Structuring of animal communities: Interspecific interactions and habitat selection among ants and small mammals

Habilitationsschrift zur Erlangung der *Venia Legendi* an der
Universität Ulm
Fakultät für Naturwissenschaften

vorgelegt von
Dr. Martin Pfeiffer
Ulm, Oktober 2007

Year's end —
Still in straw hat
And sandals.

Basho (1644-1694)

In dieser Arbeit werden die Untersuchungen zur Gemeinschaftsökologie von Ameisen und Kleinsäugern vorgestellt, die ich zwischen 1997 und 2007 durchgeführt oder betreut habe. Ich versichere, dass ich die vorliegende Arbeit ohne fremde Hilfe angefertigt und mich keiner anderen als der ausdrücklich angegebenen Hilfsmittel bedient habe.

Martin Pfeiffer Ulm, 30. Oktober 2007

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ACKNOWLEDGMENTS

I am grateful to Prof. Dr Elisabeth Kalko for the opportunity to work as a biologist at the University of Ulm, for our productive cooperation, her constant support of my work, and for the pleasure and sense of achievement while teaching and researching at the Institute for Experimental Ecology.

I also thank Prof. Dr Manfred Ayasse for our excellent cooperation and his help during the Habilitation process.

I owe a debt of gratitude to Dr Marco Tschapka and Dr Konstans Wells for our great teamwork, for the many discussions about our work, and for their comments on earlier versions of this Habilitation thesis.

Likewise, I thank all the members of the Institute for Experimental Ecology at the University of Ulm for their support and the inspiring atmosphere during our work, among others Dr Heiko Bellmann, Jakob Fahr, Dr Joanna Fietz, Dr Stefan Jarau, Prof. Dr Gerhard Maier, Dr Johannes Stökl and -last but not least- Ingrid Dillon.

I thank in particular the members of my working group for their help and for all those fun times we had during the past six years: Katrin Deufel, Dirk Mezger, Omid Paknia, Heiko Huttenlocher and Hans Peter Katzmann.

I also thank the technical staff for their various form of support: Malte Petershagen, Jolanta Schenk, Ulrike Stehle, Andrea Weiss, and Gabriele Wiest and all those who helped me during my expeditions and work in Mongolia, Malaysia, and Iran.

Many thanks especially to the many students who worked in our projects and to all our collaborators and co-workers!

Moreover, I am grateful to DAAD, DFG, the Gewinner-Stiftung, and the Pfeiffer family for their various financial supports of my studies.

Most thankful I am to my wife Irmi, who shares my life and work in various countries, “Ohne Dich geht nix!”.

This thesis has greatly benefited from the language corrections by Brian Hillcoat, Neuss.

DISENTANGLING LIFE HISTORIES, ORGANIZATION, AND FUNCTIONS IN ANIMAL COMMUNITIES OF TROPICAL RAINFORESTS AND ARID AREAS – AN OVERVIEW

Currently, an estimated number of 1.5 to 30 million species live on earth (Erwin 1983; Erwin 1991; May 1988). These species are distinctive in their morphology, physiology, and behavior and coexist in regional to local communities. Community composition is influenced by a range of ecological factors (dispersal ability and habitat selection of a species, interspecific interactions), evolutionary processes and historical events (Fig. 1).

Differences in ecological characteristics of species lead to differences in their functionality and their role in ecosystem processes (Darwin and Wallace 1858; Loreau et al. 2001). The questions of which factors structure local communities and how regional species pools contribute to local communities continue to be among the central topics in ecology (Diamond 1975).

Following Fauth et al. (1996), animal "communities" are comprised of at least two species that interact at a given geographical location. Species "assemblages" are defined as a subset of these communities consisting of animals from similar taxa, while a species "ensemble" refers to a set of species that are closely related and use similar resources.

THE NICHE CONCEPT AND ITS LIMITATIONS: A SCIENTIFIC DEBATE

Species have basic ecological requirements that have to be fulfilled to ensure their persistence in a certain local environment. Those requirements determine - in conjunction with interspecific interactions - the distribution of a species within its geographic range. The multidimensional combination of abiotic and biotic factors required for the persistence of a species has been considered as the "ecological niche" (Grinnell 1917; Hutchinson 1957). In contrast, MacArthur and Levins (1967) stressed the impacts of a species on its environment (e.g., its functional role within the food chain, see Elton 1927). Recent concepts combine both aspects in a single definition of the niche of a species as "the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal or greater than its death rate along with the set of per capita impacts of that species on these environmental conditions" (Chase and Leibold 2003).

