of the larger mound nests have galleries which extend several metres underground (Borror et al. 1981).

Males and queens in most ant colonies emerge in certain seasons and engage in mating flights. Shortly after mating the male dies and the queen starts a new colony (Holldobler and Wilson 1990). The queen sheds her wings immediately after the mating flight, locates a suitable nesting site, makes a small excavation, and produces her first brood. This first brood is cared for by the queen and consists of workers (Borror et al. 1981). Once the first workers appear they begin to carry out the work of the colony: nest construction, caring for the young, and food gathering. The queen's only role then becomes one of reproduction.

The feeding habits of ants are varied. Some are carnivorous, feeding only on other animals (alive or dead); some feed on plants; some feed on fungi; and many others feed on sap, nectar, honeydew, and similar substances. Ants in the nest often feed on the excrement of other individuals, and the exchange of food between individuals (trophallaxis) is a common occurrence (Borror et al. 1981).

Ants produce a number of secretions that function in offence, defence and communication. These are produced by various glands and are discharged principally through the mouth, anus, or sting (Dolichoderinae and Formicinae lack a sting). The sting serves as the principal means of offence and defence. All ants may bite, some severely, and others eject a foul-smelling substance which also serves as a means of defence. Many ant excretions can act as alarm substances, some stimulate group activity, and others, when left by a foraging individual, can act as an odour trail that other individuals can follow (Borror et al. 1981).

### 6.3.2 Ant function

Given their diversity and biomass it is not surprising that ants play such a large role in the functioning of ecosystems (Alonso and Agosti 2000). Ants shape ecosystems in a variety of ways including as seed dispersers, soil turners, 'keystone species' and, pathologically, as introduced species.

Ants are significant 'ecological engineers'. They rearrange the environment in ways that affect other organisms (Lawton 1994). One of the principal ways they do this is by moving and enriching soil – large ant colonies may excavate kilos if soil in their lifetime, whilst also aerating the soil and incorporating litter from the surface. Leaf cutter ants are the dominant herbivore in tropical forest whilst also excavating significant volumes of soil. For example, the earth excavated by a single six and a half year old nest of *Atta sexdens* weighed approximately 40000kg, and this young colony was estimated to have gathered 5892kg of leaves (Wilson 1971). These ants therefore also play a significant role in nutrient cycling (Kaspari 2000).

It is also likely that some ants are keystone species (Paine 1968, Lawton 1994). According to Kaspari (2000), one potential example is the army ant, *Eciton burchelli*. Army ants are nomadic species, with thousands of workers, which roam in search of prey, mainly arthropods and especially social insects. This species may be a keystone species for the following reasons. A raid by *E. burchelli* results in a wave of escaping arthropods in front of the colony, these are easy prey for many birds in mixed feeding flocks which are specialised to follow army ant swarms (Willis 1983). There is also some evidence that by preying on large ant species *E. burchelli* may provide opportunities for smaller ant species that escape predation (Franks and Bossert 1983).

In brief, ants perform several significant functional roles, particularly as predators of other arthropods and tenders of leaf-sucking insects (Hölldobler and Wilson 1990, Way and Khoo 1992, Lasalle and Gauld 1993). They are important seed dispersers. It is estimated that ants disperse the seeds of 35 percent of all herbaceous plants (Beattie 1985). It is also documented that, as well as being the foremost arthropod predator, ants scavenge in excess of 90 percent of all dead insects and other arthropods.

### 6.3.3 Leaf litter ants

Little information is available on the biology or community organisation of most neotropical ant species (Delabie et al. 2000). Previous studies have, however, indicated that, both in the Old and New World tropics, arboreal ants are distributed in a three-dimensional mosaic in which dominant ant species form mutually exclusive blocks, each with their own suite of sub-dominant and non-dominant ants (Room 1971, Majer et al. 1994).

Delabie et al. (2000) provide strong evidence that a mosaic also occurs in the leaf litter layer. Their work, carried out in Bahia, Brazil, demonstrates that this mosaic results from the interactions of two groups of ants of different origin. The first comprises ground dwelling species which generally display cryptic behaviour and interact with each other. The second group consists of a few arboreal species that are probably present on the forest floor in order to forage during unfavourable conditions in the trees (Delabie et al. 2000). This second group can dominate the ground-dwelling species and has a considerable influence on the composition of the ant community at the base of trees. At greater distances from tree bases the ant community is more characteristic of the purely ground-dwelling ant community (Delabie et al. 2000).

The same study also provides an introduction to South American soil and litter ant guilds (Delabie et al. 2000). These guilds are based on their foraging, feeding and nesting characteristics and the authors believe that the inferences they present are probably also true for a range of rain forest types of the neotropical region. Figure 6.1 summarises the nine categories of guilds distinguished below. With the exception of a few cases, the ants are considered at generic level as there is a reasonable degree of communality in foraging or nesting habits among different species of a genus. The guilds presented are detailed below. They are also discussed within the context of the data collected in this study in a later section of this chapter.

Guild 1: **Litter omnivores and scavengers** – this guild includes some of the most speciose genera (e.g. *Pheidole*, although the foraging and nesting strategies of most of these species remains completely unknown), and some species with high population densities (e.g. *Solenopsis*, sub-genus *Diplorhoptrum*). *Megalomyrmex* is also in this guild.

Guild 2: **Litter specialist predators** – this guild contains a range of cryptic species on the basis of their behaviour and foraging characteristics. They are *Acanthostichus*, *Amblyopone*, *Cerapachys*, *Discothyrea*, *Eurhopalothrix*, *Leptogenys*, *Oligomyrmex*, *Proceratium*, *Prionopelta*, *Rhopalothrix*, *Stegomyrmex*, *Thaumatomyrmex*, *Typhlomyrmex*, some highly specialised species of *Gnamptogenys*, and several Dacetonini, including *Glamyromyrmex* and *Neostruma*.

Guild 3: **Litter generalist predators** – this category includes the different species of *Hypoponera* and *Anochetus*, which are generally cryptic, and most species of *Gnamptogenys*.

Guild 4: **Army ants and army ant-like species** – this guild includes all the Ecitoninae, whether cryptic or not, namely *Eciton*, *Labidus*, *Neivamyrmex* and *Nomamyrmex*, and also the ponerine genus *Simopelta*.

Guild 5: **Soil cryptic predators** – this category contains a few species which are rarely found (but are common in a few places) and which are exclusively cryptic. Included are *Tranopelta* and *Pachycondyla holmgreni* which, because of its strong morphological convergence with *Centromyrmex*, is probably a termite predator. It is exclusively found in *Syntermes* nests (Delabie 1995).

Guild 6: **Subterranean mealybug-dependent species** – the common but extremely cryptic *Acropyga* is placed in this guild. This has a mutualistic association with highly specialised mealybugs of the tribe Rhizoecini which are found on the roots of various plant species.

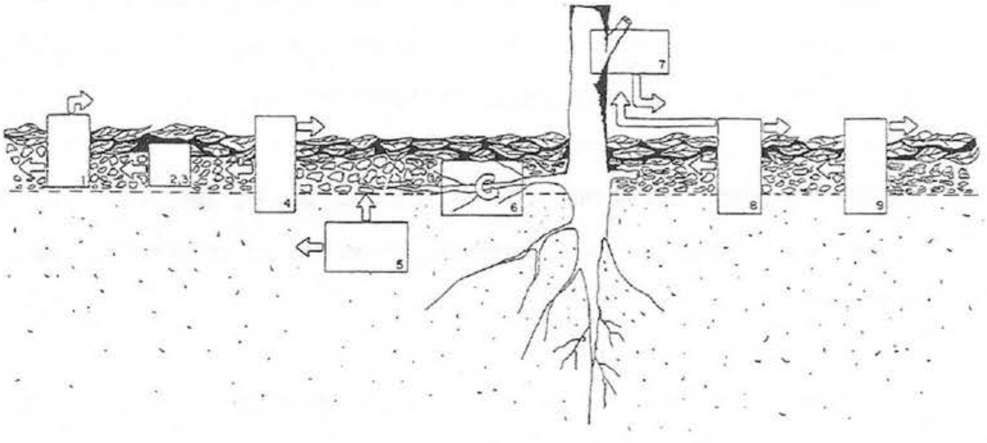
Guild 7: **Omnivorous arboreal nesting dominants foraging on the floor** – the occurrence on the forest floor of some species of dominant *Crematogaster* and *Azteca* can result from a permanent or seasonal extension of their territory. They exert a strong influence on the soil-dwelling species as a result of predation and/or food resource competition.

Guild 8: **Soil or litter dominants** – these ants forage on vegetation, on the forest floor, or in the litter. This category is divided into two groups: a) large generalist predators, such as *Odontomachus* and *Ectatomma* (some species of these genera also forage on vegetation looking for nectar); and b) true omnivores such as *Brachymyrmex*, *Camponotus*, *Monomorium*, *Paratrechina*, *Solenopsis* (larger species), and *Wasmannia*.

Guild 9: **Soil and litter nesting fungus growers** – this guild consists of members of the Attini, including the genera *Acromyrmex*, *Apterostigma*, *Atta*, *Cyphomyrmex*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex*, and *Trachymyrmex*, which use arthropod refuse and carcasses and/or dead or live plant material to cultivate their symbiotic fungus (Delabie et al. 2000).

In this overview, the importance of the leaf litter ants to ecosystem function is evident, particularly in nutrient cycling on the soil and leaf litter. The following sections present the results for the leaf litter ant data collected over five land uses representing a gradient of human disturbance. The effects of changing land use, and the related changes in environment, on the leaf litter ant fauna are discussed.

**Figure 6.1 Guild organisation of leaf litter ants in the Atlantic rain forest of Brazil** (Source: Delabie et al. 2000)



| ***Guild no.*** | ***Description of guild*** |
|---|---|
| **1** | **Litter omnivores and scavengers** (cryptic or otherwise): *Blepharidatta, Lachnomyrmex, Megalomyrmex, Pheidole, Octostruma, Solenopsis, Rogeria* |
| **2** | **Specialist litter predators** (cryptic): *Ancanthostichus, Amblyopone, Cerapachys, Cylindromyrmex, Discothyrea, Eurhopalothrix, Gnamptogenys* (few species), *Leptogenys, Hylomyrma, Octostruma, Oligomyrmex, Proceratium, Prionpelta, Rhopalothrix, Stegomyrmex, Thaumatomyrmex, Typhlomyrmex,* Dacetonini (*Glamyromyrmex, Gymnomyrmex, Neostruma, Smithistruma, Strumigenys*). |
| **3** | **Litter generalist predators** (cryptic or otherwise): *Hypoponera, Gnamptogenys* (most species), *Anochetus.* |
| **4** | **Army ants and army-like species** (cryptic or otherwise, generalist or specialist predators): Ecitoninae (*Eciton, Labidus, Neivamyrmex, Nomamyrmex*), *Simopelta.* |
| **5** | **Soil cryptic predators**: *Pachycondyla holmgreni, Centromyrmex* (exclusively in termite (*Syntermes* spp.) nests |
| **6** | **Subterranean mealybug-dependent species** (cryptic): Acropyga, Tranopelta. |
| **7** | **Omnivorous arboreal-nesting dominants**, incidentally or seasonally foraging on the floor and in the litter: *Azteca, Crematogaster.* |
| **8** | **Soil or litter dominants**, also foraging on the vegetation, the ground or the litter:<br>***A.* generalist predators**: *Odontomachus, Ectatomma*;<br>***B.* omnivores**: *Brachymyrmex, Camponotus, Monomorium, Paratrechina, Solenopsis, Wasmannia.* |
| **9** | **Soil or litter nesting fungus growers**: several genera of Attini, such as *Acromyrmex, Apterostigma, Atta, Cyphomyrmex, Mycocepurus, Myrmicocrypta, Sericomyrmex, Trachymyrmex,* which use arthropod refuse, dead or live plant material. |

## 6.4 The leaf litter ant fauna of a northern Costa Rican landscape of disturbance

The ant fauna of northern Costa Rica was assumed to follow the diversity and distribution noted earlier for neotropical forests. In order to investigate this and search for any changes caused by human disturbance, the leaf litter ant fauna of a northern Costa Rican forest landscape was sampled and sorted according to the methodology described in Chapter 4. The ants were sorted to morphospecies (referred to as 'species' in this study). A total of 16,845 ants comprising 230 species, and five of the eight neotropical subfamilies, were recorded. The dominant sub-family in the Formicidae assemblage was Myrmicinae with 135 species. Ponerinae was the next most speciose with 43 species (Table 6.1). In terms of abundance Myrmicinae has the highest number of individuals followed by Ponerinae. The most common ant was of the Ponerinae sub-family (Species no. 13, Appendix 6) which made up 20% of the total number of individuals sampled. The second most abundant ant species was of the Myrmicinae sub-family (*Monomorium sp.*, Species no. 14) and made up 10 % of the total number of individuals. The 25 most common species together made up 86% of the total number of individuals sampled whilst the 10 most common species made up 70% (Figure 6.2). Sixty-nine species were represented by single individuals.

**Table 6.1 The ant species assemblage sampled over a gradient of human disturbance from primary forest to pasture in northern Costa Rica**

| *Sub-family* | *Species Richness* | *Abundance* |
|---|---|---|
| Dolichoderinae | 11 | 157 |
| Ecitoninae | 28 | 3174 |
| Formicinae | 13 | 138 |
| Myrmicinae | 135 | 7769 |
| Ponerinae | 43 | 5607 |

Samples were taken from a large species pool as the number of species represented by a single individual in the samples (30%) and the steepness of the species accumulation curve for ant species sampled over all sites demonstrates (Fig. 6.3). As indicators of ecosystem condition (Majer 1990, Perfecto 1991a and b), ant assemblages often reflect the degree of habitat disturbance and/or succession in a community (Torres 1984 a, b). This is demonstrated by the species accumulation curves for the two primary forest sites (Figure 6.6) which are lower than the curve for the entire sample set, as would be expected if there were a significant change in species composition between the primary forest and disturbed field sites. The next section presents the ant species diversity and composition data over the five land uses sampled. It provides a more detailed examination of the ant assemblage over a gradient of human disturbance.

**Figure 6.2 Rank-abundance plot of ants sampled in northern Costa Rica, 1998-1999**

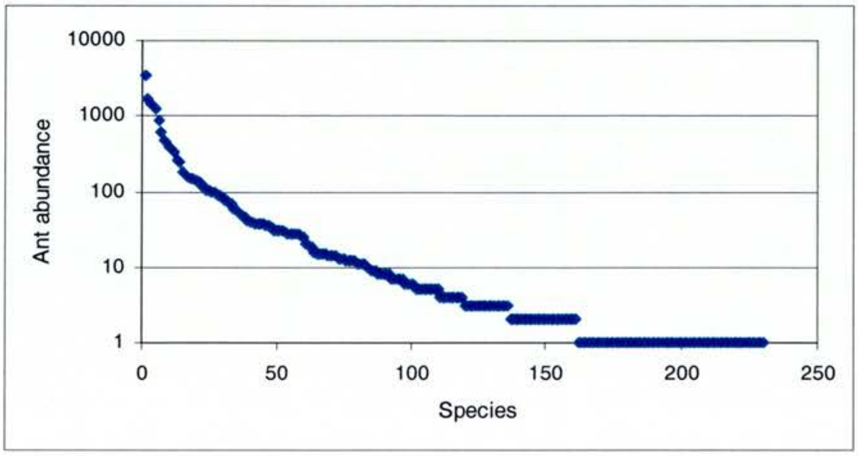
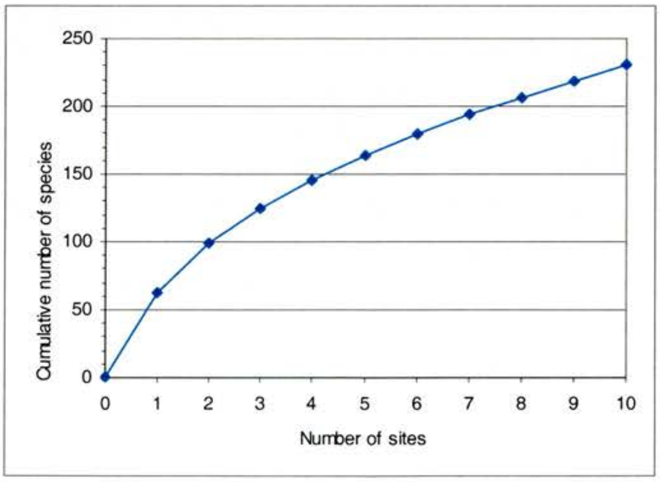


**Figure 6.3 Species accumulation curve for leaf-litter ants over a gradient of disturbance in northern Costa Rica.** Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



## 6.5 Leaf litter ant species and composition by land use

As already discussed in Chapter 4, two sites were sampled in each of five land use classifications. The two sites for each land use were selected, as far as possible, to be similar. In this section, each land use is presented in sub-sections, documenting species richness and abundance per site with each site being addressed separately and then compared. The sub-sections also examine species richness and abundance by ant subfamily, and investigate the similarity of the sites in each land use, by calculation of ant species composition similarity indices. Species accumulation curves are used to compare species richness in both sites in each land use. Finally, the numbers of species shared between each land use are presented. A final discussion section summarises and compares the findings.

### 6.5.1 Leaf litter ants in primary forest

The leaf-litter ant fauna of two primary forests in northern Costa Rica are examined below. The primary forest sites (PrimFor 1 and PrimFor 2) are described in more detail in Chapter 3 but are briefly outlined here. Site 1 was a typical lowland humid forest, with undulating topography and had not been logged. Site 2 was situated along a ridge within a larger area of forest, which had been selectively logged. The actual area of primary forest had not been logged. The sites were situated within 10 kms of each other. Patterns of species diversity and composition in the two sites were examined.

During this study 55 species and 587 individuals were collected in primary forest site 1 while 51 species and 771 individuals were collected in primary forest site 2. Overall, this comprised 87 species and 1359 individuals. These species ranged over five of the eight neotropical subfamilies. The dominant subfamily in the primary forest Formicidae assemblage was Myrmicinae with 28 species in site 1 and 31 species in site 2. Ponerinae was the next most speciose in site 1, following the pattern for all sites together, with 16 species while the next most speciose subfamily in site 2 was Ecitoninae with 9 species. This was followed closely by Ponerinae as the third most speciose in site 2 with 8 species and in site one Ecitoninae was third most speciose (Table 6.2 and Figure 6.4).

## Table 6.2 Primary forest ant species assemblage

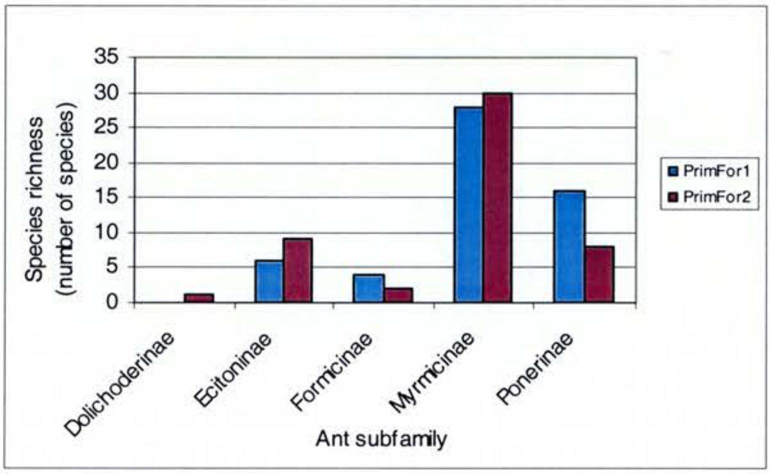
| *Sub-family* | *Primary forest 1* | | *Primary forest 2* | | *Primary forest total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Dolichoderinae | 0 | 0 | 1 | 1 | 1 | 1 |
| Ecitoninae | 7 | 255 | 9 | 323 | 15 | 578 |
| Formicinae | 4 | 7 | 2 | 7 | 5 | 14 |
| Myrmicinae | 28 | 119 | 31 | 291 | 48 | 410 |
| Ponerinae | 16 | 204 | 8 | 149 | 18 | 353 |
| **TOTALS** | **55** | **587** | **51** | **771** | **87** | **1359** |

In terms of abundance, over the two sites Ecitoninae has the highest number of individuals followed by Myrmicinae. However, the second most abundant subfamily in site 1 is Ponerinae compared to Myrmicinae in site 2 and overall (Figure 6.5). The most common species in Primary Forest site 1 was of the Ponerinae subfamily (Species 191)(Table 6.3)(Appendix 6) which made up 33% of the total number of individuals sampled. The second most abundant species in site 1 was also of the Ponerinae subfamily (*Pachycondyla sp.*, Species number 5)(Plate 6.1) and made up 23% of the total number of individuals. The 25 most common species together made up 92% of the total number of individuals sampled while the 10 most common made up 78%. Nineteen species were represented by single individuals. The most common species in site 2 was of the Ecitoninae subfamily (*Nomamyrmex sp.*, Species number 145) which made up 29% of the total number of individuals sampled. The second most abundant species was of the Myrmicinae subfamily (Species number 51) which made up 13% of the total number of individuals sampled. The 25 most common species together made up 94% of species sampled while the ten most common made up 80%. Fifteen species were represented by single individuals.

## Plate 6.1 Formicidae: *Pachycondyla sp.*

(Source: Longino 1999)

## Figure 6.4 Primary forest ant species richness by subfamily



## Figure 6.5 Primary forest ant abundance by subfamily

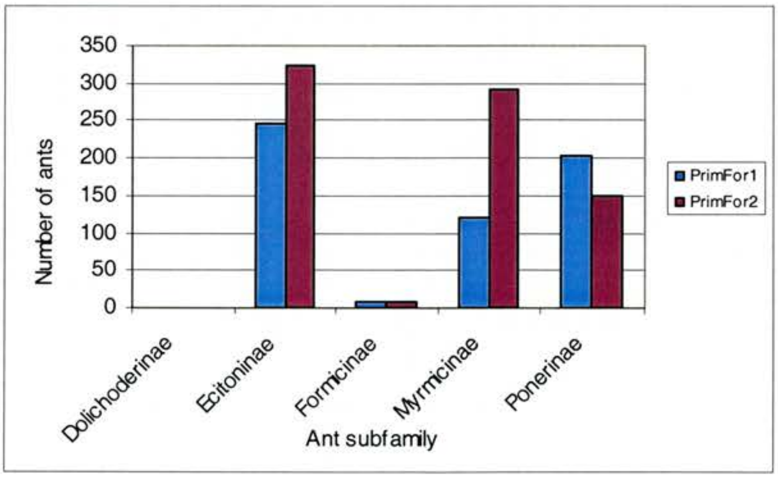


Figure 6.4 illustrates the similarities in subfamily composition between the two primary forest sites. The two subfamily data sets show a high correlation ($r=0.926$, $p<0.05$). The MannWhitney-U test (Siegl 1956) was used to examine the relationship between this subfamily composition. The two primary forest sites had a similar subfamily species distribution (Mann Whitney U-test: $p=0.936$) (Ebdon 1998).

However, by calculation of similarity indices (Krebs, 1989) it was revealed that species composition, not grouped by subfamily, between the two primary forest sites varied strongly (Table 6.15 and Table 6.16). Sorensen's coefficient gave a value of 0.362 between the two sites. This index is a qualitative measure where a value of zero indicates no similarity and a value of 1 complete similarity, although it can be affected by sample size and by species richness. In this study these effects were minimised as the samples were nearly all of equal size in all communities. As it is a binary co-efficient it only takes account of presence-absence data. Smith (1986) tested qualitative and quantitative similarity measures and concluded that the Sorensen index was the best of the existing qualitative measures.

The Morisita index of similarity gave a value of 0.144 between the two primary forest field sites indicating low similarity. Wolda (1981) recommends Morisita's index as the best overall measure of similarity for ecological use. It is independent of sample size but has a serious drawback in its high sensitivity to the abundance of the most abundant species (Magurran 1988).

Elevation is also an important factor in determining ant faunal composition. Longino and Colwell (1997) state that elevation is an important factor in faunal turnover and many species which are rare or absent in one site may be more common at a higher, or lower, elevation. In this study primary forest site 2 is found at a higher elevation (approximately 100m above sea level) than site 1 (approximately 10m above sea level). The tree species assemblage reflects this change in altitude and the corresponding change in topography (see Chapter 5), and may be one of the major factors in driving ant fauna differences between these sites of undisturbed natural forest.

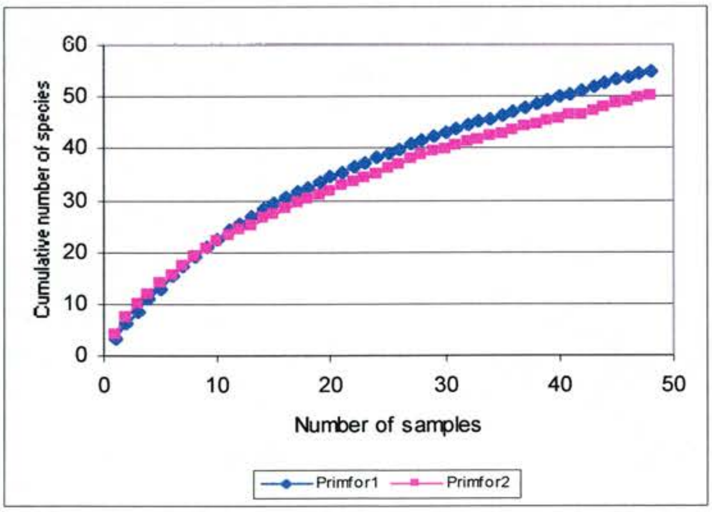
**Table 6.3 Most abundant ten species in the primary forest sites, northern Costa Rica**

| *Species number* | *PrimFor1* | *Species number* | *PrimFor2* |
|---|---|---|---|
| 4 | 9 | 3 | 23 |
| 5 | 136 | 5 | 46 |
| 12 | 25 | 12 | 39 |
| 33 | 191 | 17 | 25 |
| 44 | 14 | 45 | 34 |
| 45 | 15 | 51 | 103 |
| 77 | 9 | 55 | 41 |
| 88 | 8 | 68 | 51 |
| 89 | 44 | 142 | 31 |
| 113 | 9 | 145 | 226 |

Figure 6.6 illustrates the species accumulation curves for both the primary forest sites. These show similar gradients although primary forest site one tends towards a slightly higher overall species richness. This could be due to the altitude and topography differences mentioned earlier.

To summarise, over the two primary forest sites, 87 species were collected. 56 of these species were also found in the logged forest sites, 46 in the secondary forest sites, 31 in the plantation sites and 36 in the pasture sites (Figure 6.26). Sixteen of the species collected in primary forest were not found in any of the other land uses.

**Figure 6.6 Species accumulation curves for leaf litter ants in primary forest, northern Costa Rica**



### 6.5.2 Leaf litter ants in selectively logged forest

In this section the ant fauna of two logged forest sites (LogFor1 and LogFor2) are examined. The two logged sites in this study have been harvested for timber to varying degrees in the past. Further details of the logging activities undertaken in the two sites are given in Chapter 3. The sites are also described in more detail in Chapter 3 but, in summary, they are located within 15kms of each other. Logged forest site 1 is located in the same forest area as primary forest site 2 but as it is on undulating, easily accessible land, and about 10m above sea level, it has been selectively logged. Logged forest site 2 is situated at a higher altitude, approximately 400m above sea level, but also has an undulating topography with few very steep slopes. Patterns of species diversity and composition in the two sites are examined below.

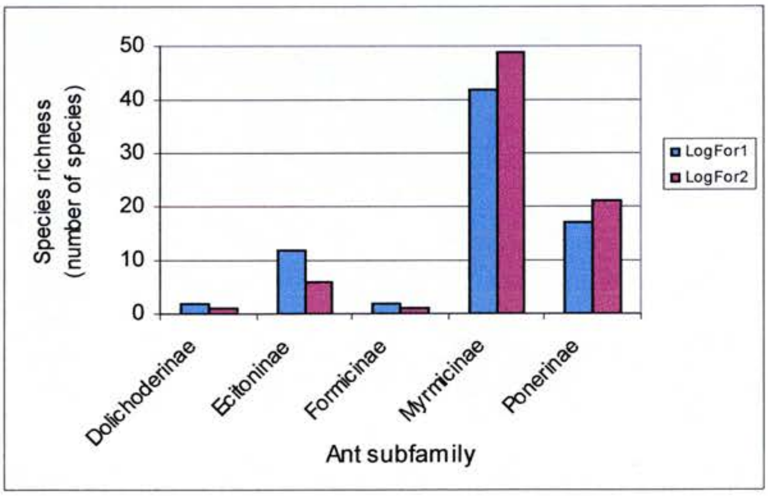
As part of this study 76 species and 904 individuals were collected in logged forest site 1 while 80 species and 1106 individuals were collected in logged forest site 2. Overall this comprised 113 species and 2010 individuals. This land use type is the most species rich of all those sampled in this study (Figure 6.19). These species also ranged over five of the eight neotropical subfamilies. The dominant subfamily in the logged forest Formicidae assemblage was Myrmicinae with 43 species in site 1 and 50 species in site 2. Ponerinae was the next most speciose in site 1 with 17 species and also in site 2 where 21 species were found (Table 6.4 and Figure 6.7).

**Table 6.4 Logged forest ant species assemblage**

| *Sub-family* | *Logged forest 1* | | *Logged forest 2* | | *Logged forest total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Dolichoderinae | 2 | 3 | 1 | 1 | 3 | 4 |
| Ecitoninae | 12 | 392 | 7 | 398 | 14 | 790 |
| Formicinae | 2 | 5 | 1 | 12 | 2 | 17 |
| Myrmicinae | 43 | 341 | 50 | 551 | 69 | 892 |
| Ponerinae | 17 | 163 | 21 | 144 | 25 | 307 |
| **TOTALS** | **76** | **904** | **80** | **1106** | **113** | **2010** |

In terms of abundance over the two sites Myrmicinae had the highest number of individuals (892) followed by Ecitoninae (790). However in site 1 Ecitoninae was the most abundant with 392 individuals followed by Myrmicinae with 341 individuals. This trend was reversed in site 2 where the Myrmicinae were most abundant with 551 individuals followed by Ecitoninae with 398 individuals (Figure 6.8). The most common species in logged forest site 1 was of the Ecitoninae subfamily (Species 55)(Table 6.5)(Appendix 6) which made up 13% of all individuals sampled. The second most abundant species in site 1 was also of the Ecitoninae subfamily (Species number 64) and made up 10% of the total number of individuals sampled. The 25 most common species in logged forest site 1 together made up 87% of the total number of individuals sampled while the 10 most common made up 66%. Twenty-three species were represented by single individuals. The most common species in logged forest site 2 was of the Ecitoninae subfamily (*Nomamyrmex sp.*, Species number 145) and made up 27% of the total number of individuals sampled. The second most abundant species in site 2 was of the Myrmicinae subfamily (Species number 41) which made up 10% of all individuals sampled. The 25 most common species made up 85% of all species sampled while the ten most common made up 63%. Twenty-five species were represented by single individuals.

**Figure 6.7 Logged forest ant species richness by subfamily**



## Figure 6.8 Logged forest ant species abundance by subfamily

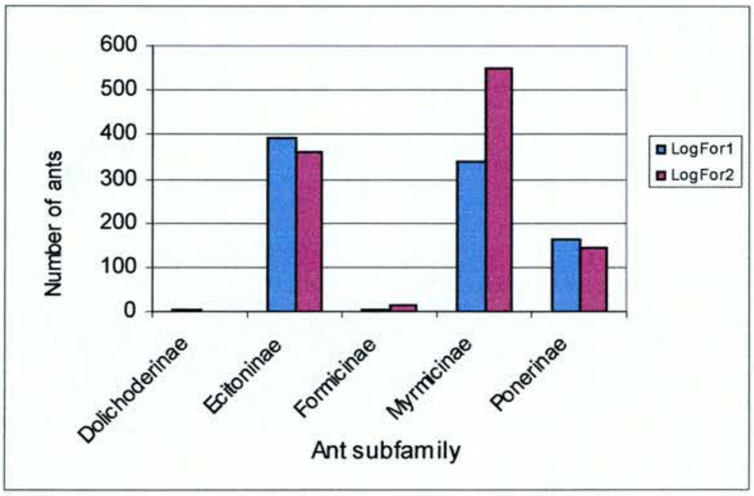


Figure 6.7 shows the proportion of species in each subfamily in the logged forest sites. As in the primary forest sites the two subfamily species data sets show a high correlation (r = 0.986, $p<0.05$). There was no significant difference in the species richness of ant subfamilies in the two different sites (Mann Whitney-U test: $p = 0.833$).

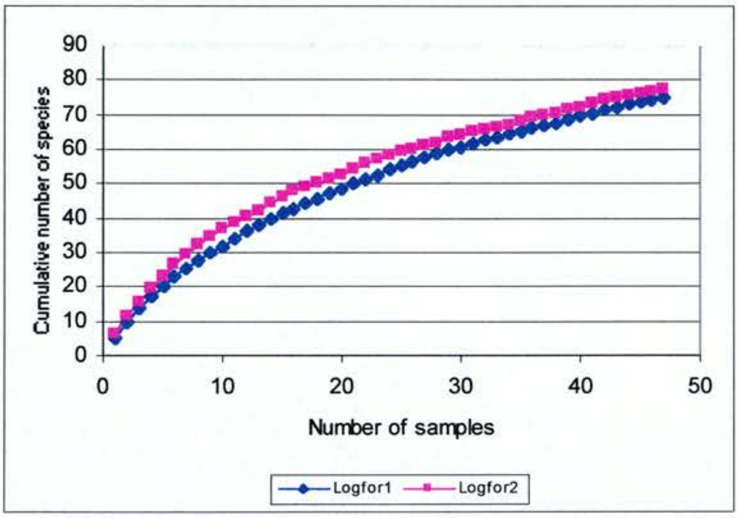
The calculation of similarity indices of species composition between the two sites shows that the two sites were similar. Sorensen's index gives a value of 0.551 and Morisita's index a value of 0.456 (Table 6.15 and Table 6.16).

## Table 6.5 Most abundant ten species in the logged forest sites, northern Costa Rica

| *Species number* | *LogFor1* | *Species number* | *LogFor2* |
|---|---|---|---|
| 55 | 119 | 145 | 304 |
| 64 | 94 | 41 | 115 |
| 145 | 71 | 5 | 66 |
| 45 | 58 | 113 | 37 |
| 232 | 55 | 51 | 36 |
| 5 | 48 | 46 | 34 |
| 13 | 46 | 44 | 31 |
| 2 | 43 | 53 | 28 |
| 113a | 35 | 64 | 27 |
| 51 | 28 | 214 | 22 |

Figure 6.9 illustrates the species accumulation curves for both the logged forest sites and, despite an initially steeper gradient in species accumulation for site 2, appear to be tending towards similar species richness.

**Figure 6.9 Species accumulation curves for leaf litter ants in selectively logged forest, northern Costa Rica**



As mentioned previously, over the two logged forest sites, 113 species were collected. Fifty six of these species were also found in the primary forest sites, 54 in the secondary forest sites, 34 in the plantation sites and 35 in the pasture sites. 30 of the species collected in the logged forest sites were not found in any of the other land uses.

### 6.5.3 Leaf litter ants in secondary forest

The two secondary forest sites (2ndFor1 and 2ndfor2) examined in this study are discussed in greater detail in Chapter 3. Site 1 has been left to regenerate for approximately five years and site 2 for approximately 8 years. Site 1 is located next to primary forest site 1 although a mud track and a strip of agriculture separates them. It is located about 10m above sea level. Site 2 is located adjacent to logged forest site 2 at about 400m above sea level. Both sites have an adjacent forest seed source and also contain remaining forest trees which were left, for shade purposes, at the time of initial forest clearance. The two sites have a similar undulating topography. This section examines the leaf-litter ant fauna of the two secondary forest sites, considering species diversity and composition.

During this study 58 ant species and 949 individuals were collected in secondary forest site 1, and 75 species with 1272 individuals in site 2. Overall this comprised 102 species and 2221 individuals. These species ranged over five of the eight neotropical subfamilies. The dominant subfamily in the secondary forest Formicidae assemblage was Myrmicinae with 31 species in site 1 and 51 species in site 2. Ponerinae was the next most speciose subfamily in both sites 1 and 2 with 14 species in site 1 and 12 species in site 2 (Table 6.6 and Figure 6.10).

## Table 6.6 Secondary forest ant species assemblage

| *Sub-family* | *2ndary forest 1* | | *2ndary forest 2* | | *2ndary forest* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Dolichoderinae | 1 | 4 | 1 | 7 | 1 | 11 |
| Ecitoninae | 8 | 46 | 8 | 215 | 12 | 261 |
| Formicinae | 4 | 18 | 3 | 23 | 6 | 41 |
| Myrmicinae | 31 | 368 | 51 | 819 | 66 | 1187 |
| Ponerinae | 14 | 513 | 12 | 208 | 17 | 721 |
| **TOTALS** | **58** | **949** | **75** | **1272** | **102** | **2221** |

Over the two sites Myrmicinae was the most abundant with 1187 individuals followed by Ponerinae with 721 individuals (Figure 6.11). Site 2 reflects this with 819 individuals in the Myrmicinae and 208 in the Ponerinae. However the most abundant subfamily in site 1 was the Ponerinae with the Myrmicinae the second most abundant. The most common species in secondary forest site 1 was from the Ponerinae (morphospecies number 13) which made up 26% of all individuals sampled in this site (Table 6.7)(Appendix 6). This species was also the most abundant over all the study sites with a total abundance in this study of 3363 individuals. The second most common species was also from the Ponerinae (*Pachycondyla* sp., morphospecies number 4) and made up 15% of all individuals samples. The 25 most common species in secondary forest site 1 together made up 94% of the total number of individuals sampled while the 10 most common made up 78%. Eighteen species were represented by single individuals. The most common species in secondary forest site 2 was from the Ecitoninae (morphospecies number 60) which made up 10% of all individuals sampled in this site (Table 6.7)(Appendix 6). The second most common species were from the Myrmicinae (morphospecies number 21 and number 27) these two species each made up 9% of all individuals samples. The 25 most common species in secondary forest site 2 together made up 90% of the total number of individuals sampled while the 10 most common made up 66%. Twenty-four species were represented by single individuals.

**Figure 6.10 Secondary forest ant species richness by subfamily**

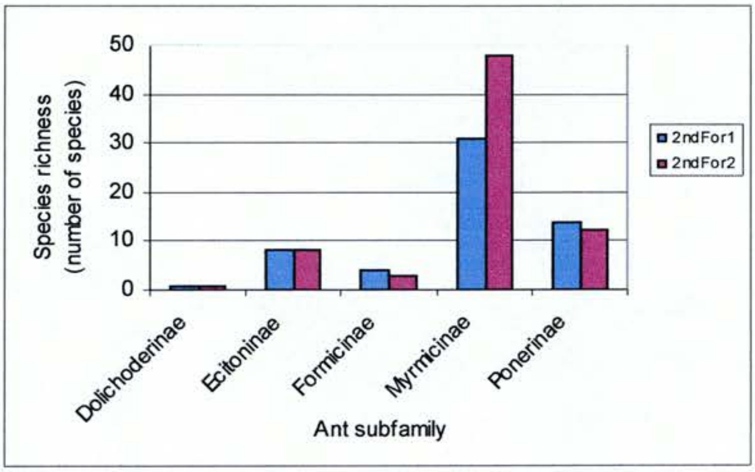


**Figure 6.11 Secondary forest ant species abundance by subfamily**

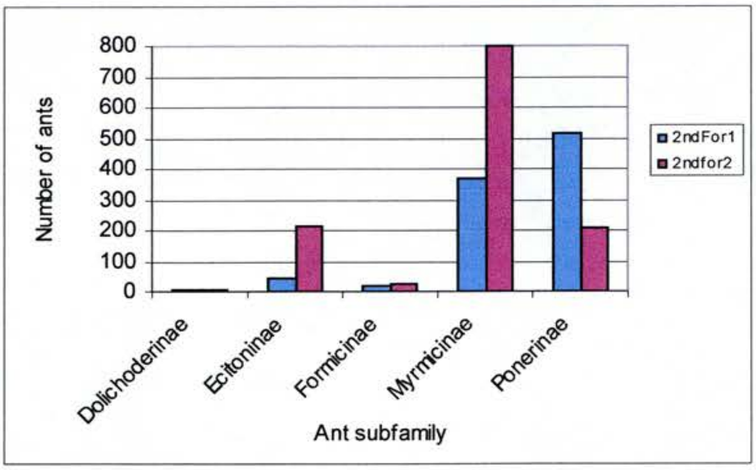


Figure 6.10 demonstrates the distribution of ant species within the subfamily grouping The two subfamily species data sets show a high correlation (r = 0.979). There was no

significant difference in the species richness of ant subfamilies in different sites (Mann Whitney-U test: $p = 1.00$).

The Sorensen index value of 0.466 and the Morisita's index value of 0.326 demonstrate the similarity between the ant species composition of the two secondary forest sites (Tables 6.15 and 6.16).

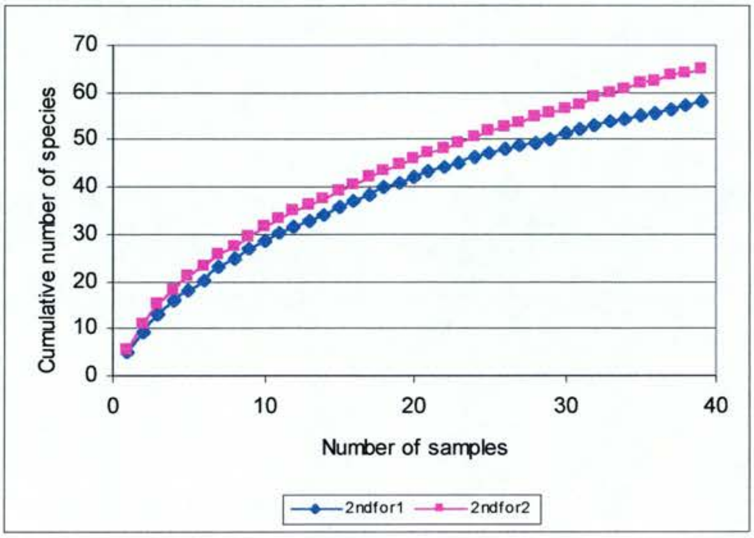
**Table 6.7 Most abundant ten species in secondary forest sites, northern Costa Rica**

| *Species number* | *LogFor1 abundance* | *Species number* | *LogFor2 abundance* |
|---|---|---|---|
| 13 | 244 | 60 | 129 |
| 4 | 141 | 21 | 112 |
| 194 | 98 | 127 | 112 |
| 21 | 84 | 47 | 100 |
| 2 | 47 | 4 | 88 |
| 5 | 46 | 51 | 68 |
| 12 | 27 | 5 | 60 |
| 14 | 20 | 135 | 59 |
| 17 | 18 | 33 | 58 |
| 3 | 17 | 75 | 55 |

Figure 6.12 illustrates the species accumulation curves for both the secondary forest sites. The curve for site 2 demonstrates a steeper gradient than that of site 1. This could be explained by the more advanced stage of regeneration present in this site. Site 2 has been regenerating for three years longer than site 1 perhaps resulting in greater species recruitment.

Over the two secondary forest sites 102 species were collected. Of these species, 46 were also found in the primary forest sites, 54 in the logged forest sites, 43 in the plantation sites and 43 in the pasture sites. Twenty-five of the species collected in secondary forest were not found in any of the other land uses.

**Figure 6.12 Species accumulation curves for leaf litter ants in secondary forest, northern Costa Rica**



### 6.5.4. Leaf litter ants in plantations of *Gmelina arborea*

This section examines the leaf-litter ant fauna of the two *Gmelina arborea* sites, considering species diversity and composition.

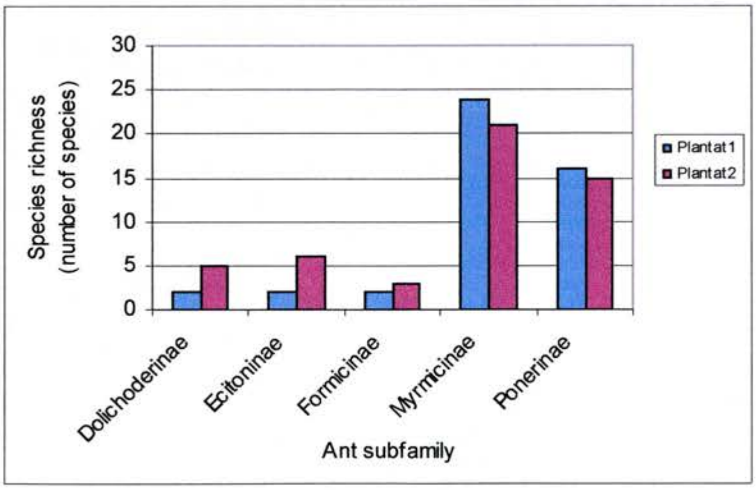
In plantation site 1, 47 leaf-litter ant species consisting of 803 individuals were collected. Fifty species and 461 individuals were collected in plantation site 2. Five of the eight neotropical ant subfamilies were covered by these species. The dominant subfamily in the plantation Formicidae assemblage was Myrmicinae with 24 species in site 1 and 21 species in site 2. Ponerinae was the next most speciose in both sites, site 1 having 16 species and site 2 15 species (Table 6.8 and Figure 6.13).

**Table 6.8 *Gmelina sp.* plantation ant species assemblage**

| *Sub-family* | *Plantation 1* | | *Plantation 2* | | *Plantatation total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Dolichoderinae | 2 | 50 | 5 | 30 | 5 | 80 |
| Ecitoninae | 3 | 30 | 6 | 88 | 9 | 118 |
| Formicinae | 2 | 2 | 3 | 15 | 5 | 17 |
| Myrmicinae | 24 | 507 | 21 | 135 | 34 | 642 |
| Ponerinae | 16 | 214 | 15 | 193 | 21 | 407 |
| **TOTALS** | **47** | **803** | **50** | **461** | **74** | **1219** |

The abundance values followed a similar pattern. Myrmicinae was the most abundant in site 1 with 507 individuals and over both sites with 642 individuals. However, in site 2 the Ponerinae were the most abundant with 193 individuals followed by the Myrmicinae with 135 individuals. In site 1 the second most abundant subfamily was the Ponerinae with 214 individuals (Figure 6.14). The most common species in site 1 was of the Myrmicinae (Species number 135) which made up 36% of the individuals sampled (Table 6.9)(Appendix 6). The second most abundant species in site 1 was of the Ponerinae (Species number 13) and made up 15% of all individuals in that site. This species was also the most abundant in this study. The 25 most common species in site 1 made up 97% of the total number of individuals sampled while the 10 most common made up 86%. Nineteen species were represented by single individuals. The most common species in plantation site 2 was from the Ponerinae (Species number 13) and made up 25% of the species collected in site 2 (Table 6.9). As mentioned, this species was the most abundant overall and it was the second most abundant in site 1. The second most abundant in site 2 was from the Myrmicinae (Species number 50) and contained 5% of the individuals sampled. The most common 25 species made up 93% of the sample and the ten most common made up 72%. Again, 19 species were represented by single individuals.

**Figure 6.13** ***Gmelina arborea*** **plantation ant species richness by subfamily**



## Figure 6.14 *Gmelina arborea* plantation ant species abundance by subfamily

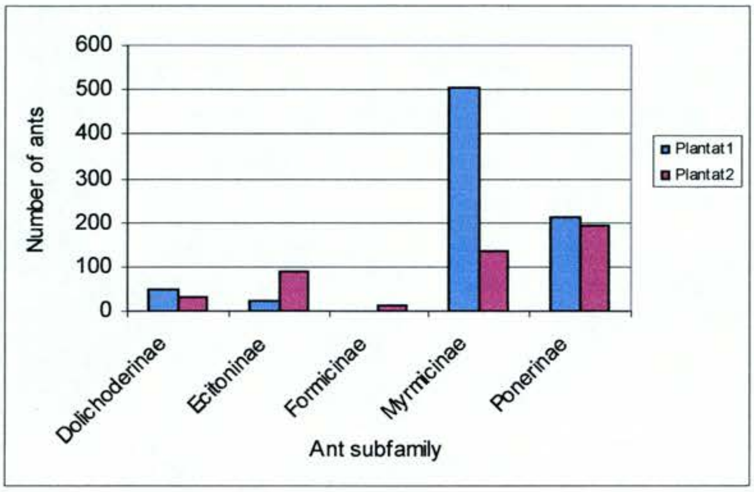


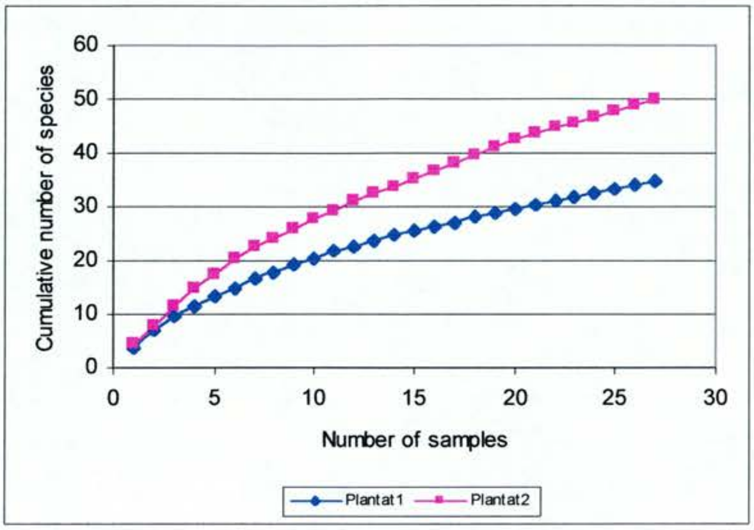
Figure 6.13 shows the similar distribution of ant species by subfamily between the two plantation sites. These datasets show a high correlation (r = 0.990, $p<0.05$). The two plantation sites also demonstrate a similar subfamily species distribution (Mann Whitney-U test: $p=0.530$). The Sorensen index value of 0.474 demonstrates the similarity in ant species composition between the two secondary forest sites as does Morisita's index which gives a value of 0.392 (Tables 6.15 and 6.16).

## Table 6.9 Most abundant ten species in plantation sites, northern Costa Rica

| *Species number* | *LogFor1 abundance* | *Species number* | *LogFor2 abundance* |
|---|---|---|---|
| 135 | 290 | 13 | 116 |
| 13 | 121 | 50 | 39 |
| 14 | 108 | 61 | 34 |
| 50 | 45 | 150 | 30 |
| 22 | 33 | 89 | 27 |
| 4 | 25 | 21 | 23 |
| 147 | 21 | 4 | 19 |
| 5 | 19 | 2 | 16 |
| 131 | 17 | 22 | 15 |
| 178 | 15 | 145 | 15 |

Figure 6.15 illustrates the species accumulation curves for both the plantation sites. Both had a steep gradient indicating that total species richness in these sites may be considerably greater than the values found by this sampling effort.

**Figure 6.15 Species accumulation curves for *Gmelina arborea* ants in plantation, northern Costa Rica**



In total, 74 species were collected in the two *Gmelina arborea* plantations. 31 of these were also found in primary forest, 34 in the logged forest sites, 43 in the secondary forest sites and 40 in the pasture sites (Figure 6.26). 16 of the species collected in the plantation sites were not found in any of the other land uses.

### 6.5.5 Leaf litter ants in pasture

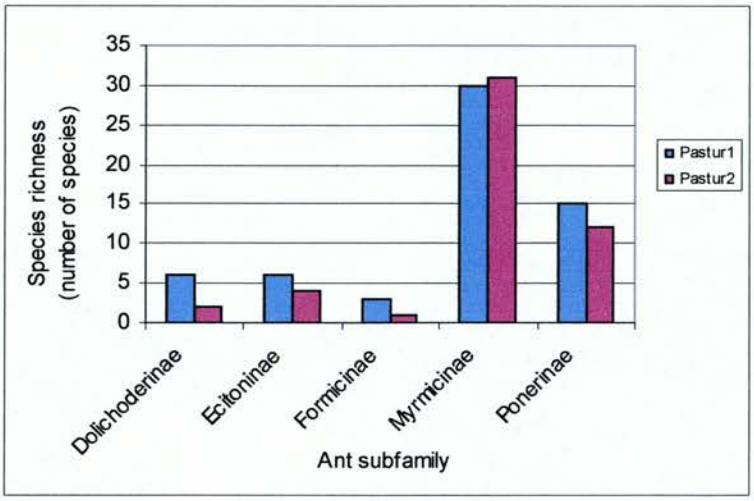
This section examines the leaf litter ant species diversity and composition which has developed in the two pasture sites sampled (Pastur1 and Pastur2). During this study 62 species and 5332 individuals were collected in pasture site 1 while 50 species and 4660 individuals were collected in pasture site 2. Overall this comprised 85 species and 9992 individuals. This represents a great increase in abundance compared to the other sites. It is also noteworthy that diversity remained at a similar level to the other sites. The species ranged over five of the eight tropical subfamilies. The dominant subfamily in the pasture Formicidae assemblage was Myrmicinae with 31 species in pasture site 1 and 31 in pasture site 2. Ponerinae was the next most speciose with 15 species in site 1 and 12 species in site 2 (Table 6.10 and Figure 6.17).

## Table 6.10 Pasture ant species assemblage

| *Sub-family* | *Pasture 1* | | *Pasture 2* | | *Pasture total* | |
|---|---|---|---|---|---|---|
| | Species Richness | Abundance | Species Richness | Abundance | Species Richness | Abundance |
| Dolichoderinae | 6 | 43 | 2 | 18 | 6 | 61 |
| Ecitoninae | 7 | 775 | 4 | 652 | 8 | 1427 |
| Formicinae | 3 | 48 | 1 | 1 | 3 | 49 |
| Myrmicinae | 31 | 3316 | 31 | 1322 | 48 | 4638 |
| Ponerinae | 15 | 1150 | 12 | 2667 | 20 | 3817 |
| **TOTALS** | **62** | **5332** | **50** | **4660** | **85** | **9992** |

Myrmicinae was the most abundant subfamily in site 1 with 3316 individuals collected during this study. However in site 2 Ponerinae was the most abundant with 2667 individuals. This trend was reversed for the second most abundant species with Ponerinae having 1150 individuals in site 1 and the Myrmicinae having 1322 individuals in site 2 (Figure 6.17). The most common species in pasture site 1 was of the Myrmicinae subfamily (*Monomorium sp.*, Species number 14)(Table 6.11)(Appendix 6) which made up 19% of total abundance from this site. The second most abundant species in site 1 was of the Myrmicinae subfamily (Species number 29) which made up 18% of total abundance. The 25 most common species in site 1 made up 99% of all individuals collected and the most common 10 species made up 93%. Twenty species were represented by single individuals. The most common species in pasture site 2 was of the Ponerinae (Species number 13) which made up 53% of the total number of individuals sampled. This species was also the most common species over all the sites sampled and was found in nine out of the ten sites. The second most common species in site 2 was of the Myrmicinae (*Monomorium sp.*, Species number 14) which made up 11% of all individuals sampled in this site. It was also the most abundant species in site 1 and was the second most abundant species overall the sites sampled. The 25 most common species made up 99% of all species sampled while the ten most common made up 95%. Twenty-one species were represented by single individuals.

## Figure 6.16 Pasture ant species richness by subfamily



## Figure 6.17 Pasture ant species abundance by subfamily

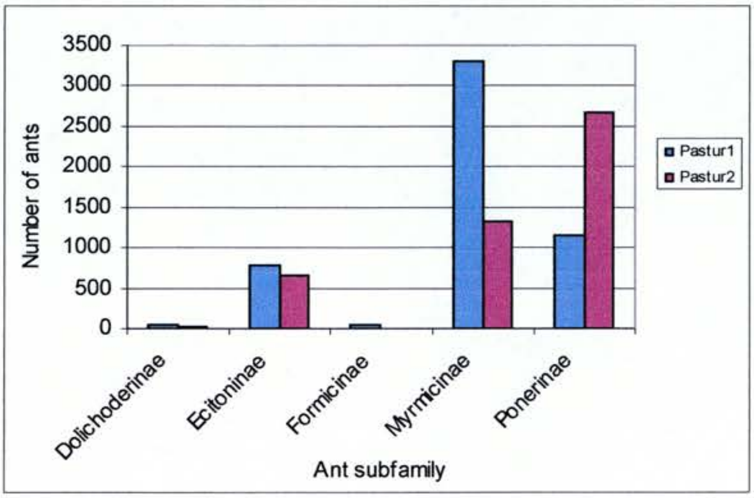


Figure 6.16 illustrates the similarity between the proportion of species in each subfamily in the pasture sites. The two subfamily data sets show a high correlation ($r = 0.995$, $p<0.05$). The two pasture sites also had a similar subfamily species distribution (Mann Whitney-U test: $p=0.531$).

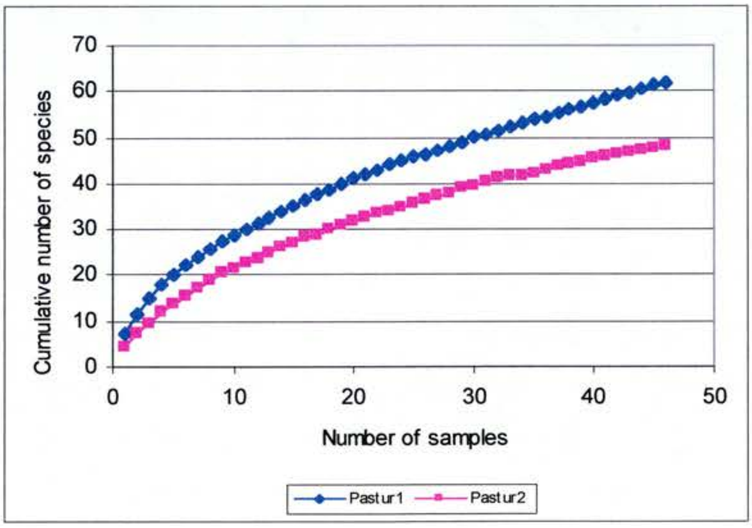
The calculation of similarity indices of species composition between the two sites shows that the two sites were similar. Sorensen's index gives a value of 0.482 and Morisita's index a value of 0.418 (Table 6.15 and Table 6.16).

**Table 6.11 Most abundant ten species in pasture sites, northern Costa Rica**

| Species number | Pastur1 abundance | Species number | Pastur2 abundance |
|---|---|---|---|
| 14 | 997 | 13 | 2468 |
| 29 | 974 | 14 | 534 |
| 4 | 759 | 33 | 488 |
| 36 | 720 | 29 | 394 |
| 33 | 651 | 4 | 170 |
| 13 | 334 | 36 | 119 |
| 149 | 280 | 64 | 114 |
| 21 | 104 | 50 | 55 |
| 64 | 87 | 149 | 52 |
| 50 | 59 | 135 | 51 |

Figure 6.18 illustrates the species accumulation curves for both the pasture sites. Pasture site 2 showed a shallower gradient than site 1. This difference may have been due to differences in site location or was, perhaps, a result of slightly different management systems between the two sites.

**Figure 6.18 Species accumulation curves for ants in cattle pasture, northern Costa Rica**



In total, 85 species were collected over the two pasture sites. Thirty-six of these species (42%) were found in the primary forest sites, 35 in the logged forest sites, 43 in the secondary forest sites and 40 in the pasture sites. Twenty of the species collected in the pasture sites were not found in any other land use.

### 6.5.6 Summary of findings: leaf litter ants by land use

This section has presented the ant data collected by land use. It has documented leaf litter ant fauna species richness and abundance, while also illustrating the similarities, and differences, between the two sites sampled from each land use type.

All land uses demonstrated a similar species richness and abundance between sites, and subfamily species richness and abundance was also similar between sites in each land use. Similarity indices generally showed medium to high similarity of ant species composition between sites. The two primary forest sites were the exception, showing low similarity. It is possible that the topographic differences between sites caused this low similarity. Choice of primary forest sites was limited as a result of the few remaining suitable areas found within the landscape studied. It is believed that these sites are sufficiently similar for the purposes of this study. This is reinforced by the fact that almost 40 percent of the species found in each site are shared between both sites. Species accumulation curves also revealed highly similar species richness between sites in all the land uses.

This section has provided a baseline study of ant species diversity and abundance in five different land uses in a northern Costa Rican landscape. It has also demonstrated the comparability of the sites chosen within each of these land uses. The next section addresses the effects of disturbance on the leaf litter ant fauna by examining species richness, abundance and composition over the five land uses, which represent different levels of human disturbance.

## 6.6 Species richness and composition

### 6.6.1 ANT SPECIES RICHNESS

As Section 6.5 has demonstrated, species richness and composition varied over the field sites and land uses sampled. Species richness ($S$) was significantly different over the field sites (One-way ANOVA, $F = 8.25$, $p < 0.001$; Table B1 in Appendix 7). However, further investigation between sites revealed that not all sites had a significantly different species richness (Tukey's multiple comparison test, $p < 0.05$; Table B3 in Appendix 7).

This may be a result of the fact that species richness did not vary greatly between sites and that changes in ant species composition are not revealed at this stage of the analysis.

The results presented here show that the logged forest sites had the highest number of species collected (*S*) followed by secondary forest and then primary forest (Table 6.12). Plantation sites had the lowest species richness (*S*) followed by pasture (Figure 6.19 and 6.20). As mentioned, this measure is of absolute species numbers collected and does not take account of species composition differences between sites. The estimated total number of species per field site, as calculated by the Jackknife richness technique (Heltshe and Forrester 1983, Krebs 1989, and Colwell and Coddington 1994) using the program *EstimateS* (Colwell 1999) is also shown in Figure 6.20. The confidence limits show that the numbers of ant species were, in nearly all cases, significantly different between the five land use types. It also confirms that the logged and secondary forest sites had significantly higher species richness than the pasture and plantation sites, with the exception of Pastur1.

Species accumulation curves for all ten field sites are shown in Figure 6.21. A preliminary assessment of season was also made, and the corresponding curves for the wet season of 1998 and dry season of 1999 are shown in Figures 6.22 and 6.23. These curves illustrate similar gradients of species accumulation over both seasons for each site, although some changes are apparent. These are particularly evident in the natural forest sites where the dry season sampling suggested a more diverse species assemblage. It is generally believed that perennially nesting ants are less prone to seasonal or long-term population fluctuations than solitary insects although studies by Levings (1983) do show some variability in tropical ant communities. The curves for all sites show a gradually flattening slope, indicating that the number of new species encountered per sample was decreasing as sample size grew larger. A logarithmic equation provided an excellent fit ($r^2 > 0.99$) to the species accumulation curve for all sites (Figure 6.24), and projecting the curve predicted that even with a significant increase in sampling effort the known fauna would not have been collected entirely.

Through structured inventory and other additional collecting Longino and Colwell (1997) give the known ant fauna of La Selva, a biological station in the north of Costa Rica approximately 100 km from the sites in this study, as over 415 species. The number of species predicted by the logarithmic equation for this study tends towards a figure exceeding 500 species, although without further sampling this figure cannot be verified.

**Figure 6.19 Ant species richness (number of species, *S*) over a land use gradient of disturbance in northern Costa Rica.** PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture. Blue bars indicate total species richness while green indicates species richness in site 1 and yellow in site 2.

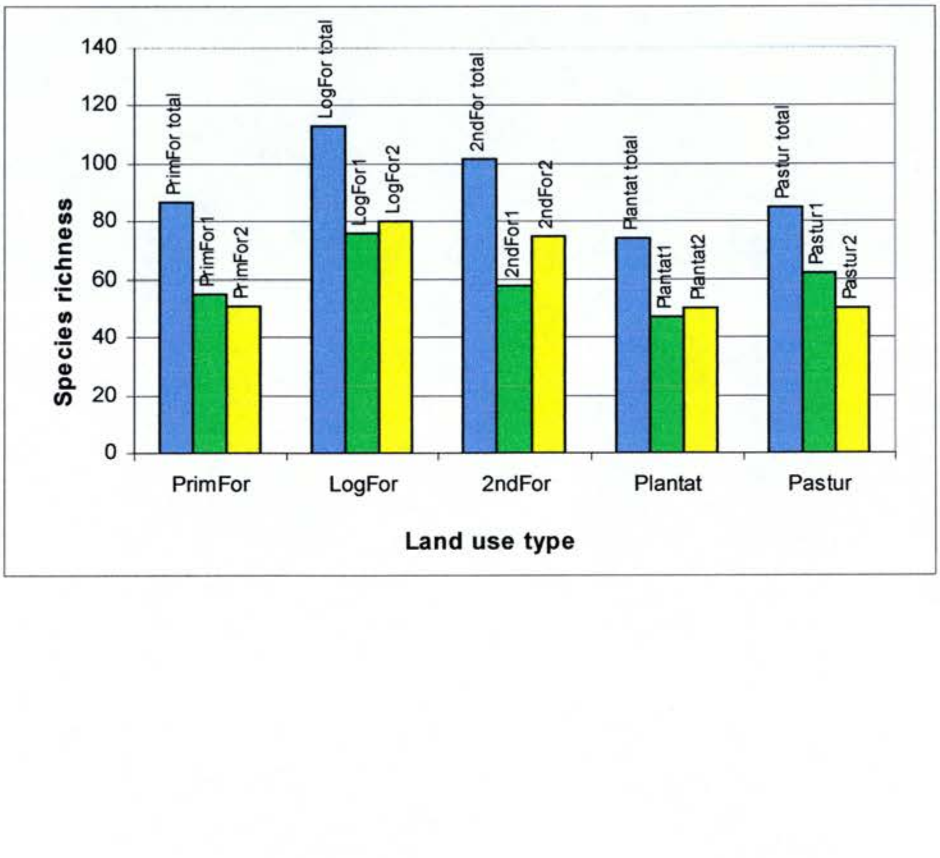


**Figure 6.20 Number of leaf-litter ant species in field sites sampled over a gradient of disturbance in northern Costa Rica.** Jackknife richness was calculated using the *EstimateS* program (Colwell 1999), the error bars denote the standard deviation. (PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture).

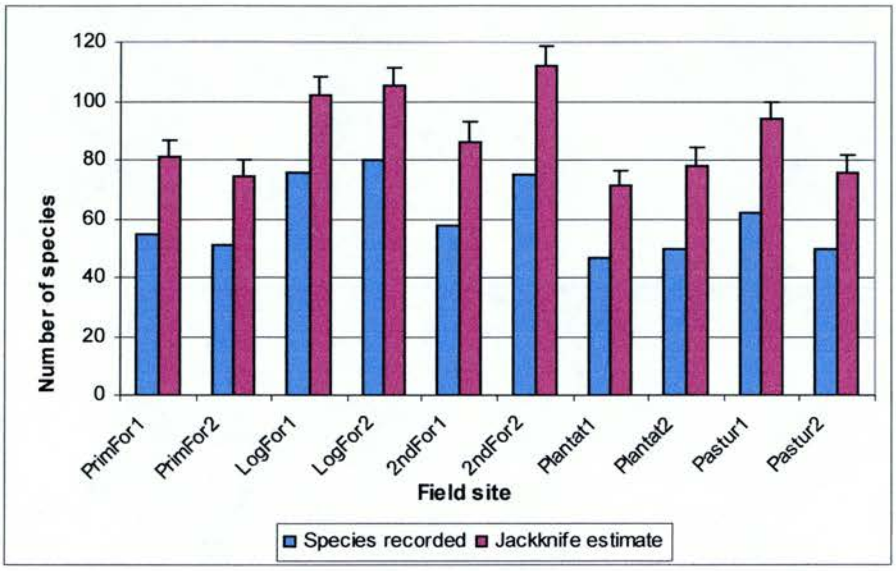
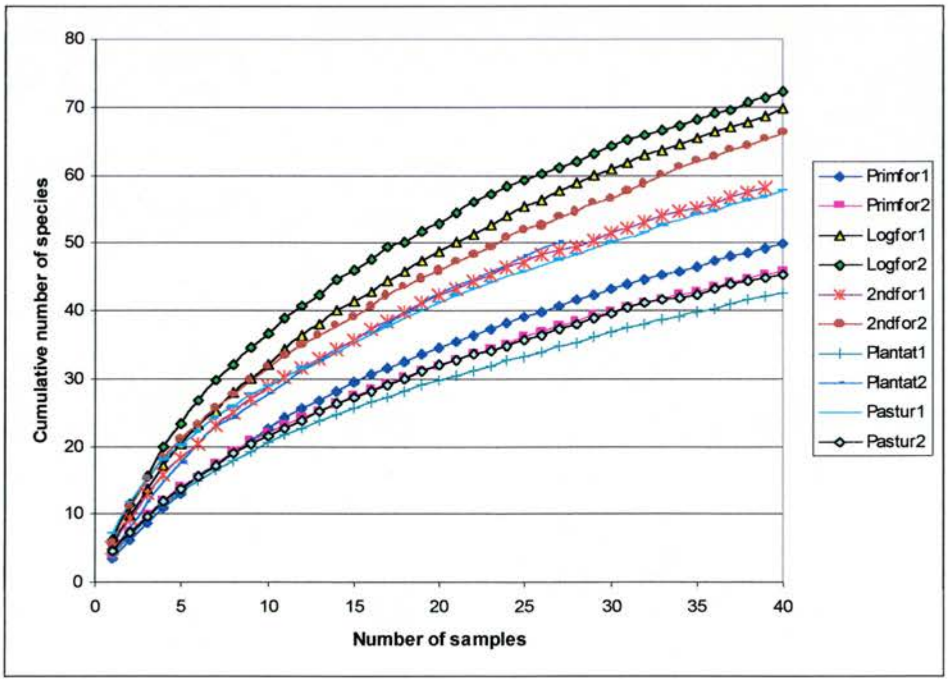


**Figure 6.21 Species accumulation curve for leaf litter ants over a gradient of disturbance from primary forest to pasture in northern Costa Rica.** Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



**Figures 6.22 and 6.23 Species accumulation curve for leaf litter ants over a gradient of disturbance from primary forest to pasture in northern Costa Rica: (6.22) Wet season 1998 and (6.23) Dry season 1999.** Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).

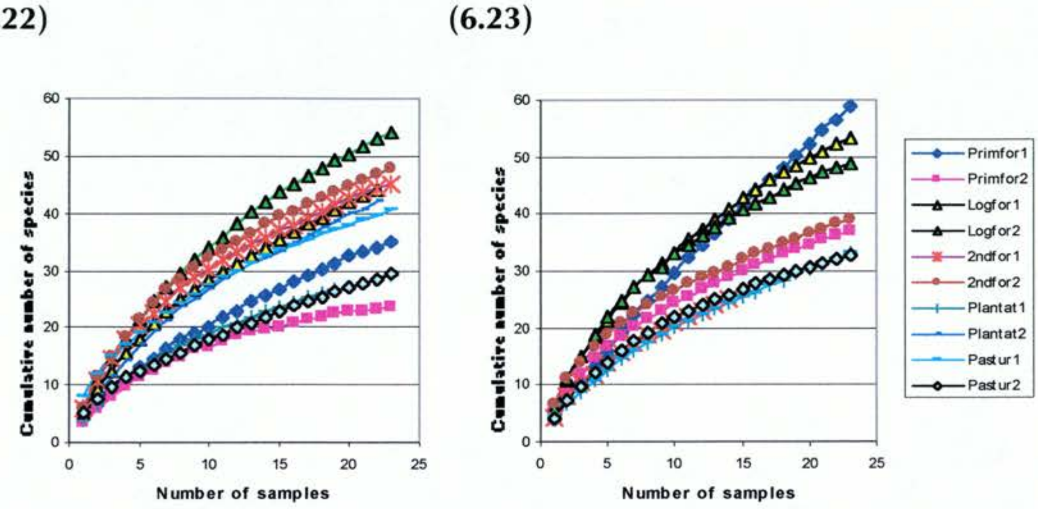
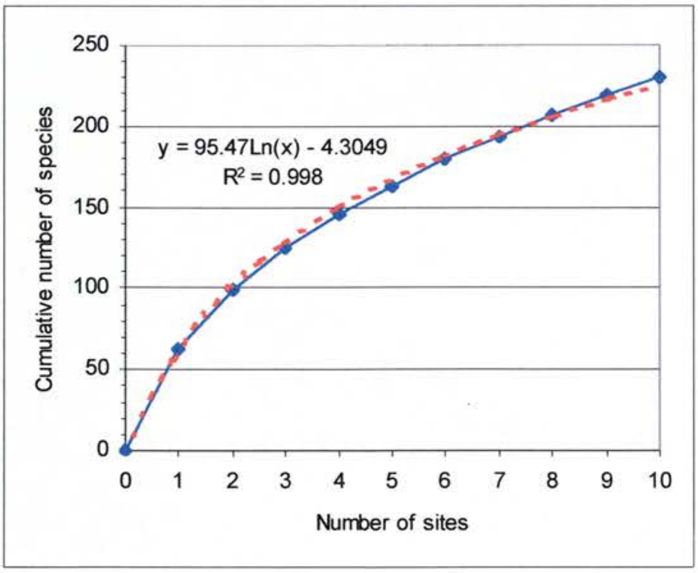

(6.22) (6.23)

**Figure 6.24 Species accumulation curve for leaf litter ants over a gradient of disturbance in northern Costa Rica.** The species accumulation curve for all sites is well fit by a logarithmic curve (indicated by dashed red line)(y = 95.47 Ln(x) – 4.3049, $R^2 > 0.99$). Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



### 6.6.2 $\alpha$ - DIVERSITY OF LEAF LITTER ANT SPECIES

Diversity, evenness and dominance indices are given in Table 6.12. These are based on pooled data from transects. Species richness has been shown to be highest in LogFor2 followed by LogFor1. However, a comparison between *S* and Shannon's index of diversity (*H*) and Simpson's index of diversity (*D*) shows that, despite highly significant correlations between *S* and these measures (Pearson's product-moment correlation coefficients between: *S* and *H*, r = 0.72, $p = 0.018$, and, *S* and *D*, r = 0.622, $p = 0.05$), different sites are identified as the most 'diverse'. Shannon's diversity index places LogFor1 followed by 2ndFor2 as having the highest diversity index, whereas Simpson's index of diversity places PrimFor2 first, closely followed by LogFor2 (Table 6.13). As discussed in Chapter 4, there are two types of diversity index which are more sensitive to either, the rare species in a community (e.g. Shannon), or the most abundant species (e.g. Simpson). This is evident in the results given. The lowest values of the Shannon index were found in the pasture sites and in one plantation site. It is probable that the higher values found in the natural forest sites were due to a recognition of the rare species found there. In contrast, the Simpson index showed a more mixed order of natural forest sites and pasture and plantation. The two plantation sites and one pasture site were ranked quite highly whereas LogFor1 and PrimFor1, both natural forest sites, had, with the exception of Pastur2, the lowest diversity indices. This outcome may have been a result of the importance the Simpson index places on species abundance. Both LogFor1 and PrimFor1 showed lower species abundance than the pasture sites although species abundance in the plantation sites was similar (Figure 6.25).

Shannon's evenness index (*E*) is a measure of the distribution of species abundances. *E* ranges between 0 and 1, with 1 representing a situation in which all species are equally abundant (Magurran 1988). The evenness indices calculated for the leaf litter ant data demonstrate a greater evenness of species distribution in the majority of the natural forest sites while the pasture sites and one plantation site had the lowest evenness (Table 6.13). These indices show that in the sites of greater human disturbance evenness was reduced. It is probable that this was caused by the increased success of a few species in the altered environment. This is supported by individual species counts where, for example, the most abundant species collected in PrimFor1 had 191 individuals (Species no. 33), while in Pastur2 the most abundant species collected had 2468 individuals. The Berger-Parker dominance measure expresses the proportional importance of the most abundant species (Magurran 1988). Low values indicate lowered dominance by any one species and are generally accompanied by increased species evenness. This was demonstrated by the dominance and evenness indices calculated here which show a highly significant negative correlation (Pearson's product-moment correlation coefficients between $E$ and $d$, $r = -0.77, p = 0.009$).

This section has presented a suite of diversity indices and measures. For the reasons discussed above, not all the sites were ranked by diversity in the same order. However, despite these differences, it is evident that the plantation and pasture sites were generally less diverse than the natural forest sites. This is taken to indicate the negative effect of human disturbance on leaf litter ant diversity. The next section examines the corresponding effects of disturbance on leaf litter ant abundance.

**Table 6.12 Diversity indices for ant species in each site.** *S* = species richness, *Jack* = first-order Jackknife richness estimator, *H* = Shannon's index of diversity, *D* = Simpson's index of diversity, *E* = Shannon's evenness index, and *d* = Berger-Parker dominance index.

| | | **INDEX:** | | | | | |
|---|---|---|---|---|---|---|---|
| **Habitat** | **Site** | ***S*** | ***Jack*** | ***H*** | ***D*** | ***E*** | ***d*** |
| Primary | PrimFor1 | 55 | 81 | 2.566 | 0.829 | 0.640 | 0.325 |
| forest | PrimFor2 | 51 | 74 | 2.748 | 0.876 | 0.699 | 0.293 |
| Logged | LogFor1 | 76 | 102 | 3.343 | 0.943 | 0.772 | 0.132 |
| forest | LogFor2 | 80 | 105 | 3.206 | 0.901 | 0.732 | 0.275 |
| Secondary | 2ndFor1 | 58 | 86 | 2.786 | 0.884 | 0.686 | 0.257 |
| forest | 2ndFor2 | 75 | 112 | 3.322 | 0.947 | 0.770 | 0.101 |
| Plantation | Plantat1 | 47 | 72 | 2.372 | 0.820 | 0.616 | 0.361 |
| | Plantat2 | 50 | 78 | 2.962 | 0.905 | 0.757 | 0.252 |
| Pasture | Pastur1 | 62 | 94 | 2.353 | 0.871 | 0.570 | 0.187 |
| | Pastur2 | 50 | 76 | 1.766 | 0.685 | 0.452 | 0.530 |

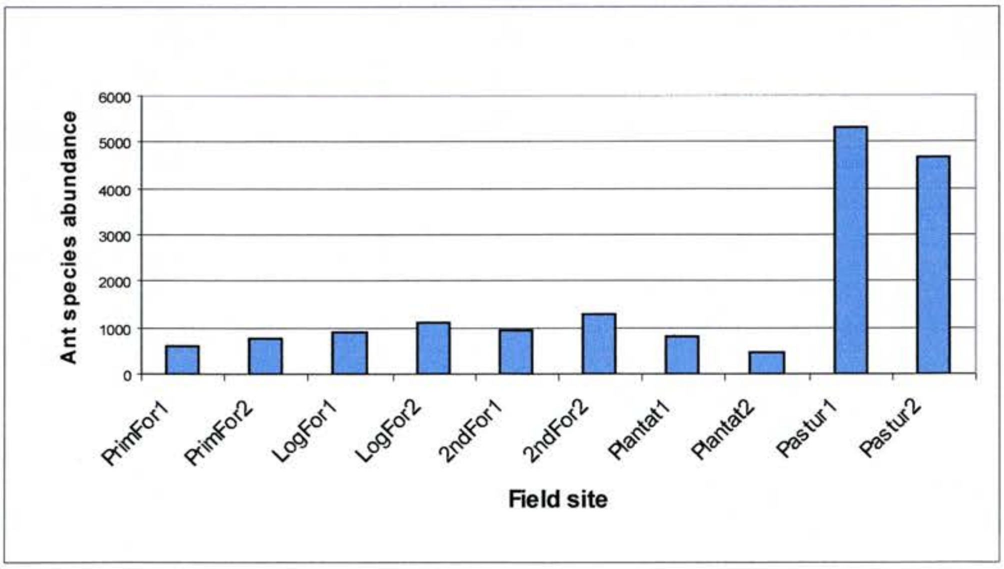
**Table 6.13 Ranking of field site by a variety of ant species diversity measures.** $S$ = species richness, $H$ = Shannon's index of diversity, $D$ = Simpson's index of diversity, $E$ = Shannon's evenness index, and $d$ = Berger-Parker dominance index.

| *Site* | *S* | *Site* | *H* | *Site* | *D* | *Site* | *E* | *Site* | *d* |
|---|---|---|---|---|---|---|---|---|---|
| LogFor2 | 80 | LogFor1 | 3.34 | PrimFor2 | 0.95 | LogFor1 | 0.77 | Pastur2 | 0.53 |
| LogFor1 | 76 | 2ndFor2 | 3.32 | LogFor2 | 0.94 | 2ndFor2 | 0.77 | Plantat1 | 0.36 |
| 2ndFor2 | 75 | LogFor2 | 3.21 | Plantat1 | 0.91 | Plantat2 | 0.76 | PrimFor1 | 0.33 |
| Pastur1 | 62 | Plantat2 | 2.96 | Plantat2 | 0.90 | LogFor2 | 0.73 | PrimFor2 | 0.29 |
| 2ndFor1 | 58 | 2ndFor1 | 2.79 | 2ndFor1 | 0.88 | PrimFor2 | 0.70 | LogFor2 | 0.28 |
| PrimFor1 | 55 | PrimFor2 | 2.75 | 2ndFor2 | 0.88 | 2ndFor1 | 0.69 | 2ndFor1 | 0.26 |
| PrimFor2 | 51 | PrimFor1 | 2.57 | Pastur1 | 0.87 | PrimFor1 | 0.64 | Plantat2 | 0.25 |
| Plantat2 | 50 | Plantat1 | 2.37 | LogFor1 | 0.83 | Plantat1 | 0.62 | Pastur1 | 0.19 |
| Pastur2 | 50 | Pastur1 | 2.35 | PrimFor1 | 0.82 | Pastur1 | 0.57 | LogFor1 | 0.13 |
| Plantat1 | 47 | Pastur2 | 1.77 | Pastur2 | 0.69 | Pastur2 | 0.45 | 2ndFor2 | 0.10 |

### 6.6.3 ANT SPECIES ABUNDANCE

Ant species abundance showed changes over the gradient of disturbance with the pasture sites showing a significant increase (Kruskal-Wallis, H = 49.08, $p < 0.001$)(Figure 6.25). This increase in total abundance was a result of significant increases in a few generalist species.

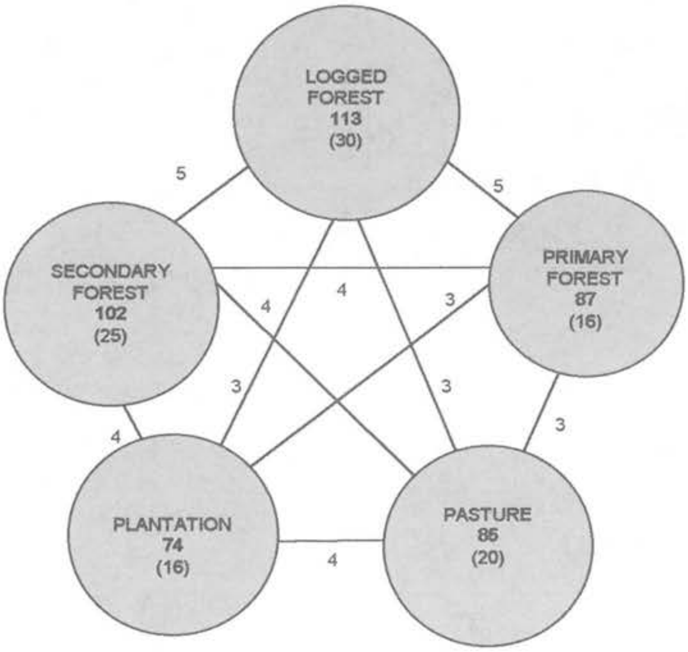
**Figure 6.25 Ant species abundance (number of individuals) in field sites sampled over a gradient of disturbance in northern Costa Rica.** PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture.



### 6.6.4 SUMMARY OF ANT SPECIES DISTRIBUTION

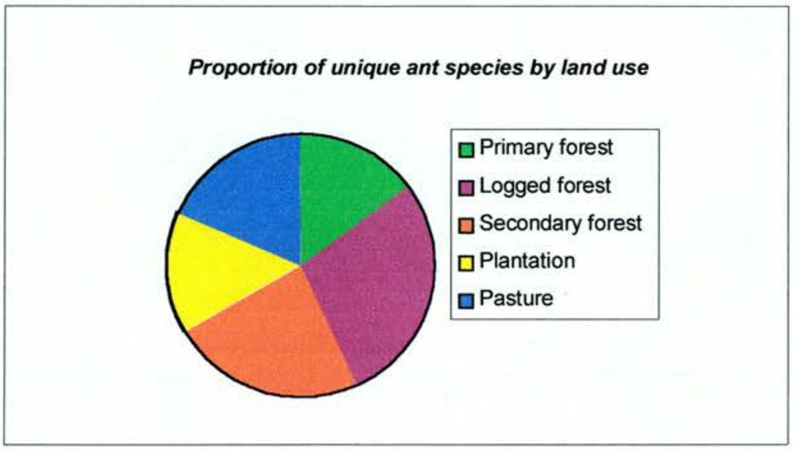
Figure 6.26 illustrates the number and composition of ant species in the different habitats considered in the study. The diagram demonstrates patterns which are more meaningful than a simple species richness value. It summarises variation in species composition in two ways: 1. by showing the number of species shared between different pairs of land uses, and 2. by the number of species unique to each land use. It demonstrates that all habitats were important in having an assemblage of species which were not present in any of the other habitats. Primary forest had 16 species that are found only in that habitat. This may illustrate that human disturbance is resulting in a loss of forest specific ant species. However, logged forest, secondary forest and pasture all demonstrated higher numbers of unique species than primary forest which may have been a result of the opening up of niches to new species by disturbance. This is summarised in Figure 6.27. Overall, the forest sites (primary, logged and secondary forest) contained 71 species which were not found in the habitats of greatest human disturbance, namely plantation and pasture.

**Figure 6.26 Ant species distribution in different land uses in Costa Rica, Central America**



**Ant species in different land uses in Costa Rica, Central America.** The number of species in each land use is given in bold, the number of species occurring in common in different habitats is given along the line joining the land uses, and the number of species unique to each land use is given in parentheses within the circles.

**Figure 6.27 Proportion of unique ant (Hymenoptera: Formicidae) species over a gradient of human disturbance in northern Costa Rica, Central America**



### 6.6.5 $\beta$ – DIVERSITY OF LEAF LITTER ANT SPECIES

In order to ascertain the degree of change in species diversity in different sites and land uses, $\beta$ - diversity was examined using the Sorensen Coefficient of Similarity (Krebs 1989)(Tables 6.14, 6.15 and 6.16 and Figs 6.28). The Morisita Index of Similarity was also calculated and used in a cluster analysis of field site and species composition. In general, $\beta$ - diversity between sites was high. According to the Sorensen's coefficients, the most similar land uses were primary forest and logged forest ($S_s$ = 0.56), and pasture and plantation ($S_s$ = 0.50). This clearly demonstrates the similarities between ant species composition in sites of similar intervention. The sites at opposite ends of the disturbance gradient demonstrated the lowest similarity, for example, logged forest and pasture ($S_s$ = 0.35). This would be expected if degree of human impact and disturbance on the forest ecosystem caused corresponding changes in leaf-litter ant species composition.

## Table 6.14 Similarities between leaf-litter ant species composition of different land uses in northern Costa Rica, as measured by the Sorensen index

| | *Primary forest* | *Logged forest* | *Secondary forest* | *Plantation* | *Pasture* |
|---|---|---|---|---|---|
| ***Primary forest*** | 1 | 0.560 | 0.487 | 0.385 | 0.419 |
| ***Logged forest*** | | 1 | 0.502 | 0.364 | 0.354 |
| ***Secondary forest*** | | | 1 | 0.455 | 0.460 |
| ***Plantation*** | | | | 1 | 0.503 |
| ***Pasture*** | | | | | 1 |

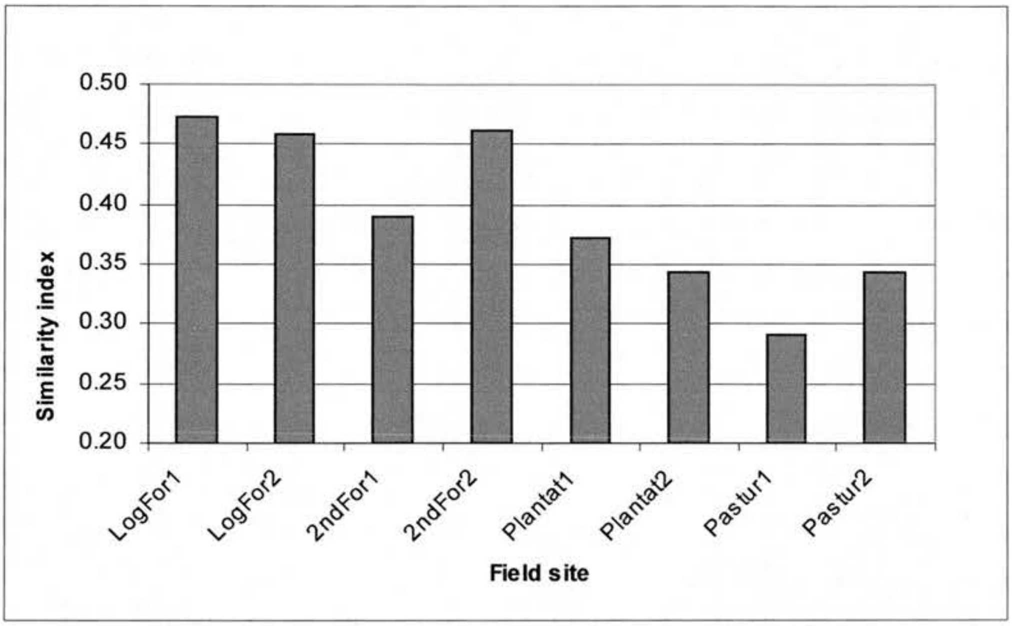
## Table 6.15 Similarities between leaf-litter ant species composition of different field sites in northern Costa Rica, as measured by the Sorensen's index

| | Prim. forest 1 | Prim. forest 2 | Log. forest 1 | Log. forest 2 | Secnd. forest 1 | Secnd. forest 2 | Plantat 1 | Plantat 2 | Pastur 1 | Pastur 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Primary forest 1*** | 1 | 0.362 | 0.473 | 0.459 | 0.389 | 0.462 | 0.373 | 0.343 | 0.291 | 0.343 |
| ***Primary forest 2*** | | 1 | 0.488 | 0.473 | 0.312 | 0.429 | 0.224 | 0.238 | 0.319 | 0.277 |
| ***Logged forest 1*** | | | 1 | 0.551 | 0.373 | 0.437 | 0.276 | 0.333 | 0.319 | 0.302 |
| ***Logged forest 2*** | | | | 1 | 0.391 | 0.516 | 0.331 | 0.292 | 0.352 | 0.323 |
| ***Secondary forest 1*** | | | | | 1 | 0.466 | 0.4 | 0.352 | 0.487 | 0.333 |
| ***Secondary forest 2*** | | | | | | 1 | 0.431 | 0.368 | 0.438 | 0.432 |
| ***Plantation 1*** | | | | | | | 1 | 0.474 | 0.477 | 0.495 |
| ***Plantation 2*** | | | | | | | | 1 | 0.357 | 0.34 |
| ***Pasture 1*** | | | | | | | | | 1 | 0.482 |
| ***Pasture 2*** | | | | | | | | | | 1 |

## Table 6.16 Similarities between leaf-litter ant species composition of different site fields in northern Costa Rica, as measured by the Morisita index

| | Prim. forest 1 | Prim. forest 2 | Log. forest 1 | Log. forest 2 | Sec. forest 1 | Sec. forest 2 | Plant 1 | Plant 2 | Pastu 1 | Pastu 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Primary forest 1*** | 1 | 0.144 | 0.156 | 0.176 | 0.154 | 0.286 | 0.066 | 0.056 | 0.291 | 0.149 |
| ***Primary forest 2*** | | 1 | 0.507 | 0.843 | 0.064 | 0.182 | 0.015 | 0.124 | 0.013 | 0.004 |
| ***Logged forest 1*** | | | 1 | 0.456 | 0.256 | 0.225 | 0.084 | 0.254 | 0.068 | 0.162 |
| ***Logged forest 2*** | | | | 1 | 0.108 | 0.194 | 0.038 | 0.175 | 0.044 | 0.055 |
| ***Secondary forest 1*** | | | | | 1 | 0.326 | 0.329 | 0.751 | 0.396 | 0.685 |
| ***Secondary forest 2*** | | | | | | 1 | 0.202 | 0.212 | 0.220 | 0.082 |
| ***Plantation 1*** | | | | | | | 1 | 0.392 | 0.289 | 0.411 |
| ***Plantation 2*** | | | | | | | | 1 | 0.218 | 0.668 |
| ***Pasture 1*** | | | | | | | | | 1 | 0.418 |
| ***Pasture 2*** | | | | | | | | | | 1 |

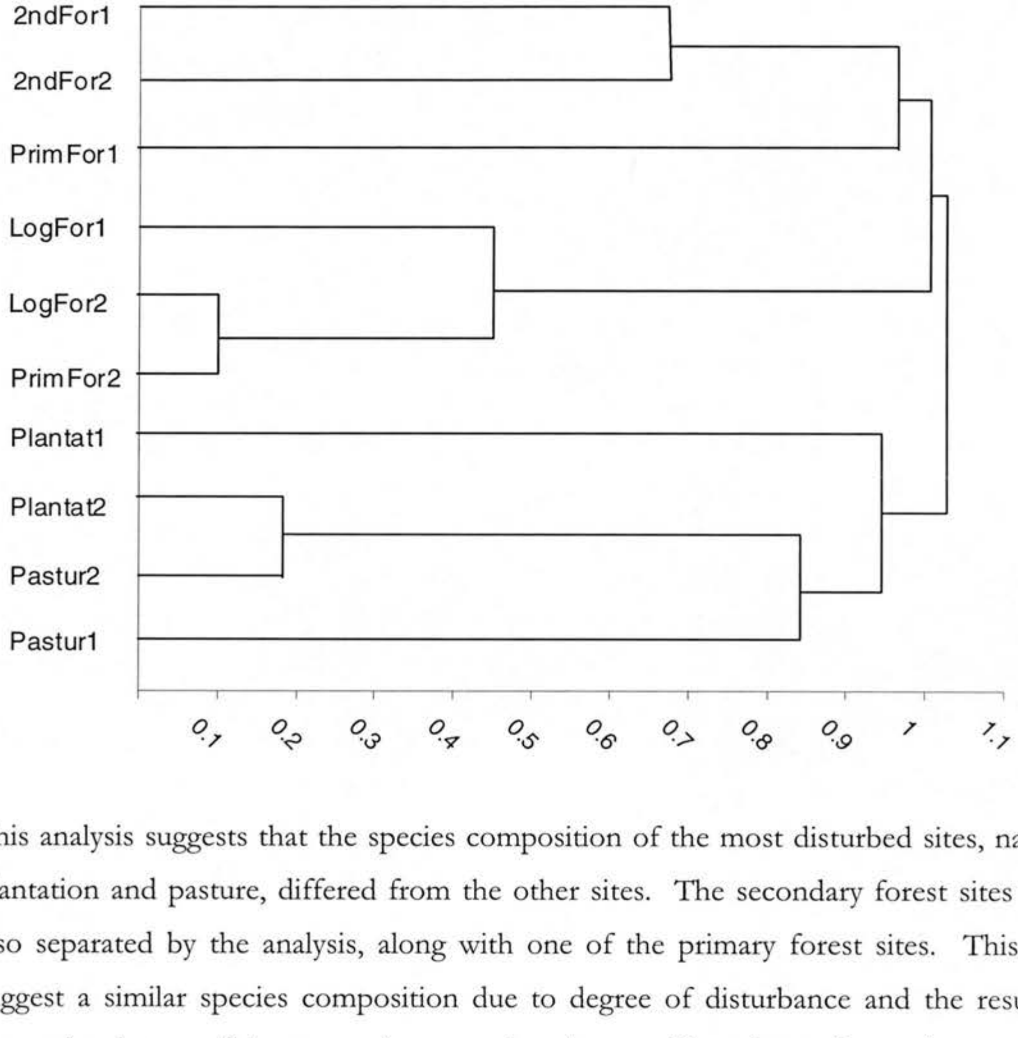
**Figure 6.28 Sorensen's similarity coefficients between primary forest (site 1) and the other 8 sites of logged forest, secondary forest, plantation and pasture.** LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture.



The examination of similarity indices has revealed a trend of lowering similarity between the natural forest sites and the more disturbed sites. Cluster analysis has been employed to analyse this trend further and to illustrate more clearly the groupings in ant species composition similarity between sites.

Cluster analysis (SAS 1990), a technique widely used to compare the species composition of plant and animal communities (e.g. Pinheiro and Ortiz 1992, Russell-Smith and Stork 1995) was applied to the Morisita Similarity Indices (Fig 6.29). The cluster analysis revealed a clear pattern of species composition separation by land use and indicated that land use change affects species composition. The field sites were divided into three main groups according to their species similarity. The two secondary forest sites (2ndFor1 and 2ndFor2) and one of the primary forest sites (PrimFor1) were grouped together, as were the two logged forest sites (LogFor1 and LogFor2) with the second primary forest site (PrimFor2). The third group consisted of both plantation (Plantat1 and Plantat2) and pasture (Pastur1 and Pastur2) sites.

**Figure 6.29 Field sites grouped according to similarity of leaf-litter ant species composition (Morisita Index and average linkage cluster analysis)**



This analysis suggests that the species composition of the most disturbed sites, namely plantation and pasture, differed from the other sites. The secondary forest sites were also separated by the analysis, along with one of the primary forest sites. This may suggest a similar species composition due to degree of disturbance and the resulting successional stage of the recovering secondary forests. The primary forest site may have been grouped with secondary forest sites due to geographical proximity. It adjoins one of the secondary forest sites (2ndFor1) which may have maintained a percentage of its original species assemblage.

## 6.7 Revealing leaf-litter ant species composition and abundance

In order to understand the response of leaf-litter ants to forest disturbance and conversion it is necessary to examine their ecological distribution. Multivariate statistical techniques were employed to achieve this. They provide a useful aid to the effective interpretation of large environmental datasets. Ant species abundance data was used in a Detrended Correspondence Analysis (DCA) to examine ant species composition of all the field sites. The next section employs Canonical Correspondence Analysis which involves the analysis of both species composition and environmental variables.

This section is divided into two parts; the first examines an ordination analysis (DCA) of the full ant species data set, and the second examines a reduced data set which excludes species where five or less individuals were collected. The reduced data set removes a particular subset of species including species which are 'tourists' and not generally present in a particular habitat. It also removes the rarest species, along with species which avoid capture, resulting in a more stable data set. This selection may also reveal the influence of rare species on the ordination groupings of species and samples.

### 6.7.1 Indirect ordination of the full ant species data set

An indirect ordination of the full ant species data was carried out using the CANOCO program (ter Braak and Smilauer 1998). The eigenvalues for this analysis are given in Table 6.17, and the scatter plots shown in Figure 5.30 a – c. The eigenvalues for axes 1 and 3 are greater than 0.5, which suggests a good separation of species along the axis. The four axes explained 35 percent of the variation.

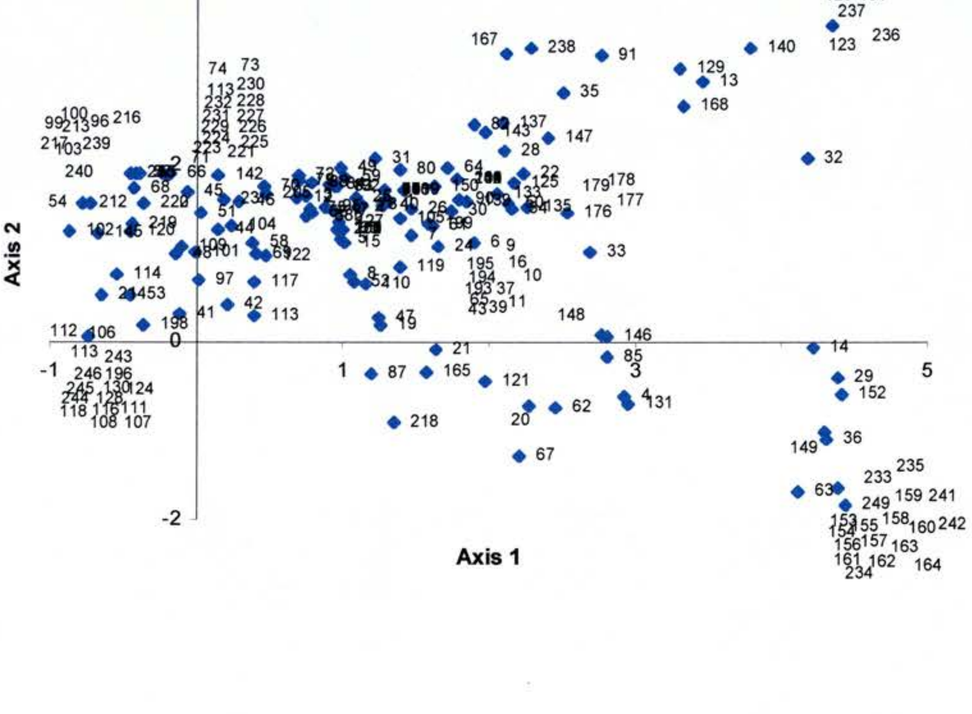
The diagrams illustrate a clear grouping of species and field sites by land use. Figure 6.30a shows significant grouping of species, both along axes 1 and axes 2. There is a clustering of species around the pasture and plantation sites, and another around one of the primary forest sites (PrimFor2) and the two logged forest sites. There is also a concentration of species in the middle of the diagram around the primary, logged and secondary forest sites. This is probably a result of generalist forest species which are found in all the natural forest sites, and are not greatly affected by disturbance until a complete removal of natural vegetation occurs, such as on the plantation and pasture sites where they are absent. Figure 6.30b not only shows the land use groupings, circled in red, but also indicates that Axes 1 is representative of the gradient of disturbance present in the field sites. Figure 6.30c illustrates both the species and sample score data in order to provide a clearer representation of species groupings by site.

**Table 6.17 Eigenvalues and percentage variance for full ant species data set**

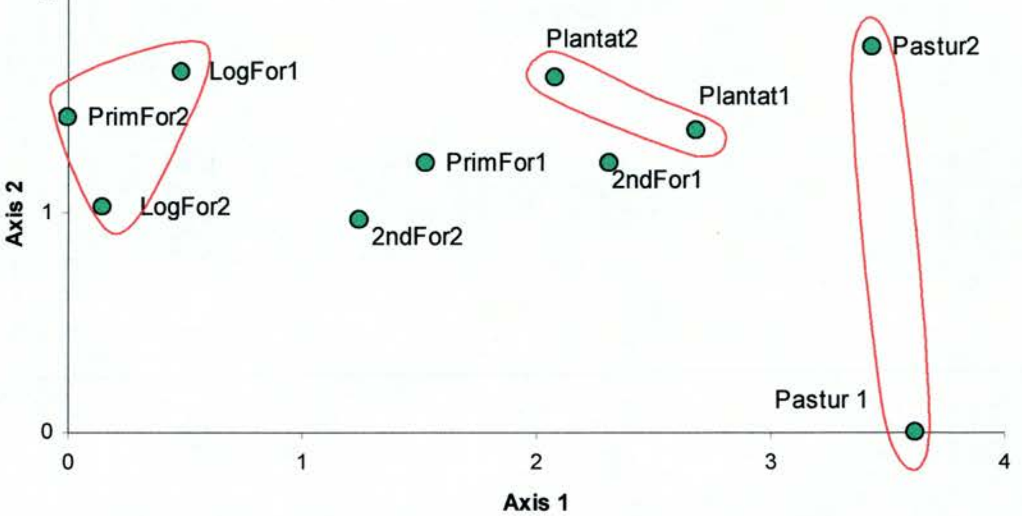
| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.732 | 0.186 | 0.56 | 0.006 | 2.803 |
| Cumulative percentage variance of species data | 26.1 | 32.8 | 34.8 | 35.0 | |
| Sum of all unconstrained eigenvalues | | | | | 2. 803 |

**Figure 6.30 DCA ordination of sites based on ant species abundances (full data set).** The species score plot is shown in (a) and the sample score plot in (b). These are then combined in (c) to illustrate the relationship between species and sites.

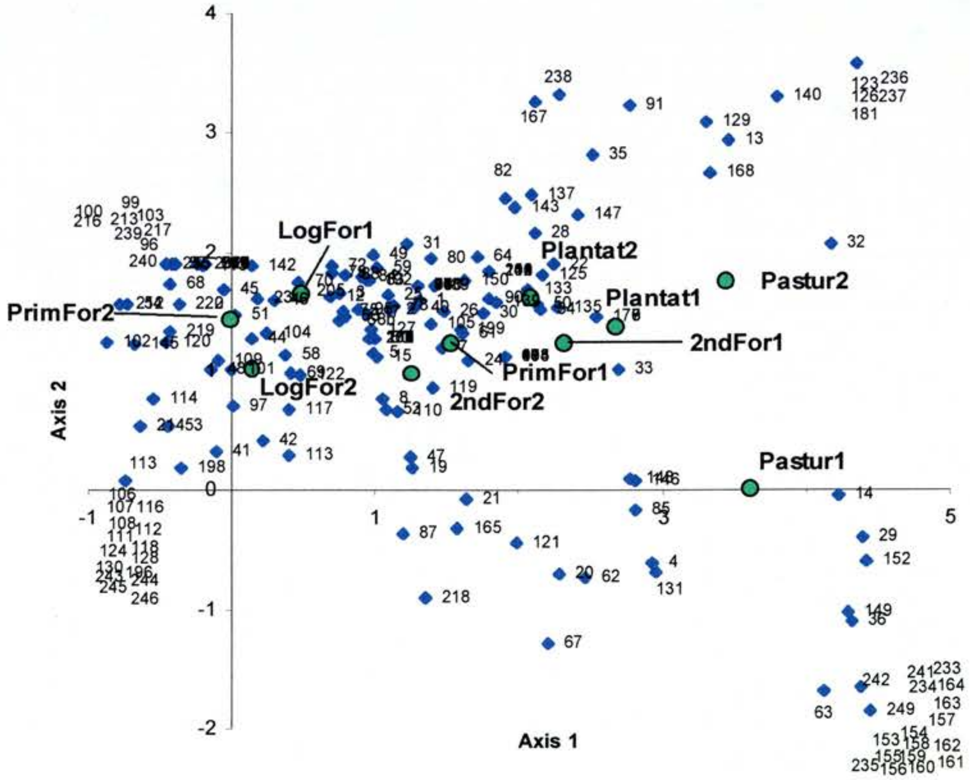
a) **Species score plot** showing the main clusters of species (these are related to land use type in Figure 6.31c).



**Sample score plot** showing the main groupings of land use type. This plot reveals the presence of a gradient along Axis 1, from the primary and logged forest sites on the left of the diagram to the more disturbed sites of plantation and pasture on the right.



c) **Sample and species score plot** showing the species and land use clusters. The relationship between species and sites is shown. The gradient of disturbance along Axis 1 is also evident.



### 6.7.2 Indirect ordination of the reduced ant species data set

The indirect ordination of the reduced ant species data set (excluding species with ≤ 5 individuals) was also carried out using the CANOCO program (ter Braak and Smilauer 1998). The number of species was reduced by over 50 percent, from 230 to 101 active species in the calculation. The eigenvalues for this analysis are given in Table 6.18, and the scatter plots shown in Figure 5.31 a – c. The eigenvalue for axis 1 is greater than 0.5, which suggests a good separation of species along the axis. The four axes explain 38 percent of the variation.

Again the resulting diagrams of species and sample scores illustrate a clear grouping of species and field sites by land use. Figure 6.31a shows significant grouping of species, both along axes 1 and axes 2. The grouping is almost identical to that shown for the full data set. There is a clustering of species around the pasture and plantation sites, and another around one of the primary forest sites (PrimFor2) and the two logged forest sites. As before, there is a concentration of species in the middle of the diagram around the primary, logged and secondary forest sites. Figure 6.31b shows the land use groupings, circled in red, and reiterates the gradient of disturbance which is apparent over axis 1. Figure 6.31c illustrates both the species and sample score data from the reduced data set. The species groupings and their proximity to the field site groupings are evident, and illustrate that the analysis of the reduced data set does not reveal any major differences from the full data set.

The species group clustered next to the pasture sites include species 4, 13, 14, 29, 32, 36, 63, 129, 131, 140, 149, and 157 (Appendix 6.1). Of these species six are in the Myrmicinae sub-family, three are in the Ponerinae, one in the Dolichoderinae, one in the Ecitoninae, and one in the Formicinae. Four of the five most abundant species over all the field sites are among these. Species 4, *Pachycondyla* sp., Ponerinae, is a soil cryptic predator which preys principally on termites, species 13 (Ponerinae) was the most abundant in the entire study, while species 14, *Monomorium* sp., Myrmicinae, is an omnivorous soil or litter dominant (Delabie et al. 2000). From the available data it appears that many of the above species may be omnivorous and therefore more adaptable to environmental changes. The fact that four out of five of the most abundant species in the study were found grouped around the pasture sites illustrates that some species are highly successful in this altered landscape. However, it is also evident from Figure 6.31, that there are less species clustered around these sites, at the right side of the DCA diagrams, compared to around the natural forest sites where the species are more concentrated. This may indicate that, although some species are successful in pasture and plantation sites, many species cannot survive in such an altered landscape.

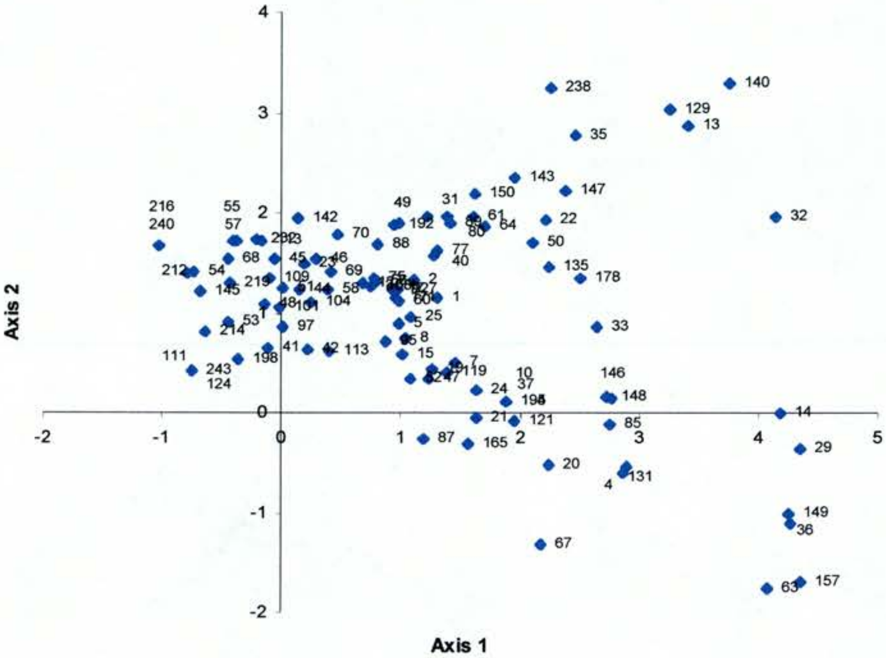
Species grouped to the left side of the diagram which, if axes 1 represents a gradient of disturbance, describes species present in the more pristine of the natural forest sites, include species 21, 53, 55, 57, 68, 111, 124, 145, 212, 214, 216, 240 and 243. Five of these species are in the Ecitoninae and eight in the Myrmicinae. Species 57, *Solenopsis* sp., Ecitoninae, is a litter omnivore/scavenger, and species 145, *Nomamyrmex* sp., Ecitoninae, is an army ant and a predator. The species grouped to the left are less abundant and also come from only two subfamilies, perhaps suggesting that they are rarer forest specialists. It is evident that these species are found in quite different positions in relation to the two axes suggesting that they respond to different environmental parameters.

**Table 6.18 Eigenvalues and percentage variance for the reduced ant species data set**

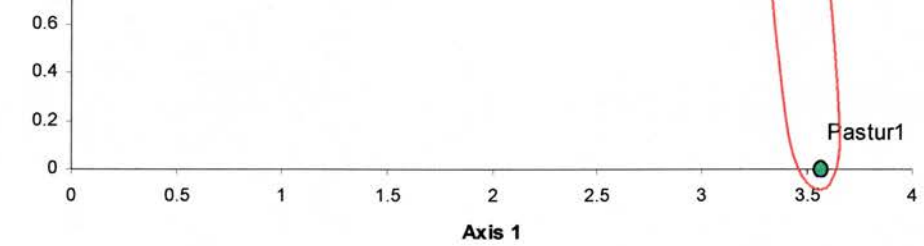
| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.729 | 0.185 | 0.076 | 0.019 | 2.681 |
| Cumulative percentage variance of species data | 27.2 | 34.1 | 36.9 | 37.6 | |
| Sum of all unconstrained eigenvalues | | | | | 2.681 |

**Figure 6.31 DCA ordination of sites based on ant species abundances (reduced data set).** The species score plot is shown in (a) and the sample score plot in (b). These are then combined in (c) to illustrate the relationship between species and sites.

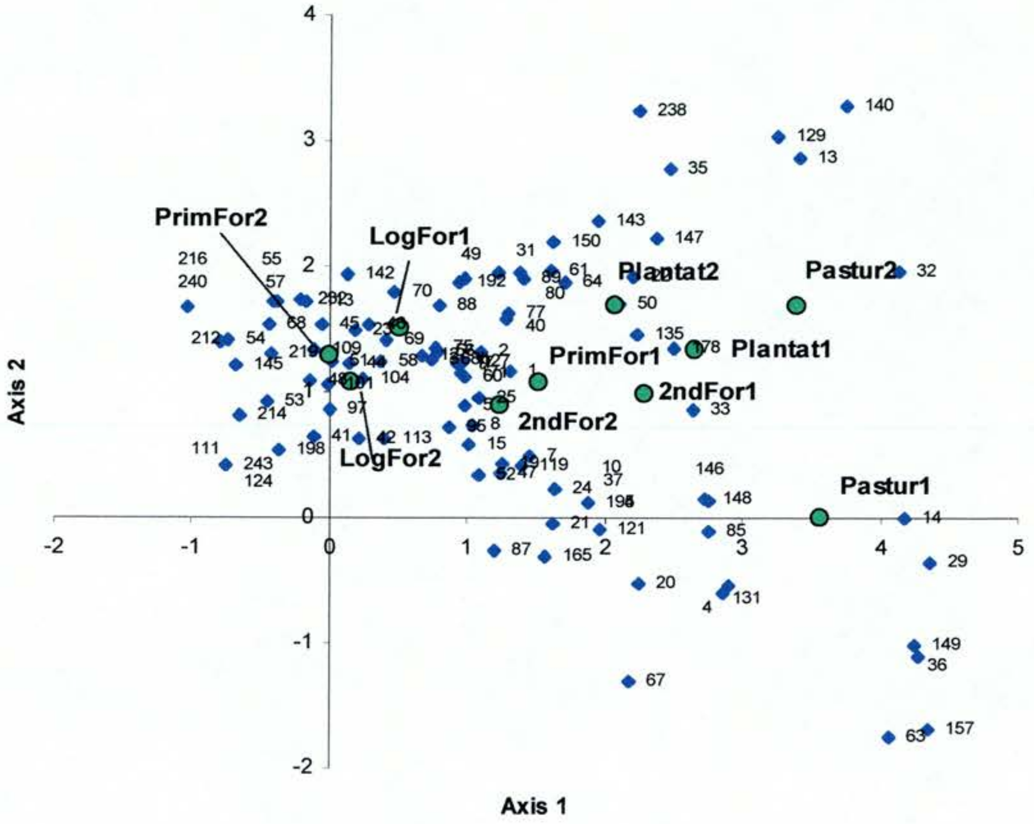
**a) Species score plot** showing the main clusters of species related to land use type.



**b) Sample score plot** showing the main groupings of land use type. These are not significantly changed by the reduced data set. This plot also reveals the presence of a gradient along Axis 1, from the primary and logged forest sites on the left of the diagram to the more disturbed sites of plantation and pasture on the right.



c) **Sample and species score plot** showing the species and land use clusters. The relationship between species and sites is shown. The gradient of disturbance along Axis 1 is also evident.



In general, the DCA analysis of both the full and reduced ant species data has shown that leaf litter ant species can be clearly divided into groups of similarly occurring species, which were found within similar land uses. The key changes indicated by the separation of species along axis 1 appeared to be a result of the gradient of human disturbance over the field sites. Particular ant assemblages were grouped with different land uses. Figures 6.30b and Figures 6.31b did not show significant differences in sample scores, although dominant species in different land uses are more evident from the reduced species score plots (Figures 6.31a). This suggests that the patterns of distribution of the leaf-litter ant species assemblages were consistent in their changes over the field sites, and corresponding land uses, and were not a result of rare species or 'tourists' biasing the data.

### 6.7.3 TWINSPAN classification of the ant species data set

TWINSPAN was used to classify samples and species (Hill 1979)(Section 4.6.3). As already discussed, this method is one of the most widely used clustering programmes in community ecology (van Tongeren 1995), and is based on the general principal that a group of sites can be characterised by a group of differential species (Jongman et al. 1995). As a hierarchical clustering technique, it essentially involves the repeated dichotomization of samples and then of species. The resulting two-way table expresses synecological relations as succinctly as possible (Hill 1979).

The database used for the classification of leaf-litter ant species consisted of 10 samples and 230 species. Pseudospecies levels were set at 0%, 2%, 5%, 10% and 20% representing 5 categories of abundance (1 = 0-2%, 2 = 2-5%, 3 = 5-10%, 4 = 10-20%, 5 = >20%). The full TWINSPAN table for all 230 species is given in Appendix 8. The results of the analysis are summarised below.

The TWINSPAN classification of samples is illustrated in Figure 6.32. The first division created two groups which divided the sites primarily by level of disturbance. The primary and logged primary forests are grouped together (*0 group), as are the pasture and plantation sites (*1 group). The two secondary forest sites are separated between the two initial groups. The next division of the left hand group (*0 group) divides the primary (PrimFor2) and logged primary (LogFor1) sites found on the *Hogar de Ancianos* ranch into one group. The second group is subdivided again, separating the other primary forest site (PrimFor1) from the sub-group which contains the logged forest site (LogFor2) and the secondary forest site (2ndFor2) which are both found on the *Luzmirio Alvarez* ranch. The next division of the right hand group (*1 group) divides the secondary forest into its own group, while the second group formed contains the two pasture sites and the two plantation sites. These are further divided as shown in Figure 6.31, and do not appear to show any groupings by geographical, or ranch, location.

An overview of this classification demonstrates that the ecological changes occurring over the gradient of disturbance found in northern Costa Rica are reflected by the resulting leaf litter ant community. There is a clear separation between the sites of greatest disturbance, namely plantation and pasture, and the remaining natural forest sites. The latter group is subdivided into further divisions, which appear to be dictated by geographical location. This is a similar result to that found for the tree species data, and may reflect the proximity of these sites to each other. It is also possible that the similarities still present between land uses are due to relict communities which have not suffered sufficient disturbance to be altered. It is noteworthy that in the sites of greatest disturbance, i.e. the groups on the right-hand side of the classification, geographical relationships have not been maintained, perhaps demonstrating that these similarities can only endure a certain level of impact. The two secondary forest sites are found on opposite sides of the first division in this classification. This may be due to the level of succession present in each site. 2ndFor2 is grouped with LogFor2 within the natural forest grouping (*0 group). This is probably a result of its geographical proximity to LogFor2, and its resulting sharing of ant species. 2ndFor1 is grouped separately within the disturbed site grouping (*1 group) perhaps as a result of its successional stage which results in a community which more closely resembles pasture than natural forest.

The TWINSPAN analysis, shown in Appendix 6.3, has revealed a number of indicator species for various site clusters. Species 45 (*Pheidole* sp., Myrmicinae) was identified as a 'perfect indicator' for the natural forest sites cluster (*0 group). This species falls into Guild 1, the litter omnivores and scavengers, according to Delabie et al. (2000). It is noteworthy that this ant was found in abundance level 5 in four out of the five sites, and in abundance level 4 in the other site in the clustering. Evidently it showed high abundance in these sites but was completely absent from any of the sites in the *1 group, the disturbed cluster. According to this analysis Species 45 was an important indicator of natural forest, although not of pristine forest as the sites it is found in include logged and secondary forest.

Species 55 (Ecitoninae) was identified as an indicator of group *00, which contained PrimFor2 and LogFor1 , within the group *0. Both of these sites were found within the same ranch (*Hogar de Ancianos*). Other species which were found primarily in the natural forest cluster (*0 group), according to the TWINSPAN output, included Species 58

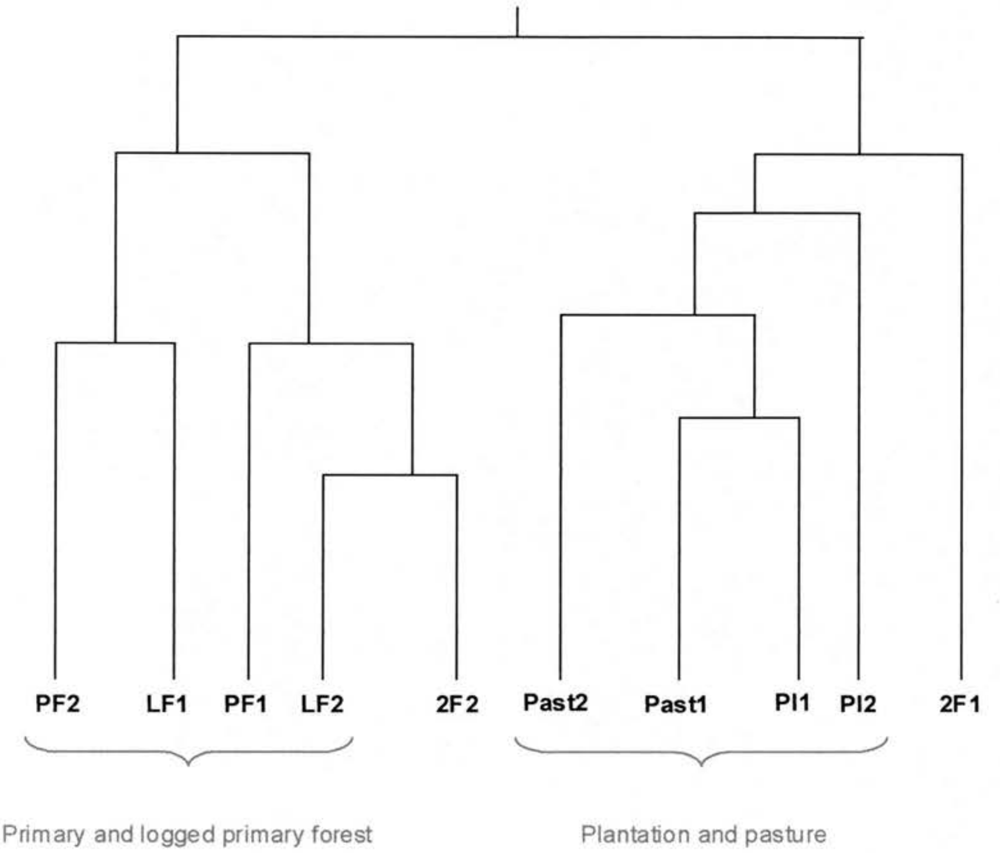
(Myrmicinae), Species 97 (Myrmicinae), Species 44 (Myrmicinae), Species 48 (Myrmicinae), Species 101 (Myrmicinae), Species 23 (Myrmicinae), and Species 68 (Myrmicinae).

In contrast, some of the ant species collected appeared to have a ubiquitous distribution, and Species 5 (*Pachycondyla* sp.2, Ponerinae) is the best example of this revealed by the TWINSPAN analysis. This ant was found in all sites. It was more abundant in the five sites clustered in group *0 where it displayed abundance level 5 in all sites. In the disturbed sites it was less abundant but was also present in all five sites. *Pachycondyla* sp. falls within Guild 5, the soil cryptic predators (Delabie et al. 2000). Species 17 (*Pachycondyla* sp.4, Ponerinae) and Species 21 (Myrmicinae) also appeared to thrive across all the different land uses sampled. Species 4 (*Pachycondyla* sp.1, Ponerinae), Species 13 (Ponerinae), which was the most abundant ant in the study, and Species 50 (Myrmicinae) were also ubiquitous over nine sites although none of the three were present in PrimFor2. It is also evident that these ant species were most abundant in the disturbed sites cluster (*0 group) where they were present, almost without exception, at the highest abundance level. It seems that they have adapted very successfully to the altered ecological and microclimatic conditions now present in these disturbed sites.

Ants that are found almost exclusively in the disturbed sites included Species 14 (*Monomorium* sp., Myrmicinae), Species 22 (*Tapinoma* sp., Dolichoderinae), Species 32 (Ecitoninae), and Species 35 (Myrmicinae)(Appendix 6.3). *Monomorium* sp. was found within Guild 8, the soil or litter dominants which also forage on the vegetation, the ground or the litter. Species 14 (*Monomorium* sp., Myrmicinae) was the second most abundant species in the overall study. It was also the only ant which was present at the highest level of abundance in four out of five of the sites within the disturbed cluster, and which was not found in any of the sites in the natural forest cluster.

The disturbed habitats, namely pasture and plantation, examined in this study had a considerably modified environment and microclimate. Both habitats were considerably drier than in native forest and temperatures were much higher. This has caused a marked change in the native ant communities. It is evident from the TWINSPAN

**Figure 6.32 Dendrogram of the TWINSPAN classification of leaf-litter ant species by site**



analysis that many species can be clearly separated by the land use in which they were found, demonstrating, in some cases, a preference for natural forest sites, or for plantation and pasture sites. Some of the species in this study have been revealed by the TWINSPAN analysis as clear indicators for the two main classifications of natural forest sites, and disturbed sites. The different habitat preferences shown by this analysis can be caused by a variety of factors. Some forest ant species cannot tolerate the increased temperatures, or the reduced humidity, related to forest conversion to plantation or pasture (Torres 1984, Andersen 2000). Changes in vegetation structure may also affect the ant assemblage, as can changes in soil properties and leaf litter. These factors are examined in relation to ant species diversity and composition in the next section.

## 6.8 Effects of environmental variables on community structure

The sites under investigation in this study have all, with the exception of the primary forest areas, been changed by human intervention. This inevitably causes alterations in the environment of the site. The previous sections have investigated the differences between ant species and composition over the different field sites and land uses studied. This section considers the effects of the environmental changes caused by human intervention on the leaf-litter ant community. Throughout the study human impact on ant species diversity and composition has been mediated by at least seven important environmental variables (Table 6.19):

- basal area of forest ($m^2$) and number of trees,
- tree species diversity,
- maximum and minimum temperature (°C),
- soil temperature (°C),
- soil organic matter(%),
- soil pH, and
- leaf litter amount ($kg/m^2$).

In addition, elevation (m), the aspect of each transect, and the mean and range of slope at each trap location was recorded to help in site characterisation (Table 6.19). These physical variables obviously remain unaltered by human action but they may affect species composition and therefore must be taken into account when attempting to explain changes in insect communities. The effect of these variables on leaf-litter ant composition is examined below.

As in the indirect ordination of the ant data, this section is divided into two parts; the first examines the direct ordination analysis of the full ant species data set, and the second examines a reduced data set which excludes species where five or less individuals were collected. It is hoped that this reduced data set will reveal the influence of rare species on the ordination groupings of species and samples while also giving a clearer picture of the more abundant species relations with site and with environmental variables.

**Table 6.19 Site characteristics.** Values indicated are means for each site ± 1 standard deviation. (Leaf litter units measure dry mass)

| *Habitat* | *Site* | *Soil temp (°C)* | *Soil pH* | *Soil organic matter (%)* | *Basal area/ha* | *Leaf litter(g)* |
|---|---|---|---|---|---|---|
| *Primary forest* | PrimFor1 | 23.8 ± 0.33 | 3.8 ± 0.46 | 2.1 ± 2.47 | 41.0 ± 0.15 | 13.0 ± 4.1 |
| | PrimFor2 | 28.1 ± 1.51 | 4.0 ± 0.26 | 1.6 ± 0.65 | 23.5 ± 0.07 | 13.9 ± 5.33 |
| *Logged forest* | LogFor1 | 26.8 ± 1.55 | 3.9 ± 0.28 | 3.2 ± 1.10 | 19.1 ± 0.07 | 8.2 ± 4.23 |
| | LogFor2 | 26.0 ± 1.62 | 4.2 ± 0.42 | 2.3 ± 1.09 | 24.3 ± 0.13 | 9.1 ± 3.19 |
| *2ndary forest* | 2ndFor1 | 29.2 ± 2.04 | 3.8 ± 0.42 | 1.7 ± 0.74 | 11.5 ± 0.08 | 8.5 ± 5.22 |
| | 2ndFor2 | 29.8 ± 1.47 | 4.2 ± 0.36 | 1.7 ± 0.72 | 37.1 ± 0.21 | 12.6 ± 7.41 |
| *Plantation* | Plantat1 | 31.6 ± 1.96 | 4.0 ± 0.26 | 1.8 ± 0.84 | 12.9 ± 0.02 | 8.5 ± 3.76 |
| | Plantat2 | 34.4 ± 2.53 | 4.0 ± 0.42 | 1.7 ± 0.71 | 11.8 ± 0.01 | 10.2 ± 4.25 |
| *Pasture* | Pastur1 | 33.9 ± 1.36 | 4.5 ± 0.39 | 1.9 ± 0.94 | 2.2 ± 0.05 | 1.8 ± 2.05 |
| | Pastur2 | 32.2 ± 2.75 | 4.4 ± 0.57 | 1.7 ± 0.86 | 0.4 ± 0.13 | 2.3 ± 2.82 |

| *Site* | *Max T (°C)* | *Min T (°C)* | *Slope (%)* | *Altitude (m)* | *Tree spp. richness.* | *Trees/ ha* |
|---|---|---|---|---|---|---|
| PrimFor1 | 27.5 ± 0.71 | 20.5 ± 0.71 | 5.2 ± 6.20 | 38.7 ± 4.17 | 53 | 478 |
| PrimFor2 | 28.3 ± 2.48 | 18.8 ± 0.35 | 29.6 ± 17.59 | 82.2 ±10.88 | 52 | 560 |
| LogFor1 | 26.3 ± 0.35 | 18.8 ± 1.06 | 13.6 ± 10.41 | 45.9 ±9.60 | 50 | 486 |
| LogFor2 | 27.5 ± 0.71 | 20.0 ± 1.41 | 13.9 ± 9.96 | 160.7 ±16.83 | 58 | 416 |
| 2ndFor1 | 29.3 ± 2.48 | 20.3 ± 0.35 | 12.1 ± 10.75 | 40.7 ± 4.90 | 34 | 186 |
| 2ndFor2 | 30.0 ± 0.00 | 18.5 ± 0.00 | 12.1 ± 7.48 | 79.4 ±27.00 | 44 | 594 |
| Plantat1 | 31.0 ± 0.00 | 20.5 ± 0.71 | 8.7 ± 6.57 | 41.5 ±5.40 | 2 | 548 |
| Plantat2 | 31.5 ± 0.00 | 19.0 ± 0.00 | 9.2 ± 8.74 | 43.8 ±3.80 | 1 | 516 |
| Pastur1 | 34.0 ± 3.54 | 20.0 ± 2.12 | 18.6 ± 12.93 | 158.6 ±12.10 | 8 | 30 |
| Pastur2 | 32.5 ± 0.00 | 21.5 ± 0.71 | 3.3 ± 4.27 | 48.2 ±9.20 | 1 | 2 |

### 6.8.1 Direct ordination of the full ant species data set

A direct ordination of the ant species data set and the environmental variables detailed above was carried out using the CANOCO program (ter Braak and Smilauer 1998). CCA selects the linear combination of environmental variables which maximise the dispersion of the species scores. It therefore incorporates the relationships between species and environment into the actual ordination. The eigenvalues for this analysis are given in Table 6.22 and the scatter plots are shown in Figure 6.33 a and b. The eigenvalue for axis 1 is greater than 0.5, suggesting a good separation of species along the axis. The four axes explain 61.8 percent of the variation.

The correlation matrix for the environmental data is shown in Table 6.20. All coefficients with a value higher than 0.7 are shown in red. Clear autocorrelations, such as between leaf litter, trees per hectare and basal area per hectare, and maximum temperature and soil temperature were reduced to one variable in the diagrams. The highest coefficients, excluding the autocorrelations, were between soil pH and leaf litter (r = -0.82), soil temperature and leaf litter (r = -0.77), soil temperature and basal area per hectare (r = -0.79), and soil temperature and tree species diversity (r = -0.89). These correlations appear to reveal an influence of leaf litter on soil pH, perhaps due to the increased accumulation of organic acids in areas of greater leaf litter. Soil temperature and leaf litter also showed a correlation possibly due to the effects of changing land use on both these variables. Soil temperature increaseed with forest disturbance due to increased insolation, while leaf litter amount was generally reduced with human impact (see Chapter 5). This also followed in the correlation of soil temperature with basal area. Basal area reduced as human disturbance increased as did soil temperature. These results agree with the results found from the tree species CCA, showing the influence of disturbance on the forest environment.

**Table 6.20 Correlation coefficients among environmental variables from the ant species (full data set) direct ordination.** CCA weighted correlation matrix output.

| | *leaf lit* | *soil OM* | *soil pH* | *soil T* | *max T* | *min T* | *slope* | *alti-tude* | *trees. ha* | *BA. ha* | *tree spp* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***leaf lit*** | 1.000 | | | | | | | | | | |
| ***soil OM*** | 0.128 | 1.000 | | | | | | | | | |
| ***soil pH*** | -0.816 | 0.300 | 1.000 | | | | | | | | |
| ***soil T*** | -0.766 | 0.486 | 0.744 | 1.000 | | | | | | | |
| ***max T*** | -0.833 | 0.531 | 0.833 | 0.949 | 1.000 | | | | | | |
| ***min T*** | -0.625 | 0.293 | 0.377 | 0.282 | 0.414 | 1.000 | | | | | |
| ***slope*** | 0.154 | 0.060 | -0.005 | 0.053 | 0.014 | -0.698 | 1.000 | | | | |
| ***altitude*** | -0.332 | 0.026 | 0.527 | 0.317 | 0.403 | -0.287 | 0.697 | 1.000 | | | |
| ***trees.ha*** | 0.946 | 0.273 | -0.748 | -0.682 | -0.790 | -0.700 | 0.189 | -0.253 | 1.000 | | |
| ***BA.ha*** | 0.927 | 0.231 | -0.662 | -0.793 | -0.780 | -0.640 | 0.138 | -0.163 | 0.892 | 1.000 | |
| ***tree spp*** | 0.814 | 0.450 | -0.650 | -0.888 | -0.875 | -0.642 | 0.333 | 0.005 | 0.748 | 0.865 | 1.000 |

**Table 6.21 Correlation coefficients of environmental variables with the CCA ordination axes from the ant species (full data set) direct ordination.** CCA weighted correlation matrix output.

| | *SPEC Axis 1* | *SPEC Axis 2* | *SPEC Axis 3* | *SPEC Axis 4* | *ENVI Axis 1* | *ENVI Axis 2* | *ENVI Axis 3* | *ENVI Axis 4* |
|---|---|---|---|---|---|---|---|---|
| ***leaf litter*** | 0.840 | 0.430 | 0.142 | -0.054 | 0.840 | 0.430 | 0.142 | -0.054 |
| ***soil OM*** | 0.457 | -0.384 | 0.016 | -0.153 | 0.457 | -0.384 | 0.016 | -0.153 |
| ***soil pH*** | -0.639 | -0.209 | -0.413 | 0.261 | -0.639 | -0.209 | -0.413 | 0.261 |
| ***soil T*** | -0.843 | 0.026 | -0.123 | 0.119 | -0.843 | 0.026 | -0.123 | 0.119 |
| ***max T*** | -0.904 | -0.024 | -0.253 | 0.202 | -0.904 | -0.024 | -0.253 | 0.203 |
| ***min T*** | -0.645 | -0.300 | 0.393 | 0.001 | -0.645 | -0.300 | 0.393 | 0.001 |
| ***slope*** | 0.302 | -0.164 | -0.541 | 0.315 | 0.302 | -0.164 | -0.541 | 0.315 |
| ***altitude*** | -0.085 | -0.224 | -0.723 | 0.563 | -0.085 | -0.224 | -0.723 | 0.563 |
| ***trees ha*** | 0.827 | 0.456 | 0.196 | 0.087 | 0.827 | 0.456 | 0.196 | 0.087 |
| ***BA ha*** | 0.813 | 0.468 | -0.113 | -0.003 | 0.813 | 0.468 | -0.113 | -0.003 |
| ***tree spp.*** | 0.935 | 0.053 | -0.220 | -0.074 | 0.935 | 0.053 | -0.220 | -0.074 |

**Table 6.22 Eigenvalues and percentage variance for the CCA analysis of ant species (full data set) and environmental variables**

| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.732 | 0.376 | 0.328 | 0.294 | 2.803 |
| Cumulative percentage variance of species data | 26.1 | 39.6 | 51.3 | 61.8 | |
| Cumulative percentage variance of species environment relation | 26.1 | 39.6 | 51.3 | 61.8 | |
| Sum of all unconstrained eigenvalues | | | | | 2.803 |

The existence of relationships between ant species diversity and composition, and the selected environmental variables was also investigated using CCA analysis. The results of the direct ordination are shown in a biplot of site and environmental variables (Figure 6.33a) and also in a biplot of species and environmental variables (Figure 6.33b). The biplot of species and environmental arrows shows the weighted averages of each species with respect to each of the environmental variables. The correlation coefficients of the environmental variables with the CCA ordination axes are shown in Table 6.21. As with the tree data, the environmental data in Figures 6.33a and 6.33b are represented by arrows which are plotted in the direction of maximum change. The length of the arrows is proportional to the magnitude of the change. The environmental variables represented by longer arrows are more important in influencing community variation. The species show their relation to the arrows by their relative positions. Those found close to the tip are strongly correlated with the variable in question (Kent and Coker 1992). The results below make it possible to develop ideas regarding the key influences on the system.

The ordination biplot of the first two axes of site and environmental variables (Figure 6.34a) reveals the existence of a correlation between the first ordination axis and the following environmental variables: leaf litter ($r = 0.84$), soil pH ($r = -0.64$), soil temperature ($r = -0.84$), minimum temperature ($r = -0.64$) and tree species diversity ($r = 0.93$)(Table 6.18). The second axis does not show a strong correlation with any of the variables although the third axis does correlate well with altitude ($r = -0.7228$). Overall, the four axes explain almost 62 percent of the variation.

The ordination diagram separates the field sites according to species composition and their response to environmental variables. Figure 6.33a reveals a distinctive separation between the two logged primary forest sites (LogFor1 and LogFor2) coupled with the second primary forest site (PrimFor2), and the pasture sites. These two groups of sites are found to the far right and far left of the diagram respectively. The first primary forest site is grouped close to 2ndFor2 on Axis 1 but is separated in Axis 2. The two plantation sites are grouped together but not as cohesively as the natural forest group and the pasture group. PrimFor1 is plotted at the tip of the arrow representing leaf litter. This arrow also represents the positioning of the basal area environmental gradient (which was removed from the diagram due to autocorrelation). It suggests that this site is defined primarily by these variables. The pasture sites are strongly correlated with soil temperature and soil pH which are important factors in defining the difference between the natural forest sites and this land use of greatest human disturbance. The plantation sites are found in the middle of the diagram and although they are located next to each other they are not plotted as closely as the other land uses, demonstrating greater diversity in environmental factors and species assemblage between them.

In general the CCA analysis of site and environmental gradients showed a trend of forest disturbance along Axis 1. The environmental gradients demonstrated that the most important factors in defining natural forest were leaf litter amount, soil organic matter content, and tree species diversity, all of which were greatly changed by forest conversion to plantation and pasture. This was reinforced by the grouping of the pasture sites at the opposite side of the diagram and their correlation with environmental variables, such as, soil temperature and soil pH. The two physical variables, slope and altitude entered into the analysis appeared to have a minimal relationship with site and species composition. The small arrows representing them revealed that they were less important than the environmental variables measured. This was to be expected, as they do not change with forest disturbance, whereas all the environmental variables are affected to a certain extent.

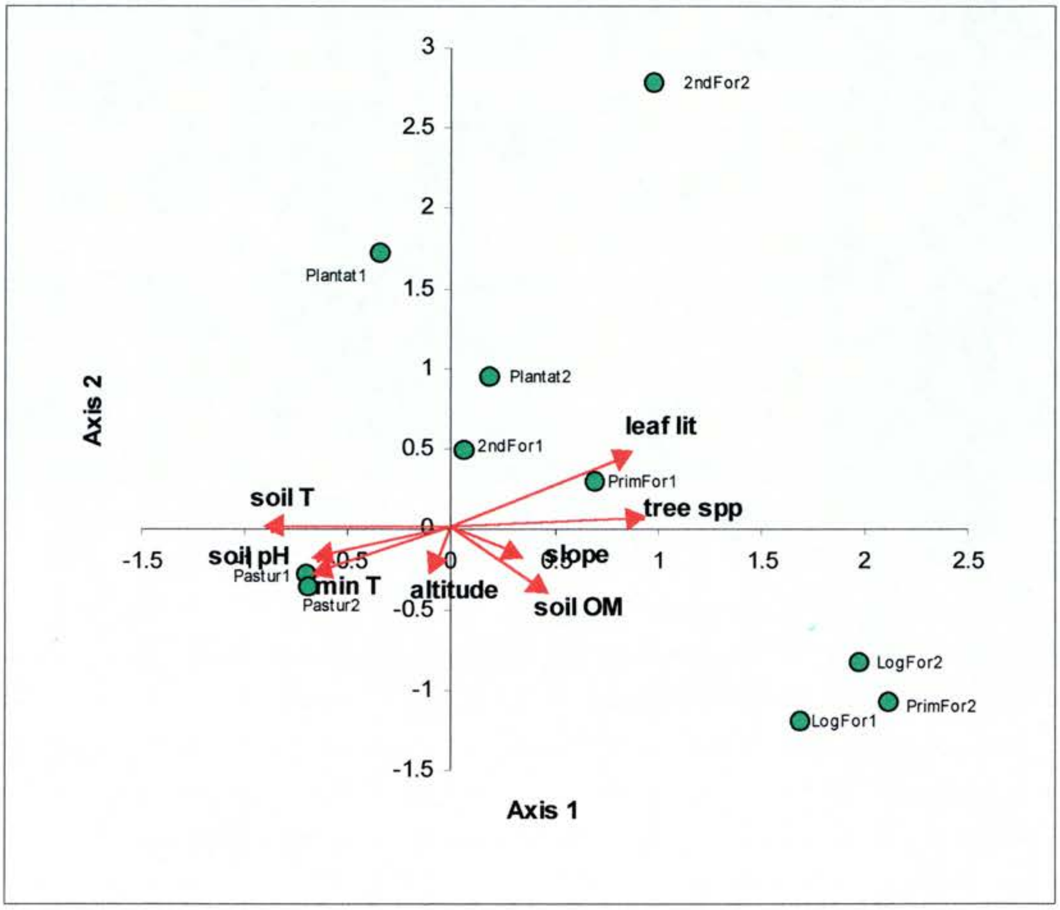
Figure 6.33b shows a clear grouping of species around the various land uses. The pasture and natural forest sites reveal very specific groupings as does 2ndFor2. Many of the species found in this analysis were unique species in the study sample or were found in abundances of less than or equal to five. The following section, which examines the CCA of the reduced species set, will discuss particular ant species grouping in more detail.

### 6.8.2 Direct ordination of the reduced ant species (>5 individuals) data set

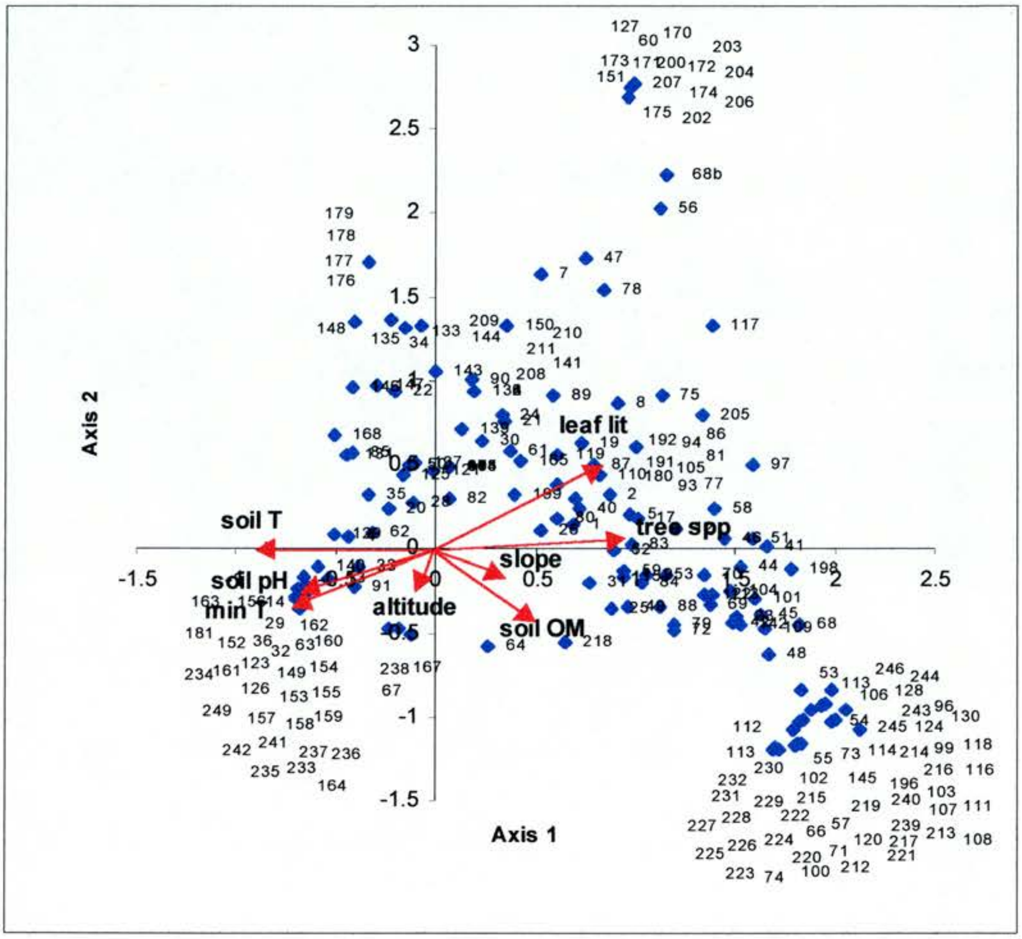
A direct ordination of the reduced ant species data set, which excludes ant species where five or less individuals were collected, and the environmental variables detailed above was carried out using the CANOCO program (ter Braak and Smilauer 1998). The eigenvalues for this analysis are given in Table 6.25 and the scatter plots are shown in Figure 6.34 a and b. The eigenvalue for axis 1 is greater than 0.5, suggesting a good separation of species along the axis. The four axes explain 63.5 percent of the variation. The correlation matrix for the environmental data is shown in Table 6.23. All coefficients with a value higher than 0.7 are shown in red. As in the previous section, clear autocorrelations, such as between leaf litter, trees per hectare and basal area per

**Figure 6.33 CCA ordination biplot of sites, ant species abundances and environmental variables (full species data set)**

a) **Site score plot showing environmental gradients.** The arrows represent the correlation between the axes and the environmental variables. They also indicate which variables are most important in influencing community variation of the sites located closest to the arrowheads.



**b) Species score plot** The arrows represent the correlation between the axes and the environmental variables. Species which are found closest to the arrowheads demonstrate a strongly positive correlation with the variable represented.



hectare, and between maximum temperature and soil temperature have been reduced to one variable in the diagrams. The highest correlation coefficients are found between the same variables as in the full data set analysis and the r values have only changed slightly.

**Table 6.23 Correlation coefficients among environmental variables from the ant species (reduced data set) direct ordination.** CCA weighted correlation matrix output.

| | *leaf lit* | *soil OM* | *soil pH* | *soil T* | *max T* | *min T* | *Slope* | *altitu* | *trees. ha* | *BA.h a* | *tree spp* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***leaf lit*** | 1 | | | | | | | | | | |
| ***soil OM*** | 0.126 | 1 | | | | | | | | | |
| ***soil pH*** | -0.816 | -0.297 | 1 | | | | | | | | |
| ***soil T*** | -0.769 | -0.482 | 0.747 | 1 | | | | | | | |
| ***max T*** | -0.834 | -0.526 | 0.834 | 0.950 | 1 | | | | | | |
| ***min T*** | -0.624 | -0.291 | 0.375 | 0.283 | 0.412 | 1 | | | | | |
| ***slope*** | 0.156 | 0.061 | -0.007 | 0.054 | 0.015 | -0.702 | 1 | | | | |
| ***altitude*** | -0.330 | 0.030 | 0.524 | 0.320 | 0.405 | -0.294 | 0.699 | 1 | | | |
| ***trees.ha*** | 0.946 | 0.270 | -0.749 | -0.685 | -0.791 | -0.699 | 0.191 | -0.251 | 1 | | |
| ***BA.ha*** | 0.927 | 0.230 | -0.662 | -0.793 | -0.781 | -0.642 | 0.141 | -0.162 | 0.893 | 1 | |
| ***tree spp*** | 0.817 | 0.446 | -0.651 | -0.886 | -0.874 | -0.646 | 0.335 | 0.005 | 0.751 | 0.867 | 1 |

**Table 6.24 Correlation coefficients of environmental variables with the CCA ordination axes from the ant species (reduced data set) direct ordination.** CCA weighted correlation matrix output.

| | *SPEC Axis 1* | *SPEC Axis 2* | *SPEC Axis 3* | *SPEC Axis 4* | *ENVI Axis 1* | *ENVI Axis 2* | *ENVI Axis 3* | *ENVI Axis 4* |
|---|---|---|---|---|---|---|---|---|
| ***leaf litter*** | 0.842 | 0.424 | 0.131 | -0.061 | 0.842 | 0.424 | 0.131 | -0.061 |
| ***soil OM*** | 0.450 | -0.366 | 0.009 | -0.053 | 0.450 | -0.366 | 0.009 | -0.053 |
| ***soil pH*** | -0.640 | -0.209 | -0.387 | 0.232 | -0.640 | -0.209 | -0.387 | 0.232 |
| ***soil T*** | -0.843 | 0.023 | -0.139 | 0.144 | -0.843 | 0.023 | -0.139 | 0.144 |
| ***max T*** | -0.902 | -0.027 | -0.253 | 0.208 | -0.902 | -0.027 | -0.253 | 0.208 |
| ***min T*** | -0.645 | -0.303 | 0.425 | -0.099 | -0.645 | -0.303 | 0.425 | -0.099 |
| ***slope*** | 0.305 | -0.159 | -0.551 | 0.411 | 0.305 | -0.159 | -0.551 | 0.410 |
| ***altitude*** | -0.084 | -0.218 | -0.712 | 0.604 | -0.084 | -0.218 | -0.712 | 0.604 |
| ***trees ha*** | 0.827 | 0.459 | 0.188 | 0.112 | 0.828 | 0.459 | 0.188 | 0.112 |
| ***BA ha*** | 0.813 | 0.469 | -0.111 | -0.004 | 0.813 | 0.469 | -0.111 | -0.004 |
| ***tree spp.*** | 0.936 | 0.055 | -0.217 | -0.066 | 0.936 | 0.056 | -0.217 | -0.066 |

**Table 6.25 Eigenvalues and percentage variance for the CCA analysis of ant species (reduced data set) and environmental variables**

| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.729 | 0.368 | 0.321 | 0.284 | 2.681 |
| Cumulative percentage variance of species data | 27.2 | 40.9 | 52.9 | 63.5 | |
| Cumulative percentage variance of species environment relation | 27.2 | 40.9 | 52.9 | 63.5 | |
| Sum of all unconstrained eigenvalues | | | | | 2.681 |

The species data set used in this analysis excludes species with ≤ 5 individuals which reduces it by over 50 percent, from 230 to 101 active species. A comparison of the biplots for the species, sites and environmental data for both the analyses (Figure 6.33 and 6.34) shows that the site groupings and the environmental gradients do not vary greatly from the results of the full data set analysis. However, Figure 6.34b reveals more clearly the dominant individual species which are correlated with the environmental variables and which are also grouped with specific field sites.

As discussed, the environmental data are represented by arrows which are plotted in the direction of maximum change with the length of the arrows being proportional to the magnitude of that change. The longer arrows are more closely correlated in the ordination that the shorter ones, and are therefore more influential in community variation. In addition, species can be related to the arrows by their relative position. Those which are found closest to the arrow tip demonstrate a strongly positive correlation with the variable represented. The most influential environmental variables in the set are leaf litter amount and tree species diversity which strongly correlate with Axis 1. As the arrows which represent them are almost of the same length they have a very similar influence in the community. Soil temperature is the next most important variable. The species found in the two pasture sites are found close to the tip of the arrow representing this variable, although they are also closely grouped around the arrow tips of soil pH and minimum temperature data. This signifies that all three of these variables are important in defining the species assemblage found in the pasture sites. The natural forest sites, PrimFor2, LogFor1 and LogFor2, are grouped separately and the variables which appear to have the most influence on this grouping are soil organic matter and tree species diversity. However, the distance of these sites from the environmental gradient arrow tips implies that the variables are not highly correlated with these sites.

Ant species, which correlate with specific environmental variables, are found near the ends of the corresponding environmental gradient arrows. The biplot shown in Figure 6.34b demonstrates the cluster of species associations with environmental factors, and also with field site. In general the species identified by TWINSPAN as being related to particular field sites are also placed in a similar cluster in the CCA analysis. For example, species 13, 14 and 32 are identified by TWINSPAN as indicators of the pasture sites and when Figure 6.34 a and b are compared it is evident that these species are also located close to the pasture sites in this analysis. The placing of the environmental gradient arrows also implies that they are influenced by soil temperature, soil pH and minimum temperature. In general, the diagrams in Figure 6.34 demonstrate significant correlations between environmental variables and related sites and species. The species assemblage is clustered by broad land use type with natural forest, and plantation and pasture being separated over the analysis. This implies that land use itself is conditioned by environmental differences. The environmental gradients also reveal which factors are most important in driving the species changes that occur across the gradient of human disturbance.

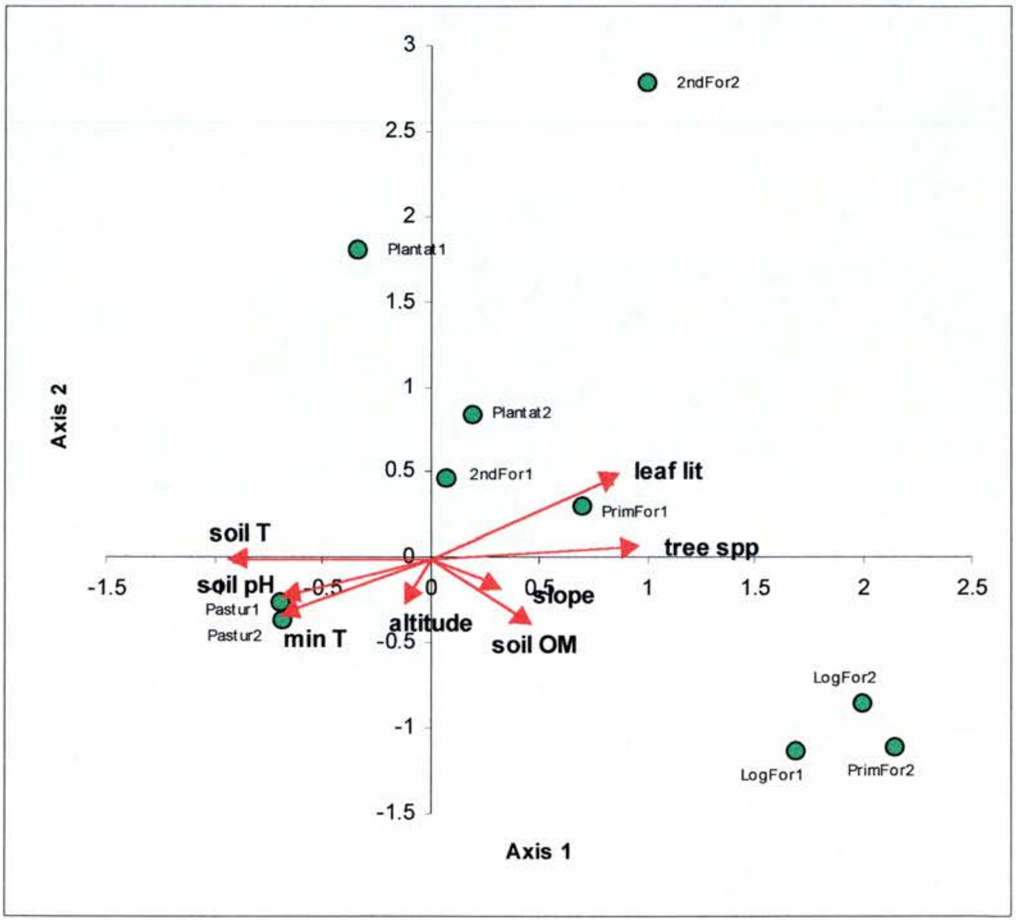
## 6.9 Summary and conclusions

### CHANGES IN ANT SPECIES RICHNESS AND COMPOSITION OVER A GRADIENT OF DISTURBANCE

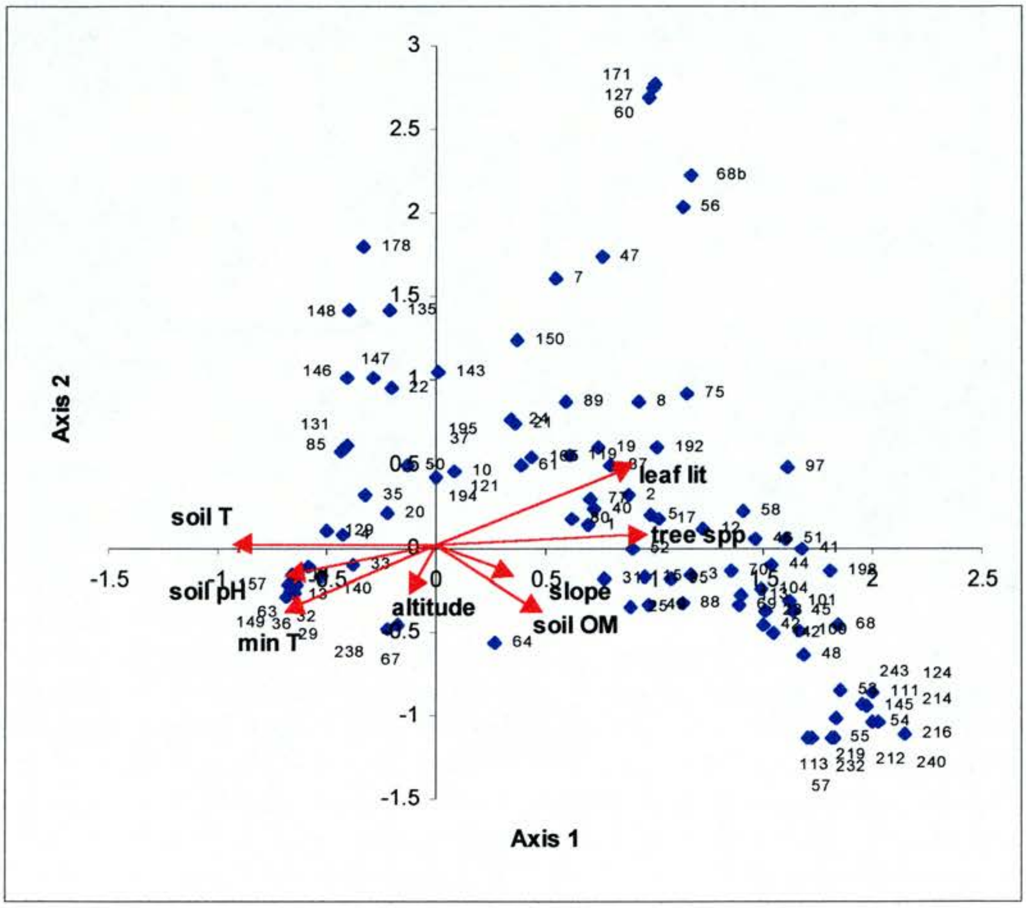
Ant species composition changed significantly over the gradient of human disturbance represented by field sites, which ranged from primary forest, to logged primary forest, secondary forest, plantation and pasture. Ants were considerably more abundant (six times) in pasture sites than in all other sites. Species richness (*S*) was also significantly different between most land uses.

## Figure 6.34 CCA ordination biplot of sites, ant species abundances and environmental variables (reduced species data set)

a) **Site score plot showing environmental gradients.** The arrows represent the correlation between the axes and the environmental variables. They also indicate which variables are most important in influencing community variation of the sites located closest to the arrowheads.



**b) Species score plot**. The arrows represent the correlation between the axes and the environmental variables. Species which are found closest to the arrowheads demonstrate a strongly positive correlation with the variable represented.



It is important to note that estimates of 'total biodiversity loss (or gain)' are not necessarily the best measures of human impact as species richness is not only dependent on loss rates of forest species, but also on invasion rates by disturbed area species. This may explain why not all sites have significantly different species richness. Figure 6.26 illustrates that the actual number of species is not greatly altered over the different land uses but that the species composition is very different.

The principal dichotomy in the TWINSPAN classification of ant species composition was between the natural forest sites (primary and logged primary forest) and the pasture and plantation sites. Secondary separation in the natural forest sites cluster was strongly geographical with closely located field sites grouped together. This may be due to pre-disturbance species assemblage similarities, or to similar environmental factors, or both. Secondary separation in the disturbed site cluster removed one of the secondary forest sites and left pasture and plantation together. These groupings were also indicated by a DCA analysis.

A CCA analysis identified the importance of a variety of environmental variables in ant species composition. Leaf litter quantity, tree species diversity and soil temperature were identified as three of the most important factors in explaining variation. Other significant variables were soil pH, air temperature, and soil organic matter. The physical site variables of slope and altitude were shown to have a smaller influence on species composition than the environmental factors. Other significant environmental variables that co-varied with leaf litter quantity were the number of trees per hectare, and basal area per hectare, while maximum air temperature co-varied with soil temperature. Ant species composition responded strongly to these differing environmental gradients, with the CCA analysis grouping specific species both along the environmental gradients and associating them with particular field sites and land uses. The nine environmental variables, coupled with the two physical variables, explained the major variation in species composition. This related primarily to leaf litter quantity, tree species diversity and soil temperature, along the first axis of the CCA, and altitude along the third axis.

### $\beta$ – DIVERSITY OF ANT SPECIES IN A LOWLAND TROPICAL FOREST LANDSCAPE

Indices of similarity between land uses and sites over a gradient of increasing disturbance show that the sites have different ant species composition. $\beta$ – diversity is higher between sites which share fewer species, and is proportional to the inverse of similarity. The analysis indicates that sites at opposite ends of the disturbance gradient demonstrate the lowest similarity. A cluster analysis using Morisita's Index of Similarity demonstrated an obvious grouping of field sites by land use and degree of human intervention (Figure 6.28). This suggests a clear effect of forest disturbance on $\beta$ – diversity.

### A CLASSIFICATION OF ANT SPECIES RESPONSES TO FOREST DISTURBANCE AND CONVERSION

The ant species collected in this study were strongly ordered along both the DCA and CCA axes. Different species showed different responses to forest disturbance and conversion, ranging from generalist species that were distributed ubiquitously over the gradient of disturbance, to specialist forest species and disturbed area species.

The TWINSPAN analysis identified species 45, *Pheidole* sp., Myrmicinae, as a 'perfect indicator' for natural forest. This species is not found in either the plantation or pasture sites. TWINSPAN also identified other species in the natural forest sites, the majority of these found in the Myrmicinae sub-family. This may suggest a preference by Myrmicinae species for natural forest, although this sub-family is the most species rich in all the land uses (Section 6.4). *Pheidole* sp. falls into the 'litter omnivore and scavenger' guild according to Delabie et al. (2000) but there are insufficient data to allocate the other natural forest species to guilds.

The ant species identified by the TWINSPAN and CANOCO analyses as being of a ubiquitous distribution are generally found in the Myrmicinae and Ponerinae sub-families. Indeed the most abundant ant in the study is a Ponerinae (Species 13). The analyses also revealed a number of species as being primarily found in the disturbed sites. These species range across four of the five ant sub-families found in the study, the only one not represented is the Ponerinae. Species 14 (*Monomorium* sp., Myrmicinae) was identified as a strong indicator of disturbance as it is particularly abundant in the pasture and plantation sites.

Due to the large dataset, many species were identified only to sub-family and morphospecies. This, coupled with the limited information available regarding ant species guilds (Delabie et al. 2000), has made it difficult to draw conclusions regarding the effects of change on specific guilds and species from the sample presented in this study. It is, however, evident that forest disturbance and conversion to plantation and pasture does significantly affect the diversity and abundance of leaf-litter ant species.

Other studies have shown varied effects of forest disturbance or conversion on leaf litter ants. Belshaw and Bolton (1993) present results showing that there was no effect on species richness or diversity of the leaf litter ant fauna after forest clearance and the establishment of cocoa farms. Watt et al. (in press) showed differences in canopy ant species composition after different methods of forest clearance although they concluded that silvicultural treatment had no consistent effect on leaf litter ant species composition. King et al. (1998) have shown that forest disturbance, particularly involving canopy clearance causes changes in ant species composition. They demonstrate that habitat disturbance favoured opportunists and that this led to colonisation by dominant Dolichoderines. Vasconcelos et al. (2000) examined the response of central Amazonian ants to selective logging. They observed that species richness and evenness did not vary with logging activity but that the population density of many species was changed. They conclude that the persistence of ant assemblages typical of undisturbed forest may depend on the degree of structural damage incurred by logging.

Roth et al. (1994) also conclude that species diversity and evenness is greatly altered in disturbed sites, such as cacao and banana plantations, but also show that abandoned cacao plantations had a similar diversity to forest sites. In general, it is believed that greater levels of disturbance, such as after conversion of mature forest into pasture or agricultural land have a negative effect on ant species richness and evenness, and that abundance is considerably altered (Mackay et al. 1991, Roth et al. 1994, Vasconcelos

1999). This study has also shown that forest disturbance, by selective logging, and conversion to plantation and pasture have a marked effect on leaf litter ant species composition and abundance. Species richness remains similar but the loss of forest species and gain of disturbed site species which occurs is not accounted for in this measure. It appears that the mosaic of land uses found in the north of Costa Rica may facilitate the conservation of the leaf litter ant fauna, however, it is evident that the natural forest sites are especially important in their maintenance. Without these forest remnants of primary, or logged primary, forest the ant species assemblage may be dramatically altered.

# CHAPTER 7

# THE RESPONSE OF LEAF LITTER INVERTEBRATES TO TROPICAL FOREST DISTURBANCE AND CONVERSION:

# I. THE BEETLES

## 7.1 Introduction

'We live in the Age of Beetles. Beetles inhabit nearly every biological niche, from the narrow fringes of polar ice caps to the broad, unexplored expanse of rain forest canopy. Using sheer numbers of species as a criterion for success beetles are the most successful animals on Earth' (Evans and Bellamy 1996).

The beetle fauna of moist tropical forests is enormously rich in species (Wagner 2000). This species richness and corresponding abundance make the beetles good ecological indicators. In addition, they are taxonomically well known, widely distributed as a group and are sensitive to environmental changes (Rykken et al. 1997). They fulfil vital roles in processes such as decomposition, pollination, seed dispersal and nutrient cycling (Sutton and Collins 1991, Didham et al. 1996).

This chapter examines the leaf litter beetle fauna of a northern Costa Rican forest landscape and its response to human disturbance. It examines the consequences of forest conversion and land use change on beetles species diversity, abundance and composition. Following the model established in Chapter 6, the response of beetles species to disturbance is related to a variety of environmental variables. Evidence is presented for the changes that occur in leaf litter Coleoptera after logging and clearing of lowland evergreen rain forest. It is interesting then to compare the results from the previous chapter, which focuses on the ant fauna, with the data presented here in order to evaluate their comparative importance in biodiversity conservation planning. This comparison will be made in the following, final chapter.

## 7.2 Objectives

The aims of this chapter are to:

- provide an overview of the neotropical beetle fauna and to discuss its importance within the forest ecosystem (Section 7.3);
- describe the changes that occur in species composition, diversity and abundance of leaf litter beetles over a landscape of human disturbance (Section 7.4, 7.5, 7.6);
- relate changes in species composition to environmental changes in forest and converted forest (Sections 7.7 and 7.8); and
- assess the effects of logging, and forest conversion to other land uses, on the beetle fauna (Section 7.9).

## 7.3 The beetles

The order Coleoptera is the largest order of insects and contains approximately 40 percent of the known species in the class Hexapoda (Borror et al. 1981). There are 166 families, and 370,000 species of beetles have been described (McGavin 2000).

One of the most distinctive features of the Coleoptera is the structure of the wings. Most have four wings, a thickened front pair known as the elytra, which meet in a straight line down the middle of the back and cover the hind wings. This order has chewing mouthparts and the mandibles are well developed. Beetles undergo complete metamorphosis (Borror et al 1981). The larvae are diverse in form in different families. The life cycle of beetles varies in length from four generations a year to one generation in several years, but the most common life cycle consists of one generation a year.

Beetles are found in almost every habitat type. They feed on various plant and animal materials. Some are phytophagous, many are predacious, some are scavengers, some feed on mould and fungi, and a few are parasitic. Of the phytophagous species many are free feeders on foliage, some are wood or fruit borers, some are leaf miners, some attack the roots, and some feed on the flowers (Borror et al. 1981).

It is evident that beetles are a vital component of the ecosystem and serve many functional roles. They have also been identified as good ecological indicators as a result of their sensitivity to changes in environmental conditions. The following sections examine the effects of habitat change on the beetle fauna of a disturbed landscape in northern Costa Rica, in order to assess the conservation potential of such landscapes.

## 7.4 The leaf litter beetle fauna of a northern Costa Rican landscape of disturbance

The leaf litter beetle fauna of a northern Costa Rican forest landscape was sampled and sorted according to the methodology described in Chapter 4. The beetles were sorted to morphospecies (hereafter referred to as 'species'). A total of 1877 beetles comprising 422 species, and 26 families, were recorded. The dominant family in the Coleoptera assemblage was the Staphylinidae with 169 species. The Nitidulidae was the next most speciose with 60 species (Table 7.1). In terms of abundance the Staphylinidae had the highest number of individuals followed by the Nitidulidae. The most common beetle was a staphylinid, or rove beetle (species no. 217, Appendix 9). There were 183 individuals of this species collected throughout the study and these made up nearly 10 percent of the total number of individuals sampled. The second most abundant beetle was also a staphylinid (species no. 318, Appendix 9), and with 71 individuals this made up four percent of the total number of individuals. The 50 most common species together made up 61 percent of the total number of individuals whilst the 25 most common species made up 48 percent (Figure 7.1). The number of species represented by a single individual was 210. The beetles sampled cover a range of trophic groups including fungivores, herbivores, predators, saprophages, xylophages and xylomeysetophages (Table 7.1)

As with the ant data, it was evident that the beetle samples were taken from a large species pool. This can be seen from the slopes of the total species accumulation curve which did not begin to reach a plateau, indicating low dominance and a high number of rare species (Figure 7.2). Fifty-two percent of these rare species were singletons (species represented by a single individual).

**Figure 7.1 Rank-abundance plot of beetles sampled in northern Costa Rica 1998-1999**

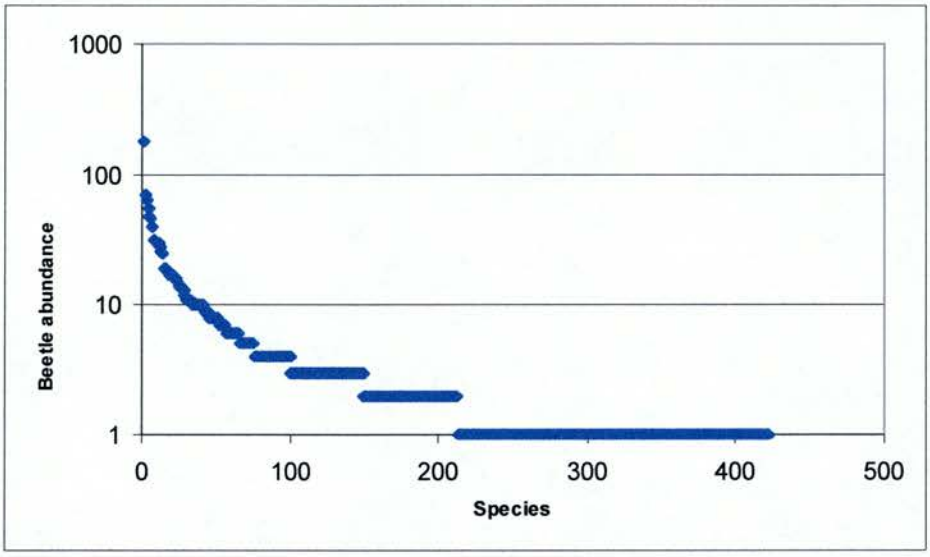
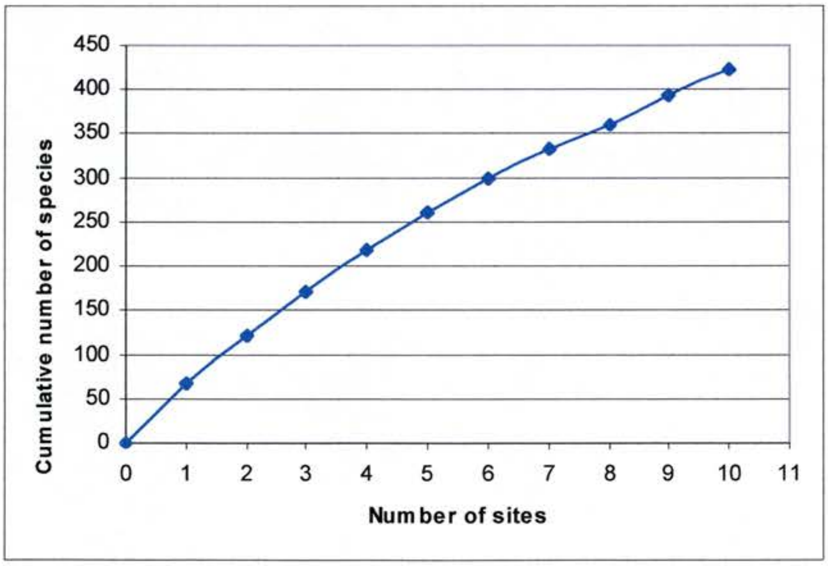


**Figure 7.2 Species accumulation curve for leaf-litter beetles over a gradient of disturbance in northern Costa Rica.**

Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



The next section presents the beetle species diversity and composition data over the five land uses sampled. It provides a more detailed examination of the leaf litter beetle assemblage in each of the field sites considering their respective level of human impact.

**Table 7.1 Beetles species assemblage sampled from ten field sites ranging over a gradient of human disturbance from primary forest to pasture in northern Costa Rica, Central America.** Trophic group assignments (Didham 1996, Hammond 1990): F = fungivore, H = herbivore, Pr = predator, S = saprophage, X = xylophage, XF = xylomeysetophage (specialists on *ambrosia* fungus in wood).

| *Family* | *Species Richness* | *Abundance* | *% Total Abundance* | *Trophic group* |
|---|---|---|---|---|
| Anthicidae | 1 | 3 | 0.2 | S |
| Biphyllidae | 2 | 2 | 0.1 | F |
| Carabidae | 41 | 94 | 5.0 | Pr |
| Chrysomelidae | 14 | 24 | 1.3 | H |
| Coccinellidae | 2 | 2 | 0.1 | Pr |
| Curculionidae | 13 | 16 | 0.9 | H, X, XF |
| Elateridae | 6 | 14 | 0.7 | H, Pr, X |
| Endomychidae | 1 | 1 | 0.1 | F |
| Histeridae | 3 | 11 | 0.6 | Pr |
| Hydrophilidae | 7 | 24 | 1.3 | Pr |
| Languriidae | 1 | 1 | 0.1 | F |
| Lathridiidae | 1 | 1 | 0.1 | F |
| Leiodidae | 15 | 226 | 12.0 | F, S |
| Limnichidae | 9 | 14 | 0.7 | S |
| Meloidae | 1 | 3 | 0.2 | ? |
| Mordellidae | 1 | 1 | 0.1 | H, F, X |
| Nitidulidae | 60 | 271 | 14.4 | F, S, H, Pr |
| Noteridae | 1 | 1 | 0.1 | ? |
| Phalacridae | 1 | 3 | 0.2 | F, H |
| Pselaphidae | 7 | 9 | 0.5 | Pr |
| Ptilidae | 3 | 3 | 0.2 | F, S |
| Scarabaeidae | 27 | 51 | 2.7 | S, H |
| Scolytidae | 20 | 109 | 5.8 | X, F |
| Scydmaenidae | 13 | 45 | 2.4 | Pr |
| Staphylinidae | 169 | 945 | 50.3 | F, Pr, S |
| Tenebrionidae | 3 | 3 | 0.2 | F, H, S |
| **TOTAL** | **422** | **1877** | **100.0** | |

## 7.5 Leaf litter beetle species and composition by land use

This section follows the model established in Section 6.5. Each land use is presented in sub-sections, documenting species richness and abundance per site with each site being addressed separately and then compared. The sub-sections also examine species richness and abundance by ant subfamily, and investigate the similarity of the sites in each land use, by calculation of beetle species composition similarity indices. Species accumulation curves are used to compare species richness in both sites in each land use. Finally, the numbers of species shared between each land use are presented. A final discussion section summarises and compares the findings.

### 7.5.1 Leaf litter beetles in primary forest

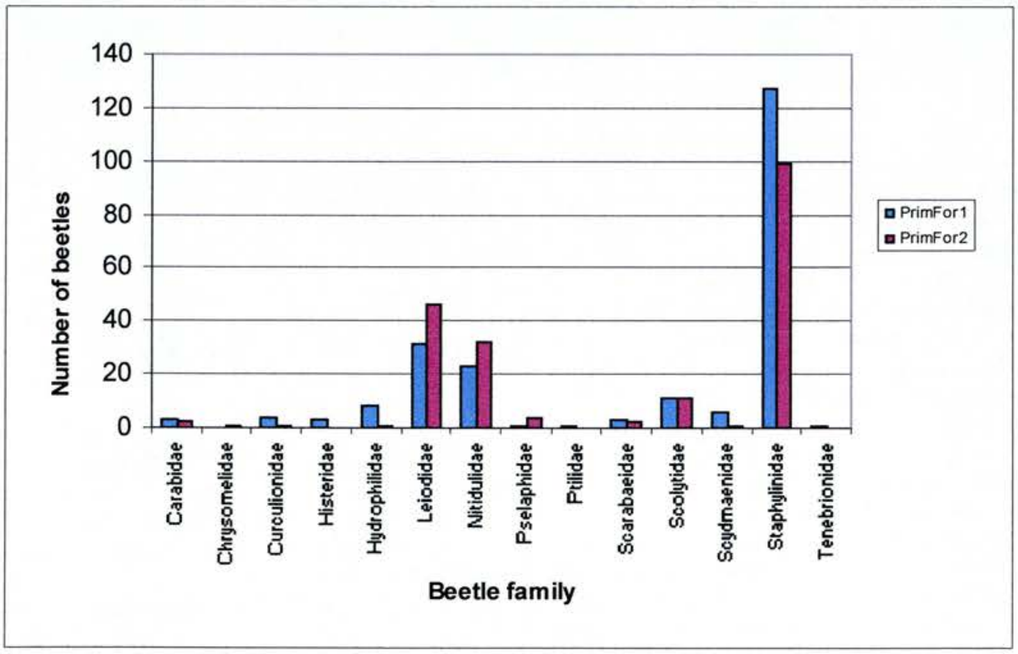
This sub-section examines the leaf litter beetle fauna of two primary forests in northern Costa Rica. The two primary forest sites considered (PrimFor1 and PrimFor2) have been discussed in greater detail in Chapters 3 and 6. Patterns of beetle species diversity and composition are examined here in order to provide baseline information on leaf litter beetle populations in the 'control' sites of minimal human impact.

During this study 94 species and 222 individuals were collected in primary forest site 1 while 77 species and 200 individuals were collected in primary forest site 2. This comprised of 148 species and 422 individuals in total. The species ranged over 13 of the 26 families collected over the study area. The dominant family in the primary forest assemblage was the Staphylinidae with 47 species in site 1 and 38 in site 2. The Nitidulidae was the next most speciose in both sites with 16 and 15 species respectively in sites 1 and 2. The third most speciose family was the Leiodidae, with 5 species in site 1 and 6 species in site 2 (Table 7.2 and Figure 7.3).

## Table 7.2 Primary forest beetle species assemblage

| Family | Primary forest 1 | | Primary forest 2 | | Primary forest total | |
|---|---|---|---|---|---|---|
| | Species Richness | Abundance | Species Richness | Abundance | Species Richness | Abundance |
| Carabidae | 2 | 3 | 2 | 2 | 4 | 5 |
| Chrysomelidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Curculionidae | 4 | 4 | 1 | 1 | 5 | 5 |
| Histeridae | 2 | 3 | 0 | 0 | 2 | 3 |
| Hydrophilidae | 3 | 8 | 1 | 1 | 3 | 9 |
| Leiodidae | 5 | 31 | 6 | 46 | 7 | 77 |
| Nitidulidae | 16 | 23 | 15 | 32 | 26 | 55 |
| Pselaphidae | 1 | 1 | 4 | 4 | 5 | 5 |
| Ptilidae | 1 | 1 | 0 | 0 | 1 | 1 |
| Scarabaeidae | 3 | 3 | 2 | 2 | 5 | 5 |
| Scolytidae | 5 | 11 | 6 | 11 | 9 | 22 |
| Scydmaenidae | 4 | 6 | 1 | 1 | 5 | 7 |
| Staphylinidae | 47 | 127 | 38 | 99 | 74 | 226 |
| Tenebrionidae | 1 | 1 | 0 | 0 | 1 | 1 |
| **TOTALS** | **94** | **222** | **77** | **200** | **148** | **422** |

## Figure 7.3 Primary forest beetle species richness by family



The pattern of abundance of beetle individuals by family was similar over the two field sites. In both cases the staphylinids were the most abundant (PrimFor1, n=127;

PrimFor2, n=99) followed by the Leiodidae (PrimFor1, n=31; PrimFor2, n=46) and then the Nitidulidae (PrimFor1, n=23; PrimFor2, n=32)(Figure 7.4). The most common species in primary forest site 1 was a staphylinid (species 27)(Table 7.3)(Appendix 9) which made up 17% of the total number of individuals sampled. The second most abundant species in site 1 was from the Leiodidae (species 39) and it made up 6% of all individuals in this site. The 25 most common species together made up 66% of the total number of individuals sampled while the 10 most common made up 78%. Of the species collected, 62 were represented by single individuals. In site 2, the most common beetle was from the Leiodidae (species 39)(Table 7.3)(Appendix 9) which made up 10% of the total number of individuals sampled. The second most abundant species in site 2 was again from the Leiodidae (species 218) and it made up 9% of all individuals in this site. The 25 most common species together made up 72% of the total number of individuals sampled while the 10 most common made up 49%. Of the species collected in this site, 47 were represented by single individuals.

**Figure 7.4 Primary forest beetle species abundance by family**

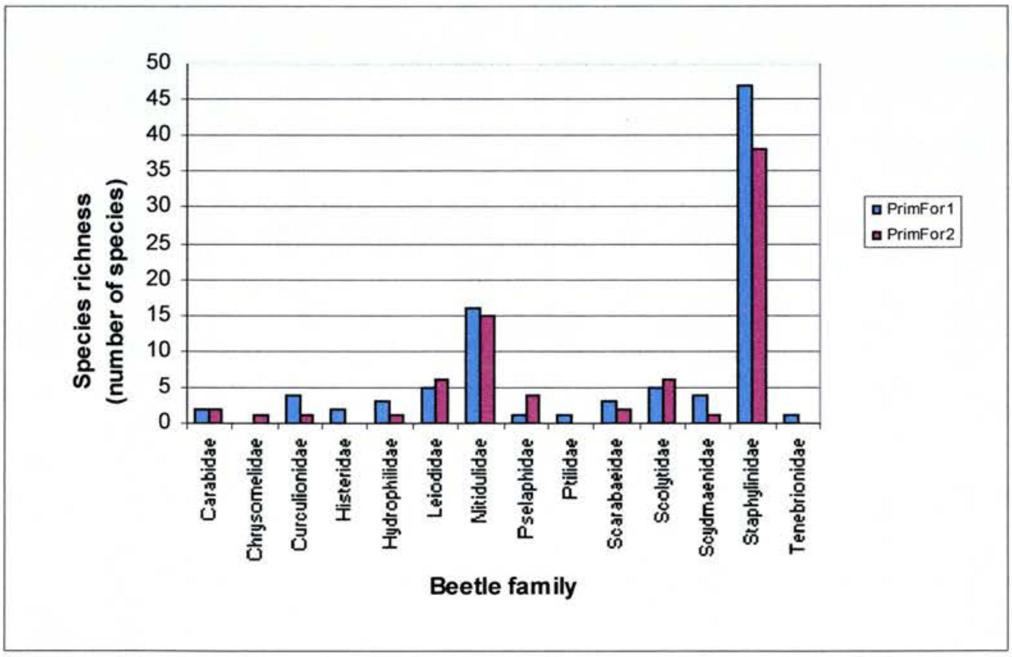


**Table 7.3 The ten most abundant beetle species in the primary forest sites, northern Costa Rica**

| Species number | PrimFor1 | Species number | PrimFor2 |
|---|---|---|---|
| 27 | 38 | 39 | 19 |
| 39 | 13 | 218 | 17 |
| 42 | 12 | 217 | 16 |
| 184 | 9 | 48 | 11 |
| 102 | 7 | 105 | 7 |
| 24 | 5 | 191 | 7 |
| 25 | 5 | 240 | 6 |
| 53 | 5 | 10 | 5 |
| 105 | 5 | 102 | 5 |
| 216 | 5 | 24 | 4 |

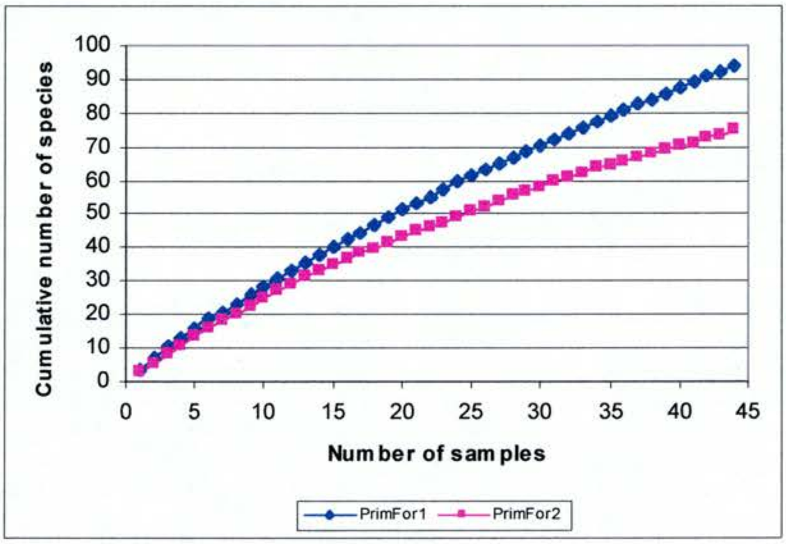
Figure 7.3 illustrates the similarities in family composition between the two primary forest sites. The two family level species data sets show a high correlation (Pearson product moment correlation coefficient, natural log (ln) transformed data: $r = 0.78$, $p = 0.006$). In addition family species distributions were shown not to be significantly different between the two primary forest sites (Mann Whitney-U test: $p = 0.814$) thus demonstrating a statistically similar family composition between sites.

Calculation of similarity indices (Krebs, 1989) revealed that compared to values calculated between many of the other sites these two sites showed a level of similarity. Sorensen's coefficient gave a value of 0.26, while Morisita's index of similarity gave a value of 0.37 (Tables 7.15 and Table 7.16). The sites shared 23 species. This represented 10% and 12% of the species found in sites 1 and 2 respectively.

Figure 7.5 illustrates the species accumulation curves for both the primary forest sites. As with the ant data, PrimFor1 tended towards a higher overall species richness, although both curves indicate that the actual species richness in these sites was much higher. Jackknife estimates of species richness (calculated by the EstimateS program, Colwell 1999) indicated species richness values for PrimFor1 of 163 ± 8.8 and for PrimFor2 of 127 ± 7.4 (Figure 7.20).

To summarise, over the two primary forest sites 148 beetles species consisting of 422 individuals were collected. The Staphylinidae were the most speciose family followed by the Nitidulidae. The beetle family composition was statistically similar between the two sites although species similarity was lower, as shown by beta diversity measures of species similarity. Jackknife estimates of species richness (Colwell 1999) reveal a highly diverse beetle community in the primary forest sites studied.

**Figure 7.5 Species accumulation curves for leaf litter beetles in primary forest, northern Costa Rica**



### 7.5.2 Leaf litter beetles in selectively logged forest

The insect fauna of selectively logged forest is an important component of the ecosystem and may indicate the intensity or standard of logging carried out. This section investigates the leaf litter beetle fauna of two logged forest sites (LogFor1 and LogFor2). The two sites have been harvested for timber in the past and these activities have been detailed in Chapter 3.

During this study 93 species and 433 individuals were collected in logged forest site 1 while 117 species and 427 individuals were collected in logged forest site 2. This comprised of 173 species and 860 individuals in total. Species represented 16 of the 26 families collected over the study area. The dominant family in the logged forest assemblage was the Staphylinidae with 41 species in site 1 and 52 in site 2. The Nitidulidae was the next most speciose in both sites with 15 and 19 species respectively in sites 1 and 2. The third most speciose family was the Scolytidae, with 10 species in site 1 and 13 species in site 2 (Table 7.4 and Figure 7.6).

## Table 7.4 Logged forest beetle species assemblage

| *Family* | *Logged forest 1* | | *Logged forest 2* | | *Logged forest total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Biphyllidae | 0 | 0 | 2 | 2 | 2 | 2 |
| Carabidae | 6 | 6 | | | 6 | 6 |
| Chrysomelidae | 2 | 5 | 4 | 4 | 6 | 9 |
| Curculionidae | 0 | 0 | 2 | 2 | 2 | 2 |
| Endomychidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Hydrophilidae | 3 | 7 | 1 | 1 | 4 | 8 |
| Leiodidae | 7 | 69 | 9 | 74 | 12 | 143 |
| Nitidulidae | 15 | 38 | 19 | 44 | 29 | 82 |
| Noteridae | 1 | 1 | 1 | 1 | 1 | 1 |
| Pselaphidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Ptilidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Scarabaeidae | 4 | 6 | 9 | 16 | 12 | 22 |
| Scolytidae | 10 | 46 | 13 | 28 | 17 | 74 |
| Scydmaenidae | 3 | 6 | 3 | 3 | 5 | 9 |
| Staphylinidae | 41 | 248 | 52 | 250 | 73 | 498 |
| Tenebrionidae | 1 | 1 | 0 | 0 | 1 | 1 |
| **TOTALS** | **93** | **433** | **117** | **427** | **173** | **860** |

The pattern of abundance of beetle individuals by family was similar over the two field sites. In both cases the staphylinids were the most abundant (LogFor1, n=248; LogFor2, n=250) followed by the Leiodidae (LogFor1, n=69; LogFor2, n=74) and then the Nitidulidae (LogFor1, n=38; LogFor2, n=44)(Figure 7.7). The most common species in logged forest site 1 was a staphylinid (species 217)(Table 7.5)(Appendix 9) which made up 29% of the total number of individuals sampled. The second most abundant species in site 1 was from the Leiodidae (species 173) and it made up 9% of all individuals in this site. The 25 most common species together made up 77% of the total number of individuals sampled while the 10 most common made up 62%. Of the species collected, 45 were represented by single individuals. Of the species collected, 62 were represented by single individuals. In site 2, the most common beetle was also a staphylinid (species 318)(Table 7.5)(Appendix 9) which made up 17% of the total number of individuals sampled. The second most abundant species in site 2 was again a staphylinid (species 217) and it made up 9% of all individuals in this site. The 25 most common species together made up 71% of the total number of individuals sampled while the 10 most common made up 53%. Of the species collected at this site, 67 were represented by single individuals.

**Figure 7.6 Logged forest beetle species richness by family**

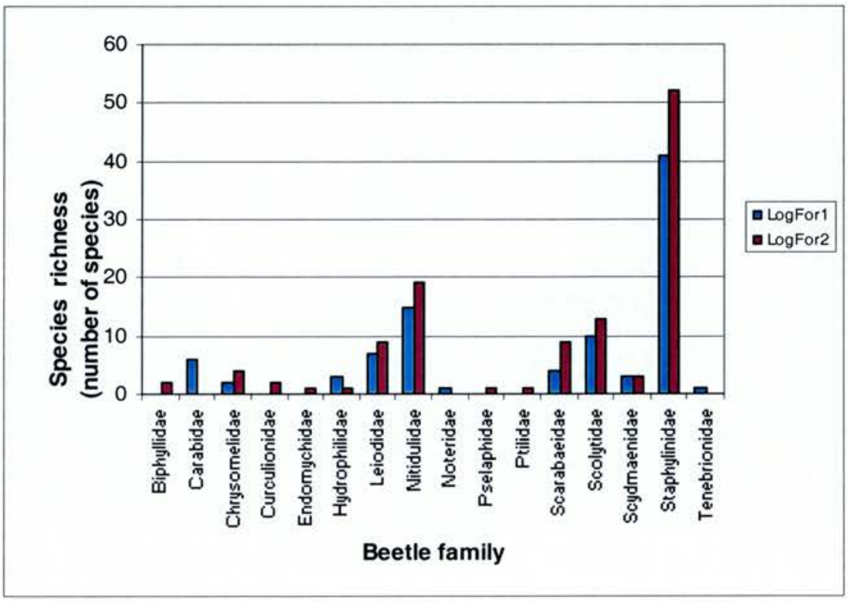


**Figure 7.7 Logged forest beetle species abundance by family**

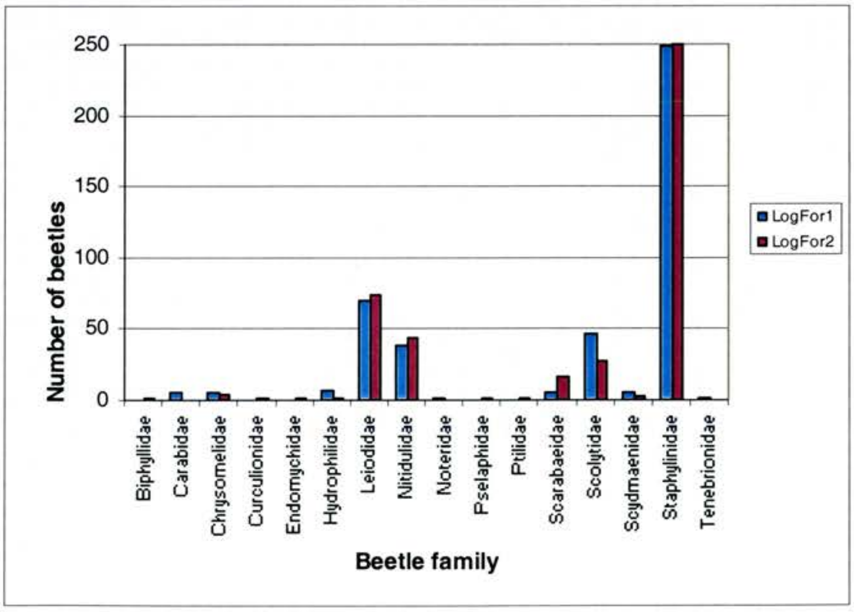


**Table 7.5 The ten most abundant beetle species in the logged forest sites, northern Costa Rica**

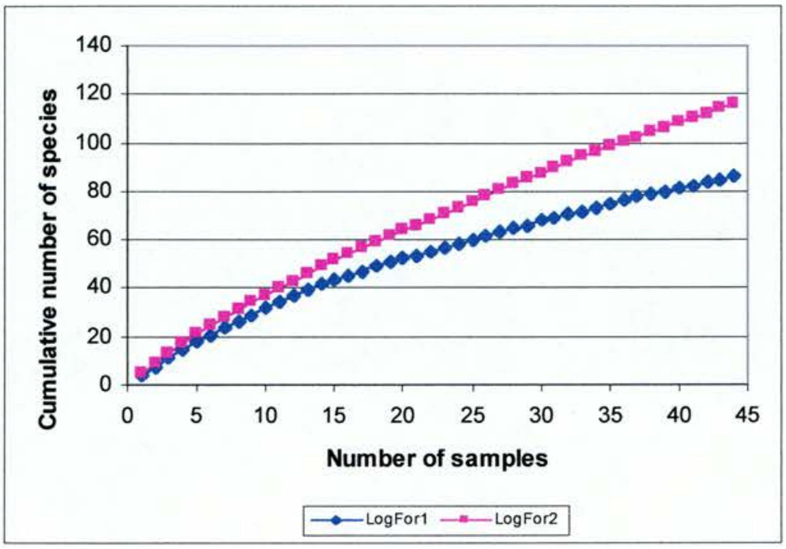
| *Species number* | *LogFor1* | *Species number* | *LogFor2* |
|---|---|---|---|
| 217 | 127 | 318 | 71 |
| 173 | 38 | 217 | 37 |
| 24 | 25 | 39 | 23 |
| 42 | 20 | 173 | 23 |
| 216 | 18 | 2b | 15 |
| 201 | 11 | 42 | 14 |
| 247 | 10 | 102 | 13 |
| 96 | 7 | 201 | 12 |
| 97 | 7 | 10 | 9 |
| 36 | 6 | 47 | 9 |

Figure 7.6 illustrates the similarities in family composition between the two logged forest sites. The two family level species data sets showed a high correlation (Pearson product moment correlation coefficient, ln transformed data: $r = 0.91$, $p = 0.001$). In addition family species distributions were shown not to be significantly different between the two logged forest sites (Mann Whitney-U test: $p = 0.703$) thus demonstrating a statistically similar family composition between sites.

Calculation of similarity indices (Krebs, 1989) revealed the similarity between the two sites. Sorensen's coefficient gave a value of 0.35, while Morisita's index of similarity gave a value of 0.47 (Tables 7.15 and Table 7.16). The sites shared 37 species, which was 9% of the species found in both sites 1 and 2.

Figure 7.8 illustrates the species accumulation curves for both the logged forest sites. LogFor1 tends towards a higher overall species richness, although both curves indicate that the actual species richness in these sites is much higher. Jackknife estimates of species richness (calculated by the EstimateS program, Colwell 1999) indicate species richness values for LogFor1 of 135 ± 8.7 and for LogFor2 of 195 ± 8.8 (Figure 7.19).

**Figure 7.8 Species accumulation curves for leaf litter beetles in logged forest, northern Costa Rica**



In summary, the two logged forest site samples contained 173 beetle species consisting of 860 individuals. As in the primary forest sites, the Staphylinidae were the most speciose family followed by the Nitidulidae. Beetle family composition was statistically similar between the two sites although species similarity was lower, as shown by beta diversity measures of species similarity. Jackknife estimates of species richness (Colwell 1999) reveal a highly diverse beetle community and indicate that the selectively logged sites contained a higher number of leaf litter layer beetle species than the undisturbed primary forest sites. This may have been a result of the increased habitats and niches which are opened to non-forest specialists by logging activities.

### 7.5.3 Leaf litter beetles in secondary forest

The two secondary forest sites examined here consist of areas of regenerating forest where previous clearance to pasture or agriculture has occurred. The two sites are discussed in greater detail in Chapter 3. This section examines the species and family composition and diversity of the leaf litter beetle fauna.

During this study 64 species and 121 individuals were collected in secondary forest site 1 while 53 species and 90 individuals were collected in secondary forest site 2. This comprised of 109 species and 211 individuals in total. The species ranged over 13 of the 26 families collected over the study area. The dominant family in the secondary forest assemblage was the Staphylinidae with 25 species in site 1 and 20 in site 2. The Nitidulidae was the next most speciose in both sites with 17 and 14 species respectively in sites 1 and 2. The third most speciose family was the Carabidae, with 6 species in site 1 and 5 species in site 2 (Table 7.6 and Figure 7.9).

### Table 7.6 Secondary forest beetle species assemblage

| *Family* | *Secondary forest 1* | | *Secondary forest 2* | | *Secondary forest total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Carabidae | 6 | 11 | 5 | 9 | 11 | 20 |
| Chrysomelidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Curculionidae | 3 | 3 | 3 | 3 | 5 | 6 |
| Hydrophilidae | 0 | 0 | 2 | 3 | 2 | 3 |
| Leiodidae | 3 | 5 | 1 | 1 | 4 | 6 |
| Nitidulidae | 17 | 41 | 14 | 31 | 27 | 72 |
| Pselaphidae | 1 | 1 | 0 | 0 | 1 | 1 |
| Ptilidae | 1 | 1 | 0 | 0 | 1 | 1 |
| Scarabaeidae | 2 | 2 | 3 | 3 | 5 | 5 |
| Scolytidae | 4 | 8 | 2 | 2 | 6 | 10 |
| Scydmaenidae | 2 | 2 | 1 | 1 | 3 | 3 |
| Staphlinidae | 25 | 47 | 20 | 35 | 42 | 82 |
| Tenebrionidae | 0 | 0 | 1 | 1 | 1 | 1 |
| **TOTALS** | **64** | **121** | **53** | **90** | **109** | **211** |

The pattern of abundance of beetle individuals by family was similar over the two field sites. In both cases the staphylinids were the most abundant (2ndFor1, n=47; 2ndFor2, n=35) followed by the Nitidulidae (2ndFor1, n=41; 2ndFor2, n=31) and then the Carabidae (2ndFor1, n=11; 2ndFor2, n=9)(Figure 7.11). The most common species in secondary forest site 1 was from the Nitidulidae (species 4)(Table 7.7)(Appendix 9) which made up 10% of the total number of individuals sampled. The second most abundant species in site 1 was a staphylinid (species 112) and it made up 6% of all individuals in this site. The 25 most common species together made up 66% of the total number of individuals sampled while the 10 most common made up 40%. Of the species collected, 37 were represented by single individuals. In site 2, the most common beetle was also from the Nitidulidae (species 188)(Table 7.7)(Appendix 9) which made up 9% of the total number of individuals sampled. The second most abundant species in site 2 was again a staphylinid (species 3) and it made up 8% of all individuals in this site. The 25 most common species together made up 69% of the total number of individuals sampled while the 10 most common made up 42%. Of the species collected at this site, 38 were represented by single individuals.

**Figure 7.9 Secondary forest beetle species richness by family**

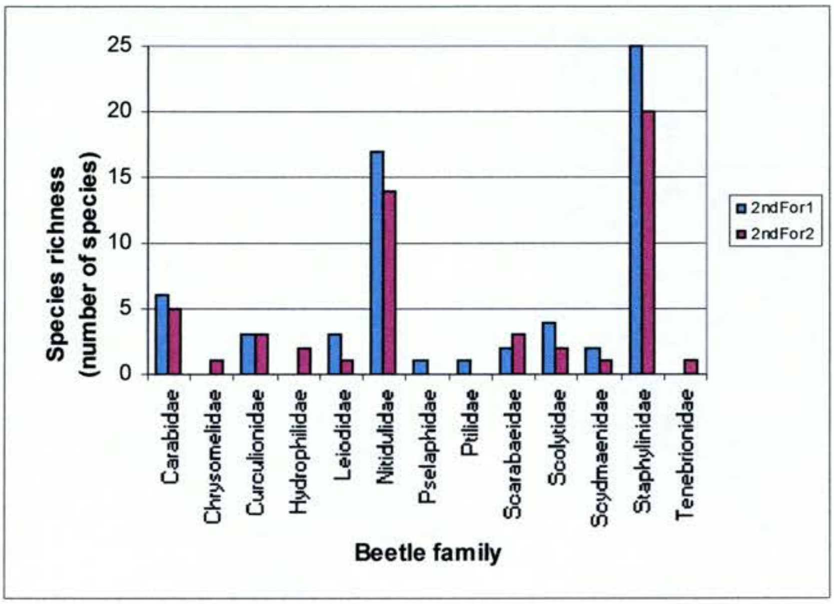


**Figure 7.10 Secondary forest beetle species abundance by family**

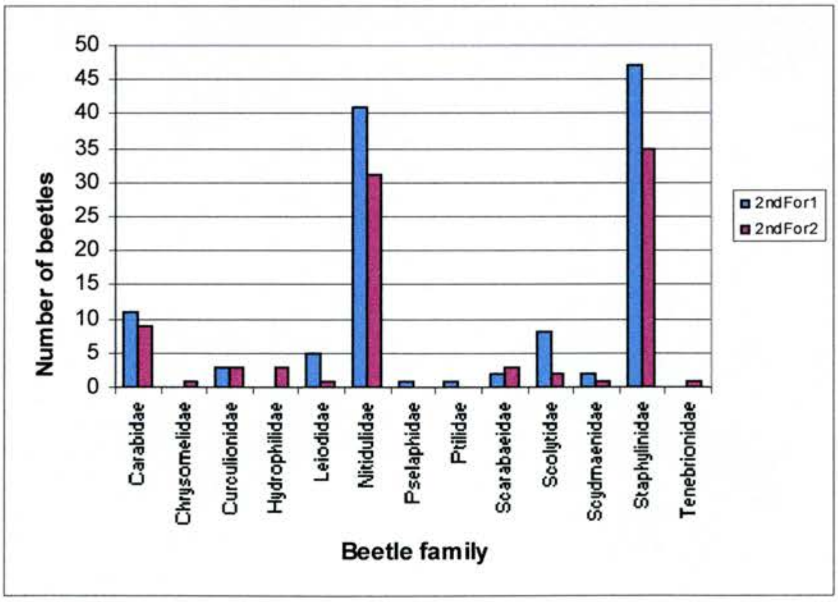


**Table 7.7 The ten most abundant beetle species in the secondary forest sites, northern Costa Rica**

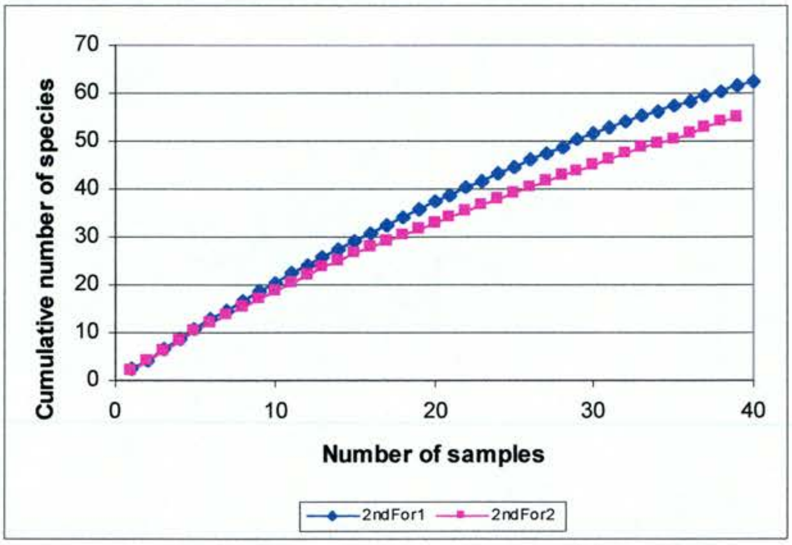
| Species number | 2ndFor1 | Species number | 2ndFor2 |
|---|---|---|---|
| 4 | 12 | 188 | 8 |
| 112 | 7 | 3 | 7 |
| 43 | 5 | 240 | 6 |
| 188 | 4 | 388 | 4 |
| 24 | 4 | 4 | 4 |
| 3 | 4 | 133a | 3 |
| 243 | 3 | 41 | 3 |
| 102 | 3 | 125 | 3 |
| 111a | 3 | 136 | 2 |
| 99 | 3 | 25 | 2 |

Figure 7.9 illustrates the similarities in family composition between the two secondary forest sites. The two family level species data sets showed a high correlation (Pearson product moment correlation coefficient, ln transformed data: $r = 0.91$, $p = 0.001$). In addition family species distributions were shown not to be significantly different between the two secondary forest sites (Mann Whitney-U test: $p = 0.451$) thus demonstrating a statistically similar family composition between sites.

Calculation of similarity indices (Krebs 1989) revealed the similarity between the two sites when demonstrated by the Morisita index. The Sorensen index revealed a lower similarity. Sorensen's coefficient gave a value of 0.14, while Morisita's index of similarity gave a value of 0.51 (Tables 7.15 and Table 7.16). The sites shared 8 species, which was 7% of the species found in both sites 1 and 2.

Figure 7.11 illustrates the species accumulation curves for both the secondary forest sites. 2ndFor1 tends towards a slightly higher overall species richness, although both curves indicate that the actual species richness in these sites was lower than that in the primary and logged forest sites. Jackknife estimates of species richness (calculated by the EstimateS program, Colwell 1999) demonstrate this as the species richness values for 2ndFor1 of 117 ± 6.8 and for 2ndFor2 of 95 ± 4.4 fall below the previous two land uses (Figure 7.19).

**Figure 7.11 Species accumulation curves for leaf litter beetles in secondary forest, northern Costa Rica**



In summary, the two secondary forest site sampled contained 109 beetle species consisting of 211 individuals. As in the primary and logged forest sites, the Staphylinidae were the most speciose family followed by the Nitidulidae. Beetle family composition was statistically similar between the two sites. Jackknife estimates of species richness (Colwell 1999) reveal a beetle community of reduced diversity and indicate that the secondary forest sites contain a lower number of leaf litter beetle species than the other natural forest sites. This is likely a result of the increased human disturbance that has occurred in these sites. Although the sites have been left to regenerate for 6 to 8 years it is evident that litter layer beetles may take a longer time to re-establish fully.

### 7.5.4 Leaf litter beetles in plantations of *Gmelina arborea*

The two plantation sites examined here are typical of plantation forestry in this area of Costa Rica. They consist of monocultures of the exotic tree species *Gmelina arborea*, and they have been established on areas which had previously been cleared for pasture from natural forest. The two sites are discussed in greater detail in Chapter 3. This section examines the patterns of species and family, composition and diversity of the leaf litter beetle fauna found in these sites.

During this study 44 species and 71 individuals were collected in plantation site 1 while 24 species and 32 individuals were collected in plantation site 2. This comprised of 59 species and 103 individuals in total. The species ranged over 12 of the 26 families collected over the study area. The dominant family in the plantation assemblage was the Staphylinidae with 17 species in site 1 and 7 species in site 2. The Nitidulidae was the next most speciose in site 1 with 10 species. In site 2 the Nitidulidae and the Carabidae both had 5 species, while in site 1 the third most speciose family was the Carabidae, with 8 (Table 7.8 and Figure 7.12).

### Table 7.8 *Gmelina arborea* plantation beetle species assemblage

| *Family* | *Plantation 1* | | *Plantation 2* | | *Plantation total* | |
|---|---|---|---|---|---|---|
| | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** | **Species Richness** | **Abundance** |
| Carabidae | 8 | 20 | 5 | 12 | 9 | 32 |
| Chrysomelidae | 1 | 1 | 0 | 0 | 1 | 1 |
| Elateridae | 0 | 0 | 1 | 1 | 1 | 1 |
| Hydrophilidae | 2 | 2 | 1 | 1 | 3 | 3 |
| Limnichidae | 1 | 1 | 0 | 0 | 1 | 1 |
| Mordellidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Nitidulidae | 10 | 15 | 5 | 5 | 12 | 20 |
| Pselaphidae | 2 | 2 | 0 | 0 | 2 | 2 |
| Scarabaeidae | 1 | 1 | 1 | 1 | 1 | 2 |
| Scolytidae | 1 | 1 | 1 | 1 | 2 | 2 |
| Scydmaenidae | 1 | 2 | 2 | 2 | 2 | 4 |
| Staphylinidae | 17 | 26 | 7 | 8 | 24 | 34 |
| **TOTALS** | **44** | **71** | **24** | **32** | **59** | **103** |

The pattern of abundance of beetle individuals by family was similar over the two field sites. In both cases the staphylinids were the most abundant (Plantat1, n=26; Plantat2, n=8) followed by the Carabidae (Plantat1, n=20; 2ndFor2, n=12) and then the Nitidulidae (Plantat1, n=15; Plantat2, n=5)(Figure 7.13). The most common species in plantation site 1 was from the Carabidae (species 7)(Table 7.9)(Appendix 9) which made up 11% of the total number of individuals sampled. The second most abundant species in site 1 was also a carabid (species 1) and it made up 6% of all individuals in this site. The 25 most common species together made up 73% of the total number of individuals sampled while the 10 most common made up 48%. Of the species collected, 31 were represented by single individuals. In site 2, the most common beetle was the same carabid as in site 1 (species 7)(Table 7.9)(Appendix 9). In this site it made up 19% of the total number of individuals sampled. The second most abundant species in site 2 was again a carabid (species 430) and it made up 9% of all individuals in this site. The 10 most common species together made up 56% of the total number of individuals sampled. Of the species collected at this site, 21 were represented by single individuals.

**Figure 7.12** ***Gmelina arborea*** **plantation beetle species richness by family**

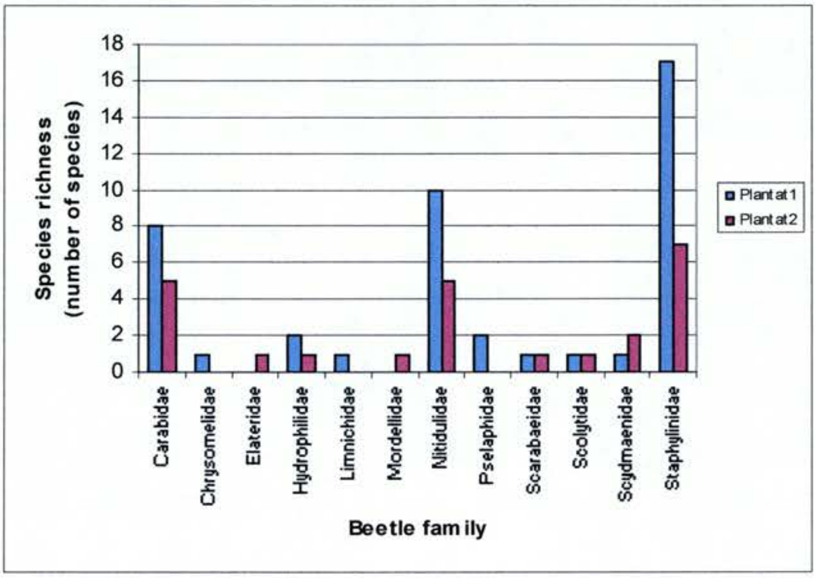


**Figure 7.13** ***Gmelina arborea*** **plantation beetle species abundance by family**

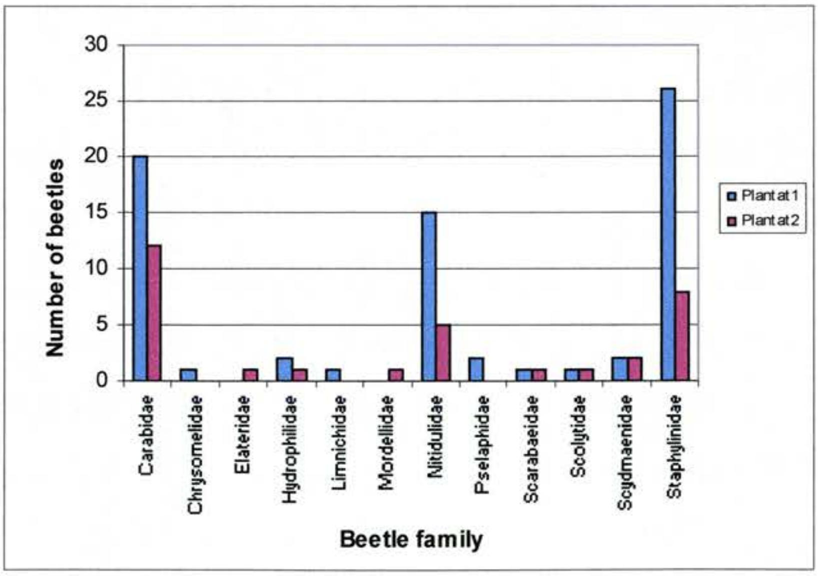


**Table 7.9 The ten most abundant beetle species in the *Gmelina arborea* plantation sites, northern Costa Rica**

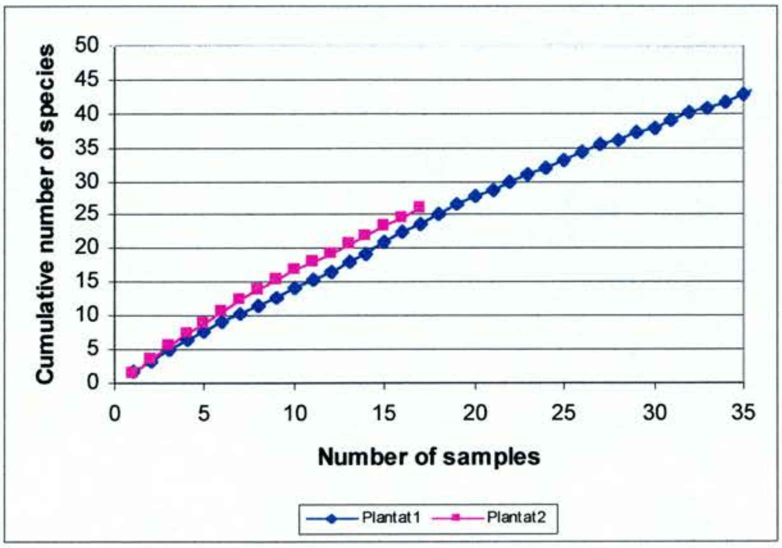
| Species number | Plantat1 | Species number | Plantat2 |
|---|---|---|---|
| 7 | 8 | 7 | 6 |
| 1 | 4 | 430 | 3 |
| 4 | 4 | 11 | 2 |
| 2a | 3 | 1 | 1 |
| 5 | 3 | 13 | 1 |
| 217 | 3 | 90 | 1 |
| 360 | 3 | 354 | 1 |
| 90 | 2 | 16 | 1 |
| 123 | 2 | 12 | 1 |
| 89 | 2 | 4 | 1 |

Figure 7.12 illustrates the similarities in family composition between the two plantation sites. In addition family species distributions were shown not to be significantly different between the two plantation sites (Mann Whitney-U test: $p = 0.658$) thus demonstrating a statistically similar family composition between sites.

Calculation of similarity indices (Krebs, 1989) revealed a high similarity between the two sites when demonstrated by the Morisita index. The Sorensen index reveals a lower similarity. Sorensen's coefficient gives a value of 0.25, while Morisita's index of similarity gives a value of 0.96 (Tables 7.15 and Table 7.16). The sites share 9 species, which is 15% of the species found in both sites 1 and 2.

Figure 7.14 illustrates the species accumulation curves for both the plantation sites. Plantat1 appears to tend towards slightly higher overall species richness. Although many of the samples from this site were lost due to damage and trampling from cattle, it was assumed, as the species accumulation curves for the two plantation sites revealed similar trends, that the data were sufficient for these analyses. The curves indicate that the actual species richness in these sites is lower than that in the primary, logged and secondary forest sites. Jackknife estimates of species richness (calculated by the EstimateS program, Colwell 1999) demonstrate this through the species richness values calculated for Plantat1 of 77 ± 6.1 and for Plantat2 of 49 ± 5.8 which fall below the previous three land uses (Figure 7.19).

**Figure 7.14 Species accumulation curves for leaf litter beetles in *Gmelina arborea* plantations, northern Costa Rica**



In summary, the two plantation site samples contained 59 beetle species consisting of 103 individuals. As in the previous three sites, the Staphylinidae were the most speciose family followed by the Nitidulidae and the Carabidae. Beetle family composition was statistically similar between the two sites. Similarity was also shown to be high between site as measured by the Morisita index of similarity. Jackknife estimates of species richness (Colwell 1999) revealed a beetle community of reduced diversity and indicated that the plantation sites contained a lower number of leaf litter beetle species than the natural and secondary forest sites. Even if the results for Plantat2 are discounted, due to the number of samples lost, the results from Plantat1 revealed that the leaf litter Coleoptera are seriously affected by the levels of disturbance which have occurred in creating the plantation sites.

### 7.5.5 Leaf litter beetles in pasture

The two pasture sites examined in this study exhibit a land use which is common in this area of Costa Rica. The natural forest has been cleared in order to graze cattle. The two sites investigated have been discussed in greater detail in Chapter 3. This section examines the patterns of leaf litter beetle composition and diversity found in these sites.

During this study 45 species and 91 individuals were collected in pasture site 1 while 84 species and 190 individuals were collected in pasture site 2. This comprised of 117 species and 281 individuals in total. The species ranged over 18 of the 26 families collected over the study area. The dominant family in the pasture assemblage was the Staphylinidae with 14 species in site 1 and 33 species in site 2. The Nitidulidae was the next most speciose in site 1 with 8 species while in site 2 the Carabidae was the next most speciose with 16 species (Table 7.10 and Figure 7.15).

**Table 7.10 Pasture beetle species assemblage**

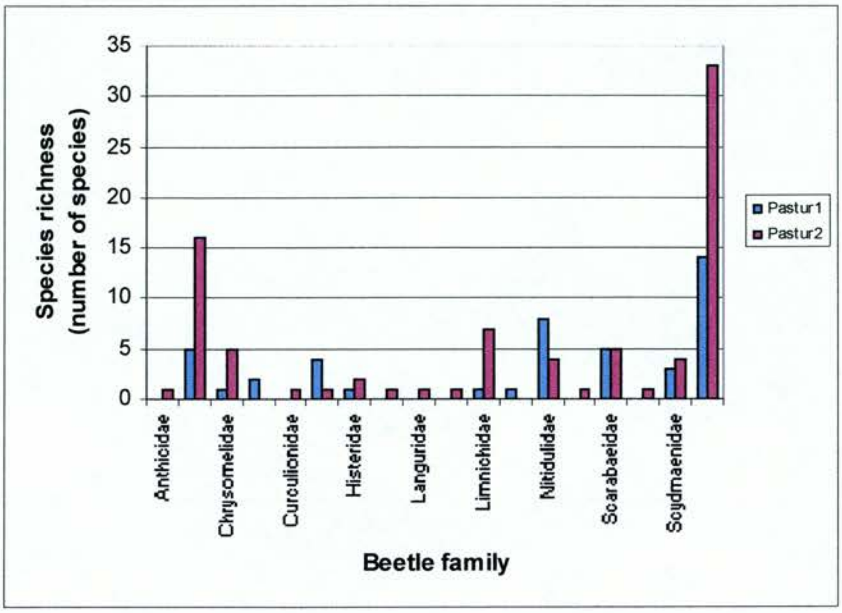
| *Family* | *Pasture 1* | | *Pasture 2* | | *Pasture total* | |
|---|---|---|---|---|---|---|
| | Species Richness | Abundance | Species Richness | Abundance | Species Richness | Abundance |
| Anthicidae | 0 | 0 | 1 | 3 | 1 | 3 |
| Carabidae | 5 | 6 | 16 | 25 | 21 | 31 |
| Chrysomelidae | 1 | 1 | 5 | 11 | 6 | 12 |
| Coccinellidae | 2 | 2 | 0 | 0 | 2 | 2 |
| Curculionidae | 0 | 0 | 1 | 3 | 1 | 3 |
| Elateridae | 4 | 6 | 1 | 7 | 5 | 13 |
| Histeridae | 1 | 2 | 2 | 6 | 2 | 8 |
| Hydrophilidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Languridae | 0 | 0 | 1 | 1 | 1 | 1 |
| Lathriidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Limnichidae | 1 | 2 | 7 | 11 | 8 | 13 |
| Meloidae | 1 | 3 | 0 | 0 | 1 | 3 |
| Nitidulidae | 8 | 34 | 4 | 8 | 10 | 42 |
| Phalacridae | 0 | 0 | 1 | 3 | 1 | 3 |
| Scarabaeidae | 5 | 9 | 5 | 8 | 9 | 17 |
| Scolytidae | 0 | 0 | 1 | 1 | 1 | 1 |
| Scydmaenidae | 3 | 4 | 4 | 18 | 6 | 22 |
| Staphylinidae | 14 | 22 | 33 | 83 | 40 | 105 |
| **TOTALS** | **45** | **91** | **84** | **190** | **117** | **281** |

The pattern of abundance of beetle individuals by family was similar over the two field sites. The Nitidulidae was the most abundant family in site 1 (Pastur1, n=34) while in site 2 the staphylinids were the most abundant (Pastur2, n=83). These were followed by the staphylinids (Plate 7.1) in site 1 (Pastur1, n=22) and the Carabidae in site 2 (Pastur2, n=25) and then the Nitidulidae (Plantat1, n=15; Plantat2, n=5)(Figure 7.17). The most common species in pasture site 1 was from the Nitidulidae (species 358)(Table

7.11)(Appendix 7.1) which made up 12% of the total number of individuals sampled. The second most abundant species in site 1 was also a nitidulid (species 240) and it made up 10% of all individuals in this site. The 25 most common species together made up 78% of the total number of individuals sampled while the 10 most common made up 53%. Of the species collected, 27 were represented by single individuals. In site 2, the most common beetle was a staphylinid (species 428)(Table 7.11)(Appendix 9). In this site it made up 9% of the total number of individuals sampled. The second most abundant species in site 2 was from the Scydmaenidae (species 68) and it made up 6% of all individuals in this site. The 25 most common species together made up 62% of the total number of individuals sampled while the 10 most common made up 40%. Of the species collected at this site, 46 were represented by single individuals.

**Plate 7.1 Coleoptera: Staphylinidae.** This family was the most species rich in both pasture sites, the most abundant in Pastur2 and the second most abundant in Pastur1. (1mm=1cm)

## Figure 7.15 Pasture beetle species richness by family



## Figure 7.16 Pasture beetle species abundance by family

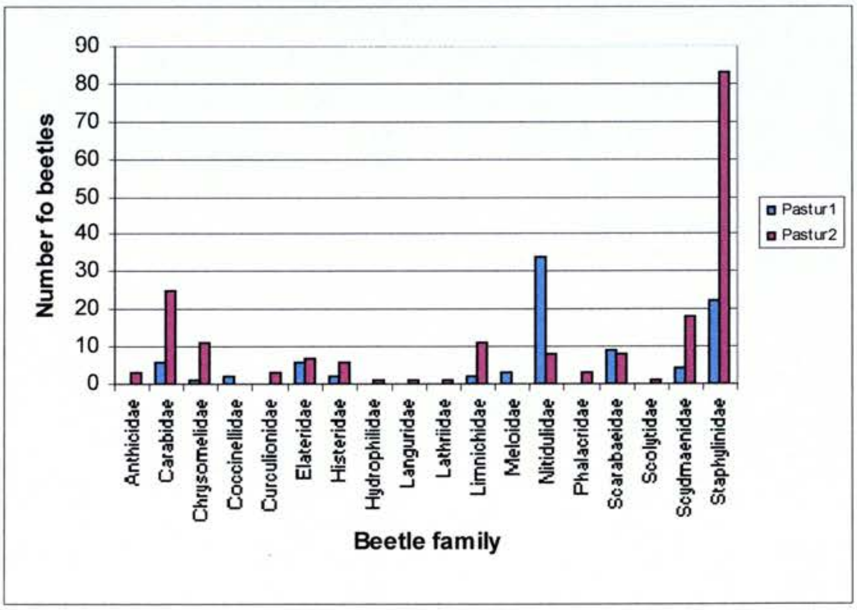


**Table 7.11 The ten most abundant beetle species in the pasture sites, northern Costa Rica**

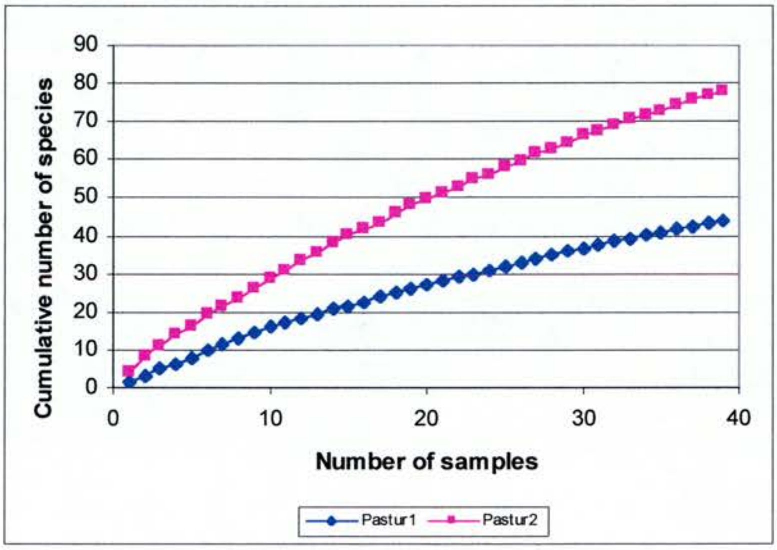
| Species number | Pastur1 | Species number | Pastur2 |
|---|---|---|---|
| 358 | 11 | 428 | 17 |
| 240 | 9 | 68 | 11 |
| 164 | 6 | 164 | 11 |
| 232 | 5 | 439 | 10 |
| 310 | 3 | 65 | 7 |
| 31 | 3 | 56a | 4 |
| 252 | 3 | 158 | 4 |
| 368 | 3 | 437 | 4 |
| 167b | 3 | 64 | 4 |
| 369 | 2 | 152 | 4 |

Figure 7.15 illustrates the similarities in family composition between the two pasture sites. Family species distributions were shown not to be significantly different between the two pasture sites (Mann Whitney-U test: $p = 0.715$) thus demonstrating a statistically similar family composition between sites.

Calculation of similarity indices (Krebs, 1989) revealed a low similarity between the two sites. Sorensen's coefficient gave a value of 0.19, while Morisita's index of similarity gave a value of 0.32 (Tables 7.15 and Table 7.16). The sites shared 12 species, which was 4% of the species found in both sites 1 and 2.

Figure 7.17 illustrates the species accumulation curves for both the pasture sites. Pastur2 tends towards higher overall species richness. The curve shown for Pastur1 reveals a similar species accumulation to the curves for the plantation sites, however the curve for Pastur2 shows a much higher species richness. Indeed, the species accumulation revealed is more similar to the natural forest sites. Both the pasture sites adjoin natural forest sites so their proximity to forest cannot explain the differences in species richness shown. Pastur1 is found at a higher altitude, which may cause a reduced level of species richness. In addition, the management levels of the two pasture sites differ. Pastur2 is operated on a rotation system which leaves areas of pasture fallow. When the grass is approximately 30 cm high the cattle are allowed to graze. Pastur 1 is more constantly grazed. Some families of beetle not previously collected have been found in Pastur2 which may consist of more generalist species or species which are better adapted to the grassland habitat developed in that site. Other studies have shown similar differences between pasture sites, and it is believed that the initial clearing method may also have a long term impact on species diversity (Furley, pers. comm.). Jackknife estimates of species richness (calculated by the EstimateS program, Colwell 1999) gave species richness values for Pastur1 of 73 ± 4.5 and for Plantat2 of 134 ± 9.2 (Figure 7.19).

**Figure 7.17 Species accumulation curves for leaf litter beetles in cattle pasture, northern Costa Rica**



In summary, the two pasture site samples contained 117 beetle species consisting of 281 individuals. As in the other sites, the Staphylinidae were the most speciose family followed by the Nitidulidae and the Carabidae. Beetle family composition was statistically similar between the two sites. The similarity measures calculated by the Sorensen index and the Morisita index of similarity were shown to be relatively low. Jackknife estimates of species richness (Colwell 1999) revealed a beetle community of reduced diversity in one of the pasture sites but indicated a higher diversity in the other. Some possible reasons for this have been suggested but these will be further investigated later in the chapter. It appears that some pasture areas do suffer from reduced beetle species diversity, however it is possible that other pasture sites are providing a habitat for generalist or non-forest beetles.

### 7.5.6 Summary of findings: leaf litter beetles by land use

This section has presented the beetle data collected by land use. It has documented leaf litter beetle fauna species richness and abundance, while also illustrating the similarities, and differences, between the two sites sampled from each land use type.

All land uses demonstrated a similar species richness and abundance between sites, and subfamily species richness and abundance was also similar between sites in each land use. Similarity indices generally showed medium to low similarity of beetle species composition between sites, although some sites demonstrated higher similarities of Morisita indices compared to Sorensen indices. This was probably a result of Morisita's sensitivity to species abundances. The generally low similarity indices between sites, compared to the ant data discussed in the previous chapter, may be a result of the significantly higher species diversity of the leaf litter beetles. A greater sample size may have addressed this problem. Species accumulation curves also revealed highly similar species richness between sites in all the land uses except pasture. The differences in the two pasture sites could be a result of the initial clearing mechanism and/or differing existing management practices. As a result of these human factors this degree of site difference, in an apparently very similar land use type, is more likely than for the other sites.

The section has provided a baseline study of beetle species diversity and abundance in five different land uses in a northern Costa Rican landscape. It has also reiterated the comparability of the sites chosen within each of these land uses. The next section addresses the effects of disturbance on the leaf litter beetle fauna by examining species richness, abundance and composition over the five land uses, which represent different levels of human disturbance.

## 7.6 Species richness and composition

### 7.6.1 BEETLE SPECIES RICHNESS

As Section 7.5 demonstrates, species richness and composition varied over the land uses and field sites sampled. Species richness ($S$) was significantly different over the field sites (One-way ANOVA, F = 14.93, $p < 0.001$; Table C1 in Appendix 10). Further investigation between sites reveals that not all sites had a significantly different species richness (Tukey's multiple comparison test, $p < 0.05$; Table C3 in Appendix 10). This may be a result of the fact that species richness did not vary greatly between sites, possibly due to the influx of disturbed-area species, and that changes in actual beetle species composition were not revealed by this analysis.

The results presented here show that the logged forest sites had the highest number of species collected followed by primary forest and then pasture (Table 7.12). Plantation sites had the lowest species richness followed by secondary forest (Figure 7.18 and 7.19). As mentioned, this measure is of absolute species numbers collected and does not take account of species composition differences between sites. The estimated total number of species per field site, as calculated by the Jackknife richness technique (Heltshe and Forrester 1983, Krebs 1989, and Colwell and Coddington 1994) using the program EstimateS (Colwell 1999) is also shown in Figure 7.19.

**Figure 7.18 Beetle species richness (number of species, *S*) over a land use gradient of disturbance in northern Costa Rica.** PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture. Blue bars indicate total species richness per land use while green indicates species richness in site 1 and yellow in site 2.

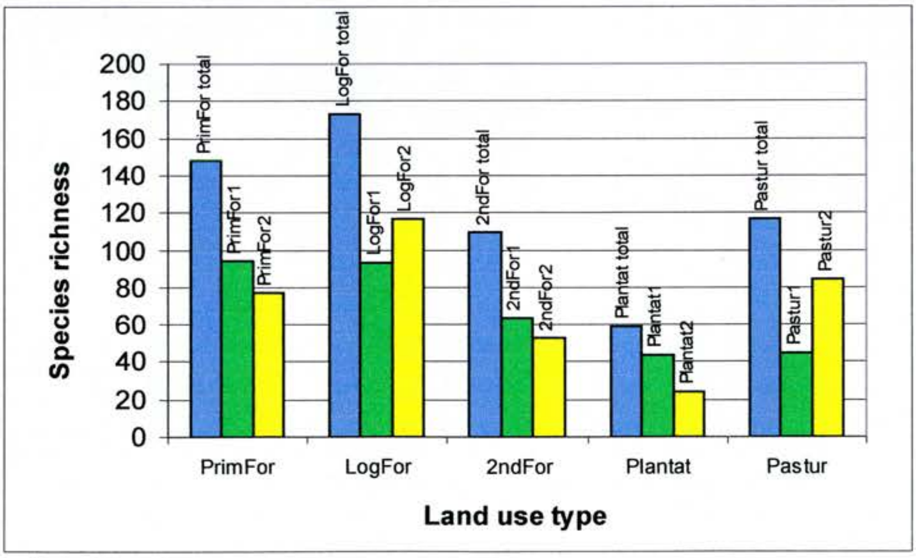
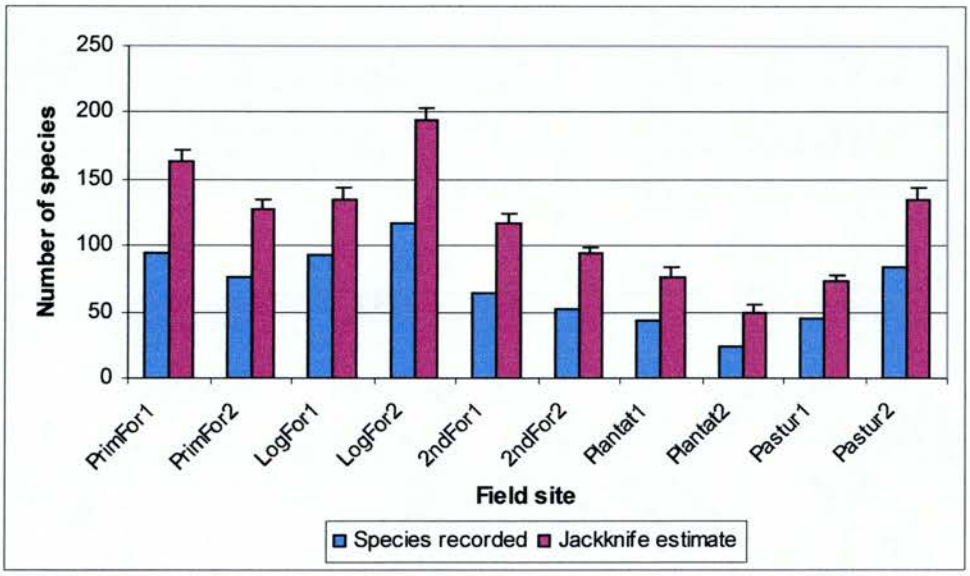
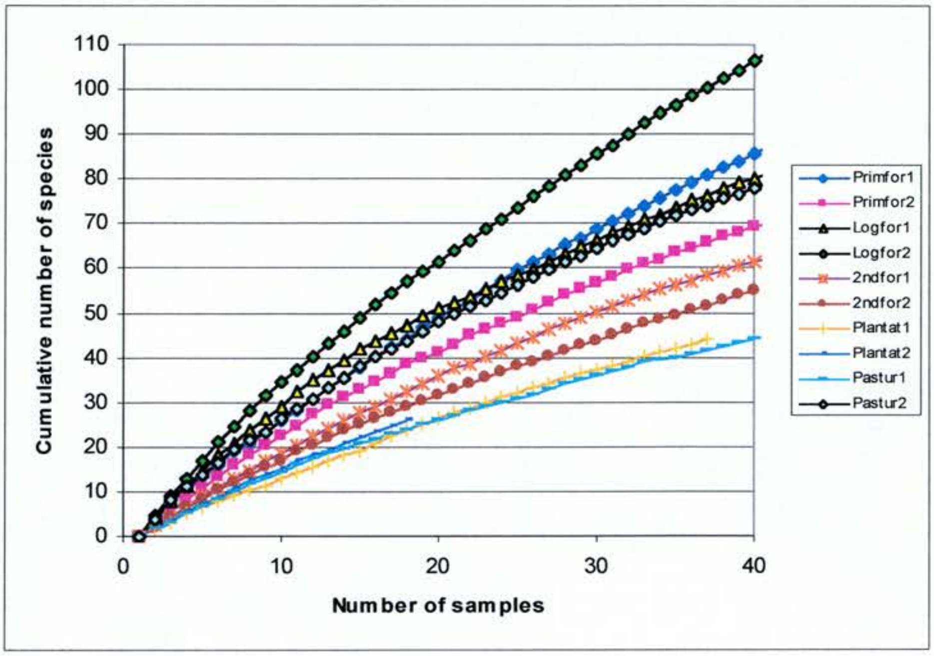


**Figure 7.19 Number of leaf-litter beetle species in field sites sampled over a gradient of disturbance in northern Costa Rica.** Jackknife richness was calculated using the EstimateS program (Colwell 1999), the error bars denote the standard deviation. (PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture).



Species accumulation curves for all ten field sites are shown in Figure 7.20. A preliminary assessment of season was also made, and the corresponding curves for the wet season of 1998 and dry season of 1999 are shown in Figures 7.21 and 7.22. These curves illustrate similar gradients of species accumulation over both seasons for each site, although some changes are apparent. These are particularly evident in the natural forest sites where the dry season sampling suggested a more diverse species assemblage. It is also evident that the two logged forest sites (LogFor1 and LogFor2) contained greater species diversity according to the EstimateS analysis. This may be due to an increase in non-forest species in areas of logging disturbance. The curves for all sites show a gradually flattening slope, indicating that the number of new species encountered per sample was decreasing as sample size grew larger. The average gradient was steeper than that of the ant data, indicating greater species diversity. A logarithmic equation provided an approximate fit ($r^2 = 0.96$) to the species accumulation curve for all sites (Figure 7.23), although the fit was less good than the equivalent regression for the ant data. The general trend indicated by the species accumulation curves indicates high species diversity although previous studies have indicated that more precise extrapolation of such data cannot be carried out with confidence (Colwell and Coddington 1994, Wagner 2000).

**Figure 7.20 Species accumulation curve for leaf litter beetles over a gradient of disturbance from primary forest to pasture in northern Costa Rica.** Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



**Figures 7.21 and 7.22 Species accumulation curve for leaf litter beetles over a gradient of disturbance from primary forest to pasture in northern Costa Rica: (7.21) Wet season 1998 and (7.22) Dry season 1999.** Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).

**(7.21)** **(7.22)**

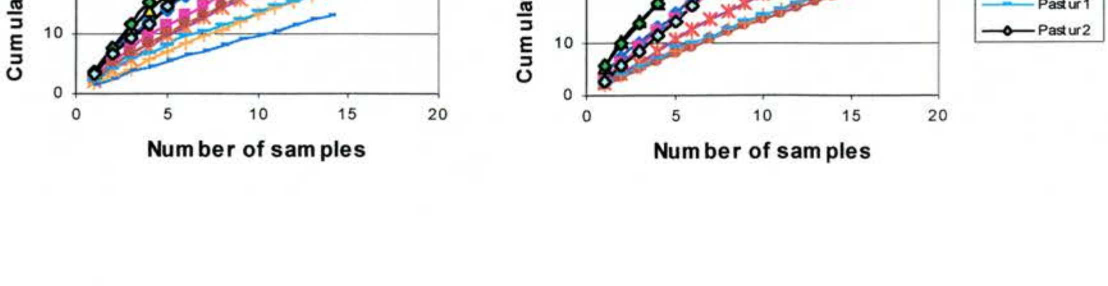
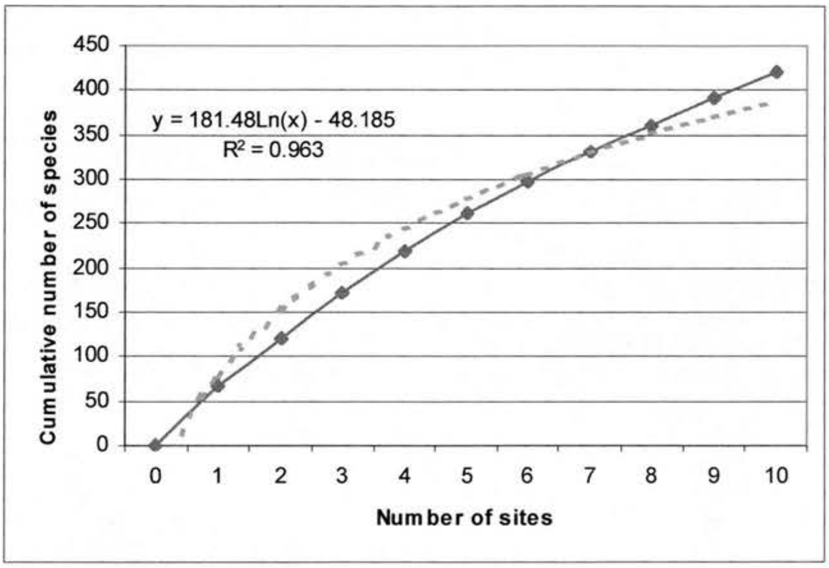


**Figure 7.23 Species accumulation curve for leaf litter beetles over a gradient of disturbance in northern Costa Rica.** The species accumulation curve for all sites is well fit by a logarithmic curve (indicated by dashed red line). Cumulative species richness was calculated using the program EstimateS 5 (Colwell, 1999).



### 7.6.2 $\alpha$ - DIVERSITY OF LEAF LITTER BEETLE SPECIES

Diversity, evenness and dominance indices are given in Table 7.12. These are based on pooled data from transects. Species richness (*S*), as mentioned previously, was highest in LogFor2 followed by PrimFor1. However, a comparison between *S* and Shannon's index of diversity (*H*) and Simpson's index of diversity (*D*) shows that these varying diversity measures identify different sites as the most 'diverse'. Shannon's diversity index places Pastur2 followed by 2ndFor1 as having the highest diversity index, whereas Simpson's index of diversity places PrimFor2 first, followed by Plantat2. As discussed in Chapter 4, there are two types of diversity index which are more sensitive to either the rare species in a community (e.g. Shannon) or the most abundant species (e.g. Simpson). This is evident in the results given. The lowest values of the Shannon index were generally found in the more disturbed sites (Table 7.13). It is probable that the higher values found in the natural forest sites were due to the inclusion of the rare species found there, although it is noteworthy that Pastur2 was identified as the most diverse site by this measure. This probably resulted from the number of new families and corresponding species found only at this site. The difference in diversity may be a result of the different altitudes of the two pasture sites, and could have been contributed to by previous land management, for example forest clearance, methods. In contrast, the Simpson index showed a more mixed order of natural forest sites and pasture and plantation. The two plantation sites were ranked quite highly whereas LogFor1, LogFor2 and PrimFor1, all natural forest sites, had, with the exception of Pastur1, the lowest diversity indices. This outcome may be a result of the importance the Simpson index places on species abundance. Both LogFor1 and PrimFor1 showed lower species abundance than the pasture sites although species abundance in the plantation sites was similar (Figure 7.24).

The evenness indices calculated for the leaf litter beetle data demonstrated a greater evenness of species distribution in the disturbed sites. The logged forest and primary forest sites demonstrated the lowest evenness (Table 7.13). This was a reversal of the pattern shown by the ant data, and may be due to the overall lower abundance and higher rarity of beetle species in the sample. It may also reflect the inability of forest beetle species to adapt to disturbed environments. A few ant species thrive in the disturbed sites at the expense of many other species, while it appears that there are no beetle species which have achieved this. The Berger-Parker dominance measure expresses the proportional importance of the most abundant species (Magurran 1988). Low values indicate lowered dominance by any one species and are generally accompanied by increased species evenness. This is demonstrated by the dominance and evenness indices calculated here which showed a significant negative correlation (Pearson's product-moment correlation coefficients between $E$ and $d$, r = -0.71, $p$ = 0.02).

This section has presented a suite of diversity indices and measures. For the reasons discussed above, not all the sites have been ranked by diversity in the same order. It remains evident, especially when considering the actual number of species collected in this study ($S$), that the plantation and pasture sites were generally less diverse than the natural forest sites, indicating the negative effect of disturbance on leaf litter beetle diversity. The next section examines the corresponding effects of disturbance on leaf litter beetle abundance.

**Table 7.12 Diversity indices for beetle species in each site.** *S* = species richness, *Jack* = first-order Jackknife richness estimator, *H* = Shannon's index of diversity, *D* = Simpson's index of diversity, *E* = Shannon's evenness index, and *d* = Berger-Parker dominance index.

| | | INDEX: | | | | | |
|---|---|---|---|---|---|---|---|
| **Habitat** | **Site** | ***S*** | ***Jack*** | ***H*** | ***D*** | ***E*** | ***d*** |
| Primary | PrimFor1 | 94 | 163 | 3.958 | 0.956 | 0.871 | 0.171 |
| forest | PrimFor2 | 77 | 127 | 3.849 | 0.965 | 0.886 | 0.095 |
| Logged | LogFor1 | 93 | 135 | 3.347 | 0.894 | 0.738 | 0.293 |
| forest | LogFor2 | 117 | 195 | 3.858 | 0.951 | 0.810 | 0.166 |
| Secondary | 2ndFor1 | 64 | 117 | 3.970 | 0.973 | 0.955 | 0.099 |
| forest | 2ndFor2 | 53 | 95 | 3.783 | 0.969 | 0.953 | 0.089 |
| Plantation | Plantat1 | 44 | 77 | 3.569 | 0.963 | 0.943 | 0.113 |
| | Plantat2 | 24 | 49 | 3.114 | 0.940 | 0.980 | 0.188 |
| Pasture | Pastur1 | 45 | 73 | 3.479 | 0.955 | 0.914 | 0.121 |
| | Pastur2 | 84 | 134 | 4.031 | 0.972 | 0.910 | 0.089 |

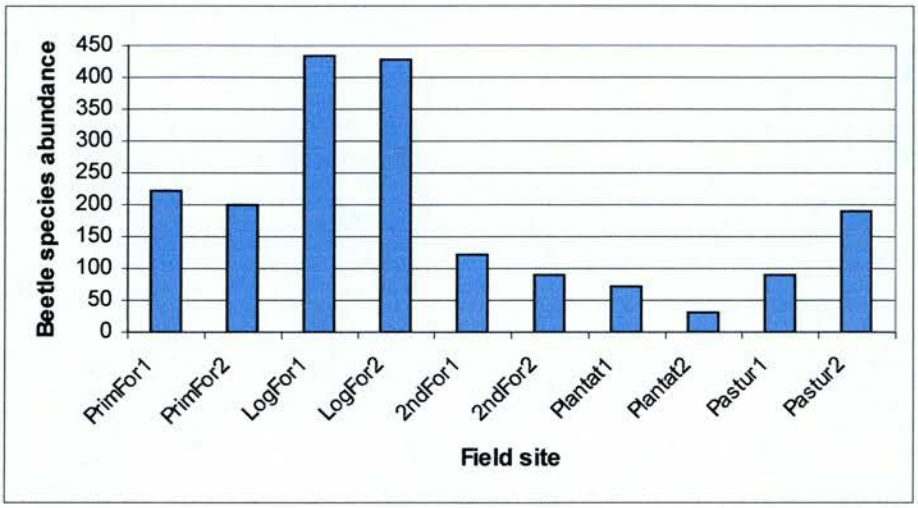
**Table 7.13 Ranking of field site by a variety of beetle species diversity measures.** *S* = species richness, *H* = Shannon's index of diversity, *D* = Simpson's index of diversity, *E* = Shannon's evenness index, and *d* = Berger-Parker dominance index.

| ***Site*** | ***S*** | ***Site*** | ***H*** | ***Site*** | ***D*** | ***Site*** | ***E*** | ***Site*** | ***d*** |
|---|---|---|---|---|---|---|---|---|---|
| LogFor2 | 117 | Pastur2 | 4.03 | PrimFor2 | 0.97 | Plantat2 | 0.98 | LogFor1 | 0.29 |
| PrimFor1 | 94 | 2ndFor1 | 3.97 | Plantat2 | 0.97 | 2ndFor1 | 0.95 | Plantat2 | 0.19 |
| LogFor1 | 93 | PrimFor1 | 3.96 | 2ndFor2 | 0.97 | 2ndFor2 | 0.95 | PrimFor1 | 0.17 |
| Pastur2 | 84 | LogFor2 | 3.86 | 2ndFor1 | 0.96 | Plantat1 | 0.94 | LogFor2 | 0.17 |
| PrimFor2 | 77 | PrimFor2 | 3.85 | Plantat1 | 0.96 | Pastur1 | 0.91 | Pastur1 | 0.12 |
| 2ndFor1 | 64 | 2ndFor2 | 3.78 | Pastur2 | 0.96 | Pastur2 | 0.91 | Plantat1 | 0.11 |
| 2ndFor2 | 53 | Plantat1 | 3.57 | LogFor1 | 0.96 | PrimFor2 | 0.89 | 2ndFor1 | 0.10 |
| Pastur1 | 45 | Pastur1 | 3.48 | LogFor2 | 0.95 | PrimFor1 | 0.87 | PrimFor2 | 0.10 |
| Plantat1 | 44 | LogFor1 | 3.35 | Pastur1 | 0.94 | LogFor2 | 0.81 | Pastur2 | 0.09 |
| Plantat2 | 24 | Plantat2 | 3.11 | PrimFor1 | 0.89 | LogFor1 | 0.74 | 2ndFor2 | 0.09 |

### 7.6.3 BEETLE SPECIES ABUNDANCE

Beetle species abundance showed changes over the gradient of disturbance with the logged forest sites showing significantly more beetles than other sites (Kruskal-Wallis, H = 66.62, $p < 0.001$)(Figure 7.24). The increase in total abundance in the logged forest sites was principally a result of increases in two staphylinid species (species 217 and 318) and is reinforced by the evenness and dominance indices discussed in the previous section.

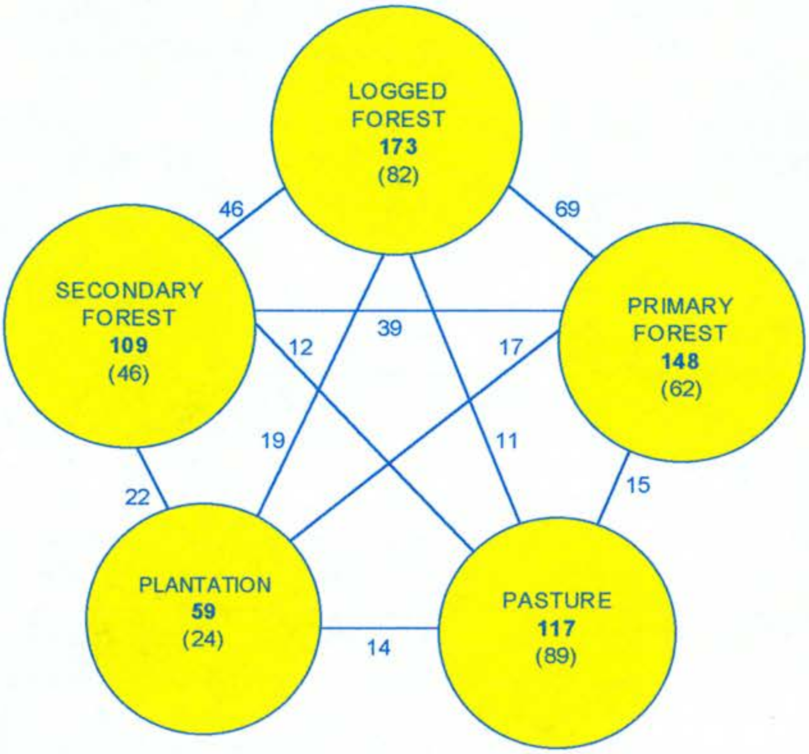
**Figure 7.24 Beetle species abundance (number of individuals) in field sites sampled over a gradient of disturbance in northern Costa Rica.** PrimFor = primary forest, LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture.



### 7.6.4 SUMMARY OF BEETLE SPECIES DISTRIBUTION

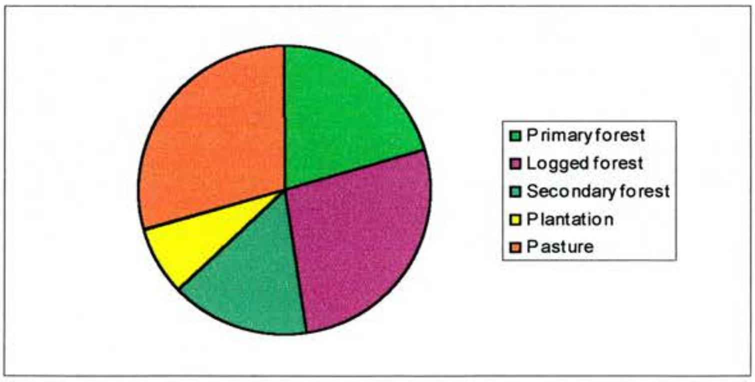
Differences in absolutes species richness between land uses was not great (despite there being significant differences between some land uses), however numbers of shared species and unique species by land use revealed the changes in species composition that have occurred after disturbance. Figure 7.25 illustrates the number of beetle species shared between different habitats considered in the study. It also shows the high numbers of species that were found only in one land use thus demonstrating patterns which are more meaningful than a simple species richness value. It illustrates that all habitats were important in having an assemblage of species which were not present in any of the other habitats. Primary forest had 62 species that were found only in that habitat. This may illustrate that human disturbance has resulted in a loss of forest specific beetle species. The pasture and logged forest sites had higher numbers of unique species than primary forest which may have been a result of the opening up of niches to new species by disturbance. This is summarised in Figure 7.26. Overall, the forest sites (primary, logged and secondary forest) contained 190 species which were not found in the habitats of greatest human disturbance, namely plantation and pasture.

## Figure 7.25 Beetle species distribution in different land uses in Costa Rica, Central America



**Beetle species in different land uses in Costa Rica, Central America.** The number of species in each land use is given in bold, the number of species occurring in common in different habitats is given along the line joining the land uses, and the number of species unique to each land use is given in parentheses within the circles.

## Figure 7.26 Proportion of unique beetle (Coleoptera) species over a gradient of human disturbance in northern Costa Rica, Central America



### 7.6.5 $\beta$ – DIVERSITY OF LEAF LITTER BEETLE SPECIES

In order to ascertain the degree of change in species diversity in different sites and land uses, and to compare the beetle species composition, $\beta$ - diversity was examined using the Sorensen Coefficient of Similarity (Krebs 1989)(Tables 7.14, 7.15 and 7.16 and Figure 7.27). The Morisita Index of Similarity was also calculated and used in a cluster analysis of field site and species composition. In general, $\beta$ - diversity between sites was high. According to the Sorensen's coefficients, the most similar land uses were primary forest and logged forest ($S_s$ = 0.43). This demonstrates the similarities between beetle species composition in the natural forest sites. The sites at opposite ends of the disturbance gradient demonstrated the lowest similarity, for example, logged forest and pasture ($S_s$ = 0.07). This reinforced the fact that the beetle species composition sampled in the pasture sites was the most dissimilar to the primary forest site, as would be expected if degree of human impact and disturbance on the forest ecosystem caused corresponding changes in leaf-litter beetle species composition.

**Table 7.14 Similarities between leaf-litter beetle species composition of different land uses in northern Costa Rica, as measured by the Sorensen index**

| | *Primary forest* | *Logged forest* | *Secondary forest* | *Plantation* | *Pasture* |
|---|---|---|---|---|---|
| ***Primary forest*** | 1 | 0.432 | 0.283 | 0.159 | 0.112 |
| ***Logged forest*** | | 1 | 0.304 | 0.154 | 0.076 |
| ***Secondary forest*** | | | 1 | 0.257 | 0.103 |
| ***Plantation*** | | | | 1 | 0.156 |
| ***Pasture*** | | | | | 1 |

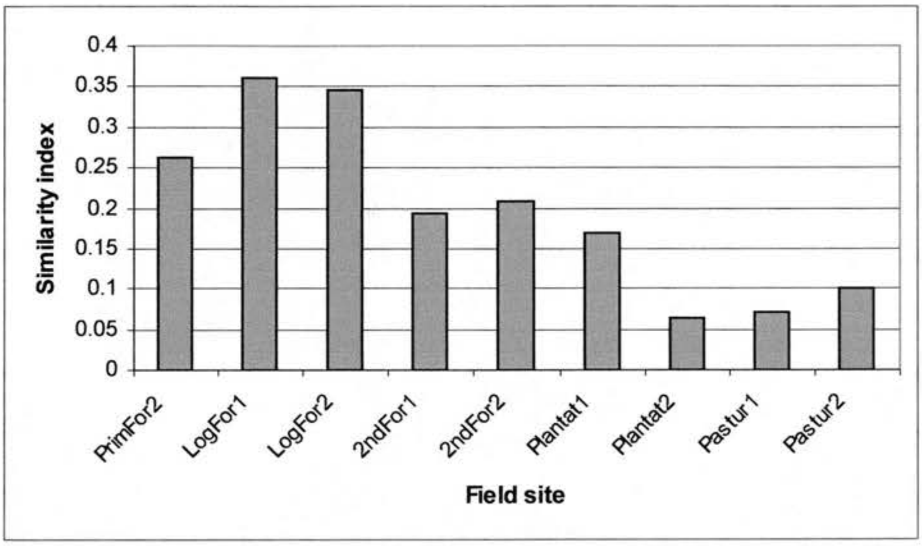
**Table 7.15 Similarities between leaf-litter beetle species composition of different land uses in northern Costa Rica, as measured by the Sorensen's index**

| | Prim. forest 1 | Prim. forest 2 | Log. forest 1 | Log. forest 2 | Secnd forest 1 | Secnd forest 2 | Plantat 1 | Plantat 2 | Pastur 1 | Pastur 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Primary forest 1*** | 1 | 0.263 | 0.360 | 0.346 | 0.193 | 0.208 | 0.170 | 0.065 | 0.070 | 0.099 |
| ***Primary forest 2*** | | 1 | 0.318 | 0.308 | 0.190 | 0.119 | 0.066 | 0.057 | 0.065 | 0.062 |
| ***Logged forest 1*** | | | 1 | 0.354 | 0.273 | 0.161 | 0.118 | 0.067 | 0.058 | 0.045 |
| ***Logged forest 2*** | | | | 1 | 0.194 | 0.149 | 0.124 | 0.042 | 0.049 | 0.030 |
| ***Secondary forest 1*** | | | | | 1 | 0.143 | 0.230 | 0.188 | 0.088 | 0.026 |
| ***Secondary forest 2*** | | | | | | 1 | 0.119 | 0.119 | 0.078 | 0.057 |
| ***Plantation 1*** | | | | | | | 1 | 0.254 | 0.225 | 0.078 |
| ***Plantation 2*** | | | | | | | | 1 | 0.111 | 0.090 |
| ***Pasture 1*** | | | | | | | | | 1 | 0.186 |
| ***Pasture 2*** | | | | | | | | | | 1 |

**Table 7.16 Similarities between leaf-litter beetle species composition of different field sites in northern Costa Rica, as measured by the Morisita index**

| | Prim forest 1 | Prim. forest 2 | Log. forest 1 | Log. forest 2 | Secnd. forest 1 | Secnd. forest 2 | Plantat 1 | Plantat 2 | Pastur 1 | Pastur 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Primary forest 1*** | 1 | 0.369 | 0.134 | 0.225 | 0.136 | 0.110 | 0.069 | 0.025 | 0.057 | 0.013 |
| ***Primary forest 2*** | | 1 | 0.415 | 0.419 | 0.141 | 0.124 | 0.142 | 0.032 | 0.134 | 0.028 |
| ***Logged forest 1*** | | | 1 | 0.470 | 0.066 | 0.042 | 0.210 | 0.004 | 0.005 | 0.002 |
| ***Logged forest 2*** | | | | 1 | 0.088 | 0.075 | 0.134 | 0.024 | 0.011 | 0.001 |
| ***Secondary forest 1*** | | | | | 1 | 0.507 | 0.538 | 0.350 | 0.046 | 0.032 |
| ***Secondary forest 2*** | | | | | | 1 | 0.226 | 0.147 | 0.312 | 0.044 |
| ***Plantation 1*** | | | | | | | 1 | 0.961 | 0.199 | 0.041 |
| ***Plantation 2*** | | | | | | | | 1 | 0.104 | 0.065 |
| ***Pasture 1*** | | | | | | | | | 1 | 0.316 |
| ***Pasture 2*** | | | | | | | | | | 1 |

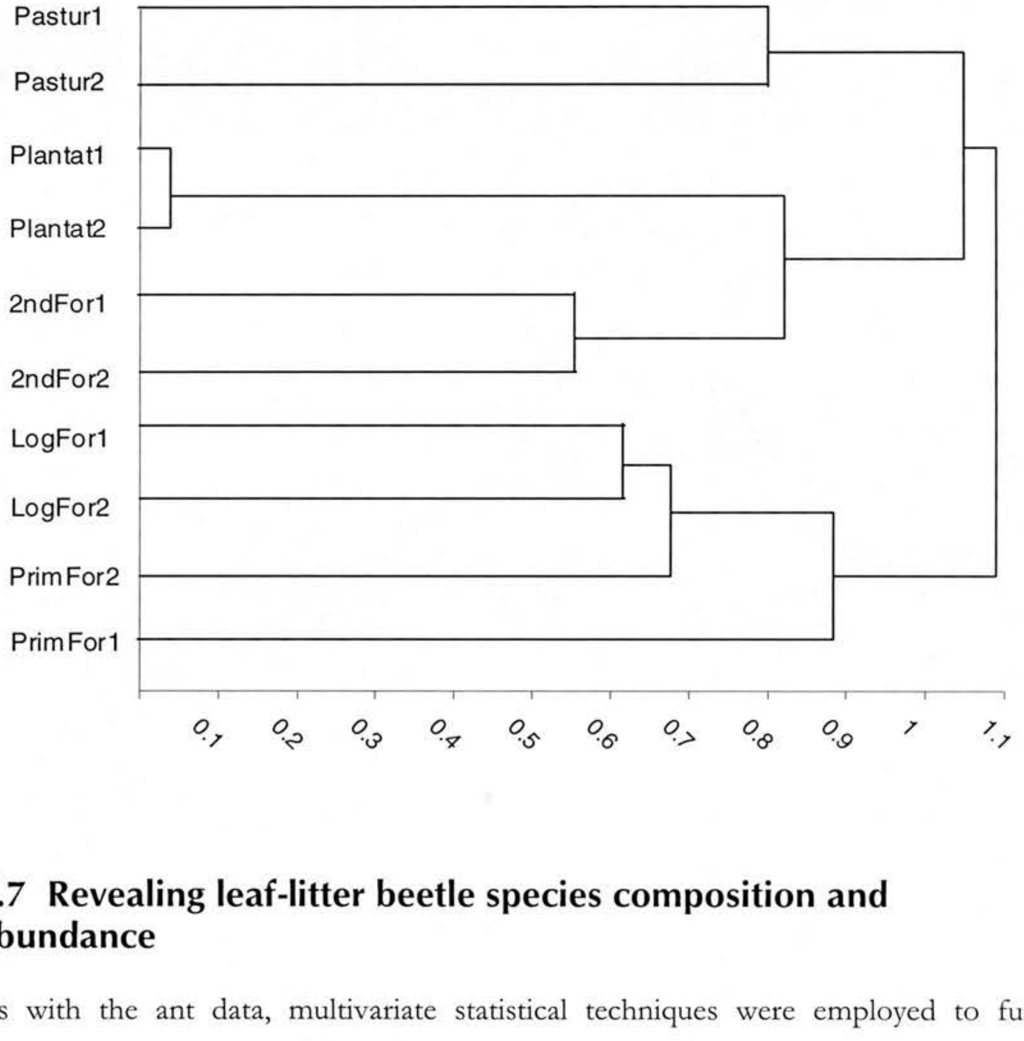
**Figure 7.27 Sorensen's similarity coefficients for beetle species between primary forest (site 1) and the other 8 sites of logged forest, secondary forest, plantation and pasture.** LogFor = selectively logged forest, 2ndFor = secondary forest, Plantat = Gmelina plantation, Pastur = pasture.



The Morisita similarity indices calculated above can also be used to carry out a cluster analysis (SAS 1990). This technique is widely used to compare the species composition of plant and animal communities (e.g. Pinheiro and Ortiz 1992, Russell-Smith and Stork 1995) and was used here to compare the beetle species composition groupings by field site (Fig 7.28). The cluster analysis revealed a clear pattern of species composition separation by land use and reinforced ideas on the effect of land use change on species composition. The cluster analysis divided the field sites into two main groups according to their species similarity. The dichotomy divided the sites broadly into natural forest in one main group, and converted forest sites on the other. The two logged forest sites (LogFor1 and LogFor2) were grouped with the two primary forest sites (PrimFor1 and PrimFor2). The two secondary forest sites (2ndFor1 and 2ndFor2) were grouped together with the plantation sites (Plantat1 and Plantat2) and this group was then linked to the pasture sites (Pastur1 and Pastur2).

The analysis suggests that the species composition of the most disturbed sites, namely secondary forest, plantation and pasture, contained a distinctive beetle species assemblage compared to the natural forest sites. This implies that human disturbance has been the principal cause of changes in the beetle community.

**Figure 7.28 Field sites grouped according to similarity of leaf-litter beetle species composition (Morisita Index and average linkage cluster analysis)**



## 7.7 Revealing leaf-litter beetle species composition and abundance

As with the ant data, multivariate statistical techniques were employed to further investigate the response of leaf-litter beetles to forest disturbance and conversion. Beetle species abundance data was used in a Detrended Correspondence Analysis (DCA) to examine the beetle species communities of all the field sites. This section is divided into two parts; the first examines an ordination analysis (DCA) of the full beetle species data set, and the second examines a reduced data set, which excludes species where only a single individual was collected.

### 7.7.1 Indirect ordination of the full beetle species data set

An indirect ordination of the full beetle species data was carried out using the CANOCO program (ter Braak and Smilauer 1998). The eigenvalues for this analysis are given in Table 7.17, and the scatter plots shown in Figure 7.29 a – c. The eigenvalue for axes 1 has a value greater than 0.5, suggesting a good separation of species along the axis. The four axes explain 30 percent of the variation. When considering the extent of possible variables in such a field study this level of explained variation is a reasonable result.

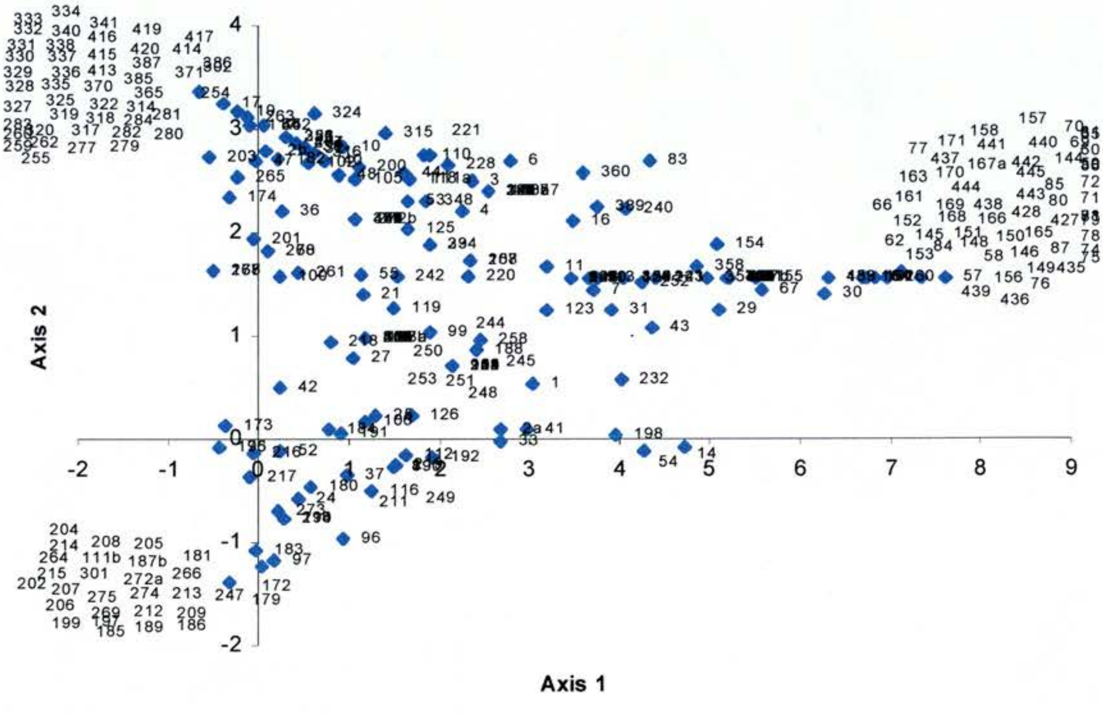
The diagrams illustrate a clear grouping of species and field sites by land use. Figure 7.29a shows significant grouping of species, both along axes 1 and axes 2. A clustering of species is revealed and by examination of Figure 7.29b it is evident that these are found around the pasture and the plantation sites. In addition a clear grouping occurs around the primary forest sites. The two logged forest sites are grouped closely in Axis 1 but are separated by Axis 2. Each site appears to show a distinct species cluster. There is some grouping of species in the middle of the diagram around the primary, logged and secondary forest sites but this is less evident than the corresponding ordination diagram for the ant species data. Many of the ant species appeared to be generalists and were found across the disturbance gradient but the beetle analysis indicates a greater species grouping according to field site and corresponding level of disturbance. This may be due to the increased sensitivity to disturbance of the beetle fauna. A gradient from the natural forest sites through secondary forest to plantation and pasture is evident in Figure 7.30b, indicating the corresponding gradient of disturbance. Another trend is also shown from one of the logged forest sites (LogFor1) below Axis 1 through the primary forest sites to the second logged forest site (LogFor2) above Axis 1 revealing a distinctive species assemblage between the two logged forest sites. Both forests have been subjected to similar logging intensities so it is unlikely that level of disturbance has caused this difference. LogFor1 is situated at a slightly higher altitude to LogFor2 and this may have resulted in some changes in insect community composition. Figure 7.29b not only shows the land use groupings, circled in red, but also indicates that Axes 1 is representative of the gradient of disturbance present in the field sites. Figure 7.29c illustrates both the species and sample score data in order to provide a clearer representation of species groupings by site.

**Table 7.17 Eigenvalues and percentage variance for full beetle species data set**

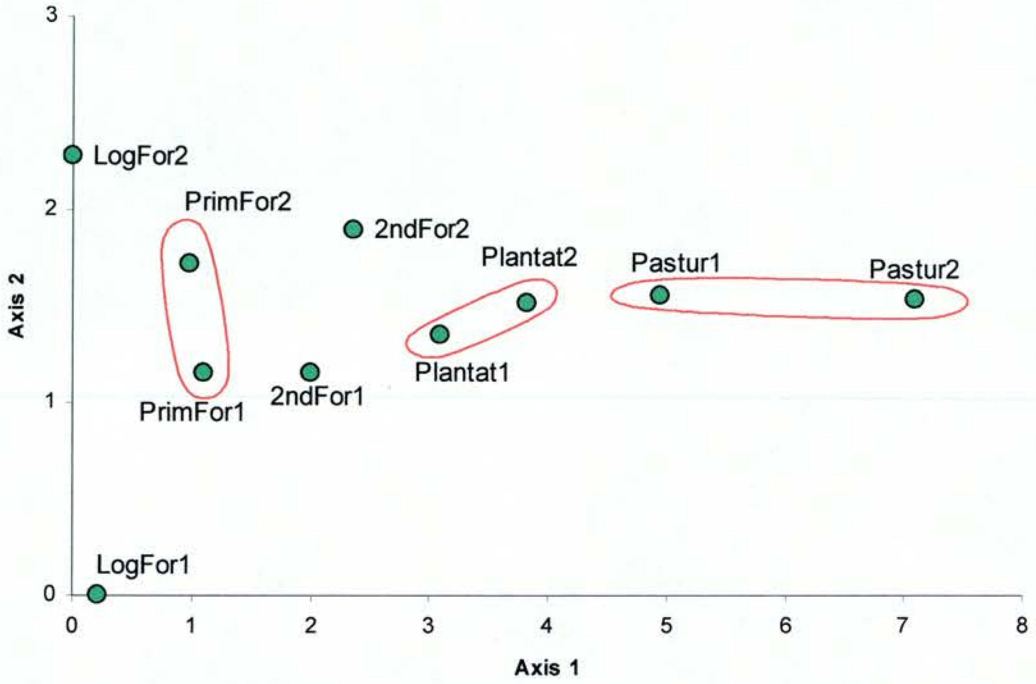
| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.888 | 0.405 | 0.132 | 0.012 | 4.717 |
| Cumulative percentage variance of species data | 18.8 | 27.4 | 30.2 | 30.5 | |
| Sum of all unconstrained eigenvalues | | | | | 4.717 |

**Figure 7.29 DCA ordination of sites based on beetle species abundances (full data set)**

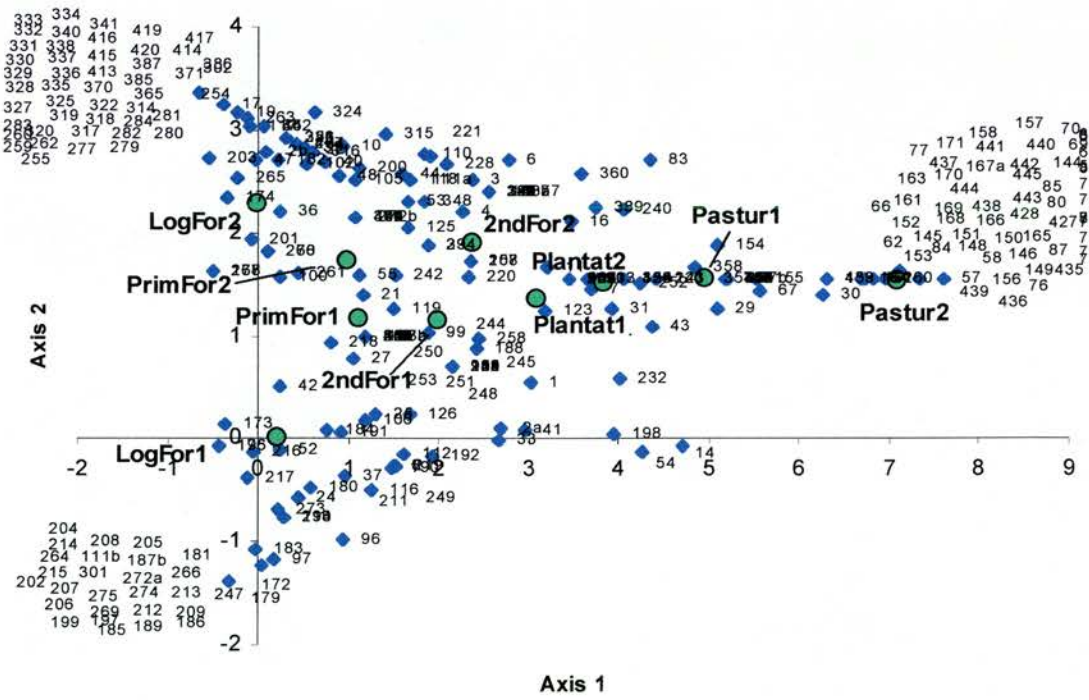
**a) Species score plot** showing the main clusters of species related to land use type.



**b) Sample score plot** showing the main groupings of land use type. This plot reveals a gradient representing disturbance along Axis 1, from the primary and logged forest sites on the left of the diagram to the more disturbed sites of plantation and pasture on the right.



**c) Sample and species score plot** showing the species and land use clusters. The relationship between species and sites is shown. The gradient of disturbance along Axis 1 is also evident.



### 7.7.1 Indirect ordination of the reduced beetle species data set

The indirect ordination of the reduced beetle species data set (excluding unique occurrences or 'singletons') was also carried out using the CANOCO program (ter Braak and Smilauer 1998). The number of species was reduced by 35 percent, from 422 to 274 active species in the calculation. The eigenvalues for this analysis are given in Table 7.18, and the scatter plots shown in Figure 7.30 a – c. The eigenvalues for axes 1 and 2 are greater than 0.5 (0.94 and 0.60 respectively) and this suggests a very good separation of species along these axes. The four axes explain 41 percent of the variation.

Again the resulting diagrams of species and sample scores illustrate a clear grouping of species and field sites by land use. Figure 7.30a shows significant grouping of species, both along axes 1 and axes 2, however the groupings revealed are different from the full data set. There now appears to be no separation between the species in the two logged forest sites. The two distinct groupings on Axis 2 which related to the logged forest species in the full data set analysis (Figure 7.29) are not evident, having been replaced by a single cluster around the primary and logged forest sites. The plantation and forest sites are also evident by individual species clusters and the gradient of disturbance is evident along Axis 1. Figure 7.30b shows the land use groupings, circled in red, and reiterates the gradient apparent over axis 1. The position of the pasture sites has changed very little, however the plantation sites have changed position in both Axes 1 and 2 from the full data set ordination diagram. All the natural forest sites (PrimFor1, PrimFor2, LogFor1, LogFor2, 2ndFor1 and 2ndFor2) have been grouped more closely with the reduced data set ordination. This reveals that the principal differences between the sites were due to the unique species occurrences, and suggests that beetle composition is clearly classified by land use type if the rarer species are excluded. It is also noteworthy that these six sites are more closely grouped together as a whole in this analysis. This may indicate a species assemblage of greater similarity among the natural forest sites of varying levels of disturbance. They are clearly separated from the plantation and pasture sites of greater human impact. Figure 7.30c illustrates both the species and sample score data from the reduced data set.

The species group clustered next to the pasture sites include species 30, 56a, 56b, 56c, 77, 151, 152, 158, 162, 167a and 170 (Appendix 9). Of these species five are from the family Staphylinidae, three are in the Carabidae, one in the Chrysomelidae (Sub-family Alticinae), one in the Curculionidae, and one in the Limnichidae. Species 30, 77, 152, 162, 170 are staphylinids and therefore either predators or saprophagous. Species 56a, 56b and 56c are carabids and therefore predators. Species 51 is from the Limnichidae and therefore saprophagous, species 158 is from the Chrysomelidae, sub-family Alticinae, and therefore herbivorous, while species 167a is from the Curculionidae and therefore probably also herbivorous or xylophagous. These feeding types cover four out of a possible six and it is notable that the missing feeding types, or trophic guilds, are the fungivores and the xylomycetophages. This may be due to the absence of a litter layer and is obviously contributed to, particularly in the case of the xylomycetophages, by the absence of trees. As with the ant data, it is also evident from Figure 7.30, that there are less species clustered around the pasture and plantation sites, at the right side of the DCA diagrams, compared to around the natural forest sites where the species are more concentrated. This may indicate that, although some species are successful in pasture and plantation sites, many species cannot survive in such an altered landscape.

Species grouped around the plantation sites include species 1, 5, 7, 8, 11, 123, 357, 360 and 430. Species 1, 7, 123 and 430 are carabids (species 1 = *Galerita* sp.3, species 123 = *Galerita* sp.2, Appendix 9) and therefore predators. Species 5, 8, 11, 357 and 360 are staphylinids and therefore either predators or saprophagous. This pattern complements the results shown for pasture, with a reduced suite of trophic groups present. The predators and sacrophages appear to dominate the plantation sites.

Species grouped around the origin to the left side of the diagram which, if axes 1 represents a gradient of disturbance, describes species present in the more pristine of the natural forest sites, include species 2b, 3, 4, 111a, 125, 133a, 200, 208, 272a, 365, 376, 378, and 449. Species 2b, 4, 111a, 133a and 376 are in the Nitidulidae which contains species covering a broad range of feeding habits, namely fungivores, saprophages, herbivores and predators. Seven of the species (species 3, 125, 200, 208, 365, 378, and 449) are staphylinids and therefore predators or saprophages while species

272a is from the Hydrophilidae and therefore a predator or a saprophage. The beetle fauna in the primary, logged and secondary forest sites appear to be dominated by staphylinids and nitidulids, with only one other family, the Hydrophilidae, being represented in this selection. Again four out of a possible six trophic groups are represented. However, in this case the absent groups are the xylophages and the xylomycetophages. This is unexpected as both the groups feed on either dead or live wood, and the forest sites do, rather obviously, contain large quantities of wood. The explanation for this absence of wood feeding beetle is probably the sampling method of pitfall trapping, which does not favour these groups. In general, it is evident that the natural forest species are found in quite different positions in relation to the two ordination axes compared to the pasture and plantation sites suggesting that they respond to different environmental parameters.

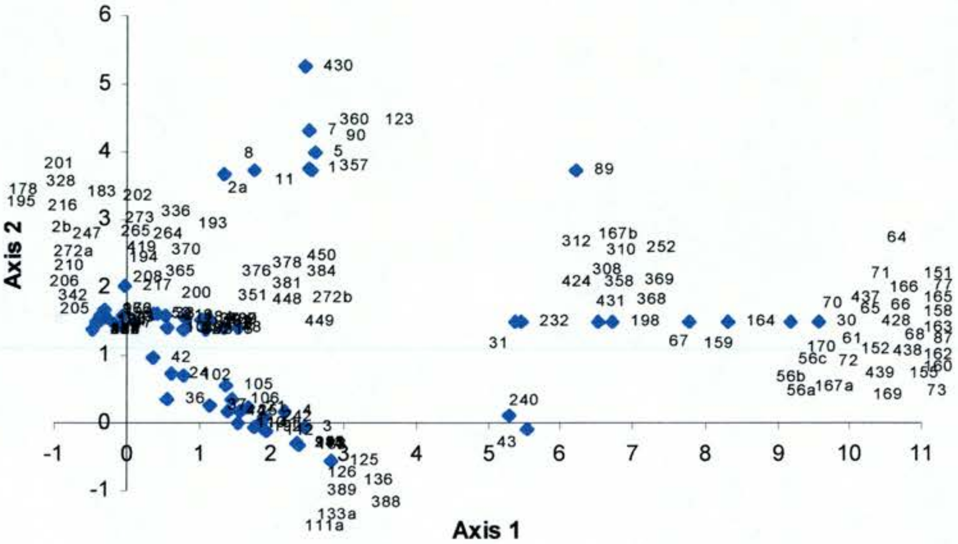
In general, the DCA analysis of both the full and reduced beetle species data has shown that leaf litter beetle species can be clearly divided into groups of similarly occurring species, which are found within similar land uses. In a similar pattern to the ant data, the key changes indicated by the separation of species along axis 1 appear to be a result of the gradient of human disturbance over the field sites. Particular beetle assemblages are grouped with different land uses. Figures 7.29b and Figures 7.30b reveal clear differences in species and sample scores between the full and reduced data sets. This may reveal that some of the differences between the sites in the full data set analysis were due to unique species occurrences, and suggest that beetle species composition can be classified by land use type if the rarer species are excluded.

**Table 7.18 Eigenvalues and percentage variance for the reduced beetle species data set (excluding unique occurrences)**

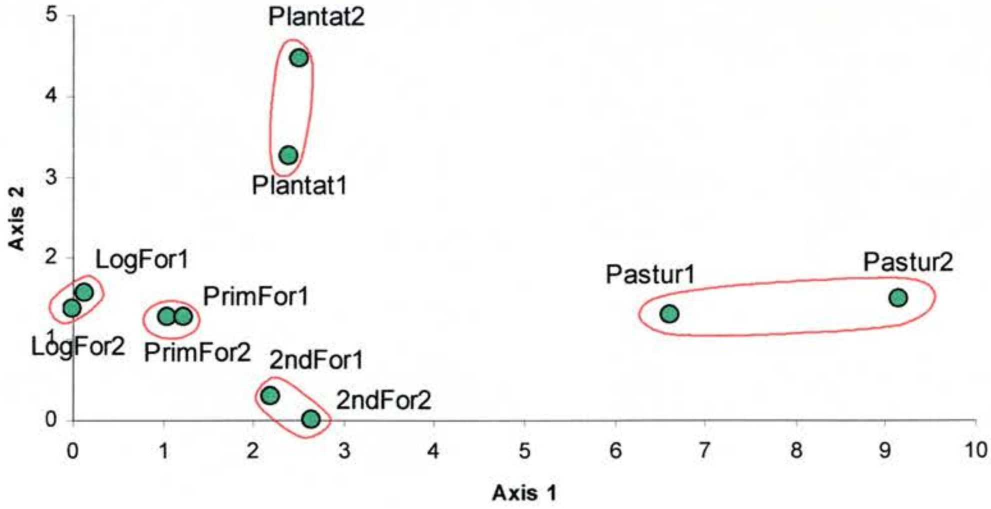
| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.940 | 0.598 | 0.337 | 0.208 | 5.028 |
| Cumulative percentage variance of species data | 18.7 | 30.6 | 37.3 | 41.4 | |
| Sum of all unconstrained eigenvalues | | | | | 5.028 |

## Figure 7.30 DCA ordination of sites based on beetle species abundances (reduced data set excluding unique occurrences)

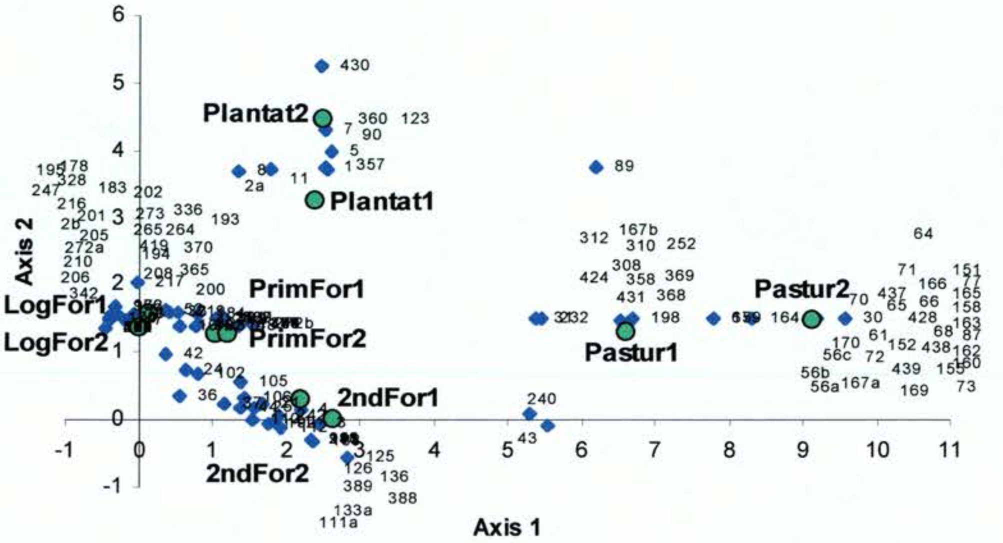
a) **Species score plot** showing the main clusters of species related to land use type.



b) **Sample score plot** showing the main groupings of land use type. The groupings have been changed by the reduced data set. The plantation and pasture sites are clearly separated while the primary, logged and secondary forest sites are clustered together. This plot also reveals the presence of a gradient along Axis 1, from the primary and logged forest sites on the left of the diagram to the more disturbed sites on the right.



**c) Sample and species score plot** showing the species and land use clusters. The relationship between species and sites is shown. The gradient of disturbance along Axis 1 is also evident.



## 7.7.2 TWINSPAN classification of the beetle species data set

TWINSPAN was used to classify samples and species (Hill 1979)(Section 4.6.3). As already discussed, this method is one of the most widely used clustering programmes in community ecology (van Tongeren 1995), and is based on the general principle that a group of sites can be characterised by a group of differential species (Jongman et al. 1995). As a hierarchical clustering technique, it essentially involves the repeated dichotomization of samples and then of species. The resulting two-way table expresses synecological relations as succinctly as possible (Hill 1979).

The database used for the classification of leaf-litter beetle species consisted of 10 samples and 274 species, which excludes unique occurrences. Pseudospecies levels were set at 0%, 2%, 5%, 10% and 20% representing 5 categories of abundance (1 = 0-2%, 2 = 2-5%, 3 = 5-10%, 4 = 10-20%, 5 = >20%). The full TWINSPAN table for all 274 species is given in Appendix 11. The results of the analysis are summarised below.

The TWINSPAN classification of samples is illustrated in Figure 7.31. The first division created two groups which divided the sites into pasture sites and all the remaining sites. The primary and logged primary, and secondary forests together with the plantation sites are grouped together (*0 group), and the pasture sites are defined as being separate from these (*1 group). The next division of the left hand group (*0 group) divides the two plantation sites from the primary, logged primary and secondary forest sites. The second group containing the forest sites is subdivided again, separating the secondary forest sites from the sub-group which contains the primary and logged forest sites.

An overview of this classification demonstrates that the ecological changes occurring over the gradient of disturbance found in northern Costa Rica are strongly reflected by the resulting leaf litter beetle community. There is a clear separation between the pasture sites and the remaining natural forest and plantation sites. This appears to indicate that beetle communities are more strongly affected by the ecological changes which occur in the sites of complete conversion from forest, namely, the pasture sites. The plantation sites are broadly grouped with the natural forest sites (*0 group) but are separated in the next subdivision (*00 group) indicating that they too show differences from the natural forest sites which are grouped together (*01 group). The latter group is subdivided further into and the secondary forests are separated from the logged and primary forest sites. Again, within this group (*011 group) there is further sub-division with one of the primary forest sites (PrimFor2) being divided from the remaining three. This does not appear to be for geographical location reasons but may reflect the slightly steeper topography in this site. It may also simply be a result of the heterogeneity of evergreen rain forest.

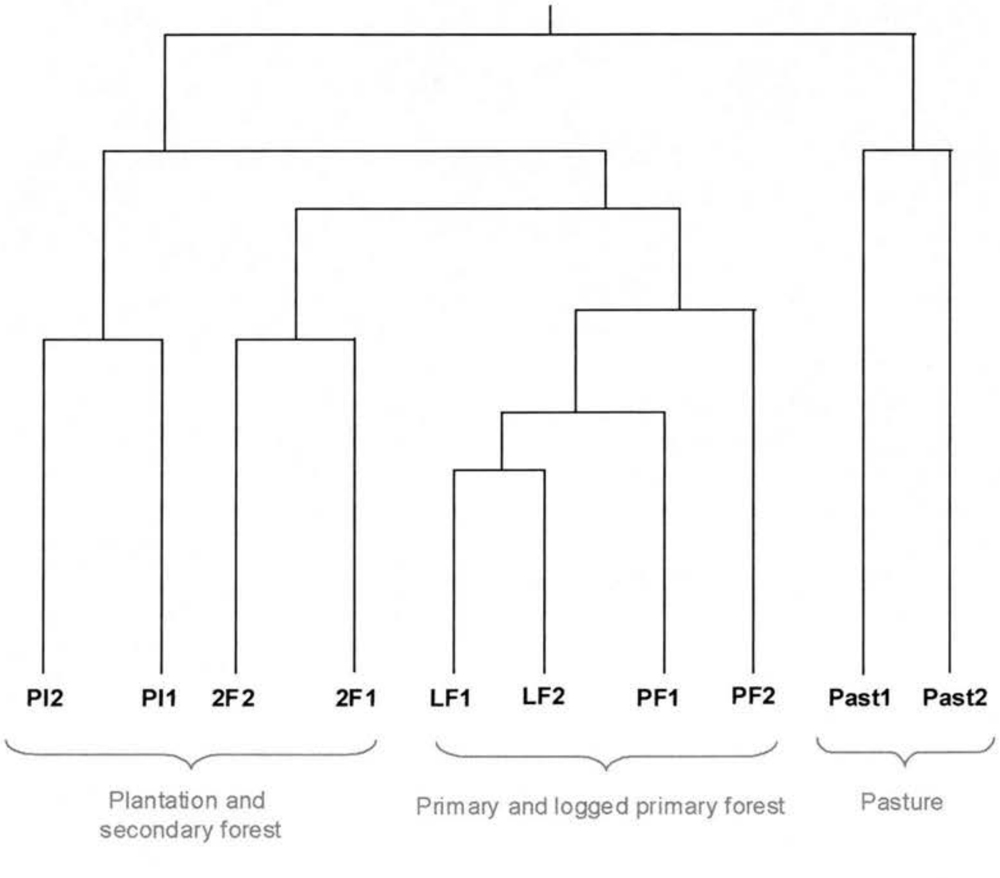
The TWINSPAN analysis, shown in Appendix 11, has revealed a number of indicator species for various site clusters. Species 7 (Carabidae) is identified as a 'perfect indicator', as defined by Hill (1979), for the natural forest and plantation sites cluster (*0 group). This species was present in both plantation sites and one of the secondary forest sites, but was not found in the primary or logged forest sites or in the pasture. As such, it may be a good indicator of intermediate disturbance. Species 201 (Staphylinidae) is exclusively found in the logged and primary forest sites and, as such, may be a good indicator species for less disturbed forest. It is noteworthy that it is present at abundance level 4 in the two primary forest sites and only abundance level 2 in the logged sites. Species 42 (Staphylinidae) has been identified by the TWINSPAN output as a 'perfect indicator' for the logged and primary forest sites (*011 group). Examination of Appendix 11 reveals that it is also present in one of the secondary forest sites (2ndFor1) but is missing in one of the primary sites (PrimFor2). Its presence in the other primary forest site and the two logged forest sites is at abundance level 4 and 5, indicating that it may also be an appropriate general indicator of natural forest cover.

Species found exclusively in the pasture sites include species 164 (Staphylinidae), 240 (Nitidulidae), 358 (Nitidulidae) and 428 (Staphylinidae). These species, along with many others (see Appendix 11) appear to be adapted to the conditions present in pasture and are not found in any of the forest sites. The presence of such species may be used in future studies to indicate high disturbance levels.

In contrast to the TWINSPAN output for the ant species, where many of the species collected appeared to have a ubiquitous distribution, no beetle species collected in this study was found in all 10 sites. The beetles appear to demonstrate specific species clusters with the three main divisions indicating species groupings into the plantation sites, the natural forest sites and the pasture sites (Figure 7.31). It seems that forest-specific beetles have not adapted very successfully to the altered ecological and microclimatic conditions now present over the range of land uses studied. They are found in clear groups which relate to land use type, and therefore to disturbance level. However, from the level of identification available here, these groups do not seem to be clearly linked to their guild membership.

The disturbed habitats, namely pasture and plantation, examined in this study have a considerably modified environment and microclimate. Both habitats are considerably drier than in native forest and temperatures are much higher. This may have caused the marked changes observed in the native beetle communities. It is evident from the TWINSPAN analysis that many species can be clearly separated by the land use in which they are found, demonstrating, in some cases, a preference for natural forest sites, or for plantation or pasture sites. Some of the species have been revealed by the TWINSPAN analysis as clear indicators for the three main classifications of natural forest sites, plantation sites and pasture sites. The different habitat preferences shown by this analysis can be a result of a variety of factors. Some forest beetle species cannot tolerate the increased temperatures, or the reduced humidity, related to forest conversion to plantation or pasture (Murcia 1995, Rodríguez et al. 1998). As with the ant fauna, changes in vegetation structure may also affect the beetle assemblage, as can changes in soil properties and leaf litter. These factors are examined in relation to beetle species diversity and composition in the next section.

**Figure 7.31 Dendrogram of the TWINSPAN classification of leaf litter beetle species by site**



## 7.8 Effects of environmental variables on beetle community structure

As already discussed, the sites under investigation in this study have all, with the exception of the primary forest areas, been changed by human intervention, although even the 'undisturbed forest' may have had a degree of impact in the past. This section considers the effects of the environmental changes caused by human intervention on the leaf-litter beetle community. As with the ants, human impact on beetle species diversity and composition has been mediated by seven environmental variables (Table 7.19):

- basal area of forest ($m^2$) and number of trees,
- tree species diversity,
- maximum and minimum temperature (°C),
- soil temperature (°C),
- soil organic matter(%),
- soil pH, and
- leaf litter quantity ($kg/m^2$).

In addition, elevation (m), the aspect of each transect, and the mean and range of slope at each trap location was recorded to help in site characterisation (Table 7.19). The effects of the variables listed above on leaf-litter beetle composition is examined below.

As in the indirect ordination of the beetle data, this section is divided into two parts; the first examines the direct ordination analysis of the full beetle species data set, and the second examines a reduced data set, excluding unique occurrences.

**Table 7.19 Site characteristics.** Values indicated are means for each site ± 1 standard deviation. (Leaf litter units measure dry mass)

| *Habitat* | *Site* | *Soil temp (°C)* | *Soil pH* | *Soil organic matter (%)* | *Basal area/ha* | *Leaf litter(g)* |
|---|---|---|---|---|---|---|
| *Primary forest* | PrimFor1 | 23.8 ± 0.33 | 3.8 ± 0.46 | 2.1 ± 2.47 | 41.0 ± 0.15 | 13.0 ± 4.1 |
| | PrimFor2 | 28.1 ± 1.51 | 4.0 ± 0.26 | 1.6 ± 0.65 | 23.5 ± 0.07 | 13.9 ± 5.33 |
| *Logged forest* | LogFor1 | 26.8 ± 1.55 | 3.9 ± 0.28 | 3.2 ± 1.10 | 19.1 ± 0.07 | 8.2 ± 4.23 |
| | LogFor2 | 26.0 ± 1.62 | 4.2 ± 0.42 | 2.3 ± 1.09 | 24.3 ± 0.13 | 9.1 ± 3.19 |
| *2ndary forest* | 2ndFor1 | 29.2 ± 2.04 | 3.8 ± 0.42 | 1.7 ± 0.74 | 11.5 ± 0.08 | 8.5 ± 5.22 |
| | 2ndFor2 | 29.8 ± 1.47 | 4.2 ± 0.36 | 1.7 ± 0.72 | 37.1 ± 0.21 | 12.6 ± 7.41 |
| *Plantation* | Plantat1 | 31.6 ± 1.96 | 4.0 ± 0.26 | 1.8 ± 0.84 | 12.9 ± 0.02 | 8.5 ± 3.76 |
| | Plantat2 | 34.4 ± 2.53 | 4.0 ± 0.42 | 1.7 ± 0.71 | 11.8 ± 0.01 | 10.2 ± 4.25 |
| *Pasture* | Pastur1 | 33.9 ± 1.36 | 4.5 ± 0.39 | 1.9 ± 0.94 | 2.2 ± 0.05 | 1.8 ± 2.05 |
| | Pastur2 | 32.2 ± 2.75 | 4.4 ± 0.57 | 1.7 ± 0.86 | 0.4 ± 0.13 | 2.3 ± 2.82 |

| *Site* | *Max T (°C)* | *Min T (°C)* | *Slope (%)* | *Altitude (m)* | *Tree spp. richness.* | *Trees/ ha* |
|---|---|---|---|---|---|---|
| PrimFor1 | 27.5 ± 0.71 | 20.5 ± 0.71 | 5.2 ± 6.20 | 38.7 ± 4.17 | 53 | 478 |
| PrimFor2 | 28.3 ± 2.48 | 18.8 ± 0.35 | 29.6 ± 17.59 | 82.2 ±10.88 | 52 | 560 |
| LogFor1 | 26.3 ± 0.35 | 18.8 ± 1.06 | 13.6 ± 10.41 | 45.9 ±9.60 | 50 | 486 |
| LogFor2 | 27.5 ± 0.71 | 20.0 ± 1.41 | 13.9 ± 9.96 | 160.7 ±16.83 | 58 | 416 |
| 2ndFor1 | 29.3 ± 2.48 | 20.3 ± 0.35 | 12.1 ± 10.75 | 40.7 ± 4.90 | 34 | 186 |
| 2ndFor2 | 30.0 ± 0.00 | 18.5 ± 0.00 | 12.1 ± 7.48 | 79.4 ±27.00 | 44 | 594 |
| Plantat1 | 31.0 ± 0.00 | 20.5 ± 0.71 | 8.7 ± 6.57 | 41.5 ±5.40 | 2 | 548 |
| Plantat2 | 31.5 ± 0.00 | 19.0 ± 0.00 | 9.2 ± 8.74 | 43.8 ±3.80 | 1 | 516 |
| Pastur1 | 34.0 ± 3.54 | 20.0 ± 2.12 | 18.6 ± 12.93 | 158.6 ±12.10 | 8 | 30 |
| Pastur2 | 32.5 ± 0.00 | 21.5 ± 0.71 | 3.3 ± 4.27 | 48.2 ±9.20 | 1 | 2 |

### 7.8.1 Direct ordination of the full ant species data set

As with the ant species data, a direct ordination of the beetle species data set and the environmental variables detailed above was carried out using the CANOCO program (ter Braak and Smilauer 1998). The eigenvalues for this analysis are given in Table 7.22 and the scatter plots are shown in Figure 7.32 a and b. The eigenvalue for axes 1, 2 and 3 are greater than 0.5, suggesting a good separation of species along the axis. The four axes explain 56.5 percent of the variation, a reasonable result for this type of analysis.

The correlation matrix for the environmental data is shown in Table 7.20. All coefficients with a value higher than 0.7 are shown in red. Clear autocorrelations, such as between trees per hectare and basal area per hectare, and maximum temperature and soil temperature were reduced to one variable in the diagrams. The highest coefficients, excluding the autocorrelations, were between soil temperature and tree species diversity (r = -0.89), soil temperature and basal area per hectare (r = -0.80), maximum temperature and trees per hectare (r = -0.72), and maximum temperature and tree species diversity (r = -0.89). Soil temperature and tree species diversity show a negative correlation which may be a result of the effects of changing land use on both these variables. As discussed in previous chapters, soil temperature increases with forest disturbance due to increased insolation (Chapter 5). This also follows in the correlation of soil temperature with basal area. Basal area reduces as human disturbance increases as does soil temperature. These results agree with the results found from the tree species and the ant species analyses, showing the influence of disturbance on the forest environment.

**Table 7.20 Correlation coefficients among environmental variables from the beetle species (full data set) direct ordination.** CCA weighted correlation matrix output.

| | *leaf lit* | *soil OM* | *soil pH* | *soil T* | *max T* | *min T* | *slope* | *altitude* | *trees.ha* | *BA.ha* | *tree spp.* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***leaf lit*** | 1 | | | | | | | | | | |
| ***soil OM*** | -0.090 | 1 | | | | | | | | | |
| ***soil pH*** | -0.644 | -0.308 | 1 | | | | | | | | |
| ***soil T*** | -0.632 | -0.450 | 0.570 | 1 | | | | | | | |
| ***max T*** | -0.580 | -0.688 | 0.638 | 0.873 | 1 | | | | | | |
| ***min T*** | -0.466 | -0.445 | 0.343 | 0.199 | 0.546 | 1 | | | | | |
| ***slope*** | 0.381 | -0.101 | -0.042 | -0.007 | -0.201 | -0.656 | 1 | | | | |
| ***altitude*** | -0.082 | -0.147 | 0.595 | -0.075 | 0.042 | 0.044 | 0.334 | 1 | | | |
| ***trees.ha*** | 0.844 | 0.302 | -0.575 | -0.587 | -0.716 | -0.708 | 0.382 | -0.065 | 1 | | |
| ***BA.ha*** | 0.859 | 0.099 | -0.523 | -0.801 | -0.614 | -0.295 | 0.044 | 0.026 | 0.748 | 1 | |
| ***tree spp*** | 0.693 | 0.414 | -0.448 | -0.894 | -0.888 | -0.514 | 0.369 | 0.279 | 0.686 | 0.757 | 1 |

**Table 7.21 Correlation coefficients of environmental variables with the CCA ordination axes from the beetle species (full data set) direct ordination.** CCA weighted correlation matrix output.

| | *SPEC Axis 1* | *SPEC Axis 2* | *SPEC Axis 3* | *SPEC Axis 4* | *ENVI Axis 1* | *ENVI Axis 2* | *ENVI Axis 3* | *ENVI Axis 4* |
|---|---|---|---|---|---|---|---|---|
| ***leaf litter*** | -0.741 | 0.021 | -0.132 | 0.255 | -0.741 | 0.021 | -0.132 | 0.255 |
| ***soil OM*** | -0.410 | -0.375 | 0.005 | -0.230 | -0.410 | -0.375 | 0.005 | -0.230 |
| ***soil pH*** | 0.633 | -0.056 | 0.316 | 0.048 | 0.633 | -0.056 | 0.316 | 0.048 |
| ***soil T*** | 0.742 | 0.517 | 0.016 | -0.048 | 0.742 | 0.517 | 0.016 | -0.048 |
| ***max T*** | 0.839 | 0.465 | 0.160 | 0.016 | 0.839 | 0.465 | 0.160 | 0.016 |
| ***min T*** | 0.645 | -0.097 | -0.124 | -0.151 | 0.645 | -0.097 | -0.124 | -0.151 |
| ***slope*** | -0.418 | 0.025 | 0.365 | -0.065 | -0.418 | 0.025 | 0.365 | -0.065 |
| ***altitude*** | -0.164 | -0.083 | 0.448 | -0.114 | -0.164 | -0.083 | 0.448 | -0.114 |
| ***trees ha*** | -0.823 | 0.028 | -0.154 | 0.086 | -0.823 | 0.028 | -0.154 | 0.086 |
| ***BA ha*** | -0.702 | -0.101 | 0.045 | 0.336 | -0.702 | -0.101 | 0.045 | 0.336 |
| ***tree spp.*** | -0.867 | -0.429 | 0.112 | 0.171 | -0.867 | -0.429 | 0.112 | 0.171 |

**Table 7.22 Eigenvalues and percentage variance for the CCA analysis of beetle species (full data set) and environmental variables**

| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.888 | 0.670 | 0.572 | 0.534 | 4.717 |
| Cumulative percentage variance of species data | 18.8 | 33.0 | 45.2 | 56.5 | |
| Cumulative percentage variance of species environment relation | 18.8 | 33.0 | 45.2 | 56.5 | |
| Sum of all unconstrained eigenvalues | | | | | 4.717 |

The existence of relationships between beetle species diversity and composition, and the selected environmental variables was also investigated using CCA analysis. The results of the direct ordination are shown in a biplot of site and environmental variables (Figure 7.32a) and also in a biplot of species and environmental variables (Figure 7.32b). The biplot of species and environmental arrows shows the weighted averages of each species with respect to each of the environmental variables. The correlation coefficients of the environmental variables with the CCA ordination axes are shown in Table 7.21. As with the tree species and ant species data, the environmental data in Figures 7.33a and 7.33b are represented by arrows, which are plotted in the direction of maximum change. The length of the arrows is proportional to the magnitude of the change. The environmental variables represented by longer arrows are more important in influencing community variation. The species show their relation to the arrows by their relative positions. Those found close to the tip are strongly correlated with the variable in question (Kent and Coker 1992). The results below make it possible to develop ideas regarding the key influences on the system.

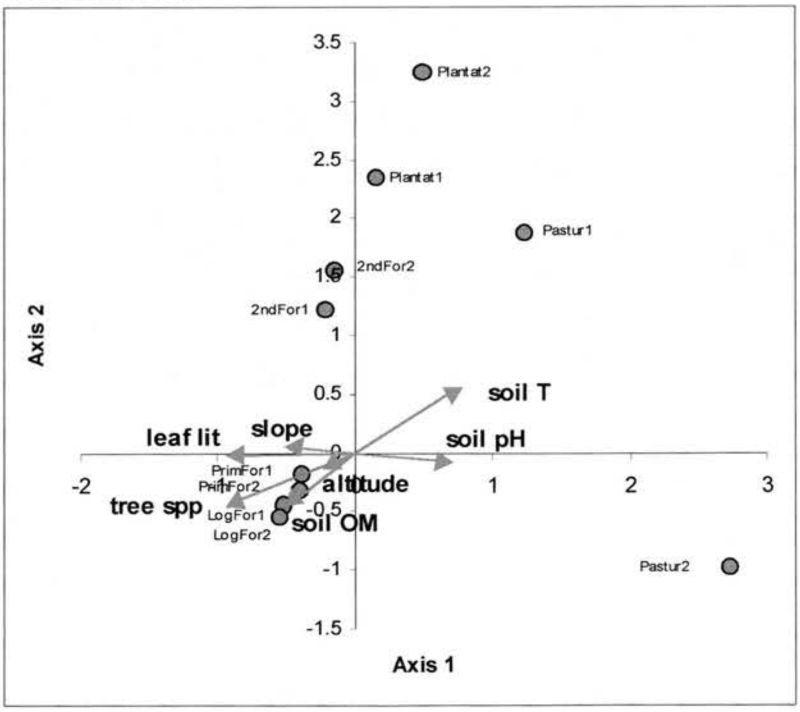
The ordination biplot of the first two axes of site and environmental variables (Figure 7.32a) reveals the existence of a correlation between the first ordination axis and the following environmental variables: leaf litter ($r = -0.74$), soil temperature ($r = 0.74$), maximum temperature ($r = 0.84$), trees per hectare ($r = -0.82$), basal area per hectare ($r = -0.70$) and tree species diversity ($r = -0.87$)(Table 7.18). The second and third axis do not show strong correlations with any of the variables. Overall, the four axes explain almost 57 percent of the variation.

The ordination diagram separates the field sites according to species composition and their response to environmental variables. Figure 7.32a reveals a distinctive separation between the logged and primary forest sites (PrimFor1, PrimFor2, LogFor1 and LogFor2) and the secondary forest, plantation and pasture sites. The cluster of logged and primary forest sites is located around the origin while the secondary and plantation sites and one of the pasture sites (Pastur1) are distributed on Axis 2. The second pasture site (Pastur2) is found in the bottom right of the diagram perhaps indicating its relationship with soil pH. In terms of environmental relationships, the proximity of the logged and primary sites to the tips of the arrows representing soil organic matter and tree species diversity indicates that these have a pronounced affect in defining these sites. Of the environmental variables measured only soil temperature appears to have any correlation with the secondary forest, plantation and one of the pasture sites. It was demonstrated in Chapter 5 that soil temperature changes significantly with land use change due to more direct insolation as a result of the removal of the forest canopy, and this may explain the correlation evident here.

In general the CCA analysis of site and environmental gradients shows a trend of forest disturbance up Axis 2, although a slightly diagonal trend is evident from the bottom left to the top right of the diagram. The environmental gradients demonstrate that the most important factors in defining natural forest are leaf litter amount, soil organic matter content, and tree species diversity, all of which are greatly changed by forest conversion to plantation and pasture. This is reinforced by the grouping of the disturbed sites at the opposite side of the diagram and their correlation with environmental variables, such as, soil temperature and soil pH. The two physical variables, slope and altitude entered into the analysis appear to have a minimal relationship with site and species composition. The small arrows representing them reveal that they are less important than the environmental variables measured although a small effect is evident in the primary and logged forest cluster. This is to be expected, as they do not change with forest disturbance, whereas all the environmental variables are affected to a certain extent.

**Figure 7.32 CCA ordination biplot of sites, beetle species abundances and environmental variables (full species data set)**

a) **Site score plot showing environmental gradients.** The arrows represent the correlation between the axes and the environmental variables. They also indicate which variables are most important in influencing the community variation of the sites located closest to the arrowheads.



b) **Species score plot.** The arrows represent the correlation between the axes and the environmental variables. Species which are found closest to the arrowheads demonstrate a strongly positive correlation with the variable represented.

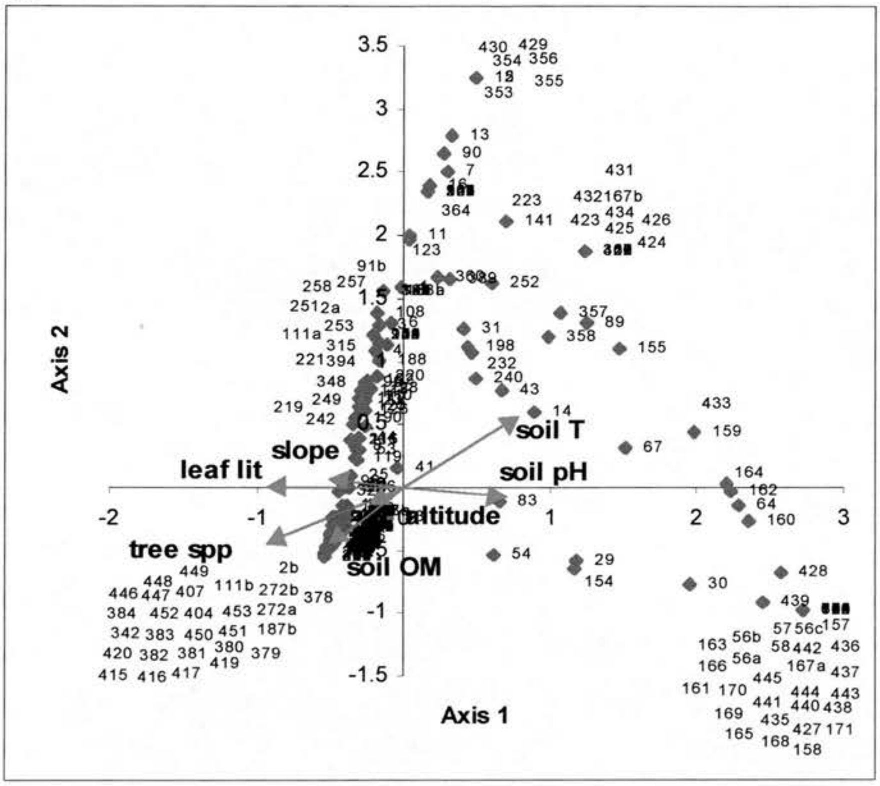


Figure 7.33b shows a clear grouping of species around the various land uses. All sites reveal quite specific grouping. Many of the species found in this analysis are unique species in the study sample. The following section, which examines the CCA of the reduced species set, will discuss particular beetle species grouping in more detail.

### 7.8.2 Direct ordination of the reduced beetle species (excluding unique occurrences) data set

A direct ordination of the reduced beetle species data set (excluding unique occurrences), and the environmental variables detailed above was carried out using the CANOCO program (ter Braak and Smilauer 1998). The eigenvalues for this analysis are given in Table 7.25 and the scatter plots are shown in Figure 7.33 a and b. The eigenvalues for axes 1 to 4 are greater than 0.5, suggesting a good separation of species along the axis. The four axes explain 58.0 percent of the variation.

The correlation matrix for the environmental data is shown in Table 7.23. All coefficients with a value higher than 0.7 are shown in red. As in the previous section, clear autocorrelations, such as between trees per hectare and basal area per hectare, and between maximum temperature and soil temperature have been reduced to one variable in the diagrams. The highest correlation coefficients are found between the same variables as in the full data set analysis and the r - values have only changed slightly.

**Table 7.23 Correlation coefficients among environmental variables from the beetle species (reduced data set) direct ordination.** CCA weighted correlation matrix output.

| | ***leaf litter*** | ***soil OM*** | ***soil pH*** | ***soil T*** | ***max T*** | ***min T*** | ***slope*** | ***altitude*** | ***trees. ha*** | ***BA. ha*** | ***tree spp.*** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***leaf lit*** | 1 | | | | | | | | | | |
| ***soil OM*** | -0.093 | 1 | | | | | | | | | |
| ***soil pH*** | -0.640 | -0.339 | 1 | | | | | | | | |
| ***soil T*** | -0.659 | -0.431 | 0.577 | 1 | | | | | | | |
| ***max T*** | -0.577 | -0.697 | 0.648 | 0.865 | 1 | | | | | | |
| ***min T*** | -0.446 | -0.504 | 0.400 | 0.237 | 0.596 | 1 | | | | | |
| ***slope*** | 0.409 | -0.109 | -0.060 | -0.001 | -0.200 | -0.656 | 1 | | | | |
| ***altitude*** | -0.054 | -0.199 | 0.602 | -0.080 | 0.059 | 0.091 | 0.310 | 1 | | | |
| ***trees.ha*** | 0.837 | 0.342 | -0.596 | -0.646 | -0.761 | -0.721 | 0.413 | -0.055 | 1 | | |
| ***BA.ha*** | 0.862 | 0.088 | -0.530 | -0.822 | -0.610 | -0.277 | 0.057 | 0.047 | 0.754 | 1 | |
| ***tree spp.*** | 0.715 | 0.401 | -0.462 | -0.894 | -0.885 | -0.537 | 0.372 | 0.280 | 0.746 | 0.765 | 1 |

The species data set used in this analysis excludes singletons therefore reducing it by 35 percent, from 422 to 274 active species. A comparison of the biplots for the species, sites and environmental data for both the analyses (Figure 7.32 and 7.33) shows that the site groupings and the environmental gradients do not vary greatly from the results of the full data set analysis. The pasture sites are the exception as they are now grouped together on the right hand side of the diagram. It is evident that the unique species were the principal factor in the wide spacing of these two pasture sites in the full species data set analysis. Figure 7.33b reveals more clearly the dominant individual species which are correlated with the environmental variables and which are also grouped with specific field sites.

**Table 7.24 Correlation coefficients of environmental variables with the CCA ordination axes from the beetle species (reduced data set) direct ordination.** CCA weighted correlation matrix output.

| | *SPEC Axis 1* | *SPEC Axis 2* | *SPEC Axis 3* | *SPEC Axis 4* | *ENVI Axis 1* | *ENVI Axis 2* | *ENVI Axis 3* | *ENVI Axis 4* |
|---|---|---|---|---|---|---|---|---|
| ***leaf litter*** | -0.756 | 0.035 | -0.027 | -0.194 | -0.756 | 0.035 | -0.027 | -0.194 |
| ***soil OM*** | -0.410 | -0.321 | -0.180 | 0.218 | -0.410 | -0.321 | -0.180 | 0.218 |
| ***soil pH*** | 0.661 | -0.155 | 0.140 | 0.117 | 0.661 | -0.155 | 0.140 | 0.117 |
| ***soil T*** | 0.761 | 0.429 | 0.246 | 0.039 | 0.761 | 0.429 | 0.246 | 0.039 |
| ***max T*** | 0.852 | 0.332 | 0.318 | 0.001 | 0.852 | 0.332 | 0.318 | 0.001 |
| ***min T*** | 0.640 | 0.058 | -0.199 | 0.066 | 0.640 | 0.058 | -0.199 | 0.066 |
| ***slope*** | -0.385 | -0.169 | 0.350 | 0.050 | -0.385 | -0.169 | 0.350 | 0.050 |
| ***altitude*** | -0.120 | -0.288 | 0.293 | 0.185 | -0.120 | -0.288 | 0.293 | 0.185 |
| ***trees ha*** | -0.865 | 0.031 | -0.082 | 0.044 | -0.865 | 0.031 | -0.082 | 0.044 |
| ***BA ha*** | -0.711 | -0.139 | 0.026 | -0.192 | -0.711 | -0.139 | 0.026 | -0.192 |
| ***tree spp.*** | -0.867 | -0.438 | -0.074 | -0.132 | -0.867 | -0.438 | -0.074 | -0.132 |

**Table 7.25 Eigenvalues and percentage variance for the CCA analysis of beetle species (reduced data set excluding unique occurrences) and environmental variables**

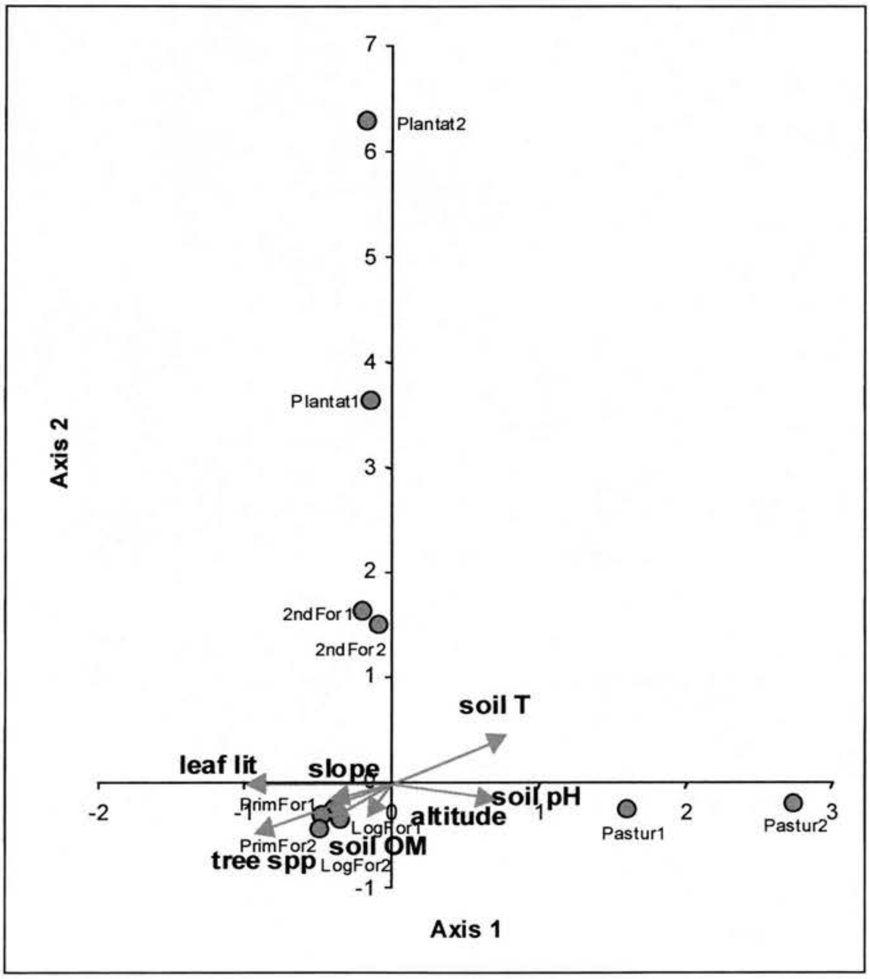
| *Axes* | *1* | *2* | *3* | *4* | *Total inertia* |
|---|---|---|---|---|---|
| Eigenvalues | 0.94 | 0.744 | 0.67 | 0.561 | 5.028 |
| Cumulative percentage variance of species data | 18.7 | 33.5 | 46.8 | 58.0 | |
| Cumulative percentage variance of species environment relation | 18.7 | 33.5 | 46.8 | 58.0 | |
| Sum of all unconstrained eigenvalues | | | | | 5.028 |

According to the analysis, the most influential environmental variables revealed are leaf litter amount and tree species diversity. Leaf litter amount is strongly correlated with Axis 1. As the arrows, which represent these variables, are almost of the same length they have a very similar influence in the community. Soil temperature is the next most important variable. This arrow is not as closely correlated to individual sites as the other two important variables but it may have some influence over both the pasture and secondary forest sites. Soil pH appears to be more important in defining the two pasture sites. The natural forest sites (PrimFor1, PrimFor2, LogFor1 and LogFor2) are grouped separately and the variables that appear to have the most influence on this grouping are soil organic matter and tree species diversity.

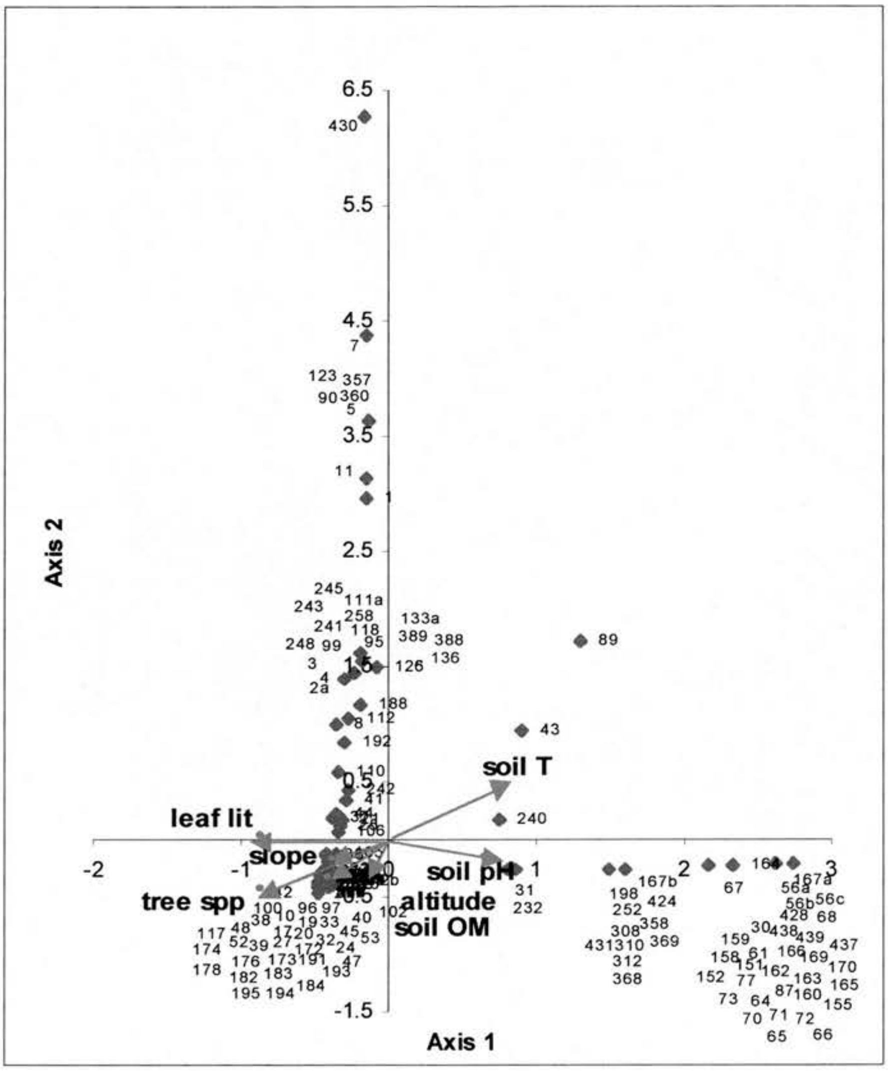
Beetle species, which correlate with specific environmental variables, are found near the ends of the corresponding environmental gradient arrows. The biplot shown in Figure 7.33b demonstrates the cluster of species associations with environmental factors, and also with field site. In general the species identified by TWINSPAN as being related to particular field sites are also placed in a similar cluster in the CCA analysis. For example, species 164, 240, 358 and 428 are identified by TWINSPAN as indicators of the pasture sites and when Figure 7.33 a and b are compared it is evident that these species are also located close to the pasture sites in this analysis. Species 240 is slightly further from the pasture sites but after examination of the TWINSPAN output it was revealed that this species was found not only in both the pasture sites but also in one of the primary forest sites (PrimFor2), and one of the secondary forest sites (2ndFor1). This explains its slightly disparate position in the CCA analysis. The placing of the environmental gradient arrows also implies that they are influenced by soil pH and soil temperature. In general, the diagrams in Figure 7.33 demonstrate significant correlations between environmental variables and related sites and species. The species assemblage is clustered by broad land use type with the logged forest and primary forest sites being grouped separately from the secondary forest, plantation and pasture sites. The environmental gradients also reveal which factors are most important in driving the species changes that occur across the gradient of human disturbance.

**Figure 7.33 CCA ordination biplot of sites, beetles species abundances and environmental variables (reduced species data set excluding single occurrences)**

a) **Site score plot showing environmental gradients.** The arrows represent the correlation between the axes and the environmental variables. They also indicate which variables are most important in influencing community variation of the sites located closest to the arrowheads.



**b) Species score plot** The arrows represent the correlation between the axes and the environmental variables. Species which are found closest to the arrowheads demonstrate a strongly positive correlation with the variable represented.



## 7.9 Summary and conclusions

CHANGES IN BEETLE SPECIES RICHNESS AND COMPOSITION OVER A GRADIENT OF DISTURBANCE

Beetle species composition changed significantly over the gradient of human disturbance represented by field sites, which ranged from primary forest (as a control), to logged primary forest, secondary forest, plantation and pasture. Beetles were considerably more abundant in logged forest and primary forest sites than in the other sites. Species richness (*S*) was also significantly different between land uses although further investigation revealed that not all sites demonstrated this difference consistently Table C3. Appendix 10). The logged and primary forest sites, along with one pasture site (Pastur2), showed the highest species richness.

As discussed in the previous chapter, estimates of 'total biodiversity loss (or gain)' are not necessarily the best measures of human impact as species richness is not only dependent on loss rates of forest species, but also on invasion rates by disturbed area species. This may explain why not all sites have significantly different species richness. The abundance and species richness of the leaf litter beetles is highest in the logged and primary forest sites. This suggests that beetles may respond more predictably to disturbance than ants, with both species richness and abundance decreasing in relation to the degree of disturbance.

The principal dichotomy in the TWINSPAN classification of beetle species composition was between the forest sites (primary, logged primary, secondary forest and plantation) and the pasture sites. Secondary separation in the forest sites cluster placed the plantation sites separately from the natural forest sites. The clustering was strongly indicative of land use, and geographical location did not seem to affect the outcome. The patterns revealed in TWINSPAN were also indicated by a DCA analysis.

A CCA analysis identified the importance of a variety of environmental variables in beetle species composition. Leaf litter quantity, tree species diversity and soil temperature were identified as three of the most important factors in explaining variation. Other significant variables were soil pH and soil organic matter percentage. As with the ant data, the physical site variables of slope and altitude were shown to have a smaller influence on species composition than other environmental factors. Further significant environmental variables that co-varied with leaf litter quantity were the number of trees per hectare, and basal area per hectare, while maximum air temperature co-varied with soil temperature. Beetle species composition responded strongly to these differing environmental gradients, with the CCA analysis grouping specific species both along the environmental gradients and associating them with particular field sites and land uses. The seven environmental variables, coupled with the two physical variables, explained the major variation in species composition. This related primarily to leaf litter quantity, tree species diversity and soil temperature, along the first axis of the CCA.

### $\beta$ - DIVERSITY OF BEETLE SPECIES IN A LOWLAND TROPICAL FOREST LANDSCAPE

Indices of similarity between land uses and sites over a gradient of increasing disturbance show that the sites have different beetle species composition. $\beta$ – diversity is higher between sites which share fewer species, and is proportional to the inverse of similarity. The analysis indicates that sites at opposite ends of the disturbance gradient demonstrate the lowest similarity. A cluster analysis using Morisita's Index of Similarity demonstrated an obvious grouping of field sites by land use and degree of human intervention. The principal division is found between the logged and primary forest site cluster and the cluster of sites of greater human disturbance, namely secondary forest, plantation and pasture (Figure 7.27). These results suggest a clear effect of forest disturbance on $\beta$ – diversity.

### A CLASSIFICATION OF BEETLE SPECIES RESPONSES TO FOREST DISTURBANCE AND CONVERSION

The beetle species collected in this study were strongly ordered along both the DCA and CCA axes. Different species showed different responses to forest disturbance and conversion. No species were distributed ubiquitously over the gradient of disturbance, while many were revealed to be specialist forest species or disturbed area species.

The TWINSPAN analysis identified species 42 (Staphylinidae) as a 'perfect indicator' for natural forest. This species is not found in either the plantation or pasture sites. TWINSPAN also identified other species in the natural forest sites, the majority of these found in the Staphylinidae. For example, species 201 (Staphylinidae) was also exclusively found in the logged and primary forest sites and may also be a good indicator species for less disturbed forest. Some species were identified as indicators of pasture, including species 164 (Staphylinidae), 240 (Nitidulidae), 358 (Nitidulidae) and 428 (Staphylinidae).

Due to the large dataset in this study, many species were identified only to sub-family and morphospecies. Therefore, although trophic guild assignments are available for the beetle data (Didham 1996, Hammond 1990) the level of identification in some cases does not allow strict assignment to one guild. This has made it difficult to draw conclusions regarding the effects of change on specific guilds and species from the sample presented in this study. It is, however, evident that forest disturbance and conversion to plantation and pasture does significantly affect the diversity and abundance of leaf-litter beetle species.

Other studies have shown varied effects of forest disturbance or conversion on beetles, although many of these studies have examined canopy-dwelling species (Lawton et al. 1997, Watt et al. 1997, Krüger and McGavin 1998, Wagner 2000). Wagner (2000) found that secondary forest in Uganda was less species rich in canopy-dwelling beetles than primary forest which in turn was less species rich than swamp forest. Their measures of $\beta$ – diversity showed distinct differences among forest types. They also showed that the taxonomic distribution of beetles in the secondary forest was more heterogeneous than in primary forest. Rodríguez et al. (1998) showed that forest-floor dwelling tiger beetles (Coleoptera: Cicindelidae) changed significantly with the degree of forest disturbance and that each stage of disturbance is characterised by a particular subset of species. They also believe that their results support the use of tiger beetles as bioindicators for monitoring the degradation and regeneration of tropical forests.

Anderson and Ashe (2000) attempt to use the leaf litter inhabiting Staphylinidae and Curculionidae as surrogates for establishing conservation priorities in tropical montane cloud forests. Results of their analyses show that the two families indicate a different ordering of site priorities based on various diversity measures. They conclude that further study is required on other taxa in order to establish a better surrogate. Perfecto et al. (1997) investigated the extent of biodiversity loss due to the transformation of a tropical agro-ecosystem. They investigated the effects of conversion from a coffee (*Coffea arabica*) agro-ecosystem characterised by high vegetational diversity to monocultural plantations where all shade trees are eliminated. A significant loss of arthropods was shown (Coleoptera, non-formicid Hymnenoptera and Formicidae). They conclude that conservation efforts should include traditional agro-ecosystems. Indeed, some of the shade trees sampled in their study showed species richness on a per tree basis to be within the same order of magnitude as that reported for trees in tropical forests. This result is important as it indicates, if the results presented can be generalised, that shade trees in cleared forests areas, whether agriculture or pasture, may greatly increase their potential to conserve biodiversity.

Beaudry et al. (1997) emphasise the importance of islands of mature forest in avoiding the extermination of old-growth carabids while Klein (1989) shows that forest fragments have fewer dung and carrion beetle species and sparser populations. He shows that this in turn results in lower rates of decomposition. Davis (2000) also investigated dung beetles. He showed that reduced impact logging better preserved the dung beetle assemblage than conventional logging techniques.

In general, it is believed that greater levels of disturbance, such as after conversion of mature forest into pasture or agricultural land, have a negative effect on beetle species richness and evenness, and that abundance is considerably altered (Didham et al. 1998, Estrada et al. 1998). This study has also shown that forest disturbance, by selective logging, and conversion to plantation and pasture has a marked effect on leaf litter beetle species composition and abundance. Species richness remained similar between most sites although the loss of forest species and gain of disturbed site species which occurred was not accounted for in this measure. Beetles appear to be more sensitive to human impact than ants and therefore may be better indicators of disturbance. This is well illustrated by the distribution of staphylinids. It is known that staphylinid beetles feed on decaying matter, living animals, fungi, algae and plants (Linssen 1959, Buse and Good 1993), and that they are considered to be more habitat generalists than other groups. The Staphylinidae are the most abundant and species rich in all sites. However, it is noteworthy that even the staphylinid species sampled do not show a ubiquitous distribution over the study sites.

It appears, as with the ant data, that the mosaic of land uses found in the north of Costa Rica may facilitate the conservation of the leaf litter beetle fauna. However, the beetle species assemblage has been shown to be greatly altered by disturbance. In order to ensure that forest specific species and their related ecological functions are not lost, the continued preservation of areas natural forest within the landscape must be a priority.

# CHAPTER 8

# IMPLICATIONS FOR BIODIVERSITY CONSERVATION: SYNTHESIS AND CONCLUSIONS

## 8.1 Introduction

'The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity' (Tilman 2000).

Biodiversity has been a source of wonderment and scientific curiosity for many generations. However, more recently, it has also become a cause for concern (Tilman 2000). The domination of the Earth's ecosystems by humans, and the corresponding changes that are occurring, are rapidly reducing the diversity of species within many habitats and increasing extinction rates (Vitousek et al. 1997, Tilman 2000). These changes in biodiversity will have a serious global impact as they alter ecosystem processes and change the resilience of ecosystems to environmental change (Chapin et al. 2000). This final chapter presents a synthesis of the findings of the research and explores some of the resulting implications. It discusses the corresponding impacts of changing invertebrate populations on the ecosystem, and the possible use of insect indicators in monitoring human disturbance. The inferences for improved forest and landscape management are also discussed.

## 8.2 Objectives

The chapter has four major objectives:

- to assess the ecological findings of Chapters 6 and 7, which examined the leaf litter ant and beetle fauna, in the light of the original objectives outlined in Chapter 1 (Section 8.3),

- to compare the ecological findings of the ant and beetle fauna in order to examine the differences in their reactions to disturbance, and to reflect on their usefulness in biodiversity monitoring (Section 8.3), and
- to discuss and identify the potential conservation and forest management implications of these results (Section 8.4).

## 8.3 Changing leaf litter invertebrate communities in a landscape of disturbance

The ecological findings of the previous chapters have demonstrated the marked changes that occurred in leaf litter invertebrate species assemblages after logging and forest clearing. The first two objectives of the thesis will be addressed below while the third objective will be addressed later. The original research objectives of this research were: 1) to enhance knowledge of the consequences of human activities on natural ecosystems; 2) to examine how forest disturbance and clearance affect invertebrate diversity and composition, by rapid inventory of leaf litter ants and beetles, and 3) to consider the implications that the results have for improved forest and converted forest biodiversity conservation.

### 8.3.1. The effects of human disturbance on leaf litter ants (Hymenoptera: Formicidae) and beetles (Coleoptera)

ANTS

The data presented in Chapter 6 illustrated the disturbance induced changes which occurred in leaf litter ant communities over a gradient of land uses from primary forest, logged forest, secondary forest, and plantation to pasture. It is evident that logging and clearance of natural forest have triggered substantial changes in the species assemblage. Both species richness (Figure 8.1) and abundance were found to change significantly over the disturbance gradient while analyses of species composition revealed clear groupings of species by land use. A number of ant species appeared to have a ubiquitous distribution over the disturbance gradient with a few thriving at great abundances in the pasture sites. There were, however, a high number of species which were found in the forest sites but were absent in the plantation and pasture sites. This indicates that, in the absence of natural forest sites (primary forest, logged primary forest, and secondary forest) many species would be lost.

**Figure 8.1 Ranking of leaf litter ant species richness over a gradient of disturbance**

*Primary logged forest* > *Secondary forest* > *Primary forest* > *Cattle pasture* > *Forest plantation*

Examination of the effects of ecological and environmental changes in the field sites, which have been discussed in Chapter 5, showed the effects of a variety of variables on ant species. The forest specialists were defined by variables such as leaf litter quantity and tree species diversity while species found in the plantation and pasture sites were correlated with variables such as soil temperature and soil pH. This reveals the strong effect of field conditions on the ant species composition found in each land use.

### BEETLES

The data presented in Chapter 7 also revealed marked changes in leaf litter beetle communities over the gradient of disturbance examined. In the case of the beetles, it was again evident that logging and clearance of natural forest has caused substantial changes in the species assemblage. Both species richness (Figure 8.2) and abundance were significantly changed by human activities. Analysis of species composition showed obvious clustering of particular species with specific land uses and a TWINSPAN classification identified species indicative of each land use or group of land uses. The beetle fauna appeared to be more affected by disturbance than the ant fauna with no species being ubiquitous over the gradient of disturbance. The specificity of habitat choice by many of the beetle species indicates that without the presence of natural forest areas within the landscape many species would be lost.

**Figure 8.2 Ranking of leaf litter beetle species richness over a gradient of disturbance**

*Primary logged forest* > *Primary forest* > *Cattle pasture* > *Secondary forest* > *Forest plantation*

Further examination of the effects of ecological and environmental changes in the field sites revealed the impact of several variables. As with the ant data, the forest specialists were defined by variables such as leaf litter quantity and tree species diversity while species found in the plantation and pasture sites were correlated with variables such as soil temperature and soil pH. This reiterates the point that beetle species composition is strongly affected by site characteristics.

The results presented demonstrate the effects of human impact on the leaf litter ant and beetle species assemblage. Other studies have shown similar changes in invertebrate communities although most have either focused on individual insect orders, selected indicator species or sampled exclusively in the forest canopy. Examples of these have been summarised in Sections 6.9 and 7.9. Many of the taxa studied by other authors are not typical of the majority of invertebrates because they are large (e.g. dung beetles, Klein 1989), functionally unique (leaf-cutter ants, Vasconcelos 1988), or specialised (euglossine bees, Powell and Powell 1987). These studies are undoubtedly of great value but they make generalisations to larger invertebrate assemblages difficult. This study has employed a multi-taxa approach to examine the effects of human disturbance on leaf litter invertebrates. It has focused on a taxonomically and trophically diverse group of insects (beetles: Coleoptera) and a numerically dominant group (ants: Hymenoptera, Formicidae) in order to produce results which may be applicable to other forest invertebrate assemblages.

Attention is now focussed on the comparison between the corresponding reactions to disturbance of the two focus groups, namely ants and beetles, and addresses their potential in biodiversity monitoring.

### 8.3.2 Comparing the leaf litter ant and beetle fauna of a northern Costa Rican landscape

The research employed rapid biodiversity assessment of two taxa, with the aim of using this information to examine the consequences of environmental change on biodiversity. The ecological responses of specific taxa have been used as indicators of responses in other taxa by some researchers (Noss 1990, Spellerberg 1992, Kaspari and Majer 2000) and some basic criteria have been decided upon to define taxon suitability. Indicator taxa should: 1) be easily sampled, 2) represent fairly diverse groups and/or groups of biological importance in the ecosystem under study, 3) have known relationships to the diversity of other taxa, and 4) should respond to environmental change in ways similar to other taxa (Alonso 2000). Conservation decisions are often based on studies of indicator taxa, but in many cases, only the first two of the above criteria have been addressed, whereas taxa which comply with criteria 3 and 4 would be the most useful. Unfortunately, few data have been collected regarding the relationships between groups of organisms (Alonso 2000).

The most comprehensive study carried out to date was conducted by Lawton et al. (1998) who investigated nine taxa, including ants and beetles in a semi-deciduous forest in Cameroon, Africa. Species richness of these taxa was compared across a gradient of habitat types of increasing intensity and frequency of disturbance. Few correlations were demonstrated between taxa when examining change in species richness across the disturbance gradient. However, of all the groups, canopy ants were positively correlated with the most other taxa including butterflies and canopy beetles. Anderson et al. (1996) also demonstrated a positive association between the species richness of ants and beetles. However, Oliver et al. (1998) did not find any significant correlations between ants and any other groups, including beetles in logged and unlogged forest. The study presented in this thesis also found that the correlation between the species richness of ants and beetles over a series of land uses representing a gradient of disturbance was not significant ($r^2=0.18$, $p=0.08$) but that individually there were clear differences over the land use gradient.

The findings that there are few strong positive correlations between ant and beetle species richness are not necessarily unexpected. Every species has a unique evolutionary history that influences its distribution (Alonso 2000). Higher taxonomic levels such as genera and families may be affected by factors that are not necessarily the same as those that affect other genera and families, even within the same habitat. Different organisms have distinct ecological requirements and are unlikely to respond to environmental change in similar ways (Lawton et al. 1998). Knowledge regarding the biology of the species under investigation is essential if a biologically meaningful interpretation of the data and understanding of the relationships between taxa are to be developed. Using changes in the species richness of one, or a limited number, of indicator taxa does not necessarily provide an accurate picture of overall change in other taxa (Lawton et al. 1998).

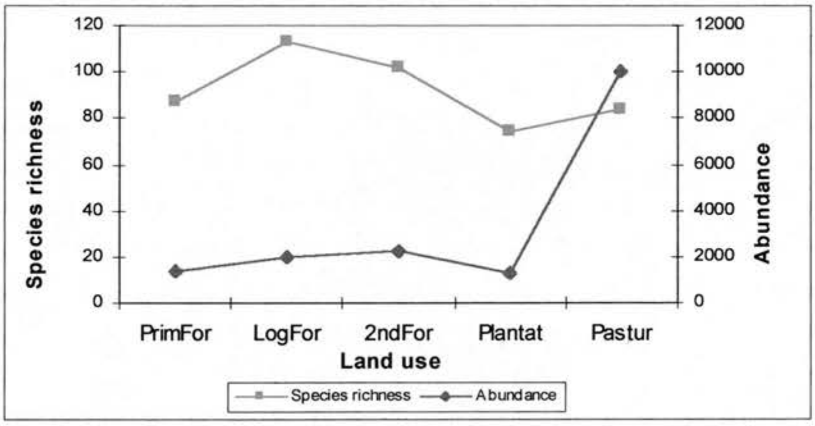
Although the results from this study cannot be extrapolated over all taxa, such as plants and vertebrates and even other invertebrates, they do present a clear picture of the change that occurs after disturbance. There can be no doubt that, although species richness change is not correlated between the groups, diversity in both groups is markedly altered by human disturbance. A summary of species richness and abundance change in both groups is given in Figure 8.3, illustrating the differences in the affects of change on the two groups.

The similar trends in species richness for both leaf litter ants and beetles, over the gradient of disturbance, are evident in Figure 8.3. Although it is generally accepted that human disturbance reduces biodiversity (Chapin et al. 2000), the data presented here show an increase in species diversity from primary forest to logged primary forest. Both ants and beetles are most species rich in logged primary forest. This is probably a result of the introduction of disturbed area species into an already rich forest environment. The trends indicate that after the relatively small disturbance caused by selective logging species richness does decrease with increasing disturbance, for example in secondary forest and plantation. The pasture sites show an increase in species richness although they do not reach the levels of the natural forest sites. This may be a result of the increase in nutrient input provided by grazing cattle or the addition of artificial fertilisers.

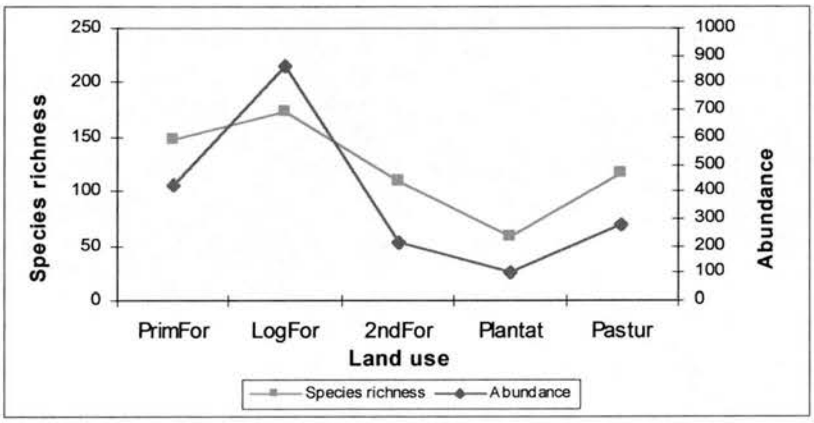
As would be expected from existing entomological knowledge, ant abundance is an order of magnitude greater than beetle abundance. However, unlike the trend demonstrated in species richness for both groups, the effects of degree of disturbance on the abundance of ants and beetles are considerably different. The ants maintain

**Figure 8.3 Leaf litter invertebrate species richness and abundance over a gradient of disturbance:**

THE ANTS



THE BEETLES



relatively stable abundance levels, which show small changes from primary forest over the disturbance gradient to plantation. However, there is a great increase in the abundance found in the pasture sites. Earlier investigation showed that this increase was due primarily to an increase in a few specific species and it is evident that these species have adapted particularly well to the altered conditions found in pasture. This change in species composition may have implications for the carrying out of the ecological functions usually provided by a more diverse and less abundant ant community. Beetle abundance is highest in logged primary forest but from there drops over the disturbance gradient to its lowest level in plantation. It then increases again in the pasture sites. It is evident that beetle species abundance levels show a very different reaction to the ant species. There are no beetle species which have been able to adapt as successfully to the changed conditions found in the plantation and pasture sites. The logged forest sites have the largest abundance of beetles and this may be a result of the introduction of disturbed area species. It is also evident that beetle abundance levels follow the trend of beetle species richness more closely than the results found for the ants. The changes in beetle species composition resulting from disturbance may affect the ecological functions performed by beetles. However, the effects of these changes will be distinctive from the corresponding effects on functions normally performed by ants.

To take the analysis of these results further, more basic information on the ecology and habitat requirements of the groups would be required. The use of morphospecies in this study has provided a rapid picture of a changing system, but the next step to achieving a reliable evaluation of sites for conservation must be the naming of species in order to assign species trophic groups and habitat preferences. This type of data would improve discussion regarding for example, the reasons for beetles being more species rich in pasture sites than in plantations.

Since both ant and beetle groups indicate distinctive variability, which can be related to type and intensity of disturbance, they have the potential to monitor the effects of anthropogenic impact.

### 8.3.3 The potential of using insect species as biodiversity indicators for monitoring human disturbance

Insects are thought to make good indicators of habitat condition because they respond quickly to environmental stress, have short generation times and are usually easily sampled (Peck et al. 1998). They have been successfully implemented as indicators of a range of environmental attributes since the beginning of the 20th century (Cairns and Pratt 1993). In aquatic systems insects are commonly used to monitor pollution levels and in indicating general water quality (Terrell and Perfetti 1989, Resh and McElravy 1993). In terrestrial systems insects have also been investigated and used in the monitoring of environmental disturbance. Among other studies, Holloway and Stork

(1991) used Lepidoptera as an indicator of change in South African habitats, Kremen (1992) explored the use of butterflies as an indicator of the health of natural areas in Madagascar rain forests, and Kromp (1990) used carabid beetles as bioindicators of farm management in Austria. Eyre et al. (1989) used carabids and curculionoids as indicators of grassland management practises, while Rodríguez et al. (1998) used tiger beetles to monitor tropical forest degradation in Venezuela. Despite this, it is frequently difficult to pinpoint a precise impact with a precise effect and many of the relationships may be multi-stage, synergistic or non-obligate.

Much of the existing work has been carried out on taxa which were perceived from the outset of the study to be good indicators. These taxa were often chosen for pragmatic reasons (ease of sampling, identification etc.) and although often good indicators of change, were not always representative of the wider invertebrate assemblage (e.g. butterflies: Lovejoy et al. 1986 and Kremen 1992, 1994; tiger beetles: Rodríguez et al. 1998). Indeed, ambiguous selection criteria and the use of inappropriate taxa have brought the use of indicator taxa under question (Hilty and Merenlender 2000). Studies of entire insect assemblages or even of selected groups involve a large investment of human resources, particularly in the sorting and identification of samples. The results from these studies often show striking changes in insect composition after human activities such as forest fragmentation, logging, or conversion to agriculture and pasture (Didham 1997, Lawton et al. 1998, Figures 6.26 and 7.26). Unfortunately these studies are time consuming to undertake and may be difficult to repeat due to the immense diversity of insects over space and time particularly in the humid tropics.

The results of this study have classified both ant and beetle species into groups which can be clearly related to particular land uses. Specific species have been identified as indicators of a particular land use type. However, it is important to note that the steepness of both the ant and beetle species accumulation curves suggest that there are many more species present in the sites sampled that have not been recorded. The information presented, especially regarding which species are adversely affected by disturbance and are therefore only found in the natural forest sites, is valuable and was not known previously. It is also important to note that the inevitable effect of complete forest clearance would be a loss of many forest ant and beetle species, and a corresponding ceasing of their roles in a variety of ecological functions.

Whilst land use classifications of insect species assemblages are important it is difficult to apply them directly to the practical management of forests for biodiversity conservation. Watt (1998) asserts that it is unnecessary to sample insects in order to discover whether or not a forest has been disturbed. This would seem a sensible conclusion as there are many other more practical ways of identifying the more obvious forms of human impact, although this does depend on the nature and intensity of the impact. Simple observation can often give a good estimate of forest disturbance although sometimes a more detailed tree species inventory is required to assess the successional stage of a recovering forest. Studies of insects are, however, important in the longer term assessment of the impact of various human activities on the forest ecosystem. In this age of ever-increasing anthropogenic impact on the environment, particularly the forest environment, information regarding the extent of damage to the ecosystem and its functioning processes is ever more vital. The insect community data presented here can be applied to reveal the extent of change caused by certain activities. This can then be applied to forest management recommendations in order to indicate what level of disturbance is acceptable in terms of avoiding a substantial loss of biodiversity.

The following section addresses the effects of biodiversity on the functioning of the ecosystem, and discusses the common assumption that diversity is related to ecosystem function.

### 8.3.4 The impacts of changing invertebrate populations on the ecosystem

In utilising the results of insect studies to monitor disturbance and damage to the ecosystem, the assumption is made that biodiversity, particularly insect diversity, is related to, and essential for, ecosystem functioning. Previous assessments of ecosystem health are considered to illustrate that changing biodiversity does have a significant impact on the ecosystem.

Both theory and empirical evidence agree that a reduction in biodiversity tends to accelerate the simplification of ecological communities (McCann 2000). There exists little doubt that the Earth's biodiversity is declining, and the international community is beginning to realise that this decrease is a huge problem for the human race. Natural ecosystems, which are ultimately our life support systems, are changing at an ever-increasing rate. It is essential that we begin to understand how the loss, or addition, of species influences the stability and function of the ecosystems on which we rely (McCann 2000). We are 'deconstructing the Earth under the implicit assumption that ecosystems have evolved the ability to withstand such assault without collapse' (McCann 2000). The diversity-stability debate, as it has become known, asserts that more diverse communities enhanced ecosystem stability (Odum 1953, Elton 1958). Many studies have concluded that diversity within an ecosystem does tend to be correlated with community stability (Tilman and Downing 1994, Tilman et al. 1996, Tilman 1996, and van der Heijden et al. 1996).

Studies in 'microcosms' have found that, regardless of scale or system type (terrestrial or aquatic), diversity is positively related to ecosystem stability (Lawton 1995, Naem and Li 1997, McGrady-Steed and Morin 2000). In general, the evidence presented by McCann (2000) does indicate the existence of the diversity-stability relationship. According to him, it appears that diversity is not the driver of this relationship but rather that stability depends upon community ability to contain species, or functional groups, that are capable of differential responses. Empirical evidence indicates that communities may be driven by trophic interactions and that the removal, or addition, of species can lead to pronounced changes in community composition and structure. Current theory agrees that drastic community changes can accompany the removal, or addition, of even a single species. If, as Elton (1958) observed, simplified communities are more vulnerable to invasion it is evident that decreasing diversity will also cause an increase in successful invaders. There are already many examples of this in modern agriculture and plantation forestry. This, in turn, will negatively affect ecosystem health.

Other researchers believe that biodiversity is not implicitly linked to ecosystem function. For example, Schwartz et al. (2000) believes that ecosystem function can be sustained at relatively low species richness. To show this they have principally utilised theoretical and mathematical models. They assert that within a single trophic level most mathematical models predict saturation of ecosystem function at a low proportion of local species richness. This may be the case in a relatively simple model but other researchers who have employed more complex models of food-web structure have shown that increasing diversity can increase food-web stability (McCann 2000). In addition, Schwartz et al. (2000) believe that one reason that high species richness may not contribute significantly to function or stability is that most communities are characterised by strong dominance such that few species provide the vast majority of the community biomass. The results presented in this thesis do not corroborate this evidence. From the ant and beetle species assemblages studied in Chapters 6 and 7, the communities have not been shown to be strongly dominant. In fact, with few exceptions, the spectrum of tropical land uses investigated show high species evenness. The only strongly dominant invertebrate community was found in the pasture sites, which represent the most disturbed sites in the study. This may suggest that the examples Schwartz et al. (2000) were drawing from were not from tropical ecosystems and can therefore not be extrapolated to these regions, or, that they were already highly disturbed habitats.

Specific tropical examples include Klein (1989) who demonstrates the importance of dung and carrion beetles in ecosystem function. He outlines the effects that a depauperate dung beetle community in forest fragments may have on the remainder of the forest community. Dung beetle function is essential in a wide range of species interconnections and their removal may cause a substantial 'ripple effect' on the species which depend upon them for dispersal and decomposition. Vasconcelos (1988) examined leaf-cutter ants, another functionally important group, while Harper (1989) and Bierregaard and Lovejoy (1989) have documented the loss of army ant-following birds in Amazonian forest fragments. It is also believed that changes in leaf litter invertebrate density will have important implications for the conservation of insectivorous vertebrate species (Didham 1997).

From the evidence examined it appears that, although the argument is still on going, there is a direct relationship between biodiversity and ecosystem function. There are many examples of human disturbance, which results in changes in biodiversity, affecting the ecosystem at all scales. Simberloff (1999) remains unconvinced and believes that in order to ensure biodiversity conservation 'we must (also) be committed to the value of biodiversity in its own right, and not as (solely) a means to some other function'. The following section investigates the possibility, assuming a negative effect of human disturbance on biodiversity and ecosystem health, that forest and landscape management can incorporate methods of improved biodiversity conservation.

## 8.4 Implications for improved biodiversity conservation through forest and landscape management

Improved natural forest management has been the focus of much research and development in the last decade (Jonkers 1988, Miller and Adam 1992, Méndez Gamboa 1993, Vanclay 1993, Alder 1995, Bruenig 1996, Camacho and Finegan, 1997, Maginnis et al. 1998 etc.). The decreasing extent of the world's forests has accelerated the urgency for sustainable forest harvesting. It is well documented that forests provide a multitude of services in addition to timber production (Breunig 1996). They provide non-timber forest products which can provide a livelihood for many communities, environmental services such as water-shed management, carbon sequestration, soil conservation and, of course, biodiversity conservation (Whitmore 1990, Bruenig 1996). This section discusses the arguments for biodiversity conservation, and then addresses the potential for an improved forest management system which can also conserve biodiversity.

### 8.4.1 Biodiversity conservation

Alongside the drive for improved forest management, there has been a huge surge in interest in biodiversity conservation in the last decade (Blench 1998). This interest has been slow to translate into action and, meanwhile, forests continue to be logged, rivers, oceans and the atmosphere polluted and rare species driven to extinction.

There are five main foci for biodiversity conservation: economic, indirect economic (protection against epidemic pathogens), ecological, aesthetic and ethical (Ehrenfield 1988, Ehrlich and Ehrlich 1992, Blench 1998) (Table 8.1).

### Table 8.1 Summary of arguments for biodiversity conservation

| ***Summary of arguments for biodiversity conservation*** | |
|---|---|
| Economic | 1. The output from the land is greater when biodiversity is conserved.<br>2. Unknown biochemical and genetic resources of potentially considerable value. |
| Protection against evolving pathogens | Genetic uniformity may allow super-pathogens to evolve and cause sudden, catastrophic deficits in food, fuel etc. |
| Ecosystem services | Biodiversity essential to ecological functioning of planetary system. |
| Aesthetic | Diversity has a value in itself. |
| Ethical | Present society is a 'steward' of earth's biological resources and we have no right to destroy them. |

Source: Blench 1998

The economic arguments are usually based in a development discourse. They have two principal elements; unmined riches, for example undiscovered genetic resources such as new drugs, and outputs from land use systems (Blench 1998). The ecological argument is that biodiversity is essential to the functioning of the planet (Ehrlich and Ehrlich 1992). The evapotranspiration of tropical forests, the maintenance of chemical balance in the atmosphere, the phytoplankton layer in the oceans, and the fertility of soils are all related to current levels of diversity. In addition, the aesthetic and ethical arguments have a strong emotional appeal to many. However, they are rarely upheld by the larger population and still less by international business. Demographic pressure will also continue to reduce natural reserves of biodiversity.

Blench (1998) concludes that, of the arguments to conserve biodiversity only those relating to protection against pathogens and the output of systems have any real validity. He believes that aesthetic values will not change real-world outcomes, and that society would rather use technology to adapt to changes than reduce its consumptive behaviour. This view is profoundly depressing however is being proved to be the case in the international arena. Perhaps the solution is to implement better natural landscape management without unanimous public support, to lead by example in demonstrating that, for example, using trees sustainably is ultimately more efficient than destroying them. Many major companies which market timber and timber products have already opted to stock timber which has been sourced from well managed forests (FSC 1999, WWF 2000), despite there initially being little public demand for them to do this. This was reliant on customers changing their preferences due to increased awareness over time and indeed the forest product market is now changing and the demand for certified timber is increasing rapidly. In response to this many forest enterprises, including both large-scale concessions and small-scale forest communities, have become, or are seeking to become, FSC certified (Ortiz 2000). Such initiatives are essential in the drive for improved forest and landscape management, and corresponding biodiversity conservation. Further loss of natural habitats and therefore biodiversity, due to increased human population pressures, will trigger increased extinction rates. These changes to the global ecosystem are permanent, extinction is a one-way process. 'In the concrete jungle there are only mechanical cockroaches' (Blench 1998).

In order to conserve the natural habitats required for biodiversity maintenance, strategies are required for managing whole landscapes (Margules and Pressey 2000). These will be considered next.

### 8.4.2 Improved forest management

Prescriptions from studies, such as the results presented in this thesis, reveal the importance of natural forest in maintaining biodiversity. The changes occurring after disturbance are significant and indicate that a total loss of forest cover would result in a great loss of species. The study reveals the importance of a mosaic of habitats in maintaining diversity and suggests that an initial prescription for forest and landscape managers should be the sustaining, at the very least, of forest patches within the broader mosaic of human land uses. This research can also be used in the formulation of guidelines to indicate the extent of change, which occurs in the ecosystem, specifically the insect community, after logging, and conversion of primary forest to other uses.

Simberloff (1999) asserts that 'forest management must change radically to maintain biodiversity'. A wealth of suggestions regarding the achieving of biodiversity conservation have employed jargon rather than real guidelines for forest management on the ground. Despite the 'revolution' in forest management many recommendations are not founded in specific scientific tests, and prescriptions are vague (Kohm and Franklin 1997, Simberloff 1999). In the past, forest management was based on the tenets of lucrative short-term wood production. Biodiversity conservation, however, requires a view of the forest as a community of species rather than simply a timber source.

In forestry, 'ecosystem management' has been lauded as a solution to conservation problems (Simberloff 1997), although there is no firm definition of what this entails (Soulé 1994). The underlying theory is that if an entire ecosystem is kept healthy, all its component species should be healthy (Simberloff 1999), and a key feature is a focus on ecological processes rather than individual species. This has alarmed many conservation biologists as it is perceived that conservation efforts to maintain specific threatened species will be discarded as part of an old-fashioned paradigm (Soulé 1994). Another area of disagreement lies in the human use of resources. Conservation biologists see ecosystem management as maintaining biodiversity while resource managers desire the production of goods and services by the ecosystem for humans (Grumbine 1997, Simberloff 1999).

In summary, conflict still exists between the various stakeholders in the application of improved forest management and it is evident that scientists believe that further research is required in order to transform ideas on managing forests for biodiversity into practical and effective tools. Tools, such as the use of indicator species, management of keystone species and umbrella species, remain hypotheses, and since few have been tested with comprehensive pilot studies are not therefore scientifically valid (Simberloff 1999). In the midst of this uncertainty regarding how to measure and monitor biodiversity effectively many practitioners are attempting to manage their forests in a sustainable manner to ensure their existence into the future. New management techniques have been recommended and although not all are grounded in science many have been tested to some extent (HMSO 1996). These, coupled with community and participatory approaches to forest management, remain the best option that many land managers have available to them (Higman et al. 1999, Salim and Ullsten 1999).

## 8.5 Future research

The ultimate goal of applied ecological research such as this is to gather knowledge of ecosystem functions and to use that knowledge to manage the forest ecosystem in a sustainable way. It is evident that the maintenance of biodiversity in a world of increasing human impact still requires extensive research. There are still many gaps in knowledge, not least in the basic taxonomy of many of the component species in a variety of natural habitats, particularly in the tropics. A focus on inventories of all forest components is crucial. This will not only fill in gaps in knowledge but will provide forest conservationists with tools to document the inevitable losses in species that will occur in the future. The lamentable case today is that species are being lost which have not yet been discovered.

Further study is also required in transforming improved forest management recommendations into scientifically based tools. This will involve careful natural history, controlled and replicated field experiment, and intensive monitoring (Simberloff 1999). Studies should be combined with the needs of local people in managing and utilising the forest resource while methodological guidelines should be geared around the full participation of local communities in natural resource management.

With specific reference to this study, further work would be useful in a variety of the areas addressed. The methodology applied utilised pitfall trapping and therefore, as stated in the original objectives of the thesis, sampled principally leaf litter invertebrates. Further work, which included the sampling of forest canopy ants and beetles using fogging techniques (Lawton et al. 1998), would provide a fuller picture of the changes that occur after human disturbance. The sample sites covered five land use types. Investigation of insect diversity in other land uses in the area, such as in agricultural fields of cassava, and in plantations of fruits such as pineapple and banana, would add to the overall assessment of diversity change caused by human impact.

Data regarding seasonal fluctuations in species diversity and composition for both ants and beetles was collected and a preliminary analysis presented. Further investigation of these data may reveal interesting patterns. The use of morphospecies has provided a rapid method to assess diversity and such studies are essential in the monitoring of landscapes which are under human pressure in order to catalogue diversity before it is too late. However, the most valuable continuation of this work would include the identification of ants and beetles to genus or species thus allowing a more detailed examination of the proportion of forest and non-forest species found in each land use. This would provide an assessment of the extent of change whilst also providing a picture of extinction and invasion rates. It would also enable the investigation of trophic groups in order to reveal any patterns or trends caused by human impact and to provide a clearer assessment of the functional effects of changing diversity on the ecosystem.

The collection of these data was outside the aim and time-scale of this study but if carried out could enhance the assessment of human impact on insect diversity in northern Costa Rica presented in this thesis, as could comparative studies in other geographical areas.

## 8.6 Conclusions

This study has provided the most detailed picture of human induced biodiversity change so far in a northern Costa Rican landscape. The rapid biodiversity assessment methodology utilised has revealed the marked changes that occur in leaf litter ant and beetles species composition, diversity and abundance after forest disturbance and conversion to other land uses. The principal conclusions drawn from the results presented in this thesis are as follows:

- Disturbance induced changes in leaf litter ant and beetle fauna are evident in measurements of species diversity, abundance and composition. A classification of species composition by site and land use particularly demonstrates level of disturbance.

- Contrary to the commonly held belief that primary forest harbours greater biodiversity than disturbed forest, logged rain forest has been shown to be richer in ant and beetle species than primary rain forest. Pasture sites have been shown to be richer in ant and beetle species than plantation sites, but less rich than secondary, logged and primary forest.

- Specific ant and beetle species can be used to indicate level of disturbance. However, information regarding the impact of disturbance on ant and beetle diversity cannot necessarily be used to imply the reaction of other taxa to similar disturbance levels.

- Forest ant and beetle species composition can be related to environmental characteristics such as amount of leaf litter and tree species diversity. Plantation and pasture ant and beetle composition can be related to different environmental characteristics notably soil pH and soil temperature.

- The mosaic of land uses found in northern Costa Rica contains a rich insect fauna. However, the changes caused by disturbance revealed in this study illustrate that natural forest patches are essential in the maintenance of species diversity.

- Improved natural forest management, which provides sustainable livelihoods for local forest communities while also conserving biodiversity and maintaining ecosystem function, should be a priority for land managers and policy-makers alike.

Successful management of tropical forests for timber, non-timber forest products, environmental services and biodiversity must be based on a good understanding of the basic biology and ecology of the component species and groups (Bazzaz 1991). The present study has provided information regarding the effects of human intervention on insect species diversity, abundance and composition. It has documented changes in the overall ant (Hymenoptera: Formicidae) and beetle (Coleoptera) assemblage and has provided baseline data regarding these leaf litter invertebrates in the mosaic of land uses present in the north of Costa Rica. As a whole, this dynamic landscape appears to be conserving a rich diversity of invertebrates. However, it is evident that the maintenance of the natural forest sites is especially important in conserving this diversity.

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# APPENDICES

# APPENDIX 1

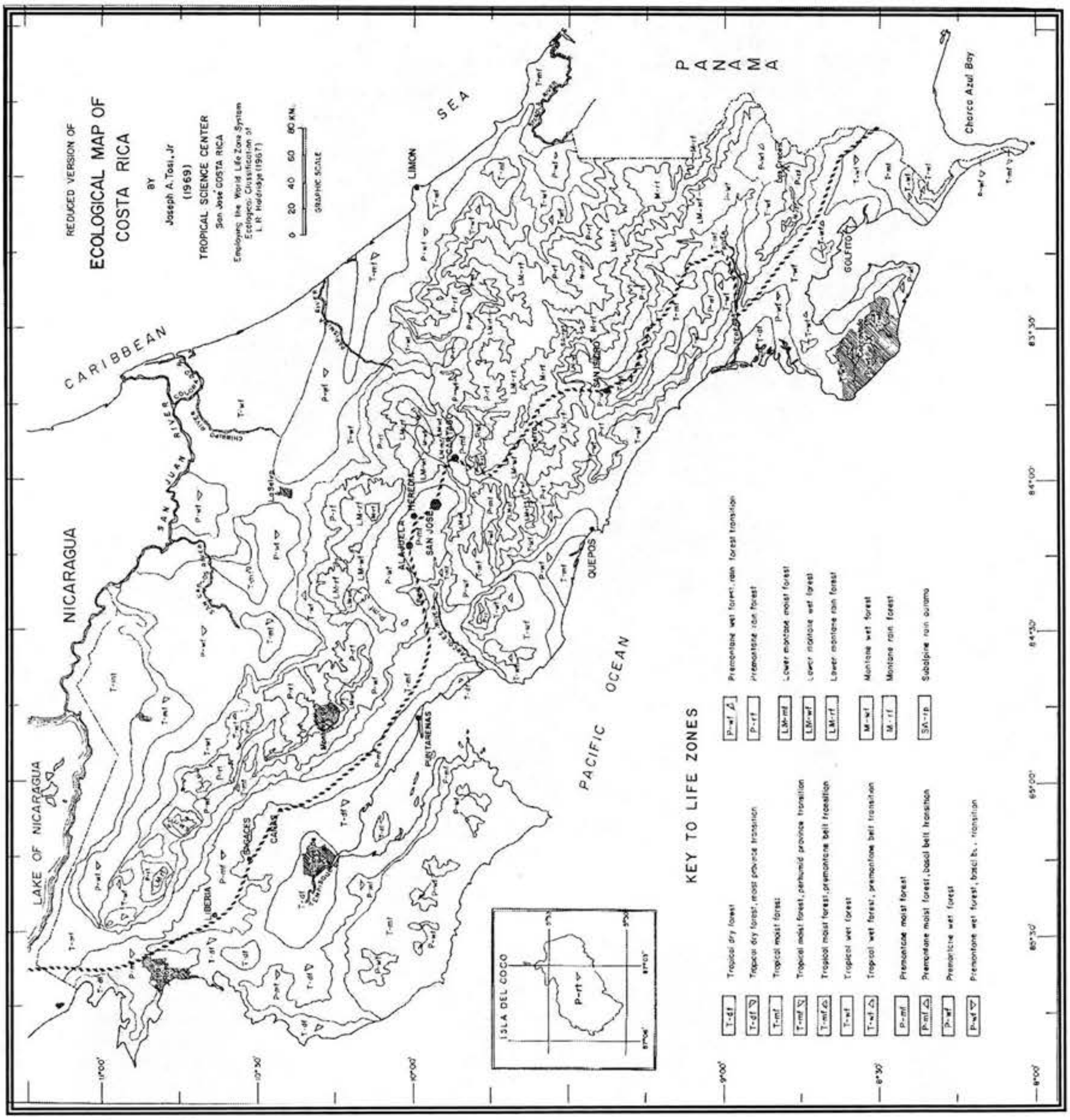
## Holdridge Life Zones occurring in Costa Rica

| | *Life Zone* | | *Units:* | | *TOTAL:* | |
|---|---|---|---|---|---|---|
| | | | *km²* | *%* | *km²* | *%* |
| 1 | **Tropical dry** | | | | 5,263 | 10.3 |
| 2 | **Tropical moist** | | | | 12,366 | 24.2 |
| | a. | non-transitional | 10,373 | 20.3 | | |
| | b. | cool-dry transition | 153 | 0.3 | | |
| | c. | cool-wet transistion | 307 | 0.6 | | |
| | d. | cool transition | 1,533 | 3.0 | | |
| 3 | **Tropical wet** | | | | 11,549 | 22.6 |
| | a. | non-transitional | 8,892 | 17.4 | | |
| | b. | cool transition | 2,657 | 5.2 | | |
| 4 | **Tropical premontane moist** | | | | 2,402 | 4.7 |
| | a. | non-transitional | | | | |
| | b. | warm transition | 716 | 1.4 | | |
| | | | 1,686 | 3.3 | | |
| 5 | **Tropical premontane wet** | | | | 6,950 | 13.6 |
| | a. | non-transitional | 2,606 | 5.1 | | |
| | b. | warm transition | 4,344 | 8.5 | | |
| 6 | **Tropical premontane rain** | | | | 5,008 | 9.8 |
| 7 | **Tropical lower montane moist** | | | | 102 | 0.2 |
| 8 | **Tropical lower montane wet** | | | | 767 | 1.5 |
| 9 | **Tropical lower montane rain** | | | | 3,781 | 7.4 |
| 10 | **Tropical montane wet** | | | | 51 | 0.1 |
| 11 | **Tropical montane rain** | | | | 2,759 | 5.4 |
| 12 | **Tropical subalpine rain paramo** | | | | 102 | 0.2 |

Source: Hartshorn 1982

# APPENDIX 2

## Ecological map of Costa Rica showing Holdridge's Life Zones



Source: Tosi 1969

# APPENDIX 3

# Tree data for all sites

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 1 | PrimFor1 | 1 | almendro | Dipteryx panamensis | Leguminosae-pap | 115.5 |
| 1 | PrimFor1 | 1 | anonillo | Rollinia pittieri | Annonaceae | 10.1 |
| 1 | PrimFor1 | 1 | anonillo | Rollinia pittieri | Annonaceae | 10.5 |
| 1 | PrimFor1 | 1 | anonillo | Rollinia pittieri | Annonaceae | 11.8 |
| 1 | PrimFor1 | 1 | anonillo | Rollinia pittieri | Annonaceae | 11.0 |
| 1 | PrimFor1 | 1 | areno | Qualea paraensis | Vochysiaceae | 16.1 |
| 1 | PrimFor1 | 1 | areno | Qualea paraensis | Vochysiaceae | 83.2 |
| 1 | PrimFor1 | 1 | baco | Couma macrocarpa | Apocynaceae | 11.9 |
| 1 | PrimFor1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 110.5 |
| 1 | PrimFor1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 90.0 |
| 1 | PrimFor1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 87.0 |
| 1 | PrimFor1 | 1 | chonta | ? | ? | 16.5 |
| 1 | PrimFor1 | 1 | chonta | ? | ? | 15.5 |
| 1 | PrimFor1 | 1 | chonta | ? | ? | 19.2 |
| 1 | PrimFor1 | 1 | fruta | Virola guatemalensis | Myristicaceae | 36.0 |
| 1 | PrimFor1 | 1 | fruta | Virola guatemalensis | Myristicaceae | 11.9 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 51.7 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.3 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 36.0 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 48.5 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 50.4 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 21.8 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 38.6 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 32.1 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 58.0 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 52.0 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 33.7 |
| 1 | PrimFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 48.0 |
| 1 | PrimFor1 | 1 | jicaro | Lecythis ampla | Lecythidaceae | 25.8 |
| 1 | PrimFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 11.5 |
| 1 | PrimFor1 | 1 | lija | Pourouma minor | Cecropiaceae | 10.5 |
| 1 | PrimFor1 | 1 | maquenque | Socratea exorrhiza | Palmae | 15.8 |
| 1 | PrimFor1 | 1 | maquenque | Socratea exorrhiza | Palmae | 13.0 |
| 1 | PrimFor1 | 1 | maquenque | Socratea exorrhiza | Palmae | 13.4 |
| 1 | PrimFor1 | 1 | melon | Rehdera trinervis | Verbenaceae | 12.0 |
| 1 | PrimFor1 | 1 | paleta | Dussia macroprophyllata | Leguminosae-pap | 10.6 |
| 1 | PrimFor1 | 1 | p. dulce | Iriartea deltoidea | Palmae | 12.6 |
| 1 | PrimFor1 | 1 | p. mantequilla | Prestoea decurrens | Palmae | 13.0 |
| 1 | PrimFor1 | 1 | panama | Sterculia apetala | Sterculiaceae | 23.7 |
| 1 | PrimFor1 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.5 |
| 1 | PrimFor1 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.2 |
| 1 | PrimFor1 | 1 | piedra de uva | Ardisia sp | Myrsinaceae | 10.2 |
| 1 | PrimFor1 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 15.3 |
| 1 | PrimFor1 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 11.4 |
| 1 | PrimFor1 | 1 | zapote | Manilkara zapota | Sapotaceae | 44.2 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 1 | PrimFor1 | 1 | zapote | Manilkara zapota | Sapotaceae | 44.0 |
| 1 | PrimFor1 | 2 | agote | ? | ? | 17.6 |
| 1 | PrimFor1 | 2 | alcanfor | Protium panamense | Burseraceae | 15.5 |
| 1 | PrimFor1 | 2 | alcantarilla | ? | ? | 11.5 |
| 1 | PrimFor1 | 2 | amarguito | Croton tonduzii | Euphorbiaceae | 19.5 |
| 1 | PrimFor1 | 2 | amarguito | Croton tonduzii | Euphorbiaceae | 36.1 |
| 1 | PrimFor1 | 2 | amarguito | Croton tonduzii | Euphorbiaceae | 20.4 |
| 1 | PrimFor1 | 2 | anonillo | Rollinia pittieri | Annonaceae | 12.5 |
| 1 | PrimFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 15.0 |
| 1 | PrimFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 13.3 |
| 1 | PrimFor1 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.1 |
| 1 | PrimFor1 | 2 | cafecillo | Faramea spp | Rubiaceae | 10.5 |
| 1 | PrimFor1 | 2 | cafecillo | Faramea spp | Rubiaceae | 10.2 |
| 1 | PrimFor1 | 2 | chonta | ? | ? | 16.1 |
| 1 | PrimFor1 | 2 | chonta | ? | ? | 19.0 |
| 1 | PrimFor1 | 2 | chonta | ? | ? | 19.1 |
| 1 | PrimFor1 | 2 | chonta | ? | ? | 15.0 |
| 1 | PrimFor1 | 2 | cuero de sapo | Licania affinis | Chrysobalanaceae | 35.1 |
| 1 | PrimFor1 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 99.0 |
| 1 | PrimFor1 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 21.2 |
| 1 | PrimFor1 | 2 | frutilla | Otoba novogranatensis | Myristicaceae | 17.2 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 78.0 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 57.6 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 50.7 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 35.0 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 63.0 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 32.9 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 44.8 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 70.0 |
| 1 | PrimFor1 | 2 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 36.5 |
| 1 | PrimFor1 | 2 | huesillo | Cupania spp | Sapindaceae | 17.8 |
| 1 | PrimFor1 | 2 | huesillo | Cupania spp | Sapindaceae | 11.1 |
| 1 | PrimFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 16.9 |
| 1 | PrimFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 12.0 |
| 1 | PrimFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 14.5 |
| 1 | PrimFor1 | 2 | magnolia | Talauma gloriensis | Magnoliaceae | 13.5 |
| 1 | PrimFor1 | 2 | mangle | Conocarpus erecta | Combretaceae | 12.3 |
| 1 | PrimFor1 | 2 | maquenque | Socratea exorrhiza | Palmae | 11.4 |
| 1 | PrimFor1 | 2 | maquenque | Socratea exorrhiza | Palmae | 14.0 |
| 1 | PrimFor1 | 2 | maquenque | Socratea exorrhiza | Palmae | 11.3 |
| 1 | PrimFor1 | 2 | melon | Rehdera trinervis | Verbenaceae | 40.0 |
| 1 | PrimFor1 | 2 | muñeco | ? | ? | 19.4 |
| 1 | PrimFor1 | 2 | nene | Ormosia macrocalyx | Leguminosae-pap | 32.2 |
| 1 | PrimFor1 | 2 | ojoche | Brosimum alicastrum | Moraceae | 52.0 |
| 1 | PrimFor1 | 2 | p. dulce | Iriartea deltoidea | Palmae | 16.5 |
| 1 | PrimFor1 | 2 | p. dulce | Iriartea deltoidea | Palmae | 17.3 |
| 1 | PrimFor1 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 12.0 |
| 1 | PrimFor1 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 13.0 |
| 1 | PrimFor1 | 2 | panama | Sterculia apetala | Sterculiaceae | 38.2 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 1 | PrimFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.8 |
| 1 | PrimFor1 | 2 | zapote | Manilkara zapota | Sapotaceae | 13.3 |
| 1 | PrimFor1 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 16.1 |
| 1 | PrimFor1 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 12.3 |
| 1 | PrimFor1 | 3 | aguacatillo | Ocotea stenoneura | Lauraceae | 10.7 |
| 1 | PrimFor1 | 3 | alcanfor | Protium panamense | Burseraceae | 11.0 |
| 1 | PrimFor1 | 3 | almendro | Dipteryx panamensis | Leguminosae-pap | 75.0 |
| 1 | PrimFor1 | 3 | anonillo | Rollinia pittieri | Annonaceae | 11.0 |
| 1 | PrimFor1 | 3 | aguacatillo | Ocotea stenoneura | Lauraceae | 11.0 |
| 1 | PrimFor1 | 3 | areno | Qualea paraensis | Vochysiaceae | 37.6 |
| 1 | PrimFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 28.8 |
| 1 | PrimFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 24.6 |
| 1 | PrimFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 47.1 |
| 1 | PrimFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 72.0 |
| 1 | PrimFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 36.9 |
| 1 | PrimFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 78.2 |
| 1 | PrimFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 85.5 |
| 1 | PrimFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 13.6 |
| 1 | PrimFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 10.5 |
| 1 | PrimFor1 | 3 | canoa | ? | ? | 21.0 |
| 1 | PrimFor1 | 3 | canoa | ? | ? | 31.5 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 16.0 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 17.0 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 17.5 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 17.0 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 16.6 |
| 1 | PrimFor1 | 3 | chonta | ? | ? | 17.7 |
| 1 | PrimFor1 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 12.0 |
| 1 | PrimFor1 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 14.6 |
| 1 | PrimFor1 | 3 | frutilla | Otoba novogranatensis | Myristicaceae | 10.5 |
| 1 | PrimFor1 | 3 | lija | Pourouma minor | Cecropiaceae | 14.8 |
| 1 | PrimFor1 | 3 | maquenque | Socratea exorrhiza | Palmae | 13.0 |
| 1 | PrimFor1 | 3 | muñeco | ? | ? | 14.2 |
| 1 | PrimFor1 | 3 | p. dulce | Iriartea deltoidea | Palmae | 16.1 |
| 1 | PrimFor1 | 3 | p. mantequilla | Prestoea decurrens | Palmae | 10.1 |
| 1 | PrimFor1 | 3 | p. mantequilla | Prestoea decurrens | Palmae | 11.1 |
| 1 | PrimFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 27.6 |
| 1 | PrimFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 45.2 |
| 1 | PrimFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.1 |
| 1 | PrimFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 10.4 |
| 1 | PrimFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 23.9 |
| 1 | PrimFor1 | 3 | piedra de uva | Ardisia sp | Myrsinaceae | 2.8 |
| 1 | PrimFor1 | 3 | piedrilla | Ardisia sp | Myrsinaceae | 11.7 |
| 1 | PrimFor1 | 3 | ponponjoche | Pachira aquatica | Bombacaceae | 11.2 |
| 1 | PrimFor1 | 3 | quizarra | Phoebe valeriana | Lauraceae | 20.0 |
| 1 | PrimFor1 | 3 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.6 |
| 1 | PrimFor1 | 3 | roble coral | Terminalia amazonia | Combretaceae | 68.5 |
| 1 | PrimFor1 | 3 | titor | Sacoglottis trichogyna | Humiriaceae | 27.5 |
| 1 | PrimFor1 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 13.7 |
| 1 | PrimFor1 | 4 | aceituno | Simarouba amara | Simaroubaceae | 25.9 |

| Site no | Site name | Tran-sect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 1 | PrimFor1 | 4 | aceituno | Simarouba amara | Simaroubaceae | 14.3 |
| 1 | PrimFor1 | 4 | anonillo | Rollinia pittieri | Annonaceae | 36.5 |
| 1 | PrimFor1 | 4 | anonillo | Rollinia pittieri | Annonaceae | 20.0 |
| 1 | PrimFor1 | 4 | anonillo | Rollinia pittieri | Annonaceae | 11.3 |
| 1 | PrimFor1 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 27.7 |
| 1 | PrimFor1 | 4 | chonta | ? | ? | 17.9 |
| 1 | PrimFor1 | 4 | chonta | ? | ? | 15.9 |
| 1 | PrimFor1 | 4 | fosforillo | Dendropanax arboreus | Araliaceae | 22.9 |
| 1 | PrimFor1 | 4 | fosforillo | Dendropanax arboreus | Araliaceae | 14.0 |
| 1 | PrimFor1 | 4 | fruta | Virola guatemalensis | Myristicaceae | 43.7 |
| 1 | PrimFor1 | 4 | fruta | Virola guatemalensis | Myristicaceae | 12.2 |
| 1 | PrimFor1 | 4 | frutilla | Otoba novogranatensis | Myristicaceae | 12.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 20.5 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 32.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 15.7 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 15.5 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 19.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 23.4 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 35.1 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 18.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 26.1 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 24.7 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 26.7 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 28.7 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 60.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 49.0 |
| 1 | PrimFor1 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 15.9 |
| 1 | PrimFor1 | 4 | guarumo | Cecropia insignis | Cecropiaceae | 26.8 |
| 1 | PrimFor1 | 4 | guayabillo montaña | Psidium sp. | Myrtaceae | 19.4 |
| 1 | PrimFor1 | 4 | lija | Pourouma minor | Cecropiaceae | 30.4 |
| 1 | PrimFor1 | 4 | manga larga | Laetia procera | Flacourtiaceae | 37.7 |
| 1 | PrimFor1 | 4 | maquenque | Socratea exorrhiza | Palmae | 14.5 |
| 1 | PrimFor1 | 4 | ojoche | Brosimum alicastrum | Moraceae | 42.5 |
| 1 | PrimFor1 | 4 | p. dulce | Iriartea deltoidea | Palmae | 19.2 |
| 1 | PrimFor1 | 4 | p. dulce | Iriartea deltoidea | Palmae | 18.1 |
| 1 | PrimFor1 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 11.7 |
| 1 | PrimFor1 | 4 | panama | Sterculia apetala | Sterculiaceae | 16.1 |
| 1 | PrimFor1 | 4 | panama | Sterculia apetala | Sterculiaceae | 11.0 |
| 1 | PrimFor1 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 22.0 |
| 1 | PrimFor1 | 4 | piedrilla | Ardisia sp | Myrsinaceae | 13.1 |
| 1 | PrimFor1 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 16.6 |
| 1 | PrimFor1 | 4 | tamarindo | Dialium guianense | Leguminosae-caes | 17.8 |
| 1 | PrimFor1 | 4 | tamarindo | Dialium guianense | Leguminosae-caes | 65.2 |
| 1 | PrimFor1 | 5 | aguacatillo | Ocotea stenoneura | Lauraceae | 25.1 |
| 1 | PrimFor1 | 5 | alcanfor | Protium panamense | Burseraceae | 12.0 |
| 1 | PrimFor1 | 5 | alcanfor | Protium panamense | Burseraceae | 16.0 |
| 1 | PrimFor1 | 5 | alcanfor | Protium panamense | Burseraceae | 14.5 |
| 1 | PrimFor1 | 5 | amargo | Aspidosperma megalocarpon | Apocynaceae | 17.6 |
| 1 | PrimFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 50.0 |

| *Site no* | *Site name* | *Transect* | *Common name* | *Scientific name* | *Family* | *DBH (cm)* |
|---|---|---|---|---|---|---|
| 1 | PrimFor1 | 5 | asufre | ? | ? | 11.2 |
| 1 | PrimFor1 | 5 | asufre | ? | ? | 14.4 |
| 1 | PrimFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 35.1 |
| 1 | PrimFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 15.0 |
| 1 | PrimFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 20.0 |
| 1 | PrimFor1 | 5 | bejuco | Cupania glabra | Sapindaceae | 12.5 |
| 1 | PrimFor1 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.9 |
| 1 | PrimFor1 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 75.0 |
| 1 | PrimFor1 | 5 | cafecillo | Faramea spp | Rubiaceae | 11.7 |
| 1 | PrimFor1 | 5 | caimito | Chrysophyllum cainito | Sapotaceae | 58.2 |
| 1 | PrimFor1 | 5 | canoa | ? | ? | 37.5 |
| 1 | PrimFor1 | 5 | chonta | ? | ? | 15.8 |
| 1 | PrimFor1 | 5 | chonta | ? | ? | 18.3 |
| 1 | PrimFor1 | 5 | chonta | ? | ? | 16.0 |
| 1 | PrimFor1 | 5 | chonta | ? | ? | 14.5 |
| 1 | PrimFor1 | 5 | chonta | ? | ? | 14.5 |
| 1 | PrimFor1 | 5 | cocobolo | Vatairea lundelli | Leguminosae-pap | 82.0 |
| 1 | PrimFor1 | 5 | cocobolo | Vatairea lundelli | Leguminosae-pap | 47.5 |
| 1 | PrimFor1 | 5 | cucaracho | Billia colombiana | Hippocastanaceae | 65.0 |
| 1 | PrimFor1 | 5 | fosforillo | Dendropanax arboreus | Araliaceae | 21.6 |
| 1 | PrimFor1 | 5 | fosforillo | Dendropanax arboreus | Araliaceae | 13.5 |
| 1 | PrimFor1 | 5 | huesillo | Cupania spp | Sapindaceae | 20.8 |
| 1 | PrimFor1 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 15.5 |
| 1 | PrimFor1 | 5 | maquenque | Socratea exorrhiza | Palmae | 14.5 |
| 1 | PrimFor1 | 5 | maquenque | Socratea exorrhiza | Palmae | 15.0 |
| 1 | PrimFor1 | 5 | maquenque | Socratea exorrhiza | Palmae | 12.0 |
| 1 | PrimFor1 | 5 | ojoche | Brosimum alicastrum | Moraceae | 42.7 |
| 1 | PrimFor1 | 5 | ojoche | Brosimum alicastrum | Moraceae | 18.9 |
| 1 | PrimFor1 | 5 | p. dulce | Iriartea deltoidea | Palmae | 14.5 |
| 1 | PrimFor1 | 5 | p. dulce | Iriartea deltoidea | Palmae | 11.1 |
| 1 | PrimFor1 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 10.2 |
| 1 | PrimFor1 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 12.5 |
| 1 | PrimFor1 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 10.0 |
| 1 | PrimFor1 | 5 | paleta | Dussia macroprophyllata | Leguminosae-pap | 33.0 |
| 1 | PrimFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.4 |
| 1 | PrimFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.4 |
| 1 | PrimFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 41.5 |
| 1 | PrimFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.5 |
| 1 | PrimFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.0 |
| 1 | PrimFor1 | 5 | tamarindo | Dialium guianense | Leguminosae-caes | 31.7 |
| 1 | PrimFor1 | 5 | titor | Sacoglottis trichogyna | Humiriaceae | 55.5 |
| 1 | PrimFor1 | 5 | zapote | Manilkara zapota | Sapotaceae | 17.3 |
| 1 | PrimFor1 | 5 | zapote | Manilkara zapota | Sapotaceae | 37.0 |
| 1 | PrimFor1 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 13.0 |
| 1 | PrimFor1 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 28.5 |
| 1 | PrimFor1 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 26.5 |
| 2 | PrimFor2 | 1 | anono | Annona sp | Annonaceae | 20.6 |
| 2 | PrimFor2 | 1 | anono | Annona sp | Annonaceae | 11.3 |
| 2 | PrimFor2 | 1 | anono | Annona sp | Annonaceae | 12.1 |

| **Site no** | *Site name* | **Tran-sect** | **Common name** | **Scientific name** | **Family** | **DBH (cm)** |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 1 | anono | Annona sp | Annonaceae | 12.2 |
| 2 | PrimFor2 | 1 | areno | Qualea paraensis | Vochysiaceae | 10.2 |
| 2 | PrimFor2 | 1 | baco | Couma macrocarpa | Apocynaceae | 18.2 |
| 2 | PrimFor2 | 1 | baco | Couma macrocarpa | Apocynaceae | 11.0 |
| 2 | PrimFor2 | 1 | bejuco | Cupania glabra | Sapindaceae | 17.3 |
| 2 | PrimFor2 | 1 | canoa | ? | ? | 24.7 |
| 2 | PrimFor2 | 1 | canoa | ? | ? | 30.0 |
| 2 | PrimFor2 | 1 | carey | Elaeoluma glabrescens | Sapotaceae | 23.7 |
| 2 | PrimFor2 | 1 | carey | Elaeoluma glabrescens | Sapotaceae | 18.8 |
| 2 | PrimFor2 | 1 | carey | Elaeoluma glabrescens | Sapotaceae | 19.7 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 24.7 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 22.7 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 44.7 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 16.9 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 42.3 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 50.3 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 45.6 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 46.0 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 44.0 |
| 2 | PrimFor2 | 1 | cedro maria | Cedrela odorata | Meliaceae | 31.5 |
| 2 | PrimFor2 | 1 | ceiba | Ceiba pentandra | Bombacaceae | 44.8 |
| 2 | PrimFor2 | 1 | chonta | ? | ? | 15.7 |
| 2 | PrimFor2 | 1 | chonta | ? | ? | 17.2 |
| 2 | PrimFor2 | 1 | cuero sapo | Licania affinis | Chrysobalanaceae | 38.0 |
| 2 | PrimFor2 | 1 | cuero sapo | Licania affinis | Chrysobalanaceae | 33.7 |
| 2 | PrimFor2 | 1 | cuero sapo | Licania affinis | Chrysobalanaceae | 17.0 |
| 2 | PrimFor2 | 1 | fosforillo | Dendropanax arboreus | Araliaceae | 29.2 |
| 2 | PrimFor2 | 1 | guabilla | Inga sp | Leguminosae-mim | 14.1 |
| 2 | PrimFor2 | 1 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 14.4 |
| 2 | PrimFor2 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 10.4 |
| 2 | PrimFor2 | 1 | lija | Pourouma minor | Cecropiaceae | 11.5 |
| 2 | PrimFor2 | 1 | nispero | Manilkara zapota | Sapotaceae | 34.6 |
| 2 | PrimFor2 | 1 | ojoche | Brosimum alicastrum | Moraceae | 17.9 |
| 2 | PrimFor2 | 1 | ojoche | Brosimum alicastrum | Moraceae | 15.1 |
| 2 | PrimFor2 | 1 | ojoche | Brosimum alicastrum | Moraceae | 24.3 |
| 2 | PrimFor2 | 1 | p. mantequilla | Prestoea decurrens | Palmae | 10.1 |
| 2 | PrimFor2 | 1 | p. mantequilla | Prestoea decurrens | Palmae | 11.2 |
| 2 | PrimFor2 | 1 | p. mantequilla | Prestoea decurrens | Palmae | 10.1 |
| 2 | PrimFor2 | 1 | p. mantequilla | Prestoea decurrens | Palmae | 10.0 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.6 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 21.2 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.5 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 18.2 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.7 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.5 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.5 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.1 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.1 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.4 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 16.8 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.1 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.5 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.4 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 10.1 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.2 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.3 |
| 2 | PrimFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.7 |
| 2 | PrimFor2 | 1 | ponponjoche | Pachira aquatica | Bombacaceae | 14.4 |
| 2 | PrimFor2 | 1 | querosene | Tetragastris panamensis | Burseraceae | 40.2 |
| 2 | PrimFor2 | 1 | quizarra | Phoebe valeriana | Lauraceae | 11.5 |
| 2 | PrimFor2 | 1 | quizarra | Phoebe valeriana | Lauraceae | 14.2 |
| 2 | PrimFor2 | 1 | quizarra | Phoebe valeriana | Lauraceae | 16.3 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 16.1 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 14.9 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 13.9 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.7 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 14.6 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 15.6 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 13.3 |
| 2 | PrimFor2 | 1 | repollito | Eschweilera costaricensis | Lecythidaceae | 13.0 |
| 2 | PrimFor2 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 20.2 |
| 2 | PrimFor2 | 2 | alcantarilla | ? | ? | 10.4 |
| 2 | PrimFor2 | 2 | alcantarilla | ? | ? | 14.5 |
| 2 | PrimFor2 | 2 | alcantarilla | ? | ? | 13.0 |
| 2 | PrimFor2 | 2 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 11.2 |
| 2 | PrimFor2 | 2 | anonillo | Rollinia pittieri | Annonaceae | 12.2 |
| 2 | PrimFor2 | 2 | areno | Qualea paraensis | Vochysiaceae | 11.7 |
| 2 | PrimFor2 | 2 | areno | Qualea paraensis | Vochysiaceae | 12.2 |
| 2 | PrimFor2 | 2 | areno | Qualea paraensis | Vochysiaceae | 29.1 |
| 2 | PrimFor2 | 2 | areno | Qualea paraensis | Vochysiaceae | 27.0 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 15.2 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 19.9 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 17.2 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 46.0 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 38.3 |
| 2 | PrimFor2 | 2 | baco | Couma macrocarpa | Apocynaceae | 10.5 |
| 2 | PrimFor2 | 2 | balsamo | Ochroma pyramidale | Bombacaceae | 16.3 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 31.1 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 28.9 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.3 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.2 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.1 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.4 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.5 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.5 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.5 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.7 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.6 |
| 2 | PrimFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 31.0 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 2 | canoa | ? | ? | 16.8 |
| 2 | PrimFor2 | 2 | canoa | ? | ? | 49.0 |
| 2 | PrimFor2 | 2 | canoa | ? | ? | 17.0 |
| 2 | PrimFor2 | 2 | canoa | ? | ? | 29.0 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 24.3 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 11.3 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 43.3 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 56.0 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 16.5 |
| 2 | PrimFor2 | 2 | carey | Elaeoluma glabrescens | Sapotaceae | 27.0 |
| 2 | PrimFor2 | 2 | ceiba | Ceiba pentandra | Bombacaceae | 42.5 |
| 2 | PrimFor2 | 2 | chonta | ? | ? | 18.7 |
| 2 | PrimFor2 | 2 | cucaracho | Billia colombiana | Hippocastanaceae | 27.3 |
| 2 | PrimFor2 | 2 | cuero sapo | Licania affinis | Chrysobalanaceae | 28.6 |
| 2 | PrimFor2 | 2 | frutilla | Otoba novogranatensis | Myristicaceae | 11.5 |
| 2 | PrimFor2 | 2 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 13.5 |
| 2 | PrimFor2 | 2 | guayabillo montaña | Psidium sp. | Myrtaceae | 11.0 |
| 2 | PrimFor2 | 2 | ira | Ocotea spp | Lauraceae | 17.2 |
| 2 | PrimFor2 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 14.5 |
| 2 | PrimFor2 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 16.0 |
| 2 | PrimFor2 | 2 | nene | Ormosia macrocalyx | Leguminosae-pap | 12.9 |
| 2 | PrimFor2 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 10.0 |
| 2 | PrimFor2 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 10.6 |
| 2 | PrimFor2 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 13.0 |
| 2 | PrimFor2 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 12.0 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 29.6 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 14.0 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.0 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.0 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.3 |
| 2 | PrimFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 20.0 |
| 2 | PrimFor2 | 2 | repollito | Eschweilera costaricensis | Lecythidaceae | 28.5 |
| 2 | PrimFor2 | 2 | repollito | Eschweilera costaricensis | Lecythidaceae | 12.7 |
| 2 | PrimFor2 | 3 | alcanfor | Protium panamense | Burseraceae | 14.3 |
| 2 | PrimFor2 | 3 | amargo | Aspidosperma megalocarpon | Apocynaceae | 18.5 |
| 2 | PrimFor2 | 3 | anonillo | Rollinia pittieri | Annonaceae | 11.3 |
| 2 | PrimFor2 | 3 | anonillo | Rollinia pittieri | Annonaceae | 18.0 |
| 2 | PrimFor2 | 3 | areno | Qualea paraensis | Vochysiaceae | 15.4 |
| 2 | PrimFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.7 |
| 2 | PrimFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.7 |
| 2 | PrimFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.4 |
| 2 | PrimFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.0 |
| 2 | PrimFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.4 |
| 2 | PrimFor2 | 3 | burio | Heliocarpus appendiculatus | Tiliaceae | 17.0 |
| 2 | PrimFor2 | 3 | cafecillo | Faramea spp | Rubiaceae | 12.0 |
| 2 | PrimFor2 | 3 | canoa | ? | ? | 40.0 |
| 2 | PrimFor2 | 3 | canoa | ? | ? | 23.0 |
| 2 | PrimFor2 | 3 | capulin | Muntingia calabura | Tiliaceae | 27.0 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 3 | cedro maria | Cedrela odorata | Meliaceae | 12.0 |
| 2 | PrimFor2 | 3 | cedro maria | Cedrela odorata | Meliaceae | 10.9 |
| 2 | PrimFor2 | 3 | chonta | ? | ? | 16.9 |
| 2 | PrimFor2 | 3 | chonta | ? | ? | 18.3 |
| 2 | PrimFor2 | 3 | chonta | ? | ? | 18.1 |
| 2 | PrimFor2 | 3 | cuero sapo | Licania affinis | Chrysobalanaceae | 31.0 |
| 2 | PrimFor2 | 3 | cuero sapo | Licania affinis | Chrysobalanaceae | 21.7 |
| 2 | PrimFor2 | 3 | guaitil | Genipa americana | Rubiaceae | 12.7 |
| 2 | PrimFor2 | 3 | guayabillo montaña | Psidium sp. | Myrtaceae | 19.2 |
| 2 | PrimFor2 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 19.5 |
| 2 | PrimFor2 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 12.8 |
| 2 | PrimFor2 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 12.3 |
| 2 | PrimFor2 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 13.7 |
| 2 | PrimFor2 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 14.0 |
| 2 | PrimFor2 | 3 | nene | Ormosia macrocalyx | Leguminosae-pap | 11.7 |
| 2 | PrimFor2 | 3 | p. mantequilla | Prestoea decurrens | Palmae | 10.5 |
| 2 | PrimFor2 | 3 | p. mantequilla | Prestoea decurrens | Palmae | 11.9 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 18.0 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 38.7 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.0 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.5 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.0 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 31.0 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.2 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.5 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 16.5 |
| 2 | PrimFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 10.5 |
| 2 | PrimFor2 | 3 | querosene | Tetragastris panamensis | Burseraceae | 39.0 |
| 2 | PrimFor2 | 3 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.0 |
| 2 | PrimFor2 | 3 | repollito | Eschweilera costaricensis | Lecythidaceae | 17.5 |
| 2 | PrimFor2 | 3 | repollito | Eschweilera costaricensis | Lecythidaceae | 12.9 |
| 2 | PrimFor2 | 3 | repollito | Eschweilera costaricensis | Lecythidaceae | 10.5 |
| 2 | PrimFor2 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 15.2 |
| 2 | PrimFor2 | 4 | alcanfor | Protium panamense | Burseraceae | 17.3 |
| 2 | PrimFor2 | 4 | almendro | Dipteryx panamensis | Leguminosae-pap | 17.0 |
| 2 | PrimFor2 | 4 | anonillo | Rollinia pittieri | Annonaceae | 12.5 |
| 2 | PrimFor2 | 4 | areno | Qualea paraensis | Vochysiaceae | 10.5 |
| 2 | PrimFor2 | 4 | areno | Qualea paraensis | Vochysiaceae | 15.6 |
| 2 | PrimFor2 | 4 | balsamo | Ochroma pyramidale | Bombacaceae | 31.5 |
| 2 | PrimFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 10.4 |
| 2 | PrimFor2 | 4 | cafecillo | Faramea spp | Rubiaceae | 14.0 |
| 2 | PrimFor2 | 4 | cafecillo | Faramea spp | Rubiaceae | 15.3 |
| 2 | PrimFor2 | 4 | cafecillo | Faramea spp | Rubiaceae | 12.4 |
| 2 | PrimFor2 | 4 | caobilla | Carapa guianensis | Meliaceae | 31.6 |
| 2 | PrimFor2 | 4 | carey | Elaeoluma glabrescens | Sapotaceae | 26.6 |
| 2 | PrimFor2 | 4 | carey | Elaeoluma glabrescens | Sapotaceae | 22.4 |
| 2 | PrimFor2 | 4 | chaperno | ? | ? | 14.5 |
| 2 | PrimFor2 | 4 | chilamate | ? | ? | 42.6 |

| **Site no** | *Site name* | **Tran-sect** | **Common name** | **Scientific name** | **Family** | **DBH (cm)** |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 4 | chonta | ? | ? | 15.1 |
| 2 | PrimFor2 | 4 | chonta | ? | ? | 15.9 |
| 2 | PrimFor2 | 4 | chonta | ? | ? | 18.8 |
| 2 | PrimFor2 | 4 | cipresillo | Podocarpus guatemalensis | Podocarpaceae | 77.0 |
| 2 | PrimFor2 | 4 | cipresillo | Podocarpus guatemalensis | Podocarpaceae | 88.0 |
| 2 | PrimFor2 | 4 | cocora | Guarea bullata | Meliaceae | 31.5 |
| 2 | PrimFor2 | 4 | cuero sapo | Licania affinis | Chrysobalanaceae | 23.0 |
| 2 | PrimFor2 | 4 | cuero sapo | Licania affinis | Chrysobalanaceae | 16.0 |
| 2 | PrimFor2 | 4 | fruta | Virola guatemalensis | Myristicaceae | 31.0 |
| 2 | PrimFor2 | 4 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 10.5 |
| 2 | PrimFor2 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 11.4 |
| 2 | PrimFor2 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 12.1 |
| 2 | PrimFor2 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 14.9 |
| 2 | PrimFor2 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 21.4 |
| 2 | PrimFor2 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 11.9 |
| 2 | PrimFor2 | 4 | nene | Ormosia macrocalyx | Leguminosae-pap | 10.7 |
| 2 | PrimFor2 | 4 | ojoche | Brosimum alicastrum | Moraceae | 15.0 |
| 2 | PrimFor2 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 10.5 |
| 2 | PrimFor2 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 10.2 |
| 2 | PrimFor2 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 11.5 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.2 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.1 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.3 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.3 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.9 |
| 2 | PrimFor2 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.0 |
| 2 | PrimFor2 | 4 | piedrilla | Ardisia sp | Myrsinaceae | 17.1 |
| 2 | PrimFor2 | 4 | querosene | Tetragastris panamensis | Burseraceae | 25.7 |
| 2 | PrimFor2 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.3 |
| 2 | PrimFor2 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.7 |
| 2 | PrimFor2 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 13.5 |
| 2 | PrimFor2 | 4 | tabacon | Cespedesia macrophylla | Ochnaceae | 12.2 |
| 2 | PrimFor2 | 4 | tabacon | Cespedesia macrophylla | Ochnaceae | 17.8 |
| 2 | PrimFor2 | 4 | zapotillo | Chrysophyllum spp | Sapotaceae | 19.7 |
| 2 | PrimFor2 | 5 | alcantarilla | ? | ? | 11.8 |
| 2 | PrimFor2 | 5 | alcantarilla | ? | ? | 13.0 |
| 2 | PrimFor2 | 5 | anonillo | Rollinia pittieri | Annonaceae | 16.5 |
| 2 | PrimFor2 | 5 | anonillo | Rollinia pittieri | Annonaceae | 16.2 |
| 2 | PrimFor2 | 5 | areno | Qualea paraensis | Vochysiaceae | 51.5 |
| 2 | PrimFor2 | 5 | areno | Qualea paraensis | Vochysiaceae | 15.3 |
| 2 | PrimFor2 | 5 | areno | Qualea paraensis | Vochysiaceae | 51.6 |
| 2 | PrimFor2 | 5 | baco | Couma macrocarpa | Apocynaceae | 14.6 |
| 2 | PrimFor2 | 5 | baco | Couma macrocarpa | Apocynaceae | 30.7 |
| 2 | PrimFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.2 |
| 2 | PrimFor2 | 5 | cafecillo | Faramea spp | Rubiaceae | 11.5 |
| 2 | PrimFor2 | 5 | carey | Elaeoluma glabrescens | Sapotaceae | 23.4 |
| 2 | PrimFor2 | 5 | carey | Elaeoluma glabrescens | Sapotaceae | 57.2 |
| 2 | PrimFor2 | 5 | carey | Elaeoluma glabrescens | Sapotaceae | 22.3 |

| Site no | Site name | Tran-sect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 2 | PrimFor2 | 5 | cedro maria | Cedrela odorata | Meliaceae | 19.9 |
| 2 | PrimFor2 | 5 | chonta | ? | ? | 13.9 |
| 2 | PrimFor2 | 5 | cocobolo | Vatairea lundelli | Leguminosae-pap | 52.0 |
| 2 | PrimFor2 | 5 | cuero sapo | Licania affinis | Chrysobalanaceae | 29.1 |
| 2 | PrimFor2 | 5 | cuero sapo | Licania affinis | Chrysobalanaceae | 38.5 |
| 2 | PrimFor2 | 5 | cuero sapo | Licania affinis | Chrysobalanaceae | 43.8 |
| 2 | PrimFor2 | 5 | fosforillo | Dendropanax arboreus | Araliaceae | 24.3 |
| 2 | PrimFor2 | 5 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 13.2 |
| 2 | PrimFor2 | 5 | guabilla | Inga sp | Leguminosae-mim | 15.5 |
| 2 | PrimFor2 | 5 | guaitil | Genipa americana | Rubiaceae | 21.8 |
| 2 | PrimFor2 | 5 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 75.0 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 14.1 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 11.5 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 22.1 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 13.0 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 11.7 |
| 2 | PrimFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 17.3 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 12.5 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 12.2 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 11.7 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 11.1 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 10.1 |
| 2 | PrimFor2 | 5 | p. mantequilla | Prestoea decurrens | Palmae | 11.9 |
| 2 | PrimFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 18.2 |
| 2 | PrimFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.9 |
| 2 | PrimFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.2 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 12.7 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 10.4 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 14.7 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.3 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 13.5 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 10.3 |
| 2 | PrimFor2 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 30.1 |
| 2 | PrimFor2 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 20.1 |
| 3 | LogFor1 | 1 | achiotillo | Vismia ferruginea | Guttiferae | 19.3 |
| 3 | LogFor1 | 1 | achiotillo | Vismia ferruginea | Guttiferae | 25.3 |
| 3 | LogFor1 | 1 | achiotillo | Vismia ferruginea | Guttiferae | 12.5 |
| 3 | LogFor1 | 1 | achiotillo | Vismia ferruginea | Guttiferae | 14.3 |
| 3 | LogFor1 | 1 | anonillo | Rollinia pittieri | Annonaceae | 11.1 |
| 3 | LogFor1 | 1 | burio | Heliocarpus appendiculatus | Tiliaceae | 13.3 |
| 3 | LogFor1 | 1 | burio | Heliocarpus appendiculatus | Tiliaceae | 10.8 |
| 3 | LogFor1 | 1 | cafecillo | Faramea spp | Rubiaceae | 11.5 |
| 3 | LogFor1 | 1 | capulin | Muntingia calabura | Tiliaceae | 20.4 |
| 3 | LogFor1 | 1 | capulin | Muntingia calabura | Tiliaceae | 21.2 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 14.0 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 14.8 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.9 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 11.6 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.2 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 14.8 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.2 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 15.4 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 13.8 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 15.3 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.2 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 12.1 |
| 3 | LogFor1 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 14.0 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 12.3 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 10.7 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 12.7 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 14.8 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 18.8 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 14.0 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 22.3 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 13.4 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 12.2 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 11.1 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 17.7 |
| 3 | LogFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 16.6 |
| 3 | LogFor1 | 1 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 15.9 |
| 3 | LogFor1 | 1 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 10.2 |
| 3 | LogFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 11.7 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 15.1 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 20.5 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 17.9 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 14.1 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 18.6 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 12.6 |
| 3 | LogFor1 | 1 | manga larga | Laetia procera | Flacourtiaceae | 16.6 |
| 3 | LogFor1 | 1 | manteco | Tapirira guianensis | Anacardiaceae | 11.9 |
| 3 | LogFor1 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.1 |
| 3 | LogFor1 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.8 |
| 3 | LogFor1 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 18.5 |
| 3 | LogFor1 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 26.5 |
| 3 | LogFor1 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 19.1 |
| 3 | LogFor1 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 16.7 |
| 3 | LogFor1 | 2 | achiotillo | Vismia ferruginea | Guttiferae | 21.0 |
| 3 | LogFor1 | 2 | alcanfor | Protium panamense | Burseraceae | 14.1 |
| 3 | LogFor1 | 2 | alcantarilla | ? | ? | 15.1 |
| 3 | LogFor1 | 2 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 10.4 |
| 3 | LogFor1 | 2 | amarguito | Croton tonduzii | Euphorbiaceae | 14.2 |
| 3 | LogFor1 | 2 | anonillo | Rollinia pittieri | Annonaceae | 15.8 |
| 3 | LogFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 34.5 |
| 3 | LogFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 12.7 |
| 3 | LogFor1 | 2 | baco | Couma macrocarpa | Apocynaceae | 50.7 |
| 3 | LogFor1 | 2 | baco | Couma macrocarpa | Apocynaceae | 50.0 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 3 | LogFor1 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.7 |
| 3 | LogFor1 | 2 | cafecillo | Faramea spp | Rubiaceae | 18.1 |
| 3 | LogFor1 | 2 | chonta | ? | ? | 16.8 |
| 3 | LogFor1 | 2 | chonta | ? | ? | 17.5 |
| 3 | LogFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 12.2 |
| 3 | LogFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 15.7 |
| 3 | LogFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 12.1 |
| 3 | LogFor1 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 42.5 |
| 3 | LogFor1 | 2 | paleta | Dussia macroprophyllata | Leguminosae-pap | 22.2 |
| 3 | LogFor1 | 2 | panama | Sterculia apetala | Sterculiaceae | 13.2 |
| 3 | LogFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.8 |
| 3 | LogFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 29.6 |
| 3 | LogFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 26.1 |
| 3 | LogFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.3 |
| 3 | LogFor1 | 2 | tamarindo | Dialium guianense | Leguminosae-caes | 24.7 |
| 3 | LogFor1 | 2 | tamarindo | Dialium guianense | Leguminosae-caes | 47.0 |
| 3 | LogFor1 | 2 | tamarindo | Dialium guianense | Leguminosae-caes | 62.0 |
| 3 | LogFor1 | 2 | titor | Sacoglottis trichogyna | Humiriaceae | 34.5 |
| 3 | LogFor1 | 2 | titor | Sacoglottis trichogyna | Humiriaceae | 43.3 |
| 3 | LogFor1 | 2 | uva | ? | ? | 20.2 |
| 3 | LogFor1 | 2 | yema huevo | Chimarrhis parviflora | Rubiaceae | 22.3 |
| 3 | LogFor1 | 2 | zapote | Manilkara zapota | Sapotaceae | 12.3 |
| 3 | LogFor1 | 2 | zapote | Manilkara zapota | Sapotaceae | 12.8 |
| 3 | LogFor1 | 2 | zapote | Manilkara zapota | Sapotaceae | 65.0 |
| 3 | LogFor1 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 12.6 |
| 3 | LogFor1 | 3 | alcantarilla | ? | ? | 12.6 |
| 3 | LogFor1 | 3 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 12.2 |
| 3 | LogFor1 | 3 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 14.1 |
| 3 | LogFor1 | 3 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 28.4 |
| 3 | LogFor1 | 3 | anonillo | Rollinia pittieri | Annonaceae | 14.8 |
| 3 | LogFor1 | 3 | anonillo | Rollinia pittieri | Annonaceae | 11.9 |
| 3 | LogFor1 | 3 | anonillo | Rollinia pittieri | Annonaceae | 12.5 |
| 3 | LogFor1 | 3 | areno | Qualea paraensis | Vochysiaceae | 13.1 |
| 3 | LogFor1 | 3 | areno | Qualea paraensis | Vochysiaceae | 41.2 |
| 3 | LogFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 40.0 |
| 3 | LogFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 24.3 |
| 3 | LogFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 13.0 |
| 3 | LogFor1 | 3 | baco | Couma macrocarpa | Apocynaceae | 15.2 |
| 3 | LogFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.0 |
| 3 | LogFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 10.6 |
| 3 | LogFor1 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 48.3 |
| 3 | LogFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 11.5 |
| 3 | LogFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 14.1 |
| 3 | LogFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 17.7 |
| 3 | LogFor1 | 3 | cafecillo | Faramea spp | Rubiaceae | 15.5 |
| 3 | LogFor1 | 3 | cedro maria | Cedrela odorata | Meliaceae | 14.2 |
| 3 | LogFor1 | 3 | chonta | ? | ? | 17.2 |
| 3 | LogFor1 | 3 | chonta | ? | ? | 16.4 |

| Site no | Site name | Tran-sect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 3 | LogFor1 | 3 | chonta | ? | ? | 17.3 |
| 3 | LogFor1 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 29.7 |
| 3 | LogFor1 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 21.7 |
| 3 | LogFor1 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 15.6 |
| 3 | LogFor1 | 3 | frutilla | Otoba novogranatensis | Myristicaceae | 20.9 |
| 3 | LogFor1 | 3 | guabilla | Inga sp | Leguminosae-mim | 11.9 |
| 3 | LogFor1 | 3 | ira | Ocotea spp | Lauraceae | 13.5 |
| 3 | LogFor1 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 10.1 |
| 3 | LogFor1 | 3 | lengua de vaca | Miconia argentea | Melastomataceae | 14.5 |
| 3 | LogFor1 | 3 | llolillo | ? | ? | 25.3 |
| 3 | LogFor1 | 3 | llolillo | ? | ? | 36.2 |
| 3 | LogFor1 | 3 | llolillo | ? | ? | 25.0 |
| 3 | LogFor1 | 3 | manteco | Tapirira guianensis | Anacardiaceae | 16.1 |
| 3 | LogFor1 | 3 | maquenque | Socratea exorrhiza | Palmae | 12.3 |
| 3 | LogFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.3 |
| 3 | LogFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 18.2 |
| 3 | LogFor1 | 3 | roble coral | Terminalia amazonia | Combretaceae | 11.5 |
| 3 | LogFor1 | 3 | roble coral | Terminalia amazonia | Combretaceae | 10.1 |
| 3 | LogFor1 | 3 | tamarindo | Dialium guianense | Leguminosae-caes | 35.7 |
| 3 | LogFor1 | 3 | vara alta | Xylopia sericophylla | Annonaceae | 12.9 |
| 3 | LogFor1 | 3 | vara alta | Xylopia sericophylla | Annonaceae | 15.4 |
| 3 | LogFor1 | 3 | yema huevo | Chimarrhis parviflora | Rubiaceae | 24.7 |
| 3 | LogFor1 | 3 | zapote | Manilkara zapota | Sapotaceae | 36.0 |
| 3 | LogFor1 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 12.7 |
| 3 | LogFor1 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 44.7 |
| 3 | LogFor1 | 4 | aguacatillo | Ocotea stenoneura | Lauraceae | 10.9 |
| 3 | LogFor1 | 4 | aguacatillo | Ocotea stenoneura | Lauraceae | 14.7 |
| 3 | LogFor1 | 4 | alcanfor | Protium panamense | Burseraceae | 11.7 |
| 3 | LogFor1 | 4 | alcanfor | Protium panamense | Burseraceae | 11.3 |
| 3 | LogFor1 | 4 | amarguito | Croton tonduzii | Euphorbiaceae | 12.3 |
| 3 | LogFor1 | 4 | anonillo | Rollinia pittieri | Annonaceae | 12.3 |
| 3 | LogFor1 | 4 | areno | Qualea paraensis | Vochysiaceae | 39.2 |
| 3 | LogFor1 | 4 | areno | Qualea paraensis | Vochysiaceae | 49.1 |
| 3 | LogFor1 | 4 | baco | Couma macrocarpa | Apocynaceae | 26.1 |
| 3 | LogFor1 | 4 | cafecillo | Faramea spp | Rubiaceae | 14.1 |
| 3 | LogFor1 | 4 | cafecillo | Faramea spp | Rubiaceae | 11.2 |
| 3 | LogFor1 | 4 | cafecillo | Faramea spp | Rubiaceae | 12.9 |
| 3 | LogFor1 | 4 | cafecillo | Faramea spp | Rubiaceae | 11.3 |
| 3 | LogFor1 | 4 | cafecillo | Faramea spp | Rubiaceae | 18.1 |
| 3 | LogFor1 | 4 | caobilla | Carapa guianensis | Meliaceae | 18.2 |
| 3 | LogFor1 | 4 | carey | Elaeoluma glabrescens | Sapotaceae | 26.8 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 19.1 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 14.1 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 16.3 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 14.9 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 17.5 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 18.4 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 14.8 |
| 3 | LogFor1 | 4 | chonta | ? | ? | 16.8 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 3 | LogFor1 | 4 | cipresillo | Podocarpus guatemalensis | Podocarpaceae | 19.5 |
| 3 | LogFor1 | 4 | cocobolo | Vatairea lundelli | Leguminosae-pap | 40.5 |
| 3 | LogFor1 | 4 | guaitil | Genipa americana | Rubiaceae | 19.5 |
| 3 | LogFor1 | 4 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 55.4 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 11.2 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 16.5 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 12.9 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 14.8 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 12.1 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 16.4 |
| 3 | LogFor1 | 4 | lengua de vaca | Miconia argentea | Melastomataceae | 16.3 |
| 3 | LogFor1 | 4 | mangle | Conocarpus erecta | Combretaceae | 14.1 |
| 3 | LogFor1 | 4 | mangle | Conocarpus erecta | Combretaceae | 11.5 |
| 3 | LogFor1 | 4 | manteco | Tapirira guianensis | Anacardiaceae | 14.1 |
| 3 | LogFor1 | 4 | maquenque | Socratea exorrhiza | Palmae | 12.3 |
| 3 | LogFor1 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 12.2 |
| 3 | LogFor1 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 11.3 |
| 3 | LogFor1 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 12.2 |
| 3 | LogFor1 | 4 | p. mantequilla | Prestoea decurrens | Palmae | 11.2 |
| 3 | LogFor1 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.8 |
| 3 | LogFor1 | 4 | piedra | Coccoloba tuerckheimii | Polygonaceae | 39.3 |
| 3 | LogFor1 | 4 | querosene | Tetragastris panamensis | Burseraceae | 11.6 |
| 3 | LogFor1 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 11.9 |
| 3 | LogFor1 | 4 | repollito | Eschweilera costaricensis | Lecythidaceae | 26.3 |
| 3 | LogFor1 | 4 | tabacon | Cespedesia macrophylla | Ochnaceae | 15.1 |
| 3 | LogFor1 | 4 | tabacon | Cespedesia macrophylla | Ochnaceae | 22.5 |
| 3 | LogFor1 | 4 | tamarindo | Dialium guianense | Leguminosae-caes | 31.3 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 24.0 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 22.3 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 10.3 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 22.3 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 38.0 |
| 3 | LogFor1 | 4 | zapote | Manilkara zapota | Sapotaceae | 14.4 |
| 3 | LogFor1 | 5 | aguacate | Persea americana | Lauraceae | 17.8 |
| 3 | LogFor1 | 5 | aguacate | Persea americana | Lauraceae | 17.8 |
| 3 | LogFor1 | 5 | aguacatillo | Ocotea stenoneura | Lauraceae | 14.4 |
| 3 | LogFor1 | 5 | alcantarilla | ? | ? | 20.3 |
| 3 | LogFor1 | 5 | alcantarilla | ? | ? | 11.9 |
| 3 | LogFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 41.2 |
| 3 | LogFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 13.1 |
| 3 | LogFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 14.7 |
| 3 | LogFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 13.4 |
| 3 | LogFor1 | 5 | areno | Qualea paraensis | Vochysiaceae | 10.2 |
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 12.4 |
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 22.0 |
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 11.0 |
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 15.1 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 10.5 |
| 3 | LogFor1 | 5 | baco | Couma macrocarpa | Apocynaceae | 12.1 |
| 3 | LogFor1 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 105.2 |
| 3 | LogFor1 | 5 | cafecillo | Faramea spp | Rubiaceae | 17.3 |
| 3 | LogFor1 | 5 | carey | Elaeoluma glabrescens | Sapotaceae | 27.0 |
| 3 | LogFor1 | 5 | cedro maria | Cedrela odorata | Meliaceae | 21.4 |
| 3 | LogFor1 | 5 | cedro maria | Cedrela odorata | Meliaceae | 33.5 |
| 3 | LogFor1 | 5 | cedro maria | Cedrela odorata | Meliaceae | 14.3 |
| 3 | LogFor1 | 5 | cedro maria | Cedrela odorata | Meliaceae | 42.8 |
| 3 | LogFor1 | 5 | chonta | ? | ? | 17.1 |
| 3 | LogFor1 | 5 | cipresillo | Podocarpus guatemalensis | Podocarpaceae | 41.5 |
| 3 | LogFor1 | 5 | guaitil | Genipa americana | Rubiaceae | 11.1 |
| 3 | LogFor1 | 5 | guayabillo montaña | Psidium sp. | Myrtaceae | 17.1 |
| 3 | LogFor1 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 11.9 |
| 3 | LogFor1 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 14.2 |
| 3 | LogFor1 | 5 | maquenque | Socratea exorrhiza | Palmae | 11.5 |
| 3 | LogFor1 | 5 | p. dulce | Iriartea deltoidea | Palmae | 18.2 |
| 3 | LogFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 23.5 |
| 3 | LogFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 26.7 |
| 3 | LogFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 22.5 |
| 3 | LogFor1 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.6 |
| 3 | LogFor1 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 10.1 |
| 3 | LogFor1 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 15.8 |
| 3 | LogFor1 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 10.9 |
| 3 | LogFor1 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 17.5 |
| 3 | LogFor1 | 5 | repollito | Eschweilera costaricensis | Lecythidaceae | 17.8 |
| 3 | LogFor1 | 5 | tabacon | Cespedesia macrophylla | Ochnaceae | 16.2 |
| 3 | LogFor1 | 5 | tabacon | Cespedesia macrophylla | Ochnaceae | 18.2 |
| 3 | LogFor1 | 5 | tabacon | Cespedesia macrophylla | Ochnaceae | 16.4 |
| 3 | LogFor1 | 5 | tabacon | Cespedesia macrophylla | Ochnaceae | 18.2 |
| 3 | LogFor1 | 5 | tabacon | Cespedesia macrophylla | Ochnaceae | 20.4 |
| 3 | LogFor1 | 5 | uva | ? | ? | 14.8 |
| 3 | LogFor1 | 5 | uva | ? | ? | 19.5 |
| 3 | LogFor1 | 5 | uva | ? | ? | 21.1 |
| 3 | LogFor1 | 5 | vaco | ? | ? | 11.0 |
| 3 | LogFor1 | 5 | zapote | Manilkara zapota | Sapotaceae | 19.8 |
| 3 | LogFor1 | 5 | zapote | Manilkara zapota | Sapotaceae | 18.2 |
| 4 | LogFor2 | 1 | aguacaton | Ocotea ira | Lauraceae | 14.8 |
| 4 | LogFor2 | 1 | bejuco | Cupania glabra | Sapindaceae | 19.1 |
| 4 | LogFor2 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.4 |
| 4 | LogFor2 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.2 |
| 4 | LogFor2 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.8 |
| 4 | LogFor2 | 1 | burio | Heliocarpus appendiculatus | Tiliaceae | 10.8 |
| 4 | LogFor2 | 1 | canoa | ? | ? | 31.0 |
| 4 | LogFor2 | 1 | carey | Elaeoluma glabrescens | Sapotaceae | 10.8 |
| 4 | LogFor2 | 1 | chonta | ? | ? | 18.1 |
| 4 | LogFor2 | 1 | chonta | ? | ? | 18.1 |
| 4 | LogFor2 | 1 | cocobolo | Vatairea lundelli | Leguminosae-pap | 43.8 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 4 | LogFor2 | 1 | cocobolo | Vatairea lundelli | Leguminosae-pap | 13.1 |
| 4 | LogFor2 | 1 | fosforillo | Dendropanax arboreus | Araliaceae | 19.1 |
| 4 | LogFor2 | 1 | fosforillo | Dendropanax arboreus | Araliaceae | 13.4 |
| 4 | LogFor2 | 1 | fruta dorada | Virola koschnyi | Myristicaceae | 59.0 |
| 4 | LogFor2 | 1 | frutilla | Otoba novogranatensis | Myristicaceae | 27.6 |
| 4 | LogFor2 | 1 | guabilla | Inga sp | Leguminosae-mim | 37.2 |
| 4 | LogFor2 | 1 | huesillo | Cupania spp | Sapindaceae | 15.2 |
| 4 | LogFor2 | 1 | lija | Pourouma minor | Cecropiaceae | 19.5 |
| 4 | LogFor2 | 1 | manteco | Tapirira guianensis | Anacardiaceae | 12.3 |
| 4 | LogFor2 | 1 | manteco | Tapirira guianensis | Anacardiaceae | 11.6 |
| 4 | LogFor2 | 1 | muneco | ? | ? | 11.1 |
| 4 | LogFor2 | 1 | ojoche | Brosimum alicastrum | Moraceae | 22.9 |
| 4 | LogFor2 | 1 | p. dulce | Iriartea deltoidea | Palmae | 17.0 |
| 4 | LogFor2 | 1 | p. dulce | Iriartea deltoidea | Palmae | 20.0 |
| 4 | LogFor2 | 1 | p. dulce | Iriartea deltoidea | Palmae | 18.3 |
| 4 | LogFor2 | 1 | p. dulce | Iriartea deltoidea | Palmae | 18.7 |
| 4 | LogFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 11.0 |
| 4 | LogFor2 | 1 | querosene | Tetragastris panamensis | Burseraceae | 18.3 |
| 4 | LogFor2 | 1 | quizarra | Phoebe valeriana | Lauraceae | 17.2 |
| 4 | LogFor2 | 1 | tabacon | Cespedesia macrophylla | Ochnaceae | 17.5 |
| 4 | LogFor2 | 1 | tabacon | Cespedesia macrophylla | Ochnaceae | 10.1 |
| 4 | LogFor2 | 1 | tamarindo | Dialium guianense | Leguminosae-caes | 54.3 |
| 4 | LogFor2 | 1 | tamarindo | Dialium guianense | Leguminosae-caes | 43.4 |
| 4 | LogFor2 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 13.6 |
| 4 | LogFor2 | 1 | vara alta | Xylopia sericophylla | Annonaceae | 25.4 |
| 4 | LogFor2 | 1 | zapote | Manilkara zapota | Sapotaceae | 15.8 |
| 4 | LogFor2 | 2 | asufre | ? | ? | 28.0 |
| 4 | LogFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.0 |
| 4 | LogFor2 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.5 |
| 4 | LogFor2 | 2 | botijo | Apeiba membranacea | Tiliaceae | 38.4 |
| 4 | LogFor2 | 2 | burio | Heliocarpus appendiculatus | Tiliaceae | 31.2 |
| 4 | LogFor2 | 2 | chonta | ? | ? | 20.4 |
| 4 | LogFor2 | 2 | chonta | ? | ? | 16.4 |
| 4 | LogFor2 | 2 | chonta | ? | ? | 17.4 |
| 4 | LogFor2 | 2 | chonta | ? | ? | 17.1 |
| 4 | LogFor2 | 2 | cocora | Guarea bullata | Meliaceae | 16.1 |
| 4 | LogFor2 | 2 | cocora | Guarea bullata | Meliaceae | 27.2 |
| 4 | LogFor2 | 2 | cocora | Guarea bullata | Meliaceae | 13.6 |
| 4 | LogFor2 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 17.5 |
| 4 | LogFor2 | 2 | fruta dorada | Virola koschnyi | Myristicaceae | 18.2 |
| 4 | LogFor2 | 2 | fruta dorada | Virola koschnyi | Myristicaceae | 16.4 |
| 4 | LogFor2 | 2 | fruta dorada | Virola koschnyi | Myristicaceae | 35.7 |
| 4 | LogFor2 | 2 | fruta dorada | Virola koschnyi | Myristicaceae | 44.7 |
| 4 | LogFor2 | 2 | frutilla | Otoba novogranatensis | Myristicaceae | 14.6 |
| 4 | LogFor2 | 2 | frutilla | Otoba novogranatensis | Myristicaceae | 17.2 |
| 4 | LogFor2 | 2 | guabilla | Inga sp | Leguminosae-mim | 32.5 |
| 4 | LogFor2 | 2 | guabilla | Inga sp | Leguminosae-mim | 18.6 |
| 4 | LogFor2 | 2 | guabilla | Inga sp | Leguminosae-mim | 18.5 |
| 4 | LogFor2 | 2 | guabilla | Inga sp | Leguminosae-mim | 12.2 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 4 | LogFor2 | 2 | huesillo | Cupania spp | Sapindaceae | 13.3 |
| 4 | LogFor2 | 2 | huesillo | Cupania spp | Sapindaceae | 11.1 |
| 4 | LogFor2 | 2 | laurel | Cordia alliodora | Boraginaceae | 48.1 |
| 4 | LogFor2 | 2 | lechoso | Brosimum utile | Moraceae | 52.5 |
| 4 | LogFor2 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 21.1 |
| 4 | LogFor2 | 2 | magnolia | Talauma gloriensis | Magnoliaceae | 15.1 |
| 4 | LogFor2 | 2 | manteco | Tapirira guianensis | Anacardiaceae | 58.0 |
| 4 | LogFor2 | 2 | maquenque | Socratea exorrhiza | Palmae | 12.4 |
| 4 | LogFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 22.3 |
| 4 | LogFor2 | 2 | p. dulce | Iriartea deltoidea | Palmae | 15.9 |
| 4 | LogFor2 | 2 | p. dulce | Iriartea deltoidea | Palmae | 20.0 |
| 4 | LogFor2 | 2 | paleta | Dussia macroprophyllata | Leguminosae-pap | 16.5 |
| 4 | LogFor2 | 2 | paleta | Dussia macroprophyllata | Leguminosae-pap | 16.5 |
| 4 | LogFor2 | 2 | paleta | Dussia macroprophyllata | Leguminosae-pap | 42.0 |
| 4 | LogFor2 | 2 | pejivaye | Bactris sp | Chrysobalanaceae | 13.8 |
| 4 | LogFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.2 |
| 4 | LogFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.9 |
| 4 | LogFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 17.1 |
| 4 | LogFor2 | 2 | quizarra | Phoebe valeriana | Lauraceae | 12.8 |
| 4 | LogFor2 | 2 | tabacon | Cespedesia macrophylla | Ochnaceae | 11.1 |
| 4 | LogFor2 | 2 | uva | ? | ? | 12.8 |
| 4 | LogFor2 | 2 | vara alta | Xylopia sericophylla | Annonaceae | 22.3 |
| 4 | LogFor2 | 3 | almendro | Dipteryx panamensis | Leguminosae-pap | 130.0 |
| 4 | LogFor2 | 3 | amarguito | Croton tonduzii | Euphorbiaceae | 18.2 |
| 4 | LogFor2 | 3 | anonillo | Rollinia pittieri | Annonaceae | 12.8 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 15.6 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 16.5 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 18.3 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 16.4 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 15.7 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 16.6 |
| 4 | LogFor2 | 3 | chonta | ? | ? | 18.0 |
| 4 | LogFor2 | 3 | cocora | Guarea bullata | Meliaceae | 33.2 |
| 4 | LogFor2 | 3 | cocora | Guarea bullata | Meliaceae | 17.1 |
| 4 | LogFor2 | 3 | cocora | Guarea bullata | Meliaceae | 27.3 |
| 4 | LogFor2 | 3 | danto | Roupala spp | Proteaceae | 24.3 |
| 4 | LogFor2 | 3 | fosforillo | Dendropanax arboreus | Araliaceae | 17.0 |
| 4 | LogFor2 | 3 | fruta dorada | Virola koschnyi | Myristicaceae | 10.9 |
| 4 | LogFor2 | 3 | fruta dorada | Virola koschnyi | Myristicaceae | 16.5 |
| 4 | LogFor2 | 3 | fruta dorada | Virola koschnyi | Myristicaceae | 10.1 |
| 4 | LogFor2 | 3 | frutilla | Otoba novogranatensis | Myristicaceae | 15.2 |
| 4 | LogFor2 | 3 | frutilla | Otoba novogranatensis | Myristicaceae | 42.3 |
| 4 | LogFor2 | 3 | huesillo | Cupania spp | Sapindaceae | 17.7 |
| 4 | LogFor2 | 3 | jicaro | Lecythis ampla | Lecythidaceae | 18.1 |
| 4 | LogFor2 | 3 | maquenque | Socratea exorrhiza | Palmae | 14.3 |
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 17.3 |
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 18.5 |
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 23.1 |
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 18.5 |

| **Site no** | Site name | **Tran-sect** | **Common name** | **Scientific name** | **Family** | **DBH (cm)** |
|---|---|---|---|---|---|---|
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 19.0 |
| 4 | LogFor2 | 3 | p. dulce | Iriartea deltoidea | Palmae | 13.2 |
| 4 | LogFor2 | 3 | paleta | Dussia macroprophyllata | Leguminosae-pap | 16.6 |
| 4 | LogFor2 | 3 | paleta | Dussia macroprophyllata | Leguminosae-pap | 22.5 |
| 4 | LogFor2 | 3 | paleta | Dussia macroprophyllata | Leguminosae-pap | 42.5 |
| 4 | LogFor2 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 15.1 |
| 4 | LogFor2 | 3 | querosene | Tetragastris panamensis | Burseraceae | 24.3 |
| 4 | LogFor2 | 3 | querosene | Tetragastris panamensis | Burseraceae | 67.6 |
| 4 | LogFor2 | 3 | quizarra | Phoebe valeriana | Lauraceae | 12.5 |
| 4 | LogFor2 | 3 | tamarindo | Dialium guianense | Leguminosae-caes | 58.5 |
| 4 | LogFor2 | 3 | titor | Sacoglottis trichogyna | Humiriaceae | 16.4 |
| 4 | LogFor2 | 3 | vara alta | Xylopia sericophylla | Annonaceae | 25.2 |
| 4 | LogFor2 | 3 | zapote | Manilkara zapota | Sapotaceae | 27.8 |
| 4 | LogFor2 | 3 | zapote | Manilkara zapota | Sapotaceae | 27.3 |
| 4 | LogFor2 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 12.3 |
| 4 | LogFor2 | 4 | amargo | Aspidosperma megalocarpon | Apocynaceae | 32.0 |
| 4 | LogFor2 | 4 | asufre | ? | ? | 12.4 |
| 4 | LogFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.6 |
| 4 | LogFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.1 |
| 4 | LogFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 110.0 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 33.2 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 10.1 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 29.0 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 38.8 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 75.0 |
| 4 | LogFor2 | 4 | botijo | Apeiba membranacea | Tiliaceae | 23.2 |
| 4 | LogFor2 | 4 | canoa | ? | ? | 70.0 |
| 4 | LogFor2 | 4 | chonta | ? | ? | 19.8 |
| 4 | LogFor2 | 4 | chonta | ? | ? | 16.1 |
| 4 | LogFor2 | 4 | chonta | ? | ? | 18.2 |
| 4 | LogFor2 | 4 | cocora | Guarea bullata | Meliaceae | 10.6 |
| 4 | LogFor2 | 4 | colpachi | Croton schiedeanus | Euphorbiaceae | 11.2 |
| 4 | LogFor2 | 4 | cucaracho | Billia colombiana | Hippocastanaceae | 65.8 |
| 4 | LogFor2 | 4 | fosforillo | Dendropanax arboreus | Araliaceae | 15.8 |
| 4 | LogFor2 | 4 | fruta dorada | Virola koschnyi | Myristicaceae | 27.6 |
| 4 | LogFor2 | 4 | fruta dorada | Virola koschnyi | Myristicaceae | 21.0 |
| 4 | LogFor2 | 4 | guabilla | Inga sp | Leguminosae-mim | 16.2 |
| 4 | LogFor2 | 4 | guabilla | Inga sp | Leguminosae-mim | 16.9 |
| 4 | LogFor2 | 4 | guabo | Inga sp2 | Leguminosae-mim | 12.1 |
| 4 | LogFor2 | 4 | guayabillo montaña | Psidium sp. | Myrtaceae | 27.5 |
| 4 | LogFor2 | 4 | huesillo | Cupania spp | Sapindaceae | 11.7 |
| 4 | LogFor2 | 4 | lechoso | Brosimum utile | Moraceae | 35.8 |
| 4 | LogFor2 | 4 | lechoso | Brosimum utile | Moraceae | 12.7 |
| 4 | LogFor2 | 4 | ojoche | Brosimum alicastrum | Moraceae | 19.2 |
| 4 | LogFor2 | 4 | ojoche | Brosimum alicastrum | Moraceae | 43.3 |
| 4 | LogFor2 | 4 | p. dulce | Iriartea deltoidea | Palmae | 18.0 |
| 4 | LogFor2 | 4 | paleta | Dussia macroprophyllata | Leguminosae-pap | 45.6 |
| 4 | LogFor2 | 4 | pava | Didymopanax morototoni | Araliaceae | 35.3 |
| 4 | LogFor2 | 4 | querosene | Tetragastris panamensis | Burseraceae | 29.3 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 4 | LogFor2 | 5 | aceituno | Simarouba amara | Simaroubaceae | 21.3 |
| 4 | LogFor2 | 5 | aceituno | Simarouba amara | Simaroubaceae | 19.9 |
| 4 | LogFor2 | 5 | aguacatillo | Ocotea stenoneura | Lauraceae | 13.5 |
| 4 | LogFor2 | 5 | alcanfor | Protium panamense | Burseraceae | 13.1 |
| 4 | LogFor2 | 5 | areno | Qualea paraensis | Vochysiaceae | 12.2 |
| 4 | LogFor2 | 5 | asufre | ? | ? | 16.0 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.2 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.3 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.0 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.6 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.6 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.6 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.8 |
| 4 | LogFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 28.3 |
| 4 | LogFor2 | 5 | cafecillo | Faramea spp | Rubiaceae | 11.3 |
| 4 | LogFor2 | 5 | capulin | Muntingia calabura | Tiliaceae | 19.4 |
| 4 | LogFor2 | 5 | ceiba | Ceiba pentandra | Bombacaceae | 13.9 |
| 4 | LogFor2 | 5 | chaperno | ? | ? | 19.5 |
| 4 | LogFor2 | 5 | chonta | ? | ? | 17.5 |
| 4 | LogFor2 | 5 | chonta | ? | ? | 17.8 |
| 4 | LogFor2 | 5 | chonta | ? | ? | 19.5 |
| 4 | LogFor2 | 5 | colpachi | Croton schiedeanus | Euphorbiaceae | 11.4 |
| 4 | LogFor2 | 5 | fosforillo | Dendropanax arboreus | Araliaceae | 15.4 |
| 4 | LogFor2 | 5 | fosforillo | Dendropanax arboreus | Araliaceae | 27.7 |
| 4 | LogFor2 | 5 | fruta dorada | Virola koschnyi | Myristicaceae | 16.5 |
| 4 | LogFor2 | 5 | guabilla | Inga sp | Leguminosae-mim | 13.3 |
| 4 | LogFor2 | 5 | guabilla | Inga sp | Leguminosae-mim | 13.1 |
| 4 | LogFor2 | 5 | guabilla | Inga sp | Leguminosae-mim | 22.5 |
| 4 | LogFor2 | 5 | huesillo | Cupania spp | Sapindaceae | 11.3 |
| 4 | LogFor2 | 5 | huesillo | Cupania spp | Sapindaceae | 15.0 |
| 4 | LogFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 12.2 |
| 4 | LogFor2 | 5 | lengua de vaca | Miconia argentea | Melastomataceae | 22.7 |
| 4 | LogFor2 | 5 | maquenque | Socratea exorrhiza | Palmae | 16.5 |
| 4 | LogFor2 | 5 | muneco | ? | ? | 18.1 |
| 4 | LogFor2 | 5 | ojoche | Brosimum alicastrum | Moraceae | 14.3 |
| 4 | LogFor2 | 5 | ojoche | Brosimum alicastrum | Moraceae | 12.3 |
| 4 | LogFor2 | 5 | ojoche | Brosimum alicastrum | Moraceae | 19.2 |
| 4 | LogFor2 | 5 | p. dulce | Iriartea deltoidea | Palmae | 17.0 |
| 4 | LogFor2 | 5 | paleta | Dussia macroprophyllata | Leguminosae-pap | 22.3 |
| 4 | LogFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 30.8 |
| 4 | LogFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 14.5 |
| 4 | LogFor2 | 5 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.8 |
| 4 | LogFor2 | 5 | quizarra | Phoebe valeriana | Lauraceae | 15.4 |
| 4 | LogFor2 | 5 | tamarindo | Dialium guianense | Leguminosae-caes | 18.3 |
| 4 | LogFor2 | 5 | tostado | Ocotea stenoneura | Lauraceae | 25.0 |
| 4 | LogFor2 | 5 | tostado | Ocotea stenoneura | Lauraceae | 24.6 |
| 4 | LogFor2 | 5 | vara alta | Xylopia sericophylla | Annonaceae | 13.6 |
| 4 | LogFor2 | 5 | zapote | Manilkara zapota | Sapotaceae | 48.0 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 4 | LogFor2 | 5 | zapote | Manilkara zapota | Sapotaceae | 16.1 |
| 5 | 2ndFor1 | 1 | aceituno | Simarouba amara | Simaroubaceae | 12.0 |
| 5 | 2ndFor1 | 1 | aceituno | Simarouba amara | Simaroubaceae | 11.5 |
| 5 | 2ndFor1 | 1 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 32.8 |
| 5 | 2ndFor1 | 1 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 13.3 |
| 5 | 2ndFor1 | 1 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 28.6 |
| 5 | 2ndFor1 | 1 | algodón | Conceveiba pleiostemona | Euphorbiaceae | 25.7 |
| 5 | 2ndFor1 | 1 | cucaracho | Billia colombiana | Hippocastanaceae | 38.9 |
| 5 | 2ndFor1 | 1 | cucaracho | Billia colombiana | Hippocastanaceae | 31.2 |
| 5 | 2ndFor1 | 1 | fruta | Virola guatemalensis | Myristicaceae | 11.5 |
| 5 | 2ndFor1 | 1 | fruta | Virola guatemalensis | Myristicaceae | 10.2 |
| 5 | 2ndFor1 | 1 | fruta | Virola guatemalensis | Myristicaceae | 41.5 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 10.3 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 11.1 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 11.4 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 12.2 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 10.4 |
| 5 | 2ndFor1 | 1 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 12.3 |
| 5 | 2ndFor1 | 1 | guabilla | Inga sp | Leguminosae-mim | 16.0 |
| 5 | 2ndFor1 | 1 | jicaro | Lecythis ampla | Lecythidaceae | 25.9 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 15.8 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 19.2 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 11.0 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 20.1 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 12.2 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 19.2 |
| 5 | 2ndFor1 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 13.6 |
| 5 | 2ndFor1 | 1 | muñeco | ? | ? | 22.0 |
| 5 | 2ndFor1 | 1 | muñeco | ? | ? | 10.8 |
| 5 | 2ndFor1 | 1 | muñeco | ? | ? | 18.0 |
| 5 | 2ndFor1 | 1 | muñeco | ? | ? | 22.0 |
| 5 | 2ndFor1 | 1 | quizarra | Phoebe valeriana | Lauraceae | 13.9 |
| 5 | 2ndFor1 | 1 | tabacon | Cespedesia macrophylla | Ochnaceae | 14.8 |
| 5 | 2ndFor1 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 10.4 |
| 5 | 2ndFor1 | 2 | aguacatillo | Ocotea stenoneura | Lauraceae | 41.3 |
| 5 | 2ndFor1 | 2 | alcanfor | Protium panamense | Burseraceae | 24.5 |
| 5 | 2ndFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 27.5 |
| 5 | 2ndFor1 | 2 | areno | Qualea paraensis | Vochysiaceae | 42.5 |
| 5 | 2ndFor1 | 2 | danto | Roupala spp | Proteaceae | 26.7 |
| 5 | 2ndFor1 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 14.0 |
| 5 | 2ndFor1 | 2 | fruta | Virola guatemalensis | Myristicaceae | 26.3 |
| 5 | 2ndFor1 | 2 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 62.0 |
| 5 | 2ndFor1 | 2 | maquenque | Socratea exorrhiza | Palmae | 14.0 |
| 5 | 2ndFor1 | 2 | ojoche | Brosimum alicastrum | Moraceae | 44.2 |
| 5 | 2ndFor1 | 2 | p. dulce | Iriartea deltoidea | Palmae | 16.0 |
| 5 | 2ndFor1 | 2 | p. mantequilla | Prestoea decurrens | Palmae | 11.0 |
| 5 | 2ndFor1 | 2 | pejivaye | Bactris sp | Chrysobalanaceae | 16.7 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 5 | 2ndFor1 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 46.5 |
| 5 | 2ndFor1 | 2 | tamarindo | Dialium guianense | Leguminosae-caes | 63.0 |
| 5 | 2ndFor1 | 2 | titor | Sacoglottis trichogyna | Humiriaceae | 33.2 |
| 5 | 2ndFor1 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 45.0 |
| 5 | 2ndFor1 | 3 | achote | ? | ? | 11.3 |
| 5 | 2ndFor1 | 3 | alcanfor | Protium panamense | Burseraceae | 27.5 |
| 5 | 2ndFor1 | 3 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 11.8 |
| 5 | 2ndFor1 | 3 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 12.5 |
| 5 | 2ndFor1 | 3 | gallinazo | Schyzolobium parahyba | Leguminosae-caes | 15.8 |
| 5 | 2ndFor1 | 3 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 42.0 |
| 5 | 2ndFor1 | 3 | maquenque | Socratea exorrhiza | Palmae | 12.5 |
| 5 | 2ndFor1 | 3 | maquenque | Socratea exorrhiza | Palmae | 11.5 |
| 5 | 2ndFor1 | 3 | maquenque | Socratea exorrhiza | Palmae | 14.3 |
| 5 | 2ndFor1 | 3 | ojoche | Brosimum alicastrum | Moraceae | 22.1 |
| 5 | 2ndFor1 | 3 | panama | Sterculia apetala | Sterculiaceae | 30.1 |
| 5 | 2ndFor1 | 3 | piedra | Coccoloba tuerckheimii | Polygonaceae | 25.9 |
| 5 | 2ndFor1 | 3 | tamarindo | Dialium guianense | Leguminosae-caes | 65.0 |
| 5 | 2ndFor1 | 3 | zapotillo | Chrysophyllum spp | Sapotaceae | 46.5 |
| 5 | 2ndFor1 | 4 | achote | ? | ? | 11.1 |
| 5 | 2ndFor1 | 4 | almendro | Dipteryx panamensis | Leguminosae-pap | 73.0 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 11.5 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 13.2 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 10.2 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 14.7 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 11.3 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 10.5 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 11.4 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 11.6 |
| 5 | 2ndFor1 | 4 | muñeco | ? | ? | 11.0 |
| 5 | 2ndFor1 | 4 | ojoche | Brosimum alicastrum | Moraceae | 23.0 |
| 5 | 2ndFor1 | 4 | ojoche | Brosimum alicastrum | Moraceae | 17.5 |
| 5 | 2ndFor1 | 4 | p. dulce | Iriartea deltoidea | Palmae | 17.2 |
| 5 | 2ndFor1 | 4 | p. dulce | Iriartea deltoidea | Palmae | 18.3 |
| 5 | 2ndFor1 | 4 | vainillo | Stryphondendron microstachyum | Leguminosae-mim | 14.4 |
| 5 | 2ndFor1 | 5 | aceituno | Simarouba amara | Simaroubaceae | 10.1 |
| 5 | 2ndFor1 | 5 | aceituno | Simarouba amara | Simaroubaceae | 12.8 |
| 5 | 2ndFor1 | 5 | alma negro | Sloanea sp. | Elaeocarpaceae | 40.3 |
| 5 | 2ndFor1 | 5 | caobilla | Carapa guianensis | Meliaceae | 34.6 |
| 5 | 2ndFor1 | 5 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 55.2 |
| 5 | 2ndFor1 | 5 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 43.0 |
| 5 | 2ndFor1 | 5 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 43.5 |
| 5 | 2ndFor1 | 5 | guabilla | Inga sp | Leguminosae-mim | 20.3 |
| 5 | 2ndFor1 | 5 | maquenque | Socratea exorrhiza | Palmae | 11.0 |
| 5 | 2ndFor1 | 5 | ojoche | Brosimum alicastrum | Moraceae | 33.5 |
| 5 | 2ndFor1 | 5 | paleta | Dussia macroprophyllata | Leguminosae-pap | 45.3 |
| 5 | 2ndFor1 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 38.5 |
| 5 | 2ndFor1 | 5 | zapotillo | Chrysophyllum spp | Sapotaceae | 45.0 |
| 6 | 2ndFor2 | 1 | aceituno | Simarouba amara | Simaroubaceae | 11.9 |
| 6 | 2ndFor2 | 1 | aguacatillo | Ocotea stenoneura | Lauraceae | 10.5 |

| Site no | Site name | Tran-sect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 1 | aguacatillo | Ocotea stenoneura | Lauraceae | 20.6 |
| 6 | 2ndFor2 | 1 | aguacatillo | Ocotea stenoneura | Lauraceae | 12.4 |
| 6 | 2ndFor2 | 1 | alcanfor | Protium panamense | Burseraceae | 10.8 |
| 6 | 2ndFor2 | 1 | alcanfor | Protium panamense | Burseraceae | 11.1 |
| 6 | 2ndFor2 | 1 | alcantarilla | ? | ? | 14.6 |
| 6 | 2ndFor2 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 64.0 |
| 6 | 2ndFor2 | 1 | canoa | ? | ? | 22.9 |
| 6 | 2ndFor2 | 1 | chilamate | ? | ? | 15.0 |
| 6 | 2ndFor2 | 1 | chilamate | ? | ? | 17.7 |
| 6 | 2ndFor2 | 1 | chonta | ? | ? | 16.5 |
| 6 | 2ndFor2 | 1 | chonta | ? | ? | 18.6 |
| 6 | 2ndFor2 | 1 | chonta | ? | ? | 15.8 |
| 6 | 2ndFor2 | 1 | chonta | ? | ? | 15.3 |
| 6 | 2ndFor2 | 1 | cocobolo | Vatairea lundelli | Leguminosae-pap | 53.0 |
| 6 | 2ndFor2 | 1 | cocora | Guarea bullata | Meliaceae | 29.1 |
| 6 | 2ndFor2 | 1 | cocora | Guarea bullata | Meliaceae | 16.2 |
| 6 | 2ndFor2 | 1 | danto | Roupala spp | Proteaceae | 22.5 |
| 6 | 2ndFor2 | 1 | frutilla | Otoba novogranatensis | Myristicaceae | 13.1 |
| 6 | 2ndFor2 | 1 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 40.3 |
| 6 | 2ndFor2 | 1 | guabilla | Inga sp | Leguminosae-mim | 25.8 |
| 6 | 2ndFor2 | 1 | lechoso | Brosimum utile | Moraceae | 36.5 |
| 6 | 2ndFor2 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 16.5 |
| 6 | 2ndFor2 | 1 | lengua de vaca | Miconia argentea | Melastomataceae | 18.1 |
| 6 | 2ndFor2 | 1 | mangle | Conocarpus erecta | Combretaceae | 14.3 |
| 6 | 2ndFor2 | 1 | manteco | Tapirira guianensis | Anacardiaceae | 60.3 |
| 6 | 2ndFor2 | 1 | manu | Minquartia guianensis | Olacaceae | 10.4 |
| 6 | 2ndFor2 | 1 | maquenque | Socratea exorrhiza | Palmae | 12.0 |
| 6 | 2ndFor2 | 1 | ojoche | Brosimum alicastrum | Moraceae | 18.3 |
| 6 | 2ndFor2 | 1 | p. dulce | Iriartea deltoidea | Palmae | 12.3 |
| 6 | 2ndFor2 | 1 | panama | Sterculia apetala | Sterculiaceae | 11.8 |
| 6 | 2ndFor2 | 1 | pejivaye | Bactris sp | Chrysobalanaceae | 19.7 |
| 6 | 2ndFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 12.4 |
| 6 | 2ndFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 28.9 |
| 6 | 2ndFor2 | 1 | piedra | Coccoloba tuerckheimii | Polygonaceae | 10.5 |
| 6 | 2ndFor2 | 1 | piedra de uva | Ardisia sp | Myrsinaceae | 17.7 |
| 6 | 2ndFor2 | 1 | querosene | Tetragastris panamensis | Burseraceae | 39.5 |
| 6 | 2ndFor2 | 1 | querosene | Tetragastris panamensis | Burseraceae | 15.2 |
| 6 | 2ndFor2 | 1 | querosene | Tetragastris panamensis | Burseraceae | 35.3 |
| 6 | 2ndFor2 | 1 | roble coral | Terminalia amazonia | Combretaceae | 12.5 |
| 6 | 2ndFor2 | 1 | tamarindo | Dialium guianense | Leguminosae-caes | 23.7 |
| 6 | 2ndFor2 | 1 | zapote | Manilkara zapota | Sapotaceae | 13.0 |
| 6 | 2ndFor2 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 11.0 |
| 6 | 2ndFor2 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 17.5 |
| 6 | 2ndFor2 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 27.0 |
| 6 | 2ndFor2 | 1 | zapotillo | Chrysophyllum spp | Sapotaceae | 28.5 |
| 6 | 2ndFor2 | 2 | aguacatillo | Ocotea stenoneura | Lauraceae | 12.5 |
| 6 | 2ndFor2 | 2 | aguacatillo | Ocotea stenoneura | Lauraceae | 10.6 |
| 6 | 2ndFor2 | 2 | aguacatillo | Ocotea stenoneura | Lauraceae | 15.7 |
| 6 | 2ndFor2 | 2 | aguacatillo | Ocotea stenoneura | Lauraceae | 13.1 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 2 | alcanfor | Protium panamense | Burseraceae | 18.5 |
| 6 | 2ndFor2 | 2 | alcanfor | Protium panamense | Burseraceae | 12.0 |
| 6 | 2ndFor2 | 2 | alcantarilla | ? | ? | 15.2 |
| 6 | 2ndFor2 | 2 | alcantarilla | ? | ? | 16.4 |
| 6 | 2ndFor2 | 2 | almendro | Dipteryx panamensis | Leguminosae-pap | 95.0 |
| 6 | 2ndFor2 | 2 | amarguito | Croton tonduzii | Euphorbiaceae | 13.0 |
| 6 | 2ndFor2 | 2 | asufre | ? | ? | 16.7 |
| 6 | 2ndFor2 | 2 | asufre | ? | ? | 25.7 |
| 6 | 2ndFor2 | 2 | canoa | ? | ? | 31.5 |
| 6 | 2ndFor2 | 2 | chonta | ? | ? | 18.3 |
| 6 | 2ndFor2 | 2 | chonta | ? | ? | 15.5 |
| 6 | 2ndFor2 | 2 | chonta | ? | ? | 16.5 |
| 6 | 2ndFor2 | 2 | chonta | ? | ? | 18.1 |
| 6 | 2ndFor2 | 2 | cocobolo | Vatairea lundelli | Leguminosae-pap | 25.3 |
| 6 | 2ndFor2 | 2 | cocora | Guarea bullata | Meliaceae | 57.0 |
| 6 | 2ndFor2 | 2 | cocora | Guarea bullata | Meliaceae | 20.4 |
| 6 | 2ndFor2 | 2 | cocora | Guarea bullata | Meliaceae | 12.9 |
| 6 | 2ndFor2 | 2 | cocora | Guarea bullata | Meliaceae | 11.8 |
| 6 | 2ndFor2 | 2 | cocora | Guarea bullata | Meliaceae | 13.1 |
| 6 | 2ndFor2 | 2 | danto | Roupala spp | Proteaceae | 12.8 |
| 6 | 2ndFor2 | 2 | danto | Roupala spp | Proteaceae | 17.6 |
| 6 | 2ndFor2 | 2 | desconocido | ? | ? | 34.5 |
| 6 | 2ndFor2 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 27.3 |
| 6 | 2ndFor2 | 2 | fosforillo | Dendropanax arboreus | Araliaceae | 18.3 |
| 6 | 2ndFor2 | 2 | fruta | Virola guatemalensis | Myristicaceae | 16.4 |
| 6 | 2ndFor2 | 2 | fruta | Virola guatemalensis | Myristicaceae | 23.4 |
| 6 | 2ndFor2 | 2 | guabilla | Inga sp | Leguminosae-mim | 32.7 |
| 6 | 2ndFor2 | 2 | huesillo | Cupania spp | Sapindaceae | 10.1 |
| 6 | 2ndFor2 | 2 | lengua de vaca | Miconia argentea | Melastomataceae | 14.6 |
| 6 | 2ndFor2 | 2 | magnolia | Talauma gloriensis | Magnoliaceae | 13.4 |
| 6 | 2ndFor2 | 2 | maquenque | Socratea exorrhiza | Palmae | 14.5 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 35.6 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 46.1 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 30.9 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 12.4 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 18.6 |
| 6 | 2ndFor2 | 2 | ojoche | Brosimum alicastrum | Moraceae | 11.0 |
| 6 | 2ndFor2 | 2 | p. dulce | Iriartea deltoidea | Palmae | 14.0 |
| 6 | 2ndFor2 | 2 | p. dulce | Iriartea deltoidea | Palmae | 14.3 |
| 6 | 2ndFor2 | 2 | panama | Sterculia apetala | Sterculiaceae | 25.6 |
| 6 | 2ndFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 24.0 |
| 6 | 2ndFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 22.3 |
| 6 | 2ndFor2 | 2 | piedra | Coccoloba tuerckheimii | Polygonaceae | 13.0 |
| 6 | 2ndFor2 | 2 | querosene | Tetragastris panamensis | Burseraceae | 15.6 |
| 6 | 2ndFor2 | 2 | querosene | Tetragastris panamensis | Burseraceae | 10.5 |
| 6 | 2ndFor2 | 2 | querosene | Tetragastris panamensis | Burseraceae | 57.3 |
| 6 | 2ndFor2 | 2 | querosene | Tetragastris panamensis | Burseraceae | 44.2 |
| 6 | 2ndFor2 | 2 | quizarra | Phoebe valeriana | Lauraceae | 17.4 |
| 6 | 2ndFor2 | 2 | tamarindo | Dialium guianense | Leguminosae-caes | 20.6 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 15.0 |
| 6 | 2ndFor2 | 2 | zapotillo | Chrysophyllum spp | Sapotaceae | 19.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.7 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.8 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.7 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.1 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 32.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 25.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 62.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.8 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.7 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.7 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.1 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.2 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.3 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.2 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.8 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.2 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.3 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.3 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.8 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 32.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 29.0 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.2 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.6 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.3 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.5 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.4 |
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.7 |

| Site no | Site name | Tran-sect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 3 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.6 |
| 6 | 2ndFor2 | 3 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 20.6 |
| 6 | 2ndFor2 | 3 | guanacaste | Enterolobium cyclocarpum | Leguminosae-mim | 72.0 |
| 6 | 2ndFor2 | 3 | lagarto | Zanthoxylum ekmanii | Rutaceae | 36.4 |
| 6 | 2ndFor2 | 3 | lagarto | Zanthoxylum ekmanii | Rutaceae | 39.0 |
| 6 | 2ndFor2 | 3 | lagarto | Zanthoxylum ekmanii | Rutaceae | 30.5 |
| 6 | 2ndFor2 | 3 | lagarto | Zanthoxylum ekmanii | Rutaceae | 39.6 |
| 6 | 2ndFor2 | 3 | ojoche | Brosimum alicastrum | Moraceae | 60.2 |
| 6 | 2ndFor2 | 3 | panama | Sterculia apetala | Sterculiaceae | 46.1 |
| 6 | 2ndFor2 | 4 | almendro | Dipteryx panamensis | Leguminosae-pap | 62.0 |
| 6 | 2ndFor2 | 4 | almendro | Dipteryx panamensis | Leguminosae-pap | 115.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.3 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 44.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 42.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.4 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.4 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.7 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.7 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 10.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 27.7 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.1 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.3 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.8 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.9 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.4 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.4 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 10.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.8 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 10.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.7 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 25.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.7 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.1 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.6 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.1 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.0 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.5 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 26.8 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.9 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.3 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 13.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.2 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.1 |
| 6 | 2ndFor2 | 4 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.6 |
| 6 | 2ndFor2 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 52.5 |
| 6 | 2ndFor2 | 4 | gavilan | Pentaclethra macroloba | Leguminosae-mim | 52.0 |
| 6 | 2ndFor2 | 4 | huesillo | Cupania spp | Sapindaceae | 12.5 |
| 6 | 2ndFor2 | 4 | manu | Minquartia guianensis | Olacaceae | 24.0 |
| 6 | 2ndFor2 | 4 | p. dulce | Iriartea deltoidea | Palmae | 15.0 |
| 6 | 2ndFor2 | 4 | tabacon | Cespedesia macrophylla | Ochnaceae | 20.0 |
| 6 | 2ndFor2 | 5 | almendro | Dipteryx panamensis | Leguminosae-pap | 205.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.1 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.8 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.4 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.8 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 12.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.6 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.1 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.3 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.6 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.4 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.8 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.1 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.9 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 20.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.1 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 19.6 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 24.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 25.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.6 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.9 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 30.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 25.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.5 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 17.6 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 21.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.2 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.8 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 18.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 11.1 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 15.7 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.0 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 22.3 |
| 6 | 2ndFor2 | 5 | botarrama | Vochysia ferruginea | Vochysiaceae | 23.0 |
| 6 | 2ndFor2 | 5 | cedro maria | Cedrela odorata | Meliaceae | 51.7 |
| 6 | 2ndFor2 | 5 | cocobolo | Vatairea lundelli | Leguminosae-pap | 25.7 |
| 6 | 2ndFor2 | 5 | cocobolo | Vatairea lundelli | Leguminosae-pap | 48.0 |
| 6 | 2ndFor2 | 5 | fruta | Virola guatemalensis | Myristicaceae | 40.1 |
| 6 | 2ndFor2 | 5 | ojoche | Brosimum alicastrum | Moraceae | 41.5 |
| 6 | 2ndFor2 | 5 | p. dulce | Iriartea deltoidea | Palmae | 14.5 |
| 6 | 2ndFor2 | 5 | p. dulce | Iriartea deltoidea | Palmae | 20.0 |
| 6 | 2ndFor2 | 5 | p. dulce | Iriartea deltoidea | Palmae | 18.0 |
| 6 | 2ndFor2 | 5 | pejivaye | Bactris sp | Chrysobalanaceae | 16.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.1 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.1 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.7 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 23.1 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.1 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 19.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.3 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 17.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 10.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 17.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 12.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 19.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.7 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.4 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 21.4 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 24.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 12.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.4 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 11.3 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 14.8 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.6 |

| ***Site no*** | *Site name* | ***Transect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 22.7 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 17.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 12.2 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.7 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 10.7 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 12.4 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 23.9 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 15.4 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 26.0 |
| 7 | Plantat1 | 1 | melina | Gmelina arborea | Verbenaceae | 18.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.9 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 27.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 17.9 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 19.5 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 18.1 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 10.2 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.5 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 21.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 15.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 18.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 25.8 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.8 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 17.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 11.5 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 20.9 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 12.1 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 13.4 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.9 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.8 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 22.5 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 17.0 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 55.0 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 14.3 |
| 7 | Plantat1 | 2 | melina | Gmelina arborea | Verbenaceae | 22.1 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 26.0 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 21.9 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 24.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.8 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 18.2 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 24.5 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.6 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 22.1 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.7 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 19.0 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 26.5 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.6 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 16.4 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 20.2 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 18.2 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 18.7 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 11.9 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 12.7 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 13.4 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 14.4 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.1 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 15.4 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 11.3 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 13.2 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 16.8 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 7 | Plantat1 | 3 | melina | Gmelina arborea | Verbenaceae | 12.0 |
| 7 | Plantat1 | 3 | roble coral | Terminalia amazonia | Combretaceae | 26.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 11.2 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.4 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 11.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 17.3 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 12.8 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 21.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.8 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.8 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 20.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 20.2 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 17.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 13.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 23.9 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 13.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 10.5 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 17.6 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 21.3 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 11.8 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 14.0 |

| **Site no** | *Site name* | **Tran-sect** | **Common name** | **Scientific name** | **Family** | **DBH (cm)** |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 21.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 12.1 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 11.4 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 15.7 |
| 7 | Plantat1 | 4 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 7 | Plantat1 | 4 | roble coral | Terminalia amazonia | Combretaceae | 14.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 12.9 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 12.9 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.7 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 13.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 20.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 17.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.9 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.1 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 13.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 21.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.9 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.1 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 12.8 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 12.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 13.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 20.1 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.8 |

| *Site no* | *Site name* | *Transect* | *Common name* | *Scientific name* | *Family* | *DBH (cm)* |
|---|---|---|---|---|---|---|
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.4 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 17.1 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.4 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 21.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 21.1 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 21.2 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.4 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 18.5 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 17.7 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 27.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 7 | Plantat1 | 5 | melina | Gmelina arborea | Verbenaceae | 14.1 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 24.7 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 13.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 18.1 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.3 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 11.2 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 25.3 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 13.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.3 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 19.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 12.8 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 13.7 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 12.4 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 21.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 16.9 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 25.7 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 19.7 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 10.8 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 25.8 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 14.7 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 12.6 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 11.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 12.7 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 10.5 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 11.6 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 8 | Plantat2 | 1 | melina | Gmelina arborea | Verbenaceae | 17.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 12.3 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 12.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 18.8 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 22.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 12.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 10.0 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 25.1 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 24.5 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 10.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 13.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 10.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 11.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 15.8 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.4 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 15.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 18.8 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 15.9 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 31.3 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 20.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 11.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 20.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 17.0 |

| Site no | Site name | Transect | Common name | Scientific name | Family | DBH (cm) |
|---|---|---|---|---|---|---|
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 24.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 18.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 17.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 20.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 18.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 14.4 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 21.2 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 23.1 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 21.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 25.6 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 20.7 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 8 | Plantat2 | 2 | melina | Gmelina arborea | Verbenaceae | 19.7 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 10.3 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 10.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.3 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 14.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.9 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.9 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 19.1 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 20.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 24.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 14.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 24.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 10.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 21.7 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 17.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.7 |

| ***Site no*** | *Site name* | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 17.1 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 25.7 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 17.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.3 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 14.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 10.9 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 14.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.4 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 10.9 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.8 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 13.7 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 11.9 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 8 | Plantat2 | 3 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 11.3 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 20.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 14.6 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.7 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.9 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 13.1 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 13.3 |

| *Site no* | *Site name* | *Tran-sect* | *Common name* | *Scientific name* | *Family* | *DBH (cm)* |
|---|---|---|---|---|---|---|
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 19.3 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 19.2 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 13.2 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 10.5 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 21.2 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 19.7 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 15.4 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 12.7 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.1 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 12.1 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.8 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.5 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 11.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 11.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 25.7 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 16.6 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 18.4 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 13.5 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 19.8 |
| 8 | Plantat2 | 4 | melina | Gmelina arborea | Verbenaceae | 12.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 16.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 16.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 20.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 12.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 16.2 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 12.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 16.4 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.6 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 14.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 14.9 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 22.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.3 |

| ***Site no*** | ***Site name*** | ***Tran-sect*** | ***Common name*** | ***Scientific name*** | ***Family*** | ***DBH (cm)*** |
|---|---|---|---|---|---|---|
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.9 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.8 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 22.9 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 25.4 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 18.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.1 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 21.1 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 19.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 20.4 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 18.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.6 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 19.4 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 14.4 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 14.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.1 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 13.9 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 23.7 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 23.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 20.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 24.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 15.5 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.2 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 17.0 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 21.3 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 28.7 |
| 8 | Plantat2 | 5 | melina | Gmelina arborea | Verbenaceae | 26.8 |
| 9 | Pastur1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 16.4 |
| 9 | Pastur1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 29.2 |
| 9 | Pastur1 | 1 | botarrama | Vochysia ferruginea | Vochysiaceae | 14.0 |
| 9 | Pastur1 | 1 | corteza | Tabebuia ochracea | Bignoniaceae | 21.0 |
| 9 | Pastur1 | 1 | laurel | Cordia alliodora | Boraginaceae | 44.2 |
| 9 | Pastur1 | 2 | aceituno | Simarouba amara | Simaroubaceae | 32.4 |
| 9 | Pastur1 | 2 | aceituno | Simarouba amara | Simaroubaceae | 31.7 |
| 9 | Pastur1 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 29.6 |
| 9 | Pastur1 | 2 | botarrama | Vochysia ferruginea | Vochysiaceae | 29.2 |
| 9 | Pastur1 | 2 | manu | Minquartia guianensis | Olacaceae | 43.1 |
| 9 | Pastur1 | 2 | roble coral | Terminalia amazonia | Combretaceae | 26.2 |
| 9 | Pastur1 | 5 | aceituno | Simarouba amara | Simaroubaceae | 30.1 |
| 9 | Pastur1 | 5 | lagarto | Zanthoxylum ekmanii | Rutaceae | 44.3 |
| 9 | Pastur1 | 5 | laurel | Cordia alliodora | Boraginaceae | 24.2 |
| 9 | Pastur1 | 5 | p. dulce | Iriartea deltoidea | Palmae | 20.2 |
| 10 | Pastur2 | 4 | guaitil | Genipa americana | Rubiaceae | 49.1 |

# APPENDIX 4

## Tree species codes used in TWINSPAN, DCA and CCA analyses

| ***Tree species code*** | ***Tree species*** | ***Family*** | ***Common name*** |
|---|---|---|---|
| *Anno na s* | *Annona sp.* | Annonaceae | Anono |
| *Apei ba m* | *Apeiba membranacea* | Tiliaceae | Botijo |
| *Ardi sia* | *Ardisia sp.* | Myrsinaceae | Piedra de uva |
| *Aspi dosp* | *Aspidosperma megalocarpon* | Apocynaceae | Amargo |
| *Bact ris* | *Bactris sp.* | Chrysobalanaceae | Pejivaye |
| *Bill ia c* | *Billia colombiana* | Hippocastanaceae | Cucaracho |
| *Bros imum* | *Brosimum alicastrum* | Moraceae | Ojoche |
| *Bros imum* | *Brosimum utile* | Moraceae | Lechoso |
| *Cara pa g* | *Carapa guianensis* | Meliaceae | Caobilla |
| *Cecr opia* | *Cecropia insignis* | Cecropiaceae | Guarumo |
| *Cedr ela* | *Cedrela odorata* | Meliaceae | Cedro maria |
| *Ceib a pe* | *Ceiba pentandra* | Bombacaceae | Ceiba |
| *Cesp edes* | *Cespedesia macrophylla* | Ochnaceae | Tabacon |
| *Chim arrh* | *Chimarrhis parviflora* | Rubiaceae | Yema huevo |
| *Chry soph* | *Chrysophyllum cainito* | Sapotaceae | Caimito |
| *Chry soph* | *Chrysophyllum sp.* | Sapotaceae | Zapotillo |
| *Cocc olob* | *Coccoloba tuerckheimii* | Polygonaceae | Piedra |
| *Conc evei* | *Conceveiba pleiostemona* | Euphorbiaceae | Algodón |
| *Cono carp* | *Conocarpus erecta* | Combretaceae | Mangle |
| *Cord ia a* | *Cordia alliodora* | Boraginaceae | Laurel |
| *Coum a ma* | *Couma macrocarpa* | Apocynaceae | Baco |
| *Crot on s* | *Croton schiedeanus* | Euphorbiaceae | Colpachi |
| *Crot on t* | *Croton tonduzii* | Euphorbiaceae | Amarguito |
| *Cupa nia* | *Cupania glabra* | Sapindaceae | Bejuco |
| *Cupa nia* | *Cupania sp.* | Sapindaceae | Huesillo |
| *Dend ropa* | *Dendropanax arboreus* | Araliaceae | Fosforillo |
| *Dial ium* | *Dialium guianense* | Leguminosae-caes | Tamarindo |
| *Didy mopa* | *Didymopanax morototoni* | Araliaceae | Pava |
| *Dipt eryx* | *Dipteryx panamensis* | Leguminosae-pap | Almendro |
| *Duss ia m* | *Dussia macroprophyllata* | Leguminosae-pap | Paleta |
| *Elae olum* | *Elaeoluma glabrescens* | Sapotaceae | Carey |
| *Ente rolo* | *Enterolobium cyclocarpum* | Leguminosae-mim | Guanacaste |
| *Esch weil* | *Eschweilera costaricensis* | Lecythidaceae | Repollito |
| *Fara mea* | *Faramea sp.* | Rubiaceae | Cafecillo |
| *Geni pa a* | *Genipa americana* | Rubiaceae | Guaitil |
| *Guar ea b* | *Guarea bullata* | Meliaceae | Cocora |
| *Heli ocar* | *Heliocarpus appendiculatus* | Tiliaceae | Burio |
| *Inga sp* | *Inga sp.1* | Leguminosae-mim | Guabilla |
| *Inga sp2* | *Inga sp.2* | Leguminosae-mim | Guabo |
| *Iria rtea* | *Iriartea deltoidea* | Palmae | Palmito dulce |
| *Laet ia p* | *Laetia procera* | Flacourtiaceae | Manga larga |
| *Lecy this* | *Lecythis ampla* | Lecythidaceae | Jicaro |
| *Lica nia* | *Licania affinis* | Chrysobalanaceae | Cuero de sapo |
| *Mani lkar* | *Manilkara zapota* | Sapotaceae | Nispero |
| *Mico nia* | *Miconia argentea* | Melastomataceae | Lengua de vaca |

| | | | |
|---|---|---|---|
| *Minq uart* | *Minquartia guianensis* | Olacaceae | Manu |
| *Munt ingi* | *Muntingia calabura* | Tiliaceae | Capulin |
| *Ochr oma* | *Ochroma pyramidale* | Bombacaceae | Balsamo |
| *Ocot ea i* | *Ocotea ira* | Lauraceae | Aguacaton |
| *Ocot ea s* | *Ocotea sp.* | Lauraceae | Ira |
| *Ocot ea s* | *Ocotea stenoneura* | Lauraceae | Aguacatillo |
| *Ormo sia* | *Ormosia macrocalyx* | Leguminosae-pap | Nene |
| *Otob a no* | *Otoba novogranatensis* | Myristicaceae | Frutilla |
| *Pach ira* | *Pachira aquatica* | Bombacaceae | Ponponjoche |
| *Pent acle* | *Pentaclethra macroloba* | Leguminosae-mim | Gavilan |
| *Pers ea a* | *Persea americana* | Lauraceae | Aguacate |
| *Phoe be v* | *Phoebe valeriana* | Lauraceae | Quizarra |
| *Podo carp* | *Podocarpus guatemalensis* | Podocarpaceae | Cipresillo |
| *Pour ouma* | *Pourouma minor* | Cecropiaceae | Lija |
| *Pres toea* | *Prestoea decurrens* | Palmae | Palmito mantequilla |
| *Prot ium* | *Protium panamense* | Burseraceae | Alcanfor |
| *Psid ium* | *Psidium sp.* | Myrtaceae | Guayabillo montaña |
| *Qual ea p* | *Qualea paraensis* | Vochysiaceae | Areno |
| *Rehd era* | *Rehdera trinervis* | Verbenaceae | Melon |
| *Roll inia* | *Rollinia pittieri* | Annonaceae | Anonillo |
| *Roup ala* | *Roupala sp.* | Proteaceae | Danto |
| *Saco glot* | *Sacoglottis trichogyna* | Humiriaceae | Titor |
| *Schy zolo* | *Schyzolobium parahyba* | Leguminosae-caes | Gallinazo |
| *Sima roub* | *Simarouba amara* | Simaroubaceae | Aceituno |
| *Sloa nea* | *Sloanea sp.* | Elaeocarpaceae | Alma negro |
| *Socr atea* | *Socratea exorrhiza* | Palmae | Maquenque |
| *Ster culi* | *Sterculia apetala* | Sterculiaceae | Panama |
| *Stry phon* | *Stryphondendron microstachyum* | Leguminosae-mim | Vainillo |
| *Tala uma* | *Talauma gloriensis* | Magnoliaceae | Magnolia |
| *Tapi rira* | *Tapirira guianensis* | Anacardiaceae | Manteco |
| *Term inal* | *Terminalia amazonia* | Combretaceae | Roble coral |
| *Tetr agas* | *Tetragastris panamensis* | Burseraceae | Querosene |
| *Vata irea* | *Vatairea lundelli* | Leguminosae-pap | Cocobolo |
| *Viro la g* | *Virola guatemalensis* | Myristicaceae | Fruta |
| *Viro la k* | *Virola koschnyi* | Myristicaceae | Fruta dorada |
| *Vism ia f* | *Vismia ferruginea* | Guttiferae | Achiotillo |
| *Voch ysia* | *Vochysia ferruginea* | Vochysiaceae | Botarrama |
| *Xylo pia* | *Xylopia sericophylla* | Annonaceae | Vara alta |
| *Zant hoxy* | *Zanthoxylum ekmanii* | Rutaceae | Lagarto |

## TWINSPAN output for tree species (102 species)

| *Twinspan No.* | *Species* | *Abundance level* | *Twinspan output* |
|---|---|---|---|
| | | *Site No.:*<br>465132 | |
| 2 | Apei ba | 3----- | 0 |
| 20 | Cord ia | 1----- | 0 |
| 22 | Crot on | 2----- | 0 |
| 28 | Didy mop | 1----- | 0 |
| 40 | Iria rte | 1----- | 0 |
| 50 | Ocot ea | 1----- | 0 |
| 82 | Voch ysi | 4----- | 0 |
| 8 | Bros imu | 21---- | 1 |
| 25 | Cupa nia | 32-2-- | 1 |
| 10 | Cecr opi | ---1-- | 100 |
| 15 | Chry sop | ---1-- | 100 |
| 65 | Roll ini | ---2-- | 100 |
| 47 | Munt ing | -2---- | 101 |
| 69 | Sima rou | --3--- | 101 |
| 71 | Socr ate | --1--- | 101 |
| 74 | Tala uma | --1--- | 101 |
| 5 | Bact ris | 121--- | 110 |
| 41 | Laet ia | 43231- | 110 |
| 67 | Saco glo | 121--- | 110 |
| 70 | Sloa nea | 2122-- | 110 |
| 43 | Lica nia | 1-11-- | 111 |
| 76 | Term ina | 11-1-- | 111 |
| 73 | Stry pho | -2121- | 1000 |
| 81 | Vism ia | -223 | 1001 |
| 16 | Chry sop | 133322 | 1010 |
| 29 | Dipt ery | 1212-1 | 1011 |
| 52 | Ormo sia | 23122- | 1011 |
| 72 | Ster cul | 22342- | 1011 |
| 6 | Bill ia | 1-21-1 | 110 |
| 7 | Bros imu | 3322-2 | 1110 |
| 37 | Heli oca | 33---1 | 1110 |
| 30 | Duss ia | 3-121- | 1111 |
| 3 | Ardi sia | -4 | 1000 |
| 56 | Pers ea | -22541 | 1001 |
| 77 | Tetr aga | 21--2- | 10100 |
| 39 | Inga sp | 422-42 | 10101 |
| 45 | Mico nia | 31-341 | 10101 |
| 17 | Cocc olo | 332445 | 10110 |
| 46 | Minq uar | 223344 | 10110 |
| 79 | Viro la | 23--12 | 10110 |
| 84 | Zant hox | 45-434 | 10110 |
| 26 | Dend rop | 321322 | 10111 |

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  27    Dial  ium          22223-      10111
  58    Podo  car          2111-2      10111
  62    Psid  ium          122322      10111
  80    Viro  la           22-211      10111
  23    Crot  on            11-22-     11000
  68    Schy  zol           1-122-     11000
  60    Pres  toe           1--2-1     11001
  54    Pach  ira          31-211       1101
   4    Aspi  dos           1--1-1       111
  24    Cupa  nia           1--1-1       111
  85    C86                 3--13-      1000
  38    Inga   sp           2---21     10010
  18    Conc  eve              -19     10011
  13    Cesp  ede          211-32       1010
  19    Cono  car           -1-12-     10110
  78    Vata  ire           -1-12-     10110
  55    Pent  acl               -2     10111
  12    Ceib  a p           1----2    110000
  53    Otob  a n               -3    110001
  61    Prot  ium             1324    110010
   9    Cara  pa               -10    110011
  32    Ente  rol              -33    110011
  63    Qual  ea            1--112    110011
  64    Rehd  era           ----44    110100
  66    Roup  ala           1--333    110101
  21    Coum  a m             -344    110110
  34    Fara  mea           1--343    110110
  48    Ochr  oma           1---21    110110
  42    Lecy  thi           ---13-    110111
  11    Cedr  ela               33    111000
  35    Geni  pa                22    111001
  51    Ocot  ea                11    111001
  59    Pour  oum               22    111001
  14    Chim  arr           ----2-     11101
  57    Phoe  be            ----2-     11101
  83    Xylo  pia           ----3-     11101
  31    Elae  olu           1---24    111100
  33    Esch  wei             -235    111101
   1    Anno  na                -2    111110
  49    Ocot  ea                -2    111110
  44    Mani  lka               -5    111111

                       000011
                       011101
                        001
                        01
```

# APPENDIX 5

**Table A1 Results of the One-way ANOVA for soil organic matter (SOM) data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Forest type | 9 | 31.11 | 3.46 | 2.70 | 0.006 |
| Error | 140 | 179.51 | 1.28 | | |
| Total | 149 | 210.62 | | | |

**Table A2 Results of the Tukey multiple comparison test (p<0.05) for the SOM One-way ANOVA.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| SITE | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -0.771 | | | | | | | | |
| | 1.89 | | | | | | | | |
| **3** | -2.379 | -2.939 | | | | | | | |
| | 0.281 | -0.278 | | | | | | | |
| **4** | -1.448 | -2.008 | -0.399 | | | | | | |
| | 1.212 | 0.653 | 2.261 | | | | | | |
| **5** | -0.879 | -1.438 | 0.17 | -0.76 | | | | | |
| | 1.782 | 1.223 | 2.831 | 1.9 | | | | | |
| **6** | -0.862 | -1.421 | 0.187 | -0.744 | -1.314 | | | | |
| | 1.799 | 1.239 | 2.848 | 1.917 | 1.347 | | | | |
| **7** | -1.002 | -1.561 | 0.047 | -0.884 | -1.454 | -1.47 | | | |
| | 1.659 | 1.099 | 2.708 | 1.777 | 1.207 | 1.19 | | | |
| **8** | -0.893 | -1.452 | 0.156 | -0.775 | -1.345 | -1.361 | -1.221 | | |
| | 1.768 | 1.208 | 2.817 | 1.886 | 1.316 | 1.3 | 1.439 | | |
| **9** | -1.054 | -1.613 | -0.005 | -0.935 | -1.505 | -1.522 | -1.382 | -1.491 | |
| | 1.607 | 1.048 | 2.656 | 1.725 | 1.155 | 1.139 | 1.279 | 1.169 | |
| **10** | -0.941 | -1.501 | 0.108 | -0.823 | -1.393 | -1.409 | -1.269 | -1.379 | -1.218 |
| | 1.72 | 1.16 | 2.769 | 1.838 | 1.268 | 1.251 | 1.391 | 1.282 | 1.443 |

Family error rate: 0.05, Individual error rate: 0.00161, Critical value: 4.55

**Table A3 Results of the one-way ANOVA for soil temperature data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Forest type | 9 | 2736.9 | 304.10 | 90.98 | 0.000 |
| Error | 240 | 802.16 | 3.34 | | |
| Total | 249 | 3539.06 | | | |

**Table A4 Results of the Tukey multiple comparison test (p<0.05) for the One-way ANOVA of soil temperature.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| SITE | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -6.013 | | | | | | | | |
| | -2.707 | | | | | | | | |
| **3** | -4.733 | -0.373 | | | | | | | |
| | -1.427 | 2.933 | | | | | | | |
| **4** | -3.853 | 0.507 | -0.773 | | | | | | |
| | -0.547 | 3.813 | 2.533 | | | | | | |
| **5** | -7.093 | -2.733 | -4.013 | -4.893 | | | | | |
| | -3.787 | 0.573 | -0.707 | -1.587 | | | | | |
| **6** | -7.693 | -3.333 | -4.613 | -5.493 | -2.253 | | | | |
| | -4.387 | -0.027 | -1.307 | -2.187 | 1.053 | | | | |
| **7** | -9.493 | -5.133 | -6.413 | -7.293 | -4.053 | -3.453 | | | |
| | -6.187 | -1.827 | -3.107 | -3.987 | -0.747 | -0.147 | | | |
| **8** | -12.293 | -7.933 | -9.213 | -10.093 | -6.853 | -6.253 | -4.453 | | |
| | -8.987 | -4.627 | -5.907 | -6.787 | -3.547 | -2.947 | -1.147 | | |
| **9** | -11.773 | -7.413 | -8.693 | -9.573 | -6.333 | -5.733 | -3.933 | -1.133 | |
| | -8.467 | -4.107 | -5.387 | -6.267 | -3.027 | -2.427 | -0.627 | 2.173 | |
| **10** | -10.093 | -5.733 | -7.013 | -7.893 | -4.653 | -4.053 | -2.253 | 0.547 | 0.027 |
| | -6.787 | -2.427 | -3.707 | -4.587 | -1.347 | -0.747 | 1.053 | 3.853 | 3.333 |

Family error rate: 0.05, Individual error rate: 0.00161, Critical value: 4.52

**Table A5 Results of the one-way ANOVA for soil pH data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Forest type | 9 | 8.085 | 0.898 | 5.76 | 0.000 |
| Error | 140 | 21.843 | 0.156 | | |
| Total | 149 | 29.928 | | | |

**Table A6 Results of the Tukey multiple comparison test (p<0.05) for the One-way ANOVA of soil pH.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| SITE | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -0.68 | | | | | | | | |
| | 0.248 | | | | | | | | |
| **3** | -0.6187 | -0.4027 | | | | | | | |
| | 0.3094 | 0.5254 | | | | | | | |
| **4** | -0.908 | -0.692 | -0.7534 | | | | | | |
| | 0.02 | 0.236 | 0.1747 | | | | | | |
| **5** | -0.4827 | -0.2667 | -0.328 | -0.0387 | | | | | |
| | 0.4454 | 0.6614 | 0.6 | 0.8894 | | | | | |
| **6** | -0.926 | -0.71 | -0.7714 | -0.482 | -0.9074 | | | | |
| | 0.002 | 0.218 | 0.1567 | 0.446 | 0.0207 | | | | |
| **7** | -0.6687 | -0.4527 | -0.514 | -0.2247 | -0.65 | -0.2067 | | | |
| | 0.2594 | 0.4754 | 0.414 | 0.7034 | 0.278 | 0.7214 | | | |
| **8** | -0.7214 | -0.5054 | -0.5667 | -0.2774 | -0.7027 | -0.2594 | -0.5167 | | |
| | 0.2067 | 0.4227 | 0.3614 | 0.6507 | 0.2254 | 0.6687 | 0.4114 | | |
| **9** | -1.17 | -0.954 | -1.0154 | -0.726 | -1.1514 | -0.708 | -0.9654 | -0.9127 | |
| | -0.242 | -0.026 | -0.0873 | 0.202 | -0.2233 | 0.22 | -0.0373 | 0.0154 | |
| **10** | -1.1107 | -0.8947 | -0.956 | -0.6667 | -1.092 | -0.6487 | -0.906 | -0.8534 | -0.4047 |
| | -0.1826 | 0.0334 | -0.028 | 0.2614 | -0.164 | 0.2794 | 0.022 | 0.0747 | 0.5234 |

Family error rate: 0.05, Individual error rate: 0.00161, Critical value: 4.55

**Table A7 Results of the one-way ANOVA for maximum air temperature data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Forest type | 9 | 107.23 | 11.91 | 4.14 | 0.023 |
| Error | 9 | 25.88 | 2.88 | | |
| Total | 18 | 133.11 | | | |

**Table A8 Results of the one-way ANOVA for minimum air temperature data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Forest type | 9 | 16.73 | 1.86 | 1.78 | 0.201 |
| Error | 9 | 9.38 | 1.04 | | |
| Total | 18 | 26.11 | | | |

**Table A9 Results of the Kruskal-Wallis test for the average slope of 10 field sites in northern Costa Rica.**

| *Site* | *Number of observations* | *Median* | *Average Rank* | *Z* |
|---|---|---|---|---|
| **1** | 20 | 2 | 59.3 | -3.33 |
| **2** | 20 | 25.5 | 160.1 | 4.92 |
| **3** | 20 | 12 | 111.1 | 0.91 |
| **4** | 20 | 13.5 | 113.4 | 1.1 |
| **5** | 19 | 8 | 99.5 | -0.04 |
| **6** | 20 | 10 | 110.4 | 0.85 |
| **7** | 20 | 6.5 | 88.5 | -0.94 |
| **8** | 20 | 7.5 | 85.2 | -1.22 |
| **9** | 20 | 19.5 | 129 | 2.37 |
| **10** | 20 | 2 | 43.6 | -4.62 |
| **Overall** | 199 | | 100 | |
| **H** | | 60.64 | | |
| **d.f.** | | 9 | | |
| **p** | | < 0.001 | | |

**Table A10 Results of the Kruskal-Wallis test for the altitude of 10 field sites in northern Costa Rica.**

| *Site* | *Number of observations* | *Median* | *Average Rank* | *Z* |
|---|---|---|---|---|
| **1** | 25 | 40 | 46.1 | -5.79 |
| **2** | 25 | 82 | 177.2 | 3.77 |
| **3** | 25 | 45 | 92.1 | -2.43 |
| **4** | 25 | 160 | 226.1 | 7.34 |
| **5** | 25 | 42 | 65.1 | -4.4 |
| **6** | 25 | 69 | 165.9 | 2.94 |
| **7** | 25 | 43 | 70.3 | -4.03 |
| **8** | 25 | 44 | 90.1 | -2.58 |
| **9** | 25 | 161 | 224.9 | 7.24 |
| **10** | 25 | 52 | 97.3 | -2.06 |
| **Overall** | 250 | | 125.5 | |
| **H** | | 193.48 | | |
| **d.f.** | | 9 | | |
| ***p*** | | < 0.001 | | |

**Table A11 Results of the one-way ANOVA for leaf litter data measured over 10 field sites in northern Costa Rica**

| **Source** | **DF** | **SS** | **MS** | **F** | ***p*** |
|---|---|---|---|---|---|
| Forest type | 9 | 2289.3 | 254.4 | 12.77 | 0.000 |
| Error | 140 | 2787.8 | 19.9 | | |
| Total | 149 | 5077.1 | | | |

**Table A12 Results of the Tukey multiple comparison test (p<0.05) for the One-way ANOVA of leaf litter.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| **SITE** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -6.093 | | | | | | | | |
| | 4.391 | | | | | | | | |
| **3** | -0.431 | 0.42 | | | | | | | |
| | 10.054 | 10.905 | | | | | | | |
| **4** | -1.361 | -0.51 | -6.172 | | | | | | |
| | 9.124 | 9.975 | 4.313 | | | | | | |
| **5** | -0.745 | 0.106 | -5.556 | -4.627 | | | | | |
| | 9.74 | 10.591 | 4.928 | 5.858 | | | | | |
| **6** | -4.837 | -3.986 | -9.648 | -8.719 | -9.334 | | | | |
| | 5.648 | 6.499 | 0.836 | 1.766 | 1.15 | | | | |
| **7** | -0.684 | 0.168 | -5.495 | -4.565 | -5.181 | -1.089 | | | |
| | 9.801 | 10.652 | 4.99 | 5.92 | 5.304 | 9.396 | | | |
| **8** | -2.456 | -1.605 | -7.268 | -6.338 | -6.954 | -2.861 | -7.015 | | |
| | 8.029 | 8.88 | 3.217 | 4.147 | 3.531 | 7.623 | 3.47 | | |
| **9** | 6.017 | 6.868 | 1.205 | 2.135 | 1.519 | 5.611 | 1.458 | 3.231 | |
| | 16.501 | 17.353 | 11.69 | 12.62 | 12.004 | 16.096 | 11.943 | 13.715 | |
| **10** | 5.48 | 6.331 | 0.669 | 1.599 | 0.983 | 5.075 | 0.922 | 2.694 | -5.779 |
| | 15.965 | 16.816 | 11.154 | 12.084 | 11.468 | 15.56 | 11.406 | 13.179 | 4.706 |

Family error rate: 0.05, Individual error rate: 0.00161, Critical value: 4.55

# APPENDIX 6

## Leaf litter ant species list

| *Species no.* | *Family* | *Sub-family* | *Genus* | *Species* |
|---|---|---|---|---|
| 1 | Formicidae | Ecitoninae | | |
| 2 | Formicidae | Myrmicinae | | |
| 3 | Formicidae | Ponerinae | *Odontomachus* | *Odontomachus* sp. |
| 4 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.1 |
| 5 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.2 |
| 6 | Formicidae | Myrmicinae | *Europalothrix* | |
| 7 | Formicidae | Myrmicinae | | |
| 8 | Formicidae | Myrmicinae | *Acanthognathus* | |
| 9 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 10 | Formicidae | Ecitoninae | | |
| 11 | Formicidae | Ecitoninae | | |
| 12 | Formicidae | Ponerinae | *Odontomachus* | *Odontomachus* sp. |
| 13 | Formicidae | Ponerinae | | |
| 14 | Formicidae | Myrmicinae | *Monomorium* | |
| 15 | Formicidae | Myrmicinae | *Solenopsis* | |
| 16 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.3 |
| 17 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.4 |
| 19 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 20 | Formicidae | Myrmicinae | *Crematogaster* | |
| 21 | Formicidae | Myrmicinae | | |
| 22 | Formicidae | Dolichoderinae | *Tapinoma* | *Tapinoma* sp. |
| 23 | Formicidae | Myrmicinae | | |
| 24 | Formicidae | Myrmicinae | | |
| 25 | Formicidae | Myrmicinae | | |
| 26 | Formicidae | Myrmicinae | | |
| 28 | Formicidae | Myrmicinae | | |
| 29 | Formicidae | Myrmicinae | | |
| 30 | Formicidae | Myrmicinae | | |
| 31 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.5 |
| 32 | Formicidae | Ecitoninae | | |
| 33 | Formicidae | Ecitoninae | | |
| 34 | Formicidae | Myrmicinae | *Solenopsis* | |
| 35 | Formicidae | Myrmicinae | | |
| 36 | Formicidae | Myrmicinae | | |
| 37 | Formicidae | Myrmicinae | | |
| 39 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.6 |
| 40 | Formicidae | Ponerinae | | |
| 41 | Formicidae | Myrmicinae | | |
| 42 | Formicidae | Myrmicinae | | |
| 43 | Formicidae | Myrmicinae | | |
| 44 | Formicidae | Myrmicinae | | |
| 45 | Formicidae | Myrmicinae | *Pheidole* | |
| 46 | Formicidae | Myrmicinae | *Solenopsis* | |
| 47 | Formicidae | Myrmicinae | | |
| 48 | Formicidae | Myrmicinae | | |
| 49 | Formicidae | Myrmicinae | *Crematogaster* | |
| 50 | Formicidae | Myrmicinae | | |
| 51 | Formicidae | Myrmicinae | | |
| 52 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.7 |

| **Species no.** | **Family** | **Sub-family** | **Genus** | **Species** |
|---|---|---|---|---|
| 53 | Formicidae | Myrmicinae | | |
| 54 | Formicidae | Ecitoninae | | |
| 55 | Formicidae | Ecitoninae | | |
| 56 | Formicidae | Myrmicinae | *Eciton* | *Eciton* sp. |
| 57 | Formicidae | Ecitoninae | *Solenopsis* | |
| 58 | Formicidae | Myrmicinae | | |
| 59 | Formicidae | Ecitoninae | | |
| 60 | Formicidae | Ecitoninae | | |
| 61 | Formicidae | Ponerinae | | |
| 62 | Formicidae | Ponerinae | *Wasmannia* | |
| 63 | Formicidae | Myrmicinae | | |
| 64 | Formicidae | Ecitoninae | | |
| 65 | Formicidae | Ecitoninae | *Odontomachus* | *Odontomachus* sp. |
| 66 | Formicidae | Ponerinae | | |
| 67 | Formicidae | Myrmicinae | *Megalomyrmex* | |
| 68 | Formicidae | Myrmicinae | | |
| 69 | Formicidae | Ponerinae | | |
| 70 | Formicidae | Myrmicinae | | |
| 71 | Formicidae | Myrmicinae | *Camponotus* | *Camponotus* sp. |
| 72 | Formicidae | Formicinae | | |
| 73 | Formicidae | Myrmicinae | | |
| 74 | Formicidae | Myrmicinae | *Wasmannia* | |
| 75 | Formicidae | Myrmicinae | *Solenopsis* | |
| 76 | Formicidae | Myrmicinae | | |
| 78 | Formicidae | Ponerinae | | *Paraponera clavata* |
| 79 | Formicidae | Myrmicinae | *Pheidole* | |
| 80 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp.9 |
| 81 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 82 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp10 |
| 83 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 84 | Formicidae | Ponerinae | | |
| 85 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp |
| 86 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp.11 |
| 87 | Formicidae | Myrmicinae | | |
| 88 | Formicidae | Myrmicinae | *Trachymyrmex* | |
| 89 | Formicidae | Ecitoninae | | |
| 90 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 91 | Formicidae | Myrmicinae | | |
| 92 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp12 |
| 94 | Formicidae | Ecitoninae | | |
| 95 | Formicidae | Myrmicinae | | |
| 96 | Formicidae | Myrmicinae | *Megalomyrmex* | |
| 97 | Formicidae | Myrmicinae | | |
| 99 | Formicidae | Myrmicinae | *Monomorium* | |
| 100 | Formicidae | Myrmicinae | | |
| 101 | Formicidae | Myrmicinae | | |
| 102 | Formicidae | Myrmicinae | *Wasmannia* | |
| 103 | Formicidae | Myrmicinae | | |
| 104 | Formicidae | Myrmicinae | | |
| 105 | Formicidae | Myrmicinae | | |
| 106 | Formicidae | Myrmicinae | | |
| 107 | Formicidae | Dolichoderinae | *Tapinoma* | *Tapinoma* sp. |
| 108 | Formicidae | Myrmicinae | | |
| 109 | Formicidae | Myrmicinae | *Tetramorium* | |

| **Species no.** | **Family** | **Sub-family** | **Genus** | **Species** |
|---|---|---|---|---|
| 110 | Formicidae | Ponerinae | | |
| 111 | Formicidae | Ecitoninae | | |
| 112 | Formicidae | Myrmicinae | | |
| 113 | Formicidae | Ecitoninae | | |
| 114 | Formicidae | Myrmicinae | | |
| 116 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp13 |
| 117 | Formicidae | Myrmicinae | *Pheidole* | *Pheidole* sp. |
| 118 | Formicidae | Myrmicinae | | |
| 119 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp14 |
| 120 | Formicidae | Myrmicinae | | |
| 121 | Formicidae | Myrmicinae | | |
| 122 | Formicidae | Myrmicinae | | |
| 123 | Formicidae | Myrmicinae | | |
| 124 | Formicidae | Myrmicinae | | |
| 125 | Formicidae | Dolichoderinae | *Tapinoma* | *Tapinoma* sp. |
| 126 | Formicidae | Myrmicinae | | |
| 127 | Formicidae | Myrmicinae | | |
| 128 | Formicidae | Myrmicinae | | |
| 129 | Formicidae | Myrmicinae | | |
| 130 | Formicidae | Myrmicinae | *Megalomyrmex* | |
| 131 | Formicidae | Dolichoderinae | *Tapinoma* | *Tapinoma* sp. |
| 132 | Formicidae | Ponerinae | | |
| 133 | Formicidae | Myrmicinae | | |
| 134 | Formicidae | Myrmicinae | | |
| 135 | Formicidae | Myrmicinae | | |
| 136 | Formicidae | Ponerinae | | |
| 137 | Formicidae | Myrmicinae | | |
| 138 | Formicidae | Dolichoderinae | *Azteca* | *Azteca* sp. |
| 139 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 140 | Formicidae | Ponerinae | | |
| 141 | Formicidae | Ponerinae | | |
| 142 | Formicidae | Ecitoninae | | |
| 143 | Formicidae | Myrmicinae | | |
| 144 | Formicidae | Myrmicinae | | |
| 145 | Formicidae | Ecitoninae | *Nomamyrmex* | *Nomamyrmex* sp. |
| 146 | Formicidae | Ponerinae | *Odontomachus* | *Odontomachus* sp. |
| 147 | Formicidae | Ecitoninae | | |
| 148 | Formicidae | Myrmicinae | | |
| 149 | Formicidae | Myrmicinae | | |
| 150 | Formicidae | Ecitoninae | | |
| 151 | Formicidae | Myrmicinae | | |
| 152 | Formicidae | Myrmicinae | | |
| 153 | Formicidae | Ecitoninae | | |
| 154 | Formicidae | Dolichoderinae | *Azteca* | *Azteca* sp. |
| 155 | Formicidae | Dolichoderinae | *Tapinoma* | *Tapinoma* sp. |
| 156 | Formicidae | Myrmicinae | *Wasmannia* | |
| 157 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 158 | Formicidae | Myrmicinae | | |
| 159 | Formicidae | Myrmicinae | | |
| 160 | Formicidae | Myrmicinae | | |
| 161 | Formicidae | Ponerinae | *Ectatomma* | *Ectatomma* sp. |
| 162 | Formicidae | Ponerinae | *Pachycondyla* | *Pachycondyla* sp15 |
| 163 | Formicidae | Ecitoninae | | |
| 164 | Formicidae | Myrmicinae | *Strumigenys* | |

| ***Species no.*** | ***Family*** | ***Sub-family*** | ***Genus*** | ***Species*** |
|---|---|---|---|---|
| 165 | Formicidae | Myrmicinae | | |
| 167 | Formicidae | Myrmicinae | | |
| 168 | Formicidae | Myrmicinae | | |
| 170 | Formicidae | Formicinae | *Camponotus* | *Camponotus* sp. |
| 171 | Formicidae | Myrmicinae | | |
| 172 | Formicidae | Ecitoninae | | |
| 173 | Formicidae | Myrmicinae | *Solenopsis* | |
| 174 | Formicidae | Formicinae | | |
| 175 | Formicidae | Myrmicinae | | |
| 176 | Formicidae | Myrmicinae | | |
| 177 | Formicidae | Myrmicinae | *Cyphomyrmex* | |
| 178 | Formicidae | Myrmicinae | | |
| 179 | Formicidae | Myrmicinae | | |
| 180 | Formicidae | Myrmicinae | | |
| 181 | Formicidae | Myrmicinae | | |
| 191 | Formicidae | Ponerinae | | |
| 192 | Formicidae | Myrmicinae | | |
| 193 | Formicidae | Formicinae | | |
| 194 | Formicidae | Myrmicinae | | |
| 195 | Formicidae | Myrmicinae | | |
| 196 | Formicidae | Myrmicinae | | |
| 198 | Formicidae | Myrmicinae | | |
| 199 | Formicidae | Ponerinae | | |
| 200 | Formicidae | Myrmicinae | | |
| 202 | Formicidae | Myrmicinae | | |
| 203 | Formicidae | Myrmicinae | | |
| 204 | Formicidae | Myrmicinae | | |
| 205 | Formicidae | Myrmicinae | | |
| 206 | Formicidae | Myrmicinae | | |
| 207 | Formicidae | Myrmicinae | | |
| 208 | Formicidae | Myrmicinae | | |
| 209 | Formicidae | Dolichoderinae | | |
| 210 | Formicidae | Ponerinae | | |
| 211 | Formicidae | Myrmicinae | | |
| 212 | Formicidae | Myrmicinae | | |
| 213 | Formicidae | Myrmicinae | | |
| 214 | Formicidae | Myrmicinae | | |
| 215 | Formicidae | Myrmicinae | | |
| 216 | Formicidae | Myrmicinae | | |
| 217 | Formicidae | Myrmicinae | | |
| 218 | Formicidae | Myrmicinae | | |
| 219 | Formicidae | Ponerinae | | |
| 220 | Formicidae | Myrmicinae | | |
| 221 | Formicidae | Myrmicinae | | |
| 222 | Formicidae | Ponerinae | | |
| 223 | Formicidae | Dolichoderinae | | |
| 224 | Formicidae | Myrmicinae | | |
| 225 | Formicidae | Myrmicinae | | |
| 226 | Formicidae | Ecitoninae | | |
| 227 | Formicidae | Ponerinae | | |
| 228 | Formicidae | Ponerinae | | |
| 229 | Formicidae | Ecitoninae | | |
| 230 | Formicidae | Myrmicinae | | |
| 231 | Formicidae | Myrmicinae | | |

| ***Species no.*** | ***Family*** | ***Sub-family*** | ***Genus*** | ***Species*** |
|---|---|---|---|---|
| 232 | Formicidae | Ecitoninae | | |
| 233 | Formicidae | Ponerinae | | |
| 234 | Formicidae | Myrmicinae | | |
| 235 | Formicidae | Dolichoderinae | | |
| 236 | Formicidae | Myrmicinae | | |
| 237 | Formicidae | Myrmicinae | | |
| 238 | Formicidae | Myrmicinae | | |
| 239 | Formicidae | Dolichoderinae | | |
| 240 | Formicidae | Ecitoninae | | |
| 241 | Formicidae | Ponerinae | | |
| 242 | Formicidae | Formicinae | | |
| 243 | Formicidae | Myrmicinae | | |
| 244 | Formicidae | Ponerinae | | |
| 245 | Formicidae | Ponerinae | | |
| 246 | Formicidae | Ponerinae | | |
| 249 | Formicidae | Myrmicinae | | |
| 68b | Formicidae | Myrmicinae | | |
| 113a | Formicidae | Ecitoninae | | |
| 113b | Formicidae | Myrmicinae | | |

# APPENDIX 7

**Table B1 Results of the One-way ANOVA for species richness (*S*) data measured over 10 field sites in northern Costa Rica**

| **Source** | **DF** | **SS** | **MS** | **F** | ***p*** |
|---|---|---|---|---|---|
| Field site | 9 | 4109.9 | 456.7 | 8.25 | 0.000 |
| Error | 89 | 4926.3 | 55.4 | | |
| Total | 98 | 9036.2 | | | |

**Table B2 Results of the Tukey multiple comparison test ($p<0.05$) for the species richness (*S*) One-way ANOVA.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| ***SITE*** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -13.2 | | | | | | | | |
| | 8.4 | | | | | | | | |
| **3** | -17.8 | -15.4 | | | | | | | |
| | 3.8 | 6.2 | | | | | | | |
| **4** | -22.6 | -20.2 | -15.6 | | | | | | |
| | -1 | 1.4 | 6 | | | | | | |
| **5** | -14.1 | -11.7 | -7.1 | -2.3 | | | | | |
| | 7.5 | 9.9 | 14.5 | 19.3 | | | | | |
| **6** | -24.4 | -22 | -17.4 | -12.6 | -21.1 | | | | |
| | -2.8 | -0.4 | 4.2 | 9 | 0.5 | | | | |
| **7** | -12 | -9.6 | -5 | -0.2 | -8.7 | 1.6 | | | |
| | 9.6 | 12 | 16.6 | 21.4 | 12.9 | 23.2 | | | |
| **8** | -6.96 | -4.56 | 0.04 | 4.84 | -3.66 | 6.64 | -5.76 | | |
| | 15.23 | 17.63 | 22.23 | 27.03 | 18.53 | 28.83 | 16.43 | | |
| **9** | -28.9 | -26.5 | -21.9 | -17.1 | -25.6 | -15.3 | -27.7 | -33.33 | |
| | -7.3 | -4.9 | -0.3 | 4.5 | -4 | 6.3 | -6.1 | -11.14 | |
| **10** | -16.1 | -13.7 | -9.1 | -4.3 | -12.8 | -2.5 | -14.9 | -20.53 | 2 |
| | 5.5 | 7.9 | 12.5 | 17.3 | 8.8 | 19.1 | 6.7 | 1.66 | 23.6 |

Family error rate: 0.05, Individual error rate: 0.00165, Critical value: 4.59

# APPENDIX 8

## TWINSPAN output for leaf litter ants (230 species)

| *Twinspan No.* | *Species* | *Abundance level* | *Twinspan output* |
|---|---|---|---|
| | | *Site No.:* | |
| | | 1 | |
| | | 2314607985 | |
| 39 | Spp4 2 | -----22--- | 0 |
| 55 | Spp5 8 | -13431---- | 1 |
| 73 | Spp7 7 | --3------- | 1 |
| 74 | Spp7 8 | --1-1----- | 1 |
| 77 | Spp8 1 | --1------- | 1 |
| 82 | Spp8 6 | --1------- | 1 |
| 88 | Spp9 3 | --2------- | 1 |
| 89 | Spp9 4 | --2------- | 1 |
| 115 | Spp1 22 | --22------ | 1 |
| 171 | Spp1 80 | --1------- | 1 |
| 173 | Spp1 91 | --1------- | 1 |
| 92 | Spp9 7 | 2-144----- | 10 |
| 100 | Spp1 06 | ---2------ | 10 |
| 101 | Spp1 07 | ---1------ | 10 |
| 102 | Spp1 08 | ---1------ | 10 |
| 105 | Spp1 11 | ---3------ | 10 |
| 106 | Spp1 12 | ---1------ | 10 |
| 109 | Spp1 16 | ---1------ | 10 |
| 110 | Spp1 17 | ---22----- | 10 |
| 111 | Spp1 18 | ---1------ | 10 |
| 117 | Spp1 24 | ---4------ | 10 |
| 121 | Spp1 28 | ---1------ | 10 |
| 123 | Spp1 30 | ---1------ | 10 |
| 144 | Spp1 51 | ----1----- | 10 |
| 161 | Spp1 70 | ----1----- | 10 |
| 162 | Spp1 71 | ----5----- | 10 |
| 163 | Spp1 72 | ----1----- | 10 |
| 164 | Spp1 73 | ----2----- | 10 |
| 165 | Spp1 74 | ----2----- | 10 |
| 166 | Spp1 75 | ----1----- | 10 |
| 178 | Spp1 96 | ---3------ | 10 |
| 179 | Spp1 98 | ---42----- | 10 |
| 181 | Spp2 00 | ----1----- | 10 |
| 182 | Spp2 02 | ----1----- | 10 |
| 183 | Spp2 03 | ----1----- | 10 |
| 184 | Spp2 04 | ----1----- | 10 |
| 186 | Spp2 06 | ----1----- | 10 |
| 187 | Spp2 07 | ----1----- | 10 |
| 223 | Spp2 43 | ---3------ | 10 |
| 224 | Spp2 44 | ---1------ | 10 |

| ***No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---|---|---|---|
| 225 | Spp2 45 | ---1------ | 10 |
| 226 | Spp2 46 | ---1------ | 10 |
| 229 | Sp11 3b | ---1------ | 10 |
| 103 | Spp1 09 | ---311---- | 11 |
| 120 | Spp1 27 | ----51---- | 11 |
| 41 | Spp4 4 | 34454----1 | 100 |
| 50 | Spp5 3 | -215-1---- | 100 |
| 53 | Spp5 6 | -2--4----- | 100 |
| 79 | Spp8 3 | 1-2------- | 100 |
| 80 | Spp8 4 | -12------- | 100 |
| 95 | Spp1 01 | 2-231----- | 100 |
| 108 | Spp1 14 | -1-2------ | 100 |
| 230 | Spp6 8b | 1---3----- | 101 |
| 57 | Spp6 0 | -2 | 110 |
| 72 | Spp7 5 | -53557 | 111 |
| 45 | Spp4 8 | 13341----- | 1000 |
| 22 | Spp2 3 | 25333----1 | 1001 |
| 42 | Spp4 5 | 55455----- | 1001 |
| 51 | Spp5 4 | 22-2------ | 1010 |
| 52 | Spp5 5 | 55-------- | 1010 |
| 54 | Spp5 7 | 23-------- | 1010 |
| 63 | Spp6 6 | -1-------- | 1010 |
| 68 | Spp7 1 | -2-------- | 1010 |
| 70 | Spp7 3 | -1-------- | 1010 |
| 71 | Spp7 4 | -2-------- | 1010 |
| 75 | Spp7 9 | -11------- | 1010 |
| 84 | Spp8 8 | -33------- | 1010 |
| 91 | Spp9 6 | 1--------- | 1010 |
| 93 | Spp9 9 | 1--------- | 1010 |
| 94 | Spp1 00 | 1--------- | 1010 |
| 97 | Spp1 03 | 1--------- | 1010 |
| 193 | Spp2 13 | 1--------- | 1010 |
| 195 | Spp2 15 | 12-------- | 1010 |
| 196 | Spp2 16 | 4--------- | 1010 |
| 197 | Spp2 17 | 2--------- | 1010 |
| 200 | Spp2 20 | -2-1------ | 1010 |
| 201 | Spp2 21 | -1-------- | 1010 |
| 202 | Spp2 22 | -2-1------ | 1010 |
| 203 | Spp2 23 | -2-------- | 1010 |
| 204 | Spp2 24 | -1-------- | 1010 |
| 205 | Spp2 25 | -2-------- | 1010 |
| 206 | Spp2 26 | -1-------- | 1010 |
| 207 | Spp2 27 | -2-------- | 1010 |
| 208 | Spp2 28 | -1-------- | 1010 |
| 209 | Spp2 29 | -2-------- | 1010 |
| 210 | Spp2 30 | -1-------- | 1010 |
| 211 | Spp2 31 | -1-------- | 1010 |
| 212 | Spp2 32 | 25-------- | 1010 |
| 219 | Spp2 39 | 1--------- | 1010 |

| ***No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---|---|---|---|
| 220 | Spp2 40 | 3--------- | 1010 |
| 228 | Sp11 3a | -5-1------ | 1010 |
| 65 | Spp6 8 | 55-44----- | 1011 |
| 96 | Spp1 02 | 1--1------ | 1011 |
| 113 | Spp1 20 | -1-1------ | 1011 |
| 185 | Spp2 05 | -1--1----- | 1011 |
| 192 | Spp2 12 | 21-2------ | 1011 |
| 194 | Spp2 14 | 23-5------ | 1011 |
| 199 | Spp2 19 | -3-3------ | 1011 |
| 12 | Spp1 2 | 545451---5 | 1100 |
| 38 | Spp4 1 | 33255--222 | 1100 |
| 48 | Spp5 1 | 553551131- | 1100 |
| 43 | Spp4 6 | 44-553-2-- | 1101 |
| 98 | Spp1 04 | 33232--1-1 | 1110 |
| 67 | Spp7 0 | -3-12---2- | 1111 |
| 46 | Spp4 9 | 22-21211-- | 10000 |
| 90 | Spp9 5 | 4--21----4 | 10001 |
| 138 | Spp1 45 | 55-5---24- | 10001 |
| 3 | Spp3 | 5333213--4 | 10010 |
| 49 | Spp5 2 | 23122-12-3 | 10010 |
| 174 | Spp1 92 | -21-2---2- | 10010 |
| 66 | Spp6 9 | -223--1-2- | 10011 |
| 69 | Spp7 2 | -2------1- | 10100 |
| 24 | Spp2 5 | -4 | 10101 |
| 135 | Spp1 42 | 5-------4- | 1011 |
| 1 | Spp1 | -46 | 11000 |
| 2 | Spp2 | -5392 | 11000 |
| 15 | Spp1 5 | -114 | 11000 |
| 17 | Spp1 7 | 54334-4234 | 11000 |
| 37 | Spp4 0 | -131 | 11000 |
| 5 | Spp5 | 5555524515 | 11001 |
| 18 | Spp1 9 | 32-44--444 | 11001 |
| 29 | Spp3 1 | 1332-22-12 | 11001 |
| 31 | Spp3 3 | 215455-5-4 | 11001 |
| 44 | Spp4 7 | 22-353-5-- | 11001 |
| 23 | Spp2 4 | -8 | 11010 |
| 7 | Spp7 | 4 | 11011 |
| 8 | Spp8 | -23 | 11100 |
| 83 | Spp8 7 | --244--4-- | 11101 |
| 107 | Spp1 13 | --35--31-- | 11110 |
| 85 | Spp8 9 | --5-4---5- | 11111 |
| 158 | Spp1 65 | 11--2-12-- | 10000 |
| 61 | Spp6 4 | 35-525-5-3 | 100010 |
| 20 | Spp2 1 | 44-554-555 | 100011 |
| 56 | Spp5 9 | -1------1- | 10010 |
| 76 | Spp8 0 | 3221-2313- | 100110 |
| 25 | Spp2 6 | -9 | 100111 |
| 47 | Spp5 0 | -22455555- | 10100 |
| 104 | Spp1 10 | ---1--1--- | 101010 |

| ***No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---|---|---|---|
| 180 | Spp1 99 | ---111-1-- | 101010 |
| 198 | Spp2 18 | ---2---2-- | 101010 |
| 86 | Spp9 0 | --1---1--- | 101011 |
| 112 | Spp1 19 | -20 | 1011 |
| 99 | Spp1 05 | 20 | 110000 |
| 28 | Spp3 0 | 3 | 110001 |
| 13 | Spp1 3 | -514455555 | 11001 |
| 19 | Spp2 0 | 1-1-1-1542 | 110100 |
| 114 | Spp1 21 | ---22-144- | 110100 |
| 143 | Spp1 50 | ----3---5- | 110100 |
| 4 | Spp4 | -232555545 | 110101 |
| 78 | Spp8 2 | --1--1--1- | 110101 |
| 87 | Spp9 1 | --1--2---- | 110101 |
| 128 | Spp1 35 | --3-55553- | 110101 |
| 136 | Spp1 43 | 201 | 110101 |
| 58 | Spp6 1 | 3--11-1351 | 110110 |
| 64 | Spp6 7 | -2-----4-- | 110110 |
| 159 | Spp1 67 | 1----2---- | 110110 |
| 140 | Spp1 47 | --2-145--- | 110111 |
| 218 | Spp2 38 | 2----5---- | 110111 |
| 118 | Spp1 25 | -----1-12- | 111000 |
| 130 | Spp1 37 | -----1--2- | 111000 |
| 14 | Spp1 4 | -560 | 111001 |
| 21 | Spp2 2 | 345441 | 111001 |
| 27 | Spp2 9 | 18 | 111001 |
| 32 | Spp3 4 | -9 | 111001 |
| 33 | Spp3 5 | 242122 | 111001 |
| 34 | Spp3 6 | 2521 | 111001 |
| 30 | Spp3 2 | -517 | 111010 |
| 60 | Spp6 3 | -5 | 111010 |
| 81 | Spp8 5 | --1--122-- | 111010 |
| 116 | Spp1 23 | -----1---- | 111010 |
| 119 | Spp1 26 | -----1---- | 111010 |
| 122 | Spp1 29 | ---1-53--- | 111010 |
| 124 | Spp1 31 | ------453- | 111010 |
| 133 | Spp1 40 | -----41-1- | 111010 |
| 139 | Spp1 46 | ----1243-- | 111010 |
| 141 | Spp1 48 | ------32-- | 111010 |
| 142 | Spp1 49 | ----25351- | 111010 |
| 145 | Spp1 52 | -----1-2-- | 111010 |
| 146 | Spp1 53 | -------2-- | 111010 |
| 147 | Spp1 54 | -------2-- | 111010 |
| 148 | Spp1 55 | -------1-- | 111010 |
| 149 | Spp1 56 | -------1-- | 111010 |
| 150 | Spp1 57 | -----115-- | 111010 |
| 151 | Spp1 58 | -------1-- | 111010 |
| 152 | Spp1 59 | -------1-- | 111010 |
| 153 | Spp1 60 | -------1-- | 111010 |
| 154 | Spp1 61 | -------1-- | 111010 |

| ***No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---|---|---|---|
| 155 | Spp1 62 | -------1-- | 111010 |
| 156 | Spp1 63 | -------2-- | 111010 |
| 157 | Spp1 64 | -------1-- | 111010 |
| 160 | Spp1 68 | -----11--- | 111010 |
| 167 | Spp1 76 | ------1--- | 111010 |
| 168 | Spp1 77 | ------1--- | 111010 |
| 169 | Spp1 78 | ------4--- | 111010 |
| 170 | Spp1 79 | ------1--- | 111010 |
| 172 | Spp1 81 | -----1---- | 111010 |
| 213 | Spp2 33 | -------2-- | 111010 |
| 214 | Spp2 34 | -------2-- | 111010 |
| 215 | Spp2 35 | -------1-- | 111010 |
| 216 | Spp2 36 | -----1---- | 111010 |
| 217 | Spp2 37 | -----1---- | 111010 |
| 221 | Spp2 41 | -------1-- | 111010 |
| 222 | Spp2 42 | -------1-- | 111010 |
| 227 | Spp2 49 | -------2-- | 111010 |
| 125 | Spp1 32 | --------1- | 111011 |
| 126 | Spp1 33 | ------1-1- | 111011 |
| 127 | Spp1 34 | --------2- | 111011 |
| 129 | Spp1 36 | --------1- | 111011 |
| 131 | Spp1 38 | --------1- | 111011 |
| 134 | Spp1 41 | --------1- | 111011 |
| 137 | Spp1 44 | --------2- | 111011 |
| 188 | Spp2 08 | --------1- | 111011 |
| 189 | Spp2 09 | --------2- | 111011 |
| 190 | Spp2 10 | --------2- | 111011 |
| 191 | Spp2 11 | --------1- | 111011 |
| 59 | Spp6 2 | -2 | 11110 |
| 26 | Spp2 8 | -3 | 111110 |
| 132 | Spp1 39 | 11 | 111110 |
| 6 | Spp6 | -2 | 111111 |
| 9 | Spp9 | -2 | 111111 |
| 10 | Spp1 0 | -3 | 111111 |
| 11 | Spp1 1 | -2 | 111111 |
| 16 | Spp1 6 | -1 | 111111 |
| 35 | Spp3 7 | -4 | 111111 |
| 36 | Spp3 9 | -1 | 111111 |
| 40 | Spp4 3 | -1 | 111111 |
| 62 | Spp6 5 | -1 | 111111 |
| 175 | Spp1 93 | -1 | 111111 |
| 176 | Spp1 94 | -5 | 111111 |
| 177 | Spp1 95 | -3 | 111111 |
|  |  | 0000011111 |  |
|  |  | 0011100001 |  |
|  |  | 010110001 |  |
|  |  | 01011 |  |
|  |  | 01 |  |

# APPENDIX 9

## Leaf litter beetle species list

| *Species no.* | *Family* | *Sub-family* | *Tribe* | *Genus* | *Species* |
|---|---|---|---|---|---|
| 1 | Carabidae | | Galerini | Galerita | Galerita sp.3 |
| 3 | Staphylinidae | | | | |
| 4 | Nitidulidae | | | | |
| 5 | Staphylinidae | | | | |
| 6 | Staphylinidae | | | | |
| 7 | Carabidae | | | | |
| 8 | Staphylinidae | | | | |
| 9 | Staphylinidae | | | | |
| 10 | Staphylinidae | | | | |
| 11 | Staphylinidae | | | | |
| 12 | Mordellidae | | | | |
| 13 | Carabidae | | Galerini | Galerita | Galerita sp.1 |
| 14 | Scolytidae | | | | |
| 15 | Staphylinidae | | | | |
| 16 | Hydrophilidae | | | | |
| 17 | Staphylinidae | | | | |
| 19 | Scarabaeidae | Coprinae | | Canthidium | Canthidium sp. |
| 20 | Staphylinidae | | | | |
| 21 | Scolytidae | | | | |
| 22 | Nitidulidae | | | | |
| 23 | Staphylinidae | | | | |
| 24 | Scolytidae | | | | |
| 25 | Hydrophilidae | | | | |
| 26 | Hydrophilidae | | | | |
| 27 | Staphylinidae | | | | |
| 28 | Staphylinidae | | | | |
| 29 | Staphylinidae | | | | |
| 30 | Staphylinidae | | | | |
| 31 | Nitidulidae | | | | |
| 32 | Nitidulidae | | | | |
| 33 | Scydmaenidae | | | | |
| 34 | Carabidae | | | | |
| 35 | Pselaphidae | | | | |
| 36 | Staphylinidae | | | | |
| 37 | Staphylinidae | | | | |
| 38 | Staphylinidae | | | | |
| 39 | Leiodidae | | | | |
| 40 | Staphylinidae | | | | |
| 41 | Staphylinidae | | | | |
| 42 | Staphylinidae | | | | |
| 43 | Nitidulidae | | | | |
| 44 | Staphylinidae | | | | |
| 45 | Staphylinidae | | | | |
| 46 | Ptilidae | | | | |
| 47 | Staphylinidae | | | | |
| 48 | Staphylinidae | | | | |
| 50 | Staphylinidae | | | | |
| 51 | Staphylinidae | | | | |

| Species no. | Family | Sub-family | Tribe | Genus | Species |
|---|---|---|---|---|---|
| 52 | Staphylinidae | | | | |
| 53 | Staphylinidae | | | | |
| 54 | Staphylinidae | | | | |
| 55 | Staphylinidae | | | | |
| 57 | Scarabaeidae | Aphodiinae | | | |
| 58 | Staphylinidae | | | | |
| 59 | Limnichidae | | | | |
| 60 | Chrysomelidae | | | | |
| 61 | Staphylinidae | | | | |
| 62 | Staphylinidae | | | | |
| 64 | Scydmaenidae | | | | |
| 65 | Elateridae | | Conoderini | Anischia | Anischia sp. |
| 66 | Scarabaeidae | Aphodiinae | | | |
| 67 | Histeridae | | | | |
| 68 | Scydmaenidae | | | | |
| 69 | Scarabaeidae | Aphodiinae | | Ataenius | Ataenius sp. |
| 70 | Carabidae | Scaritinae | Scaritini | | |
| 71 | Phalacridae | | | | |
| 72 | Chrysomelidae | | | Chaetocnema | Chaetocnema sp. |
| 73 | Limnichidae | | | | |
| 74 | Carabidae | | Tachyina | | |
| 75 | Staphylinidae | | | | |
| 76 | Staphylinidae | | | | |
| 77 | Staphylinidae | | | | |
| 78 | Staphylinidae | | | | |
| 79 | Staphylinidae | | | | |
| 80 | Carabidae | | Galerini | Galerita | Galerita sp. |
| 81 | Staphylinidae | | | | |
| 83 | Nitidulidae | | | | |
| 84 | Chrysomelidae | Alticinae | | | |
| 85 | Languridae | | | | |
| 86 | Staphylinidae | | | | |
| 87 | Staphylinidae | | | | |
| 89 | Scydmaenidae | | | | |
| 90 | Carabidae | | Harpchini | | |
| 93 | Ptilidae | | | | |
| 94 | Staphylinidae | | | | |
| 95 | Staphylinidae | | | | |
| 96 | Nitidulidae | | | | |
| 97 | Scolytidae | | | | |
| 98 | Staphylinidae | | | | |
| 99 | Staphylinidae | | | | |
| 100 | Scarabaeidae | Coprinae | | Uroxys | Uroxys sp. |
| 101 | Curculionidae | | | | |
| 102 | Leiodidae | | | | |
| 103 | Staphylinidae | | | | |
| 104 | Staphylinidae | | | | |
| 105 | Staphylinidae | | | | |
| 106 | Nitidulidae | | | | |
| 108 | Nitidulidae | | | | |
| 109 | Scydmaenidae | | | | |
| 110 | Staphylinidae | | | | |
| 112 | Staphylinidae | | | | |
| 115 | Staphylinidae | | | | |

| **Species no.** | **Family** | **Sub-family** | **Tribe** | **Genus** | **Species** |
|---|---|---|---|---|---|
| 116 | Staphylinidae | | | | |
| 117 | Scolytidae | | | | |
| 118 | Staphylinidae | | | | |
| 119 | Staphylinidae | | | | |
| 121 | Curculionidae | Baridinae | | | |
| 122 | Staphylinidae | | | | |
| 123 | Carabidae | | Galerini | Galerita | Galerita sp.2 |
| 124 | Staphylinidae | | | | |
| 125 | Staphylinidae | | | | |
| 126 | Staphylinidae | | | | |
| 128 | Staphylinidae | | | | |
| 130 | Nitidulidae | | | | |
| 131 | Nitidulidae | | | | |
| 132 | Staphylinidae | | | | |
| 134 | Carabidae | | Galerini | Galerita | Galerita sp. |
| 136 | Carabidae | | | | |
| 137 | Staphylinidae | | | | |
| 138 | Staphylinidae | | | | |
| 139 | Staphylinidae | | | | |
| 140 | Leiodidae | | | | |
| 141 | Staphylinidae | | | | |
| 142 | Limnichidae | | | | |
| 143 | Nitidulidae | | | | |
| 144 | Carabidae | | | | |
| 145 | Limnichidae | | | | |
| 146 | Limnichidae | | | | |
| 148 | Staphylinidae | | | | |
| 149 | Carabidae | Scaritinae | | | |
| 150 | Carabidae | | | | |
| 151 | Limnichidae | | | | |
| 152 | Staphylinidae | | | | |
| 153 | Limnichidae | | | | |
| 154 | Staphylinidae | | | | |
| 155 | Scarabaeidae | Aphodiinae | | Ataenius | Ataenius sp. |
| 156 | Staphylinidae | | | | |
| 157 | Staphylinidae | | | | |
| 158 | Chrysomelidae | Alticinae | | | |
| 159 | Staphylinidae | | | | |
| 160 | Staphylinidae | | | | |
| 161 | Carabidae | | | | |
| 162 | Staphylinidae | | | | |
| 163 | Anthicidae | | | | |
| 164 | Staphylinidae | | | | |
| 165 | Chrysomelidae | Alticinae | | | |
| 166 | Carabidae | | Carabini | Calosoma | Calosoma sayi |
| 168 | Staphylinidae | | | | |
| 169 | Staphylinidae | | | | |
| 170 | Staphylinidae | | | | |
| 171 | Carabidae | | Lachnophorini | | |
| 172 | Staphylinidae | | | | |
| 173 | Leiodidae | | | | |
| 174 | Scolytidae | | | | |
| 175 | Staphylinidae | | | | |
| 176 | Scolytidae | | | | |

| ***Species no.*** | ***Family*** | ***Sub-family*** | ***Tribe*** | ***Genus*** | ***Species*** |
|---|---|---|---|---|---|
| 177 | Staphylinidae | | | | |
| 178 | Staphylinidae | | | | |
| 179 | Leiodidae | | | | |
| 180 | Nitidulidae | | | | |
| 181 | Carabidae | | | | |
| 182 | Staphylinidae | | | | |
| 183 | Staphylinidae | | | | |
| 184 | Staphylinidae | | | | |
| 185 | Nitidulidae | | | | |
| 186 | Scolytidae | | | | |
| 188 | Nitidulidae | | | | |
| 189 | Scarabaeidae | | | | |
| 190 | Scarabaeidae | Coprinae | | Uroxys | Uroxys sp. |
| 191 | Staphylinidae | | | | |
| 192 | Staphylinidae | | | | |
| 193 | Staphylinidae | | | | |
| 194 | Staphylinidae | | | | |
| 195 | Staphylinidae | | | | |
| 197 | Carabidae | | | | |
| 198 | Scydmaenidae | | | | |
| 199 | Leiodidae | | | | |
| 200 | Staphylinidae | | | | |
| 201 | Staphylinidae | | | | |
| 202 | Staphylinidae | | | | |
| 203 | Staphylinidae | | | | |
| 204 | Staphylinidae | | | | |
| 205 | Chrysomelidae | | | | |
| 206 | Staphylinidae | | | | |
| 207 | Staphylinidae | | | | |
| 208 | Staphylinidae | | | | |
| 209 | Staphylinidae | | | | |
| 210 | Staphylinidae | | | | |
| 211 | Staphylinidae | | | | |
| 212 | Carabidae | | | | |
| 213 | Carabidae | | | | |
| 214 | Leiodidae | | | | |
| 215 | Tenebrionidae | | | | |
| 216 | Leiodidae | | | | |
| 217 | Staphylinidae | | | | |
| 218 | Leiodidae | | | | |
| 219 | Hydrophilidae | | | | |
| 220 | Carabidae | | | | |
| 221 | Pselaphidae | | | | |
| 222 | Chrysomelidae | Alticinae | | | |
| 223 | Carabidae | | | | |
| 224 | Nitidulidae | | | | |
| 225 | Staphylinidae | | | | |
| 226 | Hydrophilidae | | | | |
| 227 | Nitidulidae | | | | |
| 228 | Nitidulidae | | | | |
| 229 | Histeridae | | | | |
| 230 | Staphylinidae | | | | |
| 231 | Curculionidae | | | | |
| 232 | Nitidulidae | | | | |

| **Species no.** | **Family** | **Sub-family** | **Tribe** | **Genus** | **Species** |
|---|---|---|---|---|---|
| 233 | Staphylinidae | | | | |
| 234 | Tenebrionidae | | | | |
| 235 | Staphylinidae | | | | |
| 237 | Staphylinidae | | | | |
| 239 | Scydmaenidae | | | | |
| 240 | Nitidulidae | | | | |
| 241 | Nitidulidae | | | | |
| 242 | Nitidulidae | | | | |
| 243 | Carabidae | | | | |
| 244 | Pselaphidae | | | | |
| 245 | Nitidulidae | | | | |
| 247 | Nitidulidae | | | | |
| 248 | Carabidae | | | | |
| 249 | Carabidae | | | | |
| 250 | Leiodidae | | | | |
| 251 | Nitidulidae | | | | |
| 252 | Nitidulidae | | | | |
| 253 | Scarabaeidae | Aphodiinae | | Ataenius | Ataenius sp. |
| 254 | Scarabaeidae | Coprinae | | | |
| 255 | Chrysomelidae | Eumolpinae | | Percolapsis | Percolapsis sp. |
| 256 | Scolytidae | | | | |
| 257 | Curculionidae | | | | |
| 258 | Staphylinidae | | | | |
| 259 | Leiodidae | | | | |
| 260 | Endomychidae | | | | |
| 261 | Staphylinidae | | | | |
| 262 | Ptilidae | | | | |
| 263 | Staphylinidae | | | | |
| 264 | Scolytidae | | | | |
| 265 | Staphylinidae | | | | |
| 266 | Nitidulidae | | | | |
| 267 | Nitidulidae | | | | |
| 268 | Scolytidae | | | | |
| 269 | Nitidulidae | | | | |
| 270 | Nitidulidae | | | | |
| 273 | Chrysomelidae | | | | |
| 274 | Staphylinidae | | | | |
| 275 | Noteridae | | | | |
| 277 | Chrysomelidae | | | | |
| 279 | Nitidulidae | | | | |
| 280 | Nitidulidae | | | | |
| 281 | Nitidulidae | | | | |
| 282 | Nitidulidae | | | | |
| 283 | Nitidulidae | | | | |
| 284 | Biphyllidae | | | | |
| 300 | Scarabaeidae | Coprinae | | Phanaeus | Phanaeus pyroi |
| 301 | Scarabaeidae | Scarabaeinae | Canthonini | Canthon | Canthon aequinoctialis |
| 302 | Scarabaeidae | Coprinae | | Onthophagas | Onthophagas sp. |
| 303 | Scymaenidae | | | | |
| 304 | Scolytidae | | | | |
| 306 | Staphylinidae | | | | |

| **Species no.** | **Family** | **Sub-family** | **Tribe** | **Genus** | **Species** |
|---|---|---|---|---|---|
| 307 | Staphylinidae | | | | |
| 308 | Staphylinidae | | | | |
| 309 | Nitidulidae | | | | |
| 310 | Meloidae | | | Mylabris | Mylabris sp. |
| 311 | Elateridae | | | | |
| 312 | Elateridae | | | | |
| 314 | Chrysomelidae | | | | |
| 315 | Scolytidae | | | | |
| 316 | Staphylinidae | | | | |
| 317 | Staphylinidae | | | | |
| 318 | Staphylinidae | | | | |
| 319 | Biphyllidae | | | | |
| 320 | Nitidulidae | | | | |
| 321 | Staphylinidae | | | | |
| 322 | Scolytidae | | | | |
| 323 | Scymaenidae | | | | |
| 324 | Nitidulidae | | | | |
| 325 | Scarabaeidae | Scarabaeinae | | | |
| 326 | Leiodidae | | | | |
| 327 | Staphylinidae | | | | |
| 328 | Nitidulidae | | | | |
| 329 | Staphylinidae | | | | |
| 330 | Staphylinidae | | | | |
| 331 | Staphylinidae | | | | |
| 332 | Scarabaeidae | Scarabaeinae | | | |
| 333 | Staphylinidae | | | | |
| 334 | Leiodidae | | | | |
| 335 | Staphylinidae | | | | |
| 336 | Staphylinidae | | | | |
| 337 | Leiodidae | | | | |
| 338 | Scolytidae | | | | |
| 340 | Scarabaeidae | Coprinae | | | |
| 341 | Scolytidae | | | | |
| 342 | Staphylinidae | | | | |
| 343 | Curculionidae | | | | |
| 344 | Pselaphidae | | | | |
| 345 | Scarabaeidae | | | Uroxys | Uroxys sp. 2 |
| 346 | Pselaphidae | | | | |
| 347 | Staphylinidae | | | | |
| 348 | Staphylinidae | | | | |
| 349 | Nitidulidae | | | | |
| 350 | Nitidulidae | | | | |
| 351 | Leiodidae | | | | |
| 352 | Staphylinidae | | | | |
| 353 | Staphylinidae | | | | |
| 354 | Elateridae | | | | |
| 355 | Staphylinidae | | | | |
| 356 | Staphylinidae | | | | |
| 357 | Staphylinidae | | | | |
| 358 | Nitidulidae | | | | |
| 359 | Coccinellidae | | | | |
| 360 | Staphylinidae | | | | |
| 361 | Staphylinidae | | | | |
| 362 | Staphylinidae | | | | |

| **Species no.** | **Family** | **Sub-family** | **Tribe** | **Genus** | **Species** |
|---|---|---|---|---|---|
| 363 | Carabidae | | | | |
| 364 | Pselaphidae | | | | |
| 365 | Staphylinidae | | | | |
| 366 | Coccinellidae | | | | |
| 367 | Nitidulidae | | | | |
| 368 | Scarabaeidae | Aphodiinae | | | |
| 369 | Carabidae | Scaritinae | | | |
| 370 | Staphylinidae | | | | |
| 371 | Chrysomelidae | Alticinae | | | |
| 372 | Nitidulidae | | | | |
| 373 | Staphylinidae | | | | |
| 374 | Staphylinidae | | | | |
| 375 | Staphylinidae | | | | |
| 376 | Nitidulidae | | | | |
| 377 | Nitidulidae | | | | |
| 378 | Staphylinidae | | | | |
| 379 | Staphylinidae | | | | |
| 380 | Pselaphidae | | | | |
| 381 | Staphylinidae | | | | |
| 382 | Staphylinidae | | | | |
| 383 | Staphylinidae | Scaphidiinae | | | |
| 384 | Staphylinidae | | | | |
| 385 | Scarabaeidae | Coprinae | | | |
| 386 | Nitidulidae | | | | |
| 387 | Staphylinidae | | | | |
| 388 | Carabidae | | | | |
| 389 | Staphylinidae | | | | |
| 390 | Tenebrionidae | | | | |
| 391 | Curculionidae | | | | |
| 392 | Staphylinidae | | | | |
| 393 | Scarabaeidae | Coprinae | | | |
| 394 | Staphylinidae | | | | |
| 395 | Nitidulidae | | | | |
| 396 | Chrysomelidae | | | | |
| 397 | Curculionidae | | | | |
| 398 | Scolytidae | | | | |
| 399 | Nitidulidae | | | | |
| 400 | Scydmaenidae | | | | |
| 401 | Scydmaenidae | | | | |
| 402 | Nitidulidae | | | | |
| 403 | Curculionidae | | | | |
| 404 | Scolytidae | | | | |
| 405 | Staphylinidae | | | | |
| 406 | Staphylinidae | | | | |
| 407 | Scolytidae | | | | |
| 408 | Staphylinidae | | | | |
| 409 | Scarabaeidae | Coprinae | | Uroxys | Uroxys sp. |
| 410 | Nitidulidae | | | | |
| 411 | Curculionidae | | | | |
| 412 | Staphylinidae | | | | |
| 413 | Scarabaeidae | | | | |
| 414 | Curculionidae | | | | |
| 415 | Staphylinidae | | | | |
| 416 | Curculionidae | | | | |

| ***Species no.*** | ***Family*** | ***Sub-family*** | ***Tribe*** | ***Genus*** | ***Species*** |
|---|---|---|---|---|---|
| 417 | Scydmaenidae | | | | |
| 419 | Staphylinidae | | | | |
| 420 | Staphylinidae | | | | |
| 421 | Carabidae | | | | |
| 422 | Chrysomelidae | | | | |
| 423 | Elateridae | | | | |
| 424 | Elateridae | | | | |
| 425 | Scarabaeidae | Aphodiinae | | | |
| 426 | Carabidae | | | Galerita | Galerita sp. |
| 427 | Limnichidae | | | | |
| 428 | Staphylinidae | | | | |
| 429 | Nitidulidae | | | | |
| 430 | Carabidae | | | | |
| 431 | Limnichidae | | | | |
| 432 | Scarabaeidae | Coprinae | | | |
| 433 | Staphylinidae | | | | |
| 434 | Staphylinidae | | | | |
| 435 | Staphylinidae | Coprinae | | Uroxys | Uroxys sp. |
| 436 | Hydrophilidae | | | | |
| 437 | Histeridae | | | | |
| 438 | Scarabaeidae | Aphodiinae | | | |
| 439 | Staphylinidae | | | | |
| 440 | Lathriidae | | | | |
| 441 | Carabidae | | | Calosoma | Calosoma sp. |
| 442 | Carabidae | | | | |
| 443 | Carabidae | | | | |
| 444 | Carabidae | Scaritinae | | | |
| 445 | Staphylinidae | | | | |
| 446 | Nitidulidae | | | | |
| 447 | Staphylinidae | | | | |
| 448 | Staphylinidae | | | | |
| 449 | Staphylinidae | | | | |
| 450 | Staphylinidae | | | | |
| 451 | Carabidae | | | | |
| 452 | Scolytidae | | | | |
| 453 | Staphylinidae | | | | |
| 111a | Nitidulidae | | | | |
| 111b | Nitidulidae | | | | |
| 113b | Nitidulidae | | | | |
| 133a | Nitidulidae | | | | |
| 133b | Scarabaeidae | | | | Ateuchus sp. |
| 167a | Curculionidae | | | | |
| 167b | Scarabaeidae | Aphodiinae | | | |
| 187a | Curculionidae | | | | |
| 187b | Scydmaenidae | | | | |
| 272a | Hydrophilidae | | | | |
| 272b | Nitidulidae | | | | |
| 2a | Nitidulidae | | | | |
| 2b | Nitidulidae | | | | |
| 56a | Carabidae | | Scaritini | Aspidoglossa | Aspidoglossa sp. |
| 56b | Carabidae | | Scaritini | | |
| 56c | Carabidae | | Scaritini | | |
| 91b | Carabidae | | Galerini | Galerita | Galerita sp. |

## APPENDIX 10

**Table C1 Results of the One-way ANOVA for beetle species richness (*S*) data measured over 10 field sites in northern Costa Rica**

| Source | DF | SS | MS | F | *p* |
|---|---|---|---|---|---|
| Field site | 9 | 2389.6 | 265.5 | 14.93 | 0 |
| Error | 90 | 1600.2 | 17.8 | | |
| Total | 99 | 3989.8 | | | |

**Table C2 Results of the Tukey multiple comparison test ($p$<0.05) for the beetle species richness (*S*) One-way ANOVA.** These show upper and lower confidence limits for the differences between site means. Any pair of confidence intervals that has a positive and negative value indicates no significant difference, any that have either both positive or both negative values indicate a significant difference (differences which are not significant are shown in red).

| ***SITE*** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** |
|---|---|---|---|---|---|---|---|---|---|
| **2** | -4.02 | | | | | | | | |
| | 8.22 | | | | | | | | |
| **3** | -9.02 | -11.12 | | | | | | | |
| | 3.22 | 1.12 | | | | | | | |
| **4** | 10.92 | -13.02 | -8.02 | | | | | | |
| | 1.32 | -0.78 | 4.22 | | | | | | |
| **5** | -1.12 | -3.22 | 1.78 | 3.68 | | | | | |
| | 11.12 | 9.02 | 14.02 | 15.92 | | | | | |
| **6** | 0.58 | -1.52 | 3.48 | 5.38 | -4.42 | | | | |
| | 12.82 | 10.72 | 15.72 | 17.62 | 7.82 | | | | |
| **7** | 2.78 | 0.68 | 5.68 | 7.58 | -2.22 | -3.92 | | | |
| | 15.02 | 12.92 | 17.92 | 19.82 | 10.02 | 8.32 | | | |
| **8** | 4.88 | 2.78 | 7.78 | 9.68 | -0.12 | -1.82 | -4.02 | | |
| | 17.12 | 15.02 | 20.02 | 21.92 | 12.12 | 10.42 | 8.22 | | |
| **9** | 1.18 | -0.92 | 4.08 | 5.98 | -3.82 | -5.52 | -7.72 | -9.82 | |
| | 13.42 | 11.32 | 16.32 | 18.22 | 8.42 | 6.72 | 4.52 | 2.42 | |
| **10** | -4.22 | -6.32 | -1.32 | 0.58 | -9.22 | -10.92 | 13.12 | -15.22 | -11.52 |
| | 8.02 | 5.92 | 10.92 | 12.82 | 3.02 | 1.32 | -0.88 | -2.98 | 0.72 |

Family error rate: 0.05, Individual error rate: 0.00165, Critical value: 4.59

# APPENDIX 11

## TWINSPAN output for leaf litter beetles

| *Twinspan No.* | *Species* | *Abundance level* | *Twinspan output* |
|---|---|---|---|
| | | *Site No.:* | |
| | | 1 | |
| | | 8765134290 | |
| 9 | 17 | ------3--- | 0 |
| 10 | 19 | ------2--- | 0 |
| 31 | 45 | ------2--- | 0 |
| 55 | 100 | -----22--- | 0 |
| 64 | 117 | ------3--- | 0 |
| 86 | 174 | -----23--- | 0 |
| 88 | 178 | -----22--- | 0 |
| 97 | 195 | -----22--- | 0 |
| 99 | 200 | -----23--- | 0 |
| 129 | 265 | -----22--- | 0 |
| 138 | 318 | ------5--- | 0 |
| 143 | 336 | ------3--- | 0 |
| 52 | 96 | -----3---- | 1 |
| 53 | 97 | -----3---- | 1 |
| 85 | 173 | ----255--- | 1 |
| 90 | 183 | -----3---- | 1 |
| 100 | 201 | ----2442-- | 1 |
| 120 | 247 | -----4---- | 1 |
| 11 | 20 | ----2----- | 10 |
| 21 | 33 | ----22---- | 10 |
| 24 | 38 | ----2----- | 10 |
| 26 | 40 | ----2----- | 10 |
| 32 | 47 | ----223--- | 10 |
| 34 | 52 | ----22---- | 10 |
| 35 | 53 | ----3----- | 10 |
| 91 | 184 | ----32---- | 10 |
| 107 | 216 | ----343--- | 10 |
| 110 | 219 | ----22---- | 10 |
| 28 | 42 | --2-454--- | 11 |
| 17 | 27 | ----5222-- | 100 |
| 25 | 39 | ----4-54-- | 100 |
| 177 | 2b | -----342-- | 100 |
| 7 | 10 | ----2-33-- | 101 |
| 20 | 32 | ------22-- | 101 |
| 33 | 48 | ------24-- | 101 |
| 89 | 182 | ------22-- | 101 |
| 93 | 191 | -----2-3-- | 101 |
| 109 | 218 | ----2324-- | 101 |
| 136 | 316 | ------22-- | 101 |
| 108 | 217 | -2---554-- | 11 |
| 14 | 24 | ---23522-- | 100 |
| 57 | 102 | ---23243-- | 1010 |
| 60 | 105 | ---23-23-- | 1011 |
| 15 | 25 | --2-32---- | 1100 |
| 22 | 36 | --2--33--- | 1100 |

| ***Twinspan No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---:|---:|---:|---:|
| 23 | 37 | ---222---- | 1101 |
| 30 | 44 | ---22-2--- | 1101 |
| 61 | 106 | ---222-2-- | 1101 |
| 12 | 21 | ---22--2-- | 1110 |
| 27 | 41 | --2--2-2-- | 1110 |
| 51 | 95 | ---2------ | 1111 |
| 54 | 99 | ---2------ | 1111 |
| 62 | 110 | ---2--2--- | 1111 |
| 63 | 112 | ---3-2---- | 1111 |
| 65 | 118 | ---2------ | 1111 |
| 68 | 125 | --2------- | 1111 |
| 69 | 126 | --2------- | 1111 |
| 70 | 136 | --2------- | 1111 |
| 94 | 192 | ---2-2---- | 1111 |
| 117 | 242 | ---2---2-- | 1111 |
| 92 | 188 | --32-2---- | 10 |
| 176 | 2a | -2--22---- | 11000 |
| 6 | 8 | -2---2---- | 11001 |
| 4 | 5 | -2-------- | 11010 |
| 50 | 90 | -2-------- | 11010 |
| 67 | 123 | -2-------- | 11010 |
| 1 | 1 | -2-2------ | 11100 |
| 5 | 7 | 33-2------ | 11100 |
| 8 | 11 | 2-22------ | 11101 |
| 2 | 3 | -232--2--- | 11110 |
| 3 | 4 | -2242-2--- | 11111 |
| 19 | 31 | ----2---2- | 100 |
| 115 | 240 | 335 | 1010 |
| 29 | 43 | -5 | 1011 |
| 113 | 232 | ----2---3- | 11000 |
| 147 | 358 | -242 | 1101 |
| 41 | 67 | 22 | 1110 |
| 75 | 159 | 22 | 1110 |
| 79 | 164 | 34 | 1110 |
| 161 | 428 | 24 | 1110 |
| 18 | 30 | -2 | 11110 |
| 36 | 61 | -2 | 11110 |
| 38 | 64 | -2 | 11110 |
| 39 | 65 | -3 | 11110 |
| 40 | 66 | -2 | 11110 |
| 42 | 68 | -4 | 11110 |
| 43 | 70 | -2 | 11110 |
| 44 | 71 | -2 | 11110 |
| 45 | 72 | -2 | 11110 |
| 46 | 73 | -2 | 11110 |
| 47 | 77 | -2 | 11110 |
| 48 | 87 | -2 | 11110 |
| 71 | 151 | -2 | 11110 |
| 72 | 152 | -2 | 11110 |
| 73 | 155 | -2 | 11110 |
| 74 | 158 | -2 | 11110 |
| 76 | 160 | -2 | 11110 |
| 77 | 162 | -2 | 11110 |
| 166 | 439 | -4 | 11110 |

| ***Twinspan No.*** | ***Species*** | ***Abundance level*** | ***Twinspan output*** |
|---|---|---|---|
| 49 | 89 | -4 | 11111 |
| | | | |
| | | 0000000011 | |
| | | 0011111101 | |
| | | 01001111 | |
| | | 010001 | |
| | | 011 | |
| | | 01 | |