Carabid beetles (Coleoptera, Carabidae) as indicators of environmental change in Ranomafana National Park, Madagascar

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ACADEMIC DISSERTATION

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Contents

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications and manuscripts, which are referred to in the text by their Roman numerals:

I Rainio, J. & Niemelä, J. 2003: Ground beetles (Coleoptera: Carabidae) as bioindicators. – *Biodiversity and Conservation* 12: 487–506.

II Rainio, J. & Niemelä, J. 2006: Comparison of carabid beetle (Coleoptera: Carabidae) occurrence in rain forest and human-modified sites in south-eastern Madagascar. – *Journal of Insect Conservation* 10: 219–228.

III Rainio, J. 2009. Diversity, distribution and community composition of carabid beetles (Coleoptera: Carabidae) in Ranomafana National Park, Madagascar. – Submitted Manuscript.

IV Rainio, J. 2009. Seasonal variation of carabid beetle (Coleoptera: Carabidae) abundance and diversity in Ranomafana National Park, Madagascar. – Submitted Manuscript.

Contributions

The following table shows the major contributions of authors to the original articles or manuscripts (referred to as I-IV).

	I	II	III	IV
Original idea	JN	JR, JN	JR, JN	JR, JN
Data collecting	JR	JR, FR	FR, JR	FR
Analysis	JR	JR	JR	JR
Manuscript preparation	JR, JN	JR, JN	JR	JR

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Abstract

Growing human populations and increasing exploitation of natural resources threaten nature all over the world. Tropical countries are especially vulnerable to human impact because of the high number of species, most of these endemic and still unknown. Madagascar is one of the centers of high biodiversity and renowned for its unique species. However, during the last centuries many endemic species have gone extinct and more are endangered. Because of high natural values, Madagascar is one of the global conservation priorities.

The establishment of Ranomafana National Park (RNP) was intended to preserve the unique nature of Madagascar. Containing several endemic and threatened species, Ranomafana has been selected as one of UNESCO's World Natural Heritage sites. However, due to strong human pressures the region immediately surroundings the protected area has severely degraded.

Aims of this thesis were to inventory carabid fauna in RNP and evaluate their use as indicators of the environmental change. Carabid beetles were collected from protected area (secondary and primary forests) and from its degraded surrounding area. Collecting was mostly conducted by hand during years 2000-2005. Species compositions between the protected area and its surroundings were compared, and species habitat preferences and seasonal variations were studied.

In total, 4498 individuals representing 127 carabid species (of which 38 are new species) were collected. Species compositions within and outside of the protected area were markedly different. Most of the species preferred forest as their primary habitat and were mainly collected from trees and bushes. Their value as indicators is based on their different habitat requirements and sensitivity to environmental variables. Some of the species were found only in the protected forest, some occupied also the degraded forests and some preferred open areas.

Carabid fauna is very species rich in Ranomafana and there are still many species to be found. Most of the species are arboreal and probably cannot survive in the deforested areas outside the park. This is very likely also the case for other species. Establishment and continued protection of RNP is probably the only way to conserve this globally important area. However, new occupations and land use methods are urgently needed by the local people for improving their own lives while maintaining the forest intact.

1. Introduction

Global species diversity is distributed very unevenly on Earth (Brooks *et al.* 2006). In general, species richness decreases toward the poles (Hillebrand 2004) and is especially high in tropical forests (Mittermeier *et al.* 2004). There are still millions of unknown species in tropical forest canopies (Erwin 1982, Erwin 1988, Ødegaard 2000). Some of these species are potentially useful for humans but all are important parts of the ecosystem and have unique value of their own.

The concept of hotspot was developed to identify global conservation priorities (Myers 1988). Terrestrial hotspot areas are characterized by especially high number of endemic species and extensive loss of original vegetation. The latest revision identified 34 hotspots of which 22 were predominantly tropical forest biomes (Mittermeier *et al.* 2004). It is estimated that hotspot areas have lost 86% of their original vegetation currently covering only 2.3% of the planet's land surface but holding 76% of the all terrestrial mammals and 50% of the planets plant species (Mittermeier *et al.* 2004).

1.1. Species diversity and endemism in Madagascar

Madagascar is one of the world's hotspot areas and conservation priorities (Mittermeier *et al.* 2004, Brooks *et al.* 2006). It is globally known for particularly rich, unique and fascinating biota. Most of the species living in Madagascar are endemic, (i.e. cannot be found anywhere else in the world (Brooks *et al.* 2002, Goodman & Benstead 2003)). The uniqueness of the Malagasy biota is explained by the long period of geographic isolation, topographical variation, several climatic zones and great diversity of habitats, from the hot and dry southern region to rainforests (Lowry *et al.* 1997, Gautier & Goodman 2003).

Madagascar was part of the Gondwana supercontinent until rifting from the African mainland 165 million years ago (Krause 2003). Approximately 70 million years later Madagascar separated also from India and achieved its current location ~400 km from the southeastern African coast. Thus Madagascar has been geographically isolated since before the global extinction of non-avian dinosaurs 65 Ma (Krause 2003).

The contemporary Malagasy fauna is primarily derived from occasional individuals, which crossed the marine barrier from Africa during the last 65 million years (Paulian & Viette 2003, Yoder & Nowak 2006). Crossings have occurred under widely different ecological conditions and at widely different times. This has resulted high levels of radiation in some groups while some other groups, which are widely represented on the African mainland, are nonexistent or poorly present in Madagascar. For example, there are no large carnivores (canids, felids) in Madagascar, and only a few ungulates, all of which are already extinct reached the island (Krause 2003).

1.2. Humans, extinctions and deforestation in Madagascar

Humans settled Madagascar fairly recently. Records of the earliest human presence on Madagascar date back to 2300 yr BP in the southwest (Burney *et al.* 2004). It is still unknown where these settlers came from Indonesia or east Africa (Dewar 1997). During the eleventh and twelfth centuries, settlements spread widely along the coasts (Wright & Rakotoarisoa 2003).

Subsequent to the establishment of a human population, several species have gone extinct. These include many species of birds (Goodman & Rakotozafy 1997), lemurs (Godfrey *et al.* 1997), giant tortoises (Burney 1997) and dwarf hippopotami (MacPhee & Burney 1991). However, the causes of these extinctions seem to be complex, such combinations of climate change and direct and indirect consequences of human activities, including hunting, burning, and introduced species, which have acted in concert and varied from place to place (Dewar 1997, Burney *et al*. 2004).

During the French colonial period (1896-1960), over four million hectares were cleared due to logging, forest product extraction, crop production for export, shifting cultivation, grazing and burning (Jarosz 1993). Although clearing land by fire was prohibited in 1913, illegal burning of primary and secondary forest and grassland became a symbol of peasant protest against the state authorities (Jarosz 1993).

After becoming independent, loss of evergreen forest has been approximately 102, 000 ha per year (Dufils 2003). Estimates of forest destruction indicate that 50-80 % of Madagascar's original forest cover has disappeared after human arrival (Green & Sussman 1990), and by the early 1990s only 10% of the whole of Madagascar remained forested (Nelson & Horning 1993).

Rates of deforestation have been directly related to population density and the slope of the land (Sussman *et al*. 1994). In the southeast, the only forest remaining (outside the protected areas) is on very steep slopes (Sussman *et al*. 1994). Although data are patchy and it is difficult to estimate the total original forest cover and loss, it is clear that since human arrival forest cover has substantially decreased (Nelson & Horning 1993).

The main reason for forest decline is upland slash-and-burn cultivation (*tavy* in Malagasy). Tavy (Figure 1) is the traditional and predominant land use practice in eastern Madagascar. Primary forest or secondary vegetation is cut, dried by the sun, burned, and rice and a variety of complementary crops are grown (Hanson 2007). After the harvest, the land is left fallow.

Figure 1. Tavy field in Ranomafana region.

Tavy provides several short-term benefits to farmers including release of nutrients to otherwise poor soil and eliminates many pests such as mosquitoes, and locusts (Hanson 2007). However, it is only sustainable under conditions of low population density and abundant land. Current short fallow periods collapse the traditional tavy system (Styger *et al*. 2007). Due to human population growth tavy is recognized as the principal cause of deforestation and subsequent upland degradation (Gade 1996).

Besides burning, there are other causes of degradation including overgrazing by cattle and goats, and overharvesting of endemic species (Richard & O'Connor 1997). Because of direct and indirect human action, large areas are covered by species-poor secondary vegetation (Lowry *et al*. 1997, Schatz 2001). They represent a number of successional stages and compose various types of secondary formations. Frequent use of fire is replacing native species with introduced ones, and creating treeless landscapes, which have minimal productivity and ecological value (Styger *et al*. 2007).

Deforestation has also caused silting the rivers and irrigation canals, which decrease crop productivity (Kusky & Raharimahefa 2006) and threatens specialized taxa in rivers (Benstead *et al.* 2003, Elouard & Gibon 2003). Since human arrival, several introduced species have also naturalized in Madagascar. This “biotic homogenization” scenario is happening around the world meaning that cosmopolitan generalist species become more common replacing rare, native specialist species (McKinney & Lockwood 1999).

Madagascar is one of the countries, which have lost most terrestrial vertebrates since 1500 AD (Brooks *et al*. 2002), and have particularly high proportions of threatened species across multiple taxa (Baillie *et al*. 2004). High species richness and endemism along with serious threats to wildlife make Madagascar one of the top priorities for conservation action (Mittermeier *et al.* 2004, Brooks *et al*. 2006, Burgess *et al.* 2006).

1.3. Conservation in Madagascar

Globally the greatest numbers of threatened mammal, bird and amphibian species occur in the tropical continents (Baillie *et al*. 2004). One of the greatest problems for protecting the world’s natural heritage is that the biologically richest countries are also the economically poorest (Baillie *et al*. 2004). This is true for Madagascar, which is one of the world’s poorest countries, having GNI (Gross National Income) per capita $280 and population growth 2.6 % in 2006 (World Bank 2007).

On Madagascar, the negative effects of deforestation were recorded already by the 1800s and legislation in 1907 banned all fires except for locust control and pasture renewal (Kull 2003). In November 2002, the Malagasy government implemented a law which prohibited setting fire after cutting trees. Although farmers still light fires, it is decreased in several highland areas (Kull 2003).

The first strict nature reserves were established in 1927 during the French colonial period, and in 2003 there were already 18 national parks, 5 strict protected areas and 23 special reserves covering a surface area of 17,103 km^2 (3%) in total (ANGAP 2003). However, there are still several areas which need further protection (Wilmé *et al*. 2006, Kremen *et al.* 2008). To fill this gap, Madagascar aims to increase it’s protected area surface from 3% to 10% (IUCN 2005).

In the 1990s, the National Association for the Management of Protected areas (l'Association Nationale pour la Gestion des Aires Protégées, ANGAP) was founded to manage Madagascar’s protected area system. Its stated mission is “*To establish, conserve and sustainably manage a national network of parks and reserves representative of the biological diversity and the natural heritage of Madagascar*”. One of the principal goals is to enable local communities to benefit directly from conservation. Fifty percent of the park entrance fees collected by ANGAP go to the local communities, and visitors are not allowed to enter a park without hiring a local guide (ANGAP 2003).

To protect unique nature and improve livelihood of the people, the government of Madagascar has established a development strategy for 2007-2012, the Madagascar Action Plan (MAP), a second-generation Poverty Reduction Strategy (IMF 2007). World Bank (2007) has reported good progress in the implementation of the roads program, education for all, nutrition, and health. By family planning, increasing health, improving rice-cultivation and increasing protected land area, the government of Madagascar aims to maintain biodiversity and improve the livelihoods of people.

1.4. Ranomafana National Park

The Ranomafana National Park (RNP) was created in 1991 "to preserve the biology and ecosystem of the park through a program linking conservation of the core park area with improved standards of living and income alternatives within the surrounding peripheral zone" (Grenfell 1995). It was thereby established as an ICDP (Integrated Conservation and Development Project), which aims to link conservation of the protected area to social and economic development for people living adjacent to the protected area.

RNP is located in Fianarantsoa province and situated on the southeastern escarpment of Madagascar (47°29´ E longitude, 21°16´ S latitude) (Figure 2). The core area (43,500 ha) is mountainous and contains relatively undisturbed lowland rain forests, cloud forests and high plateau forests (Grenfell 1995). The altitudinal gradient varies between 500 and 1500 m though most of the park lies between 900 and 1200 m. The park is surrounded by a 3 km wide buffer or peripheral zone, which includes villages and cultivations of local people.

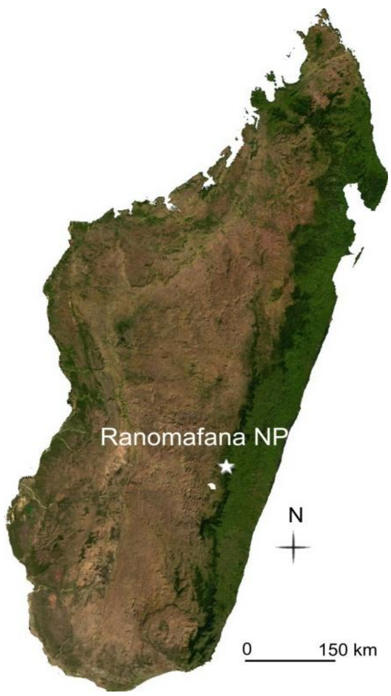

Figure 2. Satellite image of Madagascar showing green belt of forest in Eastern Madagascar. Original map: http://commons.wikimedia.org/wiki/File:Madagascar_sat.png 10.10.2009

The temperature of the area is subtropical, with average between 14–20°C and minimum temperatures (~4° C) in June–September and maximum in December–February (up to ~40° C). Annual rainfall is between 2300-4000 mm but is highly variable from year to year, depending on tropical depressions and cyclones. Monthly rainfall is high from December to March (400 mm) and lowest from May to October (90 mm). Relative humidity is over 90% throughout the year (Grenfell 1995).

RNP is recognized both nationally and internationally as one of the most important areas to conserve because of its exceptionally high species diversity and the immediate threat from human activity. Madagascar's Environmental Action Plan gave highest priority to the preservation of the Ranomafana rain forest and UNESCO has chosen it as a world heritage site. RNP is one of the most important watershed areas of southeastern Madagascar because of the Namorona River. The river arises in the forest and descends to the southeast, providing essential hydropower for southeastern Madagascar (Grenfell 1995). Protecting the forest also prevents erosion and stabilizes water flow.

Since 1986, when a new lemur species, the golden bamboo lemur (*Hapalemur Aureus*) (Meier *et al*. 1987) was discovered there, new species, representing many taxa, have been recorded frequently (e.g. Griswold 1997, Glaw & Vences 2005). In addition, several rare and threatened species occur in the park including species of primates, birds, trees, orchids and invertebrates (Grenfell 1995).

Within the 3 km wide buffer zone surrounding the RNP there are 96 villages, with approximately 25 000 inhabitants. Also in RNP tavy (slash-and-burn cultivation) has been the primary cause of deforestation (Peters 1999). Many people living in the Ranomafana region have depended at least partially on tavy to supply their food. However, soil in the area is very poor, containing toxic levels of aluminum, and very low levels of phosphorus (Johnson 2000). Also the steepness of the slopes and lack of fertilizers make agriculture difficult and crops can be grown only for a period of a few years on the burned sites (Johnson 2000).

The establishment of RNP and banning tavy, cattle grazing and collecting plants and wood from the forest have affected the lives of the local people. To compensate for these losses, several development projects have been conducted in RNP (Peters 1998). In addition, tourism and research bring income and work opportunities for local people (Wright & Andriamihaja 2003). As a consequence of growing population and need of land for cultivation, areas surrounding RNP are severely degraded but within the protected area 98% is intact (Wright & Andriamihaja 2003).

1.5. Carabid beetles as study organisms

Carabid beetles (Coleoptera: Carabidae) are one of the most species-rich families of beetles. There are more than 40 000 described species on Earth and they occur in all major habitats, except the driest parts of deserts (Thiele 1977, Lövei & Sunderland 1996). Carabids are among the most common beetle families present in canopy samplings in tropical and subtropical rainforests (Basset 2001). It is suggested that carabid beetles are ancestrally ground-dwelling (Erwin 1979) as they still are in boreal forests, but adapted to living in the trees in tropical forests (Stork 1987, Ober 2003).

In the temperate and boreal zones carabids are widely used for indicating alterations in the environment. This is based on their easy collecting (by pitfall traps) and responses of alterations in environment. Many biotic and abiotic factors regulate carabid species abundances. These factors include soil moisture (Luff 1996, Sroka & Finch 2006), soil type (Thiele 1977), heterogeneity of habitats (Epstein & Kulman 1990), and predation (Parmenter & MacMahon 1988). However, there is high variation among species' sensitivities to these factors.

On Madagascar, there are approximately 1320 described carabid species, of which 95% are endemic (Jeannel 1946, 1948 and 1949; Basilewsky 1973, 1985). The distribution ranges of most of the species are limited to a single or few localities. Species having broader distribution range occur also on the African mainland and/or in the nearby Comoros, Mauritius and Reunion islands. Very little is known of their ecology, life histories and habitat preferences. They suitability as bioindicators is thus also unknown. Understanding function of the tropical forest requires the knowledge of its organisms and their interactions, but this discipline is still largely obscure.

2. Aim of the thesis

This thesis is part of the ECOMADA-project (Ecological and health-related changes in the threatened rainforests of Madagascar), the research focus of which is to study ecological, health and social impacts of the establishment of RNP. The aim of this thesis was to assess the ecological impacts of the establishment of RNP using carabid beetles as indicators. The health and social aspects were assessed in the thesis of Korhonen (2006).

The suitability of carabids as bioindicators was first assessed by literature review. Because there is no information available concerning carabid species before establishing RNP, the ecological impacts were assessed by comparing carabid species compositions in the protected area and nearby deforested area, where the forest has been severely degraded due to human habitat alteration. In addition, because the carabid fauna of Madagascar and RNP is poorly known, the other objective was to conduct a species inventory, examine distribution patterns of species, and to collect information of their seasonal variation.

This thesis is based on four articles that have been published or submitted. The specific questions addressed by each of these papers, referred to as I-IV, are: **(I)** How suitable are carabid beetles as bioindicators? This paper is a review article considering the suitability and limitations of carabids as bioindicators. It also provides a background for this thesis. **(II)** How does carabid species composition differ between protected forests and human altered areas? **(III)** What are the community composition, distribution patterns and abundances of carabids in RNP. **(IV)** Do carabid beetle species and abundances vary during the year? In addition, descriptions of new species will be published in separate papers.

3. Material and methods

3.1. Carabid beetles as bioindicators (Paper I)

The first paper is a literature review consisting of an evaluation of the suitability of carabid beetles as bioindicators. Reviewed articles covered studies of wide range of habitat types, including different kinds of forests and grasslands, and the most common management practices (e.g. forest cutting, agriculture etc).

The suitability of carabids as environmental, ecological and biodiversity indicators was tested by McGeoch's (1998) suitability test. In the procedure (Table 2 in **Paper I**), two or three studies per type of indicator were selected to test the suitability of carabids as bioindicators. Their suitability as environmental indicators was examined using fragmentation studies (Davies & Margules 1998, Halme & Niemelä 1993, Abildsnes & Tømmeros 2000). Their suitability as ecological indicators was examined using studies which tested whether or not responses of carabid beetle assemblages to management practices resemble the responses of other species (Rushton *et al.* 1989, Niemelä *et al.* 1996). Finally, their suitability as biodiversity indicators was tested using studies that determined whether or not carabid diversity reflects the diversity of other species groups (Duelli & Obrist 1998, Niemelä & Baur 1998).

3.2. Field methods in RNP

The study was conducted in the Ranomafana National Park (RNP) and in the surrounding buffer (or peripheral) zone (Figure 3). Collecting areas were located in secondary forest (Talatakely), primary forests (Vatoharanana and Valohoaka) and in the village region (buffer zone. Talatakely is a low montane secondary forest, which was selectively logged in 1986-

1989. Vatoharanana and Valohoaka are montane primary rain forests four and eight km south of Talatakely, respectively. In Vatoharanana, there have been slight loggings, but Valohoaka is undisturbed (Balko 1998). The buffer zone consists of a varied mosaic of cultivations, abandoned tavy-fields and forest edges.

In each study, hand-collecting was selected as the main collecting method, because the actual location of each collected specimen is then recorded. Pitfall traps (**Paper II**) and trunk traps (**Paper III**) were tested as additional methods. The collection effort was standardized so that one sample consisted of one hour collecting/one person at each study site (10 X 10 meters). Hand-collecting included beating and shaking trees, turning stones, breaking into decaying logs, and removing bunches of dead leaves from bushes to a height up to 3 m. Collection was conducted during the day time only.

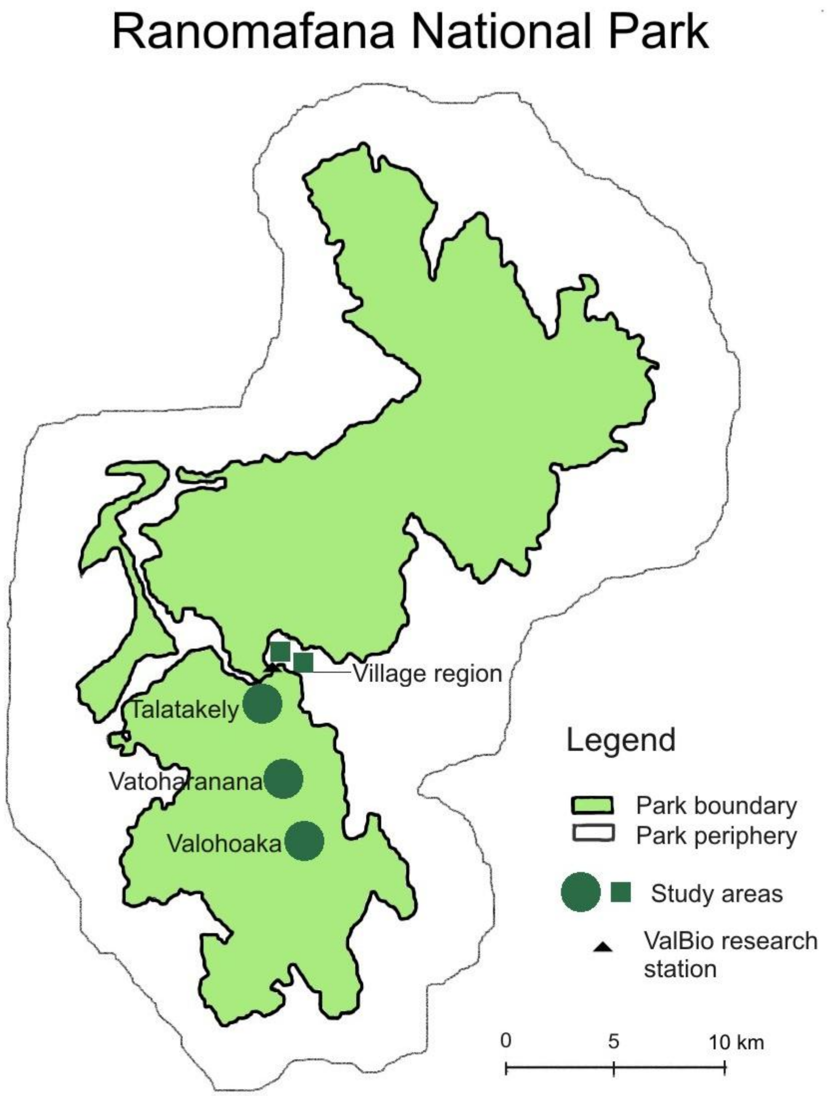

Figure 3. Map of Ranomafana National Park with study areas: Talatakely, Vatoharanana, Valohoaka and village region.

3.2.1. Comparison of carabid occurrence in forest and village sites (Paper II)

This study was conducted in March 2004 in two study areas: (1) the secondary forest of Talatakely and (2) the buffer zone. In both areas, ten different kinds of study sites were established to represent the heterogeneity of the forest and the variability of the secondary vegetation in the buffer zone. Sampling sites in these forests differed regarding vegetation, humidity and canopy cover. One of the forest sites was partly, and another almost completely, dominated by the introduced guava (*Psidium cattleianum*).

In the village area (buffer zone), vegetation was highly varied, including different cultivations, secondary grassy fields, and young trees and forest edges. Most of the sites were relatively dry and the moistest site was in a banana cultivation surrounded by forest. In each site, three collectors spent one hour during the first visit and 2 hours during the second visit in manual collecting. Ten pitfall traps (diameter 65 mm, depth 70 mm) were placed for seven days at each site arranged in two rows at a distance of one meter from each other.

3.2.2. Diversity, distribution and community composition of carabid beetles (Paper III)

Carabids were collected from four study areas (a total of 209 study sites). Most of the sites (147) were located in Talatakely, 39 sites were in Vatoharanana and 7 sites were in Valohoaka. The fourth study area was in the buffer zone with 16 sites. Carabids were collected by hand and by trunk traps during the years 2000-2005. The collecting period was continued throughout the year. In total, 765 hours were spent in collecting. Several sites were visited more than once during the years.

Two different sizes of circle trunk traps (Figure 4) were tested by attaching them directly to the trunks of living trees. The larger trap was 82 cm and the smaller one 35 cm wide at the base. Both trap types were left for 24 hours, inverted, and left for another 24 hours. In total, two traps were left for 48 hours in 24 sites (six sites in each of the four areas).

This data was also used for "Seasonal variation of carabids" (**Paper IV**). However, only those samples which were regularly collected from the same sites, were used. The data were collected within the protected area from Valohoaka, Vatoharanana and Talatakely. In each area, six study sites were visited during the year 2005, in February, March, May, June, July, September and November, and in 2004 in November. In addition, monthly temperatures (minimum, maximum and average) and amount of rainfall (total and average) were measured at the nearby ValBio research station.

Figure 4. Trunk trap attached to tree.

3.3. Species identification

All specimens were identified to species-level, except for a small part (~2%) that could not be reliably identified. Because of the high number of species new to science, species descriptions are still under preparation, and some species appear in the papers without a scientific name. Species identification was based on several morphological characteristics, including male and female genitalia using the keys of Jeannel (1946, 1948, and 1949) and Basilewsky (1973, 1985). I also visited the California Academy of Sciences to refer to their collection of carabid beetles from RNP. Furthermore, I twice visited the Museum of Natural History in Paris, where the primary (holo)types of almost all Malagasy carabids are stored.

Most of the species were identified in collaboration with Dr. David Kavanaugh (California Academy of Sciences, USA), who is also responsible for the descriptions of most of the new species. In addition, part of the material was identified by the following taxonomic specialist: Prof. Achille Casale, University of Sassari, Italy (*Callidiola*), Dr. Thierry Deuve, Museum of Natural History of Paris, France (*Eucamptognathus* and *Tshitscherinellus*), and Jiří Moravec (*Pogonostoma*).

3.4. Habitat affinity of carabids

Classification of species as forest specialist species, forest generalists, generalists or open habitat species is provided in Papers II and III and in Appendix 1. This classification is based on the habitat type in which most of the specimens of each species were collected. This classification is tentative and perhaps not reliable for those species caught in low numbers.

The forest specialists were those which were found only in forest (i.e. within the protected area). Forest generalists were those which were found in different types of forest (i.e. within the protected area and in the degraded forest sites in the buffer zone region). Generalist species were collected from the forest and in the buffer zone area including fields or bushy sites. Open habitat species preferred open sites in the buffer zone region.

3.5. Statistical methods

A cluster analysis (**Paper II**) with Pearson's correlation using average linkage (between groups) was used to compare species composition between study sites. SPSS software package (SPSS for Windows, www.spss.com) was used to perform the cluster analysis and to construct the dendrogram.

Carabid community structure (**Paper III**) was studied by dividing species into abundance classes. The first class consisted of species represented by less than ten individuals, the second class 10-19 individuals, the third one 20-29 and so on. Distribution patterns (**Paper III**) of species were investigated by calculating the numbers of sites from which each species was found. Differences of species occurrences in different vegetation types (secondary forest, primary forests and village area) were also studied.

Species accumulation curves (or sample-based rarefaction curve) for observed species richness and estimated species richness (number of species) were computed using EstimateS (Colwell 2005) (**Paper III**). I used Chao1 (Chao 1984) to estimate total species richness, because it is based on the number of rare species (singletons and doubletons), which are predominant in tropical species communities.

$$\hat{S}_{Chao1} = S_{obs} + (\alpha^2 / 2\beta),$$

where S_{obs} is the observed number of species in a sample, α is the number of observed species that are represented by single individuals (i.e. singletons) and β is the number of observed species represented by two individuals (i.e. doubletons) in that sample.

Interspecific relationship between abundance and occupancy (**Paper III**) was analyzed by Pearson correlation coefficient. Occupancy (i.e. number of sites where species were present) was correlated with 1) total number of specimens per species and 2) average number of specimens per species per sample. A linear regression line with 95% mean prediction interval was fitted to the resulting scatterplot. The software used was provided by SPSS.

Relationships between number of species and individuals and several factors including monthly rainfall, previous month's rainfall, monthly average temperature and previous month's average temperature were tested by Pearson correlation coefficient (**Paper IV**). Monthly temperatures (minimum, maximum and average) and amount of rainfall (total and average) were measured at ValBio research station in RNP. The distance between ValBio and study sites ranged from a few hundred meters to eight kilometers.

4. Summary of the main results

In this section, I present summaries of the main results of each paper. In total 4498, carabid individuals of 127 species, including 38 new species were collected (Appendix 1).

4.1. Review of carabids as bioindicators

Bioindicators can be defined as organisms that respond to alterations of habitat, indicate responses of other species or reflect diversity of other species. The use of bioindicators is based on their cost-effectiveness, and the possibility of providing early warning of changes in the environment. Selecting the most suitable species as bioindicator depends on the aims of the study – different species reflect different changes in the environment.

Carabid beetles fulfil many of the requirements suggested for a good indicator, including well-known taxonomy and ecology, easy and cost-effective collecting by pitfall traps, sensitivity to environmental factors, broad range of habitat requirements and importance as pest predators. However, there are also several disadvantages including seasonal variation, patchy distribution, and high number of generalist species. In addition, in tropical regions their taxonomy and ecology are poorly known, and they can not be efficiently collected by pitfall trapping.

According to previous studies, the general impacts of forest cutting and fragmentation on carabid beetles are changes in 1) species composition, although species number might remain the same, 2) species abundances changes in some but not all species, 3) decline in specialist species and 4) increased incidence of open habitat species. The results of the suitability test (McGeoch 1998) showed that carabid beetles can be used as environmental bioindicators, but that there is not enough knowledge to facilitate their use as ecological (i.e. how well they reflect the response of other species) or biodiversity indicators.

4.2. Comparison of carabid occurrence in forest and village sites

In total, 245 individuals of 54 species were collected. Comparison of the study areas showed clear differences in their species assemblages; 38 species were collected exclusively from the secondary forest (Talatakely), 28 from the village region and 12 species occurred in both habitats.

There was a high variation in the species richness between sites in both areas. In the forest, the most species-rich site (Figure 5) was a moist area, containing a wide variety of microhabitats (large trees, smaller trees and plenty of logs). The two most species-poor sites in the forest were partly or entirely dominated by the introduced guava (*Psidium cattleianum*). In the village region, the most species-rich site was a moist banana cultivation, mostly surrounded by forest, and the most species-poor sites were a rice field and a pine cultivation. Most of the species were collected from trees. In the village sites, most of the species were from relatively moist spots such as at edges of stones, and under banana leaves.

There was also a high turnover between the same sites at different collection times (i.e. only a few species were found at both of the sampling times). Only six specimens (three species) were collected by pitfall traps. Almost all the trapped carabids were from the same forest site, in which the ground layer was dominated by dead bamboo. Only one specimen was collected from the village area (banana cultivation) by pitfall trapping.

Figure 5. The most species-rich study site in Talatakely.

4.3. Diversity, distribution and community composition of carabid beetles

In total, 4314 individuals belonging to 125 species, including 38 new species, were collected. Only six specimens and two species were collected by trunk traps. The Chao 1 estimate for total species richness was clearly higher than the observed number of species. This indicates that only part of the carabid assemblages were represented in the collected data. Carabid community consisted of three very common species, almost 100 rare species (less than 10 specimens) and a few species of intermediate abundance.

There were 31 species which were represented by only one specimen, while the three most common species were represented by ca 500 specimens each. Almost 40% of the species were found from only one site and 100 species were recorded from ten sites or less. The three most common species had very different distribution patterns; one was widely distributed (found from 43% of the sites), the second was intermediately distributed (found from 24% of the sites), and the third was quite restricted to certain sites (found from 11% of the sites). Despite a high variation between species distribution patterns, there was a positive correlation between abundance and occupancy.

A comparison of the different study areas showed that ~75% of the species were found only from forests, and most were accordingly classified as forest specialists (Appendix 1.). Almost 20% of the species were found both from the forests and from the village area (generalist species) and a minority (<10%) of the species were found only from the open village area (open habitat species).

4.4. Seasonal variation of carabids

In total, 1175 individuals of 50 species were collected. Numbers of individuals and monthly rainfall were highly variable during the year. Number of species was more stable (from 15 to 25) month to month, although species composition changed during the year. Lowest number of individuals was found in May, which is in the "dry season" and the highest number was in February, which is in the rainy season. Numbers of species were lowest in May and June, but highest in September. However, in February, March and November, there were only a few species less. Most (60%) of the species occurred during February–March. Species abundances vary considerably during the year, with 28% of the species found in only one month, and only one species collected in every collecting time.

There was no correlation found between total number of species/individuals and temperature/rainfall using Pearson correlation coefficient nor between the previous month's rainfall/temperature and number of individuals. The only statistically significant correlation (at the 0.05 level) found was between number of species and number of individuals. The abundances of some of the species were positively or negatively correlated with amount of rainfall and/or temperature.

There was considerable monthly variation among abundances of species. Many of the species had their lowest abundance in May and highest in February, but some had maximum abundance during cooler winter months (June-September). Some of the species had one clear peak, while some other species had more than one peak. Only one species (*Lobocolpodes murex*) was found in every sampling time while 28% of species were found only during one month.

5. Discussion

5.1. Suitability of carabids as bioindicators

Carabid beetles can be used for indicating changes in many kinds of alterations in the environment. This is due to high number of species with varying habitat requirements and sensitivity to different environmental factors (moisture, soil quality). Alteration in a certain environmental variable may have different consequences for different species – abundances may increase, decrease or remain the same (Pocock & Jennings 2008). This means that species indicate different patterns of the environment and some species have higher value as bioindicators than others (Chen *et al.* 2006, Pohl *et al.* 2007).

In addition, carabid beetles might not be the most suitable bioindicator in all habitats nor indicate all changes in the environment. For instance, in their study Follner & Henle (2006) found that floodplain grasslands plants were more indicative of the duration of inundation and depth of groundwater than carabid beetle species.

Species which have similar ecological requirements might reflect the response of each other in abundances, and might be used as ecological indicators of each other. However, comparison of the responses of different taxa to changes in environmental variables has shown high variation between species responses (Chen *et al.* 2006, Pohl *et al.* 2007, Pocock & Jennings 2008) and no taxon have proved to be a good indicator for other groups (Billeter *et al.* 2008).

Because of the wide variation of species responses, it is highly unlikely that carabid beetles as a group would indicate response of some other groups. However, there might be some carabid species, which could reflect the response of some other particular species. It is also unlikely that carabid beetles could be used as biodiversity indicators to all other species groups. Studies comparing biodiversity and responses of different taxa, have showed low level of congruence (Barlow *et al*. 2007).

Selection of the proper bioindicator depends on the aims of the study. Because species are sensitive to different ecological factors (e.g. moisture, light, temperature), selection of bioindicator should be based on the sensitivity of the species to that environmental variable that is to be examined in the study.

5.2. Comparison of carabid occurrence in forest and village sites

Forest loss in Madagascar and around RNP has tremendously decreased the primary forest habitat of many species. It is also noticed that plant species diversity is significantly higher inside the protected area than in remnant forests near villages (Brown *et al.* 2009). Comparison of the species compositions of carabids in the protected forest and in the village area showed clear differences in species occurrence and habitat preferences. Of the 54 species only 12 were collected from both areas and clearly more species were found in the forest than in the village area. Human caused habitat alteration has detrimental impact on many carabid species that cannot occupy open areas. However, some moist but degraded sites surrounded by forest contained many species. Moisture is probably one of the most important factors affecting carabid species abundances.

In addition to forest degradation, another major form of human impact in RNP is the introduced guava (*Psidium cattleianum*). Because of the dense stands it forms within forests, it threatens indigenous vegetation (Turk 1996). In guava dominated sites carabid beetle communities were much species poorer than elsewhere in the forest. Because of extensive 'monocultures' there were very few native trees in these sites and, therefore, only little available shelter for carabids, and presumably also for other arthropod species.

5.3. Diversity, distribution and community composition of carabid beetles

Over 4 000 individuals of 125 species were collected, including 38 new species. The species accumulation curves and the high proportion of new species, indicate that only a part of the species assemblages was collected. Because most of the species (88, ca 69%) were recorded in very low abundances (<10 specimens), rarity is a community character also in Malagasy carabid beetles. Relatively high numbers of singletons have been earlier noted in many arthropod groups in the tropics (Novotný & Basset 2000).

Figure 6. *Lobocolpodes murex* was the most common species.

The relationship between average abundance per sample (number of individuals of a species) and occupancy (number of sites occupied by a species) was positively correlated. This means that numerous species are also wider distributed than rarer species. However, the three most common species had very different distribution ranges. *Lobocolpodes murex* (Figure 6) was a forest generalist and found in many of the sites and different kind of forest habitats, while *Neocolpodes* n.sp.1 was very patchily distributed and *Mallopelmus dactaleurys* was intermediate between these two. Therefore, in general, it might be difficult to estimate abundances on the basis of occurrence information, which was also observed by Warren *et al*. (2003).

Most of the species collected were from trees or bushes and are probably arboreal. Arboreal organisms spend at least half of their time during at least one stage of their life cycle in trees (Moffett 2000). Also poor collecting results by pitfall trapping in the forest and buffer zone indicate that only a minority of carabids in RNP are ground-dwelling. However, very little is known about life cycles of Malagasy carabids, their movements and habitat preferences.

A few of the specimens collected could not be reliably identified. This might be due to high variation within species or hybridization between species. Hybridization between two different species or sub-species may cause sterility and lower fitness than parental types, and thereby lead to reduced hybridization (Noor 1995, Higgie *et al.* 2000). However, hybridization may also generate new species (Schwarz *et al.* 2005), and hybrid populations may offer a greater genetic variability for the operation of natural selection (Ayala 1965, Chapman & Burke 2007, Pfennig *et al.* 2007).

Although hybridization is considered to be rare in carabid beetles, there is evidence of hybridization both in nature (Imyra 1989, Mossakowski *et al.* 1990, Obydov 2001, Sota *et al*. 2000, Veyrier *et al.* 2005) and in laboratory conditions (Sota *et al*. 2000). In tropical carabids, hybridization has not been studied or tested by breeding experiments in laboratory.

5.4. Seasonal variation

There was a high variation in abundances of carabid species and individuals throughout the year. Species composition also changed, which appears to be a characteristic of tropical carabid assemblages (Erwin & Scott 1980). Some of the species had only one peak in their abundances, some had two peaks and some had a more even distribution throughout the year. These variations have also been observed in other carabid studies (e.g. Boivin & Hance 2003). Because, species life-cycles (i.e. breeding times, larval development, dormancy period etc.) occur in different times of the year, there might be less competition and more species to coexist.

The high number of individuals in the rainy season and low number in the dry season is in accordance with other studies of seasonal variation of arthropods in tropical region (Tanaka & Tanaka 1982, Pearson & Derr 1986). Temperature and rainfall correlated with abundance of some of the species but not with all. Thus, there are species level differences in response to drought/moisture, as has been observed by Kadar & Szentkiralyi (1997).

According to previous studies, seasonal patterns of carabids are influenced by a variety of factors, including different breeding times (Vennila & Rajagopal 2003), different times of diapause (Vennila & Rajagopal 2003), prey availability (Guillemain *et al.* 1997, Symondson *et al*. 2002), and competition (Currie *et al*. 1996). It is also unknown do species move between habitats during their life cycle. In the future, this could be monitored by radio-telemetrically (Rink & Sinsch 2007, Negro *et al*. 2008). The interactions and implications of these factors are complicated and because the life history patterns of most of the Malagasy carabid fauna are unknown, the causes of their seasonal variation remain unknown.

6. Conclusions

The primary aim of this thesis was to study the effect of the establishment of RNP on the biota using carabid beetles as bioindicators. There is not enough knowledge about how well their diversity or responses represent other species, but they can be used as indicators of the environmental change. This is based on the observation that many of the species prefer certain habitat types and therefore depend on certain environmental variables.

Species inventory of the carabid fauna of RNP revealed high species richness, with a high number of new species. Adaptation to living in the trees and adult activity at different times of year might be reasons of high species diversity in RNP and in tropical areas in general. Most of the species were collected from trees and bushes and it is very probable that most of the forest dwelling species can not adapt for survival in the deforested areas around the protected areas. Without protection of the forest, many of the carabid species would vanish from the area and some might also go extinct. Deforestation, therefore, has a detrimental impact on many species and the establishment of RNP was essential for the survival of these species.

Results of this thesis are mostly based on hand collecting. Use of other methods such as light traps, Malaise traps or canopy fogging, would probably give different results and increase the total number of species found. Time of the year is another affecting factor. This was observed in the seasonal variation of species abundances during the year. There were several species which were caught only during a short time period, and a representative inventory of the whole carabid fauna of RNP would demand a survey covering the whole year or several years.

Forest fragmentation is an especially severe environmental problem in the tropics (Achard 2002). In Madagascar, it is a major threat to all forest ecosystems and only through corridor connections can gene flow be maintained (Hannah *et al*. 1998). Therefore it would be crucial to protect corridor between RNP and the Andringitra National Park and the Ivohibe special reserve.

Protecting the forest not only benefits endemic species, but also plays an important role at local and global levels. Locally, forest cover stabilizes water throughout the year, decreases erosion, and prevents silting of rivers. Forests are also important resources for tourism and research, providing employment and income to local people. Globally, forests reduce global warming but may also have a tremendous potential for medicinal plants.

The establishment of the RNP, prohibiting tavy and the use of natural resources from the national park, has impacted the lives of many people. However, due to the growing human population, tavy is no longer a sustainable landuse practice and without protection forested areas would continue to decrease tremendously. Generating alternative ways of living is the only sustainable way to maintain the forest and improve the livelihoods of local people. Combining nature conservation and improving the livelihood of local people is an extremely slow and difficult process. However, both of these; conservation actions and satisfying the needs of the local people – are necessary for sustainable development and maintaining the unique nature of Madagascar.

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Appendix 1. List of species.

C=classification (F=forest specialist species, FG= forest generalist, G=generalist species and O=open habitat species), total number of specimens/species, Co=collection method (H=Hand collected, P=pitfall trap, T=trunk trap) and numbers of individuals collected from each area.

Species	C	Total	Co	valo	vato	tala	Village
Andrewesinulus n.sp.1_	F	1	H	0	0	1	0
Antimerina elegans Alluad, 1897	F	8	H	2	1	5	0
Astigis sp.1	F	3	H	0	0	3	0
Belonognatha signatipennis Chaudoir, 1869	F	20	H	16	2	2	0
Belonognatha stellulata Fairmaire, 1897	F	7	H	3	2	2	0
Brachypelus n. sp.1		1	P	0	0	1	0
Caelostomus ambiguus Tschitschérine, 1900	F	57	H	33	6	18	0
Caelostomus anthracinus Klug, 1833		1	H	1	0	0	0
Caelostomus cribratus Jeannel, 1948	F	55	H	9	10	36	0
Caelostomus hova Tschitschérine, 1898	F	4	H	1	2	1	0
Caelostomus n.sp.1	F	2	H, P	0	1	1	0
Caelostomus n.sp.2	F	2	H	0	2	0	0
Caelostomus n.sp.3	F	2	H, T	0	0	2	0
Caelostomus nr. Distinctus Brancsik, 1892	FG	5	H	0	0	2	3
Callidiola marginalis Jeannel, 1949		1	H	0	1	0	0
Callidiola olsoufieffi Jeannel, 1949	FG	14	H	2	1	7	4
Calliodiola violaceipennis Jeannel, 1949	FG	14	H	1	2	9	2
Callidiola n.sp.1		1	H	1	0	0	0
Catacolpodes carayoni Basilewski, 1985	F	4	H	1	0	3	0
Catacolpodes scitus Jeannel, 1948	F	98	H	18	55	24	1
Catacolpodes n.sp.1	F	15	H	7	8	0	0
Celiochesis immaculatus Jeannel, 1949		1	H	0	0	0	1
Chlaenius sp.1		1	H	0	0	0	1
Coptoderina umbrina Fairmaire, 1899	F	2	H	2	0	0	0
Crepidogaster kavanaughi Deuve, 2005	F	3	H, T	0	2	1	0
Crepidogaster n.sp.1		1	H	0	0	1	0
Dactyleurus n.sp.1	F	20	H	5	0	15	0
Deuveilla n.sp.1	F	3	H	0	0	3	0
Dinoscaris atrox Bänninger, 1934		1	H	0	1	0	0
Drypta cyanella Chaudoir, 1843	O	5	H	0	0	0	5
Egadroma iridescens Klug, 1833	O	22	H	0	0	1	21
Eucamptognathus n.sp.1		1	H	0	0	1	0
Eucamptognathus n.sp.2		1	H	1	0	0	0
Eucolliuris rudicollis Fairmaire, 1898		1	H	0	0	0	1
Eunostus n.sp.1		1	H	0	1	0	0
Eurydera armata Castelnau, 1831	F	16	H	1	15	0	0
Eurydera foveicollis Jeannel, 1949	F	2	H	0	2	0	0
Eurydera n. sp.1		1	H	0	1	0	0
Eurydera n. sp.2	F	2	H	0	2	0	0
Eurydera n.sp.3	F	2	H	0	0	2	0
Eurydera n.sp.4		1	H	1	0	0	0
Eurydera n.sp.5		1	H	0	0	1	0
Eurydera n.sp.6	F	4	H	0	4	0	0
Eurydera n.sp.7	F	2	H	0	2	0	0
Eurydera n.sp.8	F	2	H	0	0	2	0

Eurydera near armata,		1	H	0	1	0	0
Haplocolpodes perrieri Alluaud, 1899	F	296	H	35	11	250	0
Harpaline sp.1		1	H	0	0	0	1
Hemitelestus hova Alluaud, 1897	F	10	H	0	4	6	0
Lebia madagascariensis Chaudoir, 1850	FG	271	H	45	101	121	4
Lebia sp.1	F	3	H	3	0	0	0
Lebia sp.2.		1	H	0	1	0	0
Lebia sp.3	F	84	H	12	44	28	0
Lebia sp.4		1	H	0	0	1	0
Lebia vadoni Alluaud, *1936*	F	3	H	0	1	2	0
Liagonum hova Alluaud, 1897	FG	102	H	21	25	49	7
Liagonum subsolanum Jeannel, 1948	FG	210	H	74	38	95	3
Liagonum vadoni Basilewski, 1985	G	8	H	1	0	6	1
Lobocolpodes murex Alluaud, 1909	FG	558	H	215	150	161	32
Madecassina alluadi Jeannel, 1949		1	H	0	0	0	1
Madecassina picta Alluaud, 1897	F	9	H	5	2	2	0
Madecassina nr. Tanala Alluaud, 1935	F	99	H	50	38	10	1
Mallopelmus dactaleurys Alluaud, 1936	FG	501	H	128	45	315	13
Mallopelmus n.sp.1	FG	2	H	0	0	1	1
Megalonychus madagascariensis Chaudoir, 1843	G	2	H	0	0	0	2
Michrochila denticollis Jeannel, 1949	F	8	H	0	5	3	0
Microlestes madecassus Alluaud, 1935		1	H	0	0	0	1
Morion n.sp.1	F	2	H	0	2	0	0
Neocolpodes bessoni Alluaud, 1909	F	16	H	10	6	0	0
Neocolpodes eucharis Alluaud, 1935	F	12	H	0	0	12	0
Neocolpodes gemmula Alluaud, 1897	G	22	H	1	4	15	2
Neocolpodes imerinae Alluaud, 1897	F	15	H	5	7	2	1
Neocolpodes isakae Jeannel, 1948	F	9	H	4	2	2	1
Neocolpodes leptoterus Alluaud, 1935	F	76	H	13	0	62	1
Neocolpodes micaauri Alluaud, 1897	G	19	H	0	13	3	3
Neocolpodes nr. phaedrus Alluaud, 1932*	FG	183	H	62	19	91	11
Neocolpodes n.sp.1	F	542	H	124	204	212	2
Neocolpodes n.sp.2	G	18	H	3	0	4	11
Neocolpodes n.sp.3	G	27	H	3	0	8	16
Neocolpodes n.sp.4	G	6	H	0	0	2	4
Neocolpodes n.sp.5	F	3	H	3	0	0	0
Neocolpodes n.sp.6		1	H	0	0	0	1
Neocolpodes n.sp.7	F	5	H	3	2	0	0
Neocolpodes parenthesis Alluaud, 1897	G	111	H	36	53	8	14
Neocolpodes porphyreticus Alluaud, 1935	G	2	H	0	1	0	1
Neocolpodes sp.1	F	54	H	7	33	13	1
Neocolpodes sp.2	FG	123	H	31	82	4	6
Neocolpodes sp.3	G	9	H	7	0	1	1
Neocolpodes sp.4	O	31	H	0	0	0	31
Neocolpodes sublaevis Alluaud, 1909	F	134	H	30	98	6	0
Neocolpodes tanalensis Jeannel, 1948	F	28	H	16	12	0	0
Neocolpodes vagus Alluaud, 1909	F	96	H	26	41	27	2
Nesiodrypta cupripennis Jeannel, 1949	F	2	H	0	1	1	0
Nesiodrypta waterhousei R. Oberthur, 1881	G	58	H	44	7	0	7
Notocolpodes hylonomus Alluaud, 1935	F	140	H	1	0	137	2
Notocolpodes olsoufieffi Alluaud, 1935	F	2	H	0	0	2	0
Nycteis brevicollis Castelnau, 1834		1	H	0	0	0	1
Nycteoscema alluadi Jeannel, 1949	F	3	H	2	0	1	0
Notaphus mixtus Schaum, 1863		1	H	0	0	0	1

Parena alluadi Jeannel, 1949	F	2	H	0	1	1	0
Harpalus tenuestriatus Jeannel, 1948	O	23	H	0	0	0	23
Peliocypas angulosus Jeannel 1949	O	2	H	0	0	0	2
Peliocypas dissimilis Klug, 1833	O	5	H	0	0	0	5
Peliocypas insularis Fairmaire, 1897	G	41	H	15	12	2	12
Peliocypas sicardi Jeannel, 1949	O	2	H	0	0	0	2
Peliocypas n.sp.1		1	H	0	0	0	1
Pentagonica vadoni Jeannel, 1949	G	5	H	0	1	0	4
Pioprosopus aemulus Tschitschérine, 1902	F	5	P	0	0	5	0
Platynine sp.1		1	H	0	1	0	0
Pogonostoma chalybaeum Klug, 1835	G	6	T	2	0	0	4
Pogonostoma sawadai Moravec, 2008	F	4	H	3	1	0	0
Pogonostoma zasterai Moravec, 2003	G	3	T, H	0	0	1	2
Pristacrus n.sp.1		1	H	0	0	1	0
Prodyscherus externus Fairmaire, 1901		1	P	0	0	1	0
Pseudomasoreus catalai Jeannel, 1949		1	H	0	0	1	0
Pseudomasoreus inopinatus Jeannel, 1941	F	3	H	0	0	3	0
Pseudozaena goryi Castelnau, 1834	F	6	H	1	0	5	0
Ripogena n.sp.1	F	4	H	0	4	0	0
Ripogena n.sp.2		1	H	0	1	0	0
Tachys exiguus R. F. Sahlberg, 1844		1	H	0	1	0	0
Tachyura bibula Coquerel, 1866	F	2	H	0	0	2	0
Thyroptecerus perrieri Jeannel, 1949	G	2	H	0	0	1	1
Thysanotus sp.1.	F	26	H	9	7	10	0
Thysanotus n.sp.1	F	7	H	7	0	0	0
Thysanotus n.sp.2	F	2	H	2	0	0	0
Thysanotus n.sp.3	F	4	H	0	1	3	0
Tshitscherinella n.sp.1	G	3	H, P	1	0	1	1
Total number of specimens		4498		1165	1206	1844	283
Total number of species		127		58	64	75	54

*This species may contain hybrid specimens or closely related species.