Starting from the early studies of Hutchinson (1959) and MacArthur (1958; MacArthur 1972a), research efforts in community ecology have attempted to reveal the mechanisms that allow the coexistence of species in local habitats and ecosystems (Brown 1995). Much of the last decades of community ecology have been devoted to the analysis and interpretation of the structure and composition of animal and plant communities.

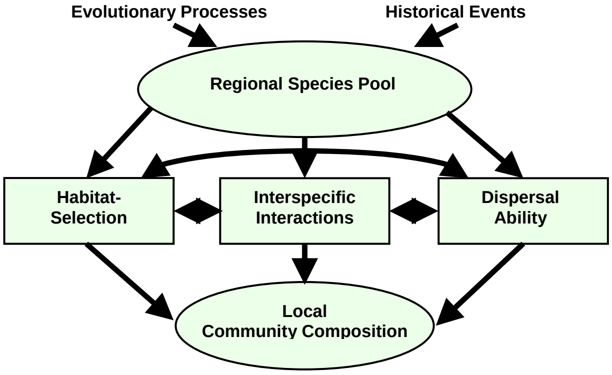

Fig. 1 The recruitment of a local community from a regional species pool is a consequence of many interacting factors (Adapted from Morin 1999).

There are contrasting doctrines on this matter: the "deterministic" view argues that competition is the main driving force in the structuring of communities. This view is linked with the "competitive exclusion principle" as proposed by Gause (1936) and formulated by Hardin (1960). The concept states that two species must differ in some traits related to their fitness in order to coexist. Consequently, coexisting organisms should differ in their ecological requirements (Biesmeijer et al. 1999; Gotelli and McCabe 2002; Graves and Gotelli 1993). As part of this view, community structure is seen as a non-random association of locally coexisting species (Brown 1995). Furthermore, assembly rules have been derived that reflect the tendency of communities to exhibit non-random ecological or taxonomic attributes (Diamond 1975).

Other scientists underline the ecological similarity of coexisting species within local communities compared with a larger species pool. For instance, analyses based on phylogenetic relationships revealed that some communities consist of more related species than expected (Harvey 1996; Williams 1947). This is in conjunction with phylogenetic studies that underline the conservative nature of many ecological species traits within various groups of animals and plants (Barraclough et al. 1999; Lindeman 2000; Silvertown et al. 1997; Webb et al. 2002). A positive assocation between coexistence of species within communities and their phylogenetic relatedness has been postulated (Leibold 1998). This assumption has been confirmed, for instance, for temperate grass communities (Silvertown et al. 2001) and tree communities of tropical rainforests (Webb 2000).

A range of mechanisms has been suggested to better understand the underlying reasons for the co-occurrence of closely related, ecologically similar species (e.g., Chesson 2000; Hubbell 2001; McPeek 2000). In particular, non-equilibrium explanations for the maintenance of diversity have been suggested for particularly species-rich communities where animals with seemingly similar attributes coexist in habitats (Connell 1978; Hutchinson 1961). Here, the so-called "lottery models", which consider community composition as a random draw from a larger species pool, are best at explaining the patterns of co-occurrence in species-rich communities in coral reefs and tropical forests (Brokaw and Busing 2000; Chesson and Warner 1981). These models assume that random events (e.g., tree falls) constantly disturb the habitat, thus preventing the establishment of a climax community and providing free space for colonization by random sets of species from the regional species pool.

With regard to the high biodiversity in the tropics, a strong positive relationship between biodiversity and ecosystem functioning has emerged as a major scientific issue (Loreau 2000; Loreau et al. 2001). Consequently, "functional redundancy" of species in highly diverse ecosystems could provide a buffer that ensures ecosystem functioning even under changing environmental conditions. This assumption is based on non-equilibrium models of community patterns (Loreau 2004). Moreover, recent analyses of ecosystem multi-functionality have revealed that different species affect different processes in an ecosystem, and that more diverse ecosystems can maintain more ecological functions (Hector and Bagchi 2007; Hooper et al. 2005).

In contrast to the classical niche assembly paradigm, Hubbell's (2001) "Unified Neutral Theory of Biodiversity and Biogeography" does not require niche differences to generate realistic predictions regarding species coexistence and relative abundances. It does, however, incorporate immigration and extinction processes, which are termed "ecological drift". Within neutral theory, species traits are treated as neutral and species are hence considered as functionally equivalent in terms of birth, death, dispersal, and speciation (Hubbell 2005)[1]. So far, predictions based on the neutral theory have been only partially applicable, for instance with regard to alpha-diversity patterns of bat species in tropical rainforests[2] (Hubbell 2001), but they failed to describe coral reef beta diversity (Dornelas et al. 2006). Moreover, they were not congruent with beta-diversity patterns of trees in forests of Panama and Amazonia (Condit et al. 2002). As this often-cited and debated model is the most simplified approach to understanding community assembly in species-rich communities; its predictions are likely to be used as null hypotheses for a larger number of community studies as soon as the mathematical tools are available to a greater number of scientists.

Biological diversity varies in space and time at different scales. For example, distribution of species and organization of species assemblages may differ from a local to a regional to a global scale (Blackburn and Gaston 2002; Leibold et al. 2004; Rahbek 2005). Patch heterogeneity has been found to support ecosystem stability. Theoretical models predict that competing species can coexist at regional spatial scales, while crucial trade-offs come into effect at individual, local scales (Kneitel and Chase 2004). These results, and the ideas of the metacommunity concept (Leibold et al. 2004), suggest that some ideas of the "niche" and the competitive exclusion principle need to be revised (Bascompte and Solé 1995; Cottenie 2005; Hubbell 2001).

STUDYING STRUCTURE AND DIVERSITY OF ANIMAL COMMUNITIES

The niche concept, and the question of which factors structure animal communities, provide the framework for the ecological studies that I, together with my co-workers, have conducted over the past six years. A central point of my research focuses on the questions of how local animal assemblages recruit from the larger regional species pool, and how coexisting species partition resources (see Fig. 1). My emphasis is on two main points: 1) habitat selection and its link to species-specific traits, and 2) interspecific interactions that may be responsible for the exclusion of species from local communities.

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[1] Hubbell (2001) suggested that a community can maintain high diversity for long periods of time, while many species are actually on a very slow trajectory towards extinction.

[2] Data from Kalko et al. 1996.

I am conducting my studies in ecosystems 1) with high productivity and species diversity (tropical rainforest), 2) with low productivity and species diversity (desert, steppe), and 3) in temperate regions. Studying communities in areas with contrasting environments (including differences in species diversity and productivity) are likely to reveal crucial elements that contribute to local community composition. I have chosen two groups of animals as focal organisms for my research: ants and small mammals. On the one hand, both groups differ in terms of species richness and biomass, with ants being the group with higher species richness and biomass. On the other hand, both groups show a range of similar traits. They are mobile and use habitats in various ways. Furthermore, they comprise members of different trophic levels and show a rather high degree of omnivory. Species of both taxa are territorial, live in social groups, and are considered to be "ecosystem engineers", exerting a high impact on the structure and function of the ecosystems in which they occur.

I am studying species assemblages of ants and small mammals in their natural habitats to assess the species richness and diversity of their communities and to sample information on species' life history traits. Which kinds of species live together in local assemblages and how do they coexist? How do they partition resources and how do they interact? Is the community mainly structured by partitioning of space or by other functional traits of the species? Is species composition in local communities random or predictable, following niche theory? What about the impact of phylogeny on species structure? What is the impact of scale when looking at the relations between regional and local species pools? These questions are fundamental to a functional understanding of community structure.

My methods towards achieving these research aims comprise a wide range of sampling methods for vertebrates and invertebrates, such as mark-recapture techniques for small mammals with cage-trapping and transponder marking, sampling of ants at baits, with Barber traps or hand collection, and extraction of leaf-litter ants from soil samples with the Winkler apparatus. They also include behavioral observation, radio tracking, stable isotope analysis, microscopy, gaschromatography (GC-MS), the use of statistical methods (null models, multivariate statistics, diversity indices), the application of geostatistical methods (e.g., GIS), and biodiversity informatics.

RESEARCH TOPICS

In the following section I give a brief summary of my studies and research topics, highlighting the most important questions. The chapters refer to publications and manuscripts (see annex) that I have produced during the past six years. Details of the chapters are given after the summary.

In **Chapter 2** www.antbase.net is introduced, a tool to solve the taxonomic problems connected with the study of ants. Communities are composed of species as their basic units. However, especially in the species-rich tropics, proper taxonomic identification is a major problem for community ecologists. This is particularly true for invertebrates, in this case ants. The internet site www.antbase.net, a taxonomic database, summarizes my current research efforts to compile taxonomic and ecological information and provide detailed photographs of more than 400 species of ants. The establishment of this extensive database forms a fundamental part of my work to ultimately overcome the impediment of species identification in this species-rich group. So far, the main emphasis of this new tool focuses mainly on ants from Southeast and Central Asia, where most of my studies have been conducted.

Chapter 3 deals with the assessment of ant communities along environmental gradients in Mongolia and Iran. Based on comprehensive checklists, together with colleagues I clarified the taxonomic identity of the ant fauna of Mongolia and Iran, recording more than a dozen new species for the two countries (Paknia et al. submitted; Pfeiffer et al. 2007). This work establishes the basis for a detailed assessment of ant assemblages in these arid regions, which provide limited resources for a less diverse species pool.

The functional traits of species within these regional species pools can be highlighted by studying communities along a steep environmental gradient that favors different sets of species. We therefore assessed the ant fauna along a north-south transect in Mongolia and found a clear separation into ant assemblages adapted to steppe, semi-desert, and desert biomes. Each assemblage was dominated by different functional groups of ant species that showed contrasting species traits (Pfeiffer et al. 2003). At present a similar study is being conducted in Iran that will supply more information on ant niche patterns of the Middle East, where ecological studies on ants are still lacking.

Besides species traits, animal communities are also structured by ecological interactions. Null models provide an opportunity to study these interspecific relationships by comparing the structure of a real community with those of randomly generated communities. In **Chapter 4** I present null model studies of niche structure in tropical ant assemblages.

The "Ant mosaic theory" postulates that in disturbed habitats with limited resources, such as plantations, dominant species should exclude each other, while still coexisting with a defined set of non-dominant species (e.g., Dejean and Corbara 2003). We found clear evidence for this theory of spatial partitioning in arboreal ant assemblages in a detailed null model study using a comprehensive data set from oil palm plantations in Malaysia (Pfeiffer et al. in press).

Resource partitioning arising from the "size-matching" of ant species and their loads was found to structure assemblages of desert ants (Davidson 1977). In a study on soil ants in Borneo, I investigated whether seed-collecting ant ensembles in the leaf litter of tropical forests are also structured by a similar partitioning of resources. Although ant species showed size-matching between species body size and load size, application of null models revealed that ant ensembles significantly overlap in their food size use, a result that is in contrast to niche models (Pfeiffer et al. 2006).

To answer the question "why can so many ant species coexist in tropical rain forests?" I conducted a comparative study on soil ants in Sarawak. In **Chapter 5** we compare community structure of soil ant assemblages in different forest types. I have gathered with colleagues information about the potential niches of ant species by autecological studies of their temperature and food preferences, and by assessing their trophic status with stable-isotope measurements (Fry 2006). We also sampled soil ant assemblages with Winkler bag extraction and Barber traps to examine community patterns and investigate whether these communities are structured by niche patterns and competitive exclusion of species or by random co-occurrence. Preliminary results of the temperature preferences of ants and their status in soil food webs in Gunung Mulu National Park, Sarawak, suggest that ant species and genera differ significantly in their temperature preferences and occupy different trophic positions in the soil food web.

Ant-plant mutualism is a species interaction that promotes species diversity in different habitats (Beattie and Hughes 2002). In **Chapter 6** I look at "myrmecochory", the dispersal of plant seeds by ants. This interaction is mediated by an ant reward, the "elaiosome", a nutrient-rich appendix of the seed. Starting from a physiological point of view, I focus on the question of which chemical cues in the diaspore trigger the removal of seeds by ants. First results from a set of European spring ephemerals revealed that oleic acid is the main trigger of removal behavior in ants of the species *Formica polyctena* (Pfeiffer et al. manuscript). In this study we compared 10 species of ant-dispersed seeds and found to our surprise that some plant species appear to "cheat" their ant mutualists as they do not provide them with a reward for their seed dispersal (Pfeiffer et al. manuscript).

Another part of this chapter deals with ant-dispersed plants in tropical rainforests and their interaction with ant species. We were the first to describe myrmecochory in Asian ginger (Zingiberaceae) species. Furthermore, we demonstrated that dispersal distances of diaspores are correlated with the size of the dispersing ant species (Pfeiffer et al. 2004).

Small mammals are an important faunistic element of the Bornean rainforest, and pose a variety of questions concerning their community structure. **Chapter 7** discusses the spatial patterns and nesting behavior of small mammals in an assemblage in Kinabalu National Park, Malaysia.

In the first paper in this section, we focused on resource partitioning within a regional community inhabiting a heterogeneous forest habitat. We wanted to know how many species interact in the three-dimensional space of this highly complex habitat, and whether the assemblage was structured by vertical stratification of species and/or differential use of habitat structures. We found 20 species in six families of small mammals that partly overlapped in their microhabitat use and their preference for arboreal or terrestrial habitat (Wells et al. 2004b).

How large are the home ranges of the large pencil-tailed tree mouse, *Chiropodomys major*, the most abundant arboreal species in this area, and how is its use of space organized? The results point towards resource partitioning within a species and at differences based on social structure. We found that home range areas of both sexes overlapped with those of consexuals and with individuals of the opposite sex, suggesting that individuals do not maintain exclusive ranges. However, home range size varied between sexes, with males generally having larger home ranges than females (Wells et al. 2004a).

The last paper in this chapter deals with the form and type of nest sites used by rodents and tree shrews in Borneo. To answer this question we located 83 nests of seven species of non-volant small mammals and categorized them into five main nest types (Wells et al. 2006a).

Habitat destruction by logging of tropical forests is a major concern in animal conservation.

Chapter 8 compares community structure, movement patterns, and parasitic infestation of small mammals in logged and unlogged rainforest. Here, as in other projects, our main focus was on the comparison of species traits and the resulting community structure in contrasting habitats.

Do species diversity, species composition, or variability of small mammal communities differ between pristine and logged rainforests? Our data suggest that species richness of small mammals was significantly higher in pristine forests, but that secondary forests were still able to sustain most of the common species (Wells et al. 2007a). In this study we compared community patterns at local and regional scales. We found similar patterns in diversity and assemblage variability. Due to the pronounced habitat heterogeneity, assemblage compositions in logged and unlogged forest, as revealed by multidimensional scaling, were indistinguishable from each other at the local scale. The differed, however, at aregional scale (Wells et al. 2007a).

Do logging-induced habitat differences influence use of space and movement trajectories of common small mammals? Our results show that all species were affected by altered forest structure in logged forests, reacting species-specifically in their movement trajectories (Wells et al. 2006b).

What are the effects of logging on the movement and range of the giant rat *Leopoldamys sabanus*? We investigated these questions on two scales with both spool-and line tracking and radio tracking. Our results showed that on a small scale, paths had shorter straight-line sections in logged than in unlogged forest. On a larger scale, however, rats showed a high individual variability in movement behavior and did not differ in their movement speed in both forest types (Wells et al. accepted).

In the last paper we investigated the impact of logging on the prevalence and species richness of helminth parasites in small mammals. We found that species composition and abundance patterns of endoparasite assemblages were significantly influenced by logging, with contrasting changes in infection patterns among different host species in unlogged vs. logged forests (Wells et al. 2007b).

SUMMARY

The papers that I present in this thesis focus on two different groups of animals that strongly differ in their species traits: ants and small mammals. I examined community structures in both groups at regional and local scales, and assessed local habitat features in terms of composition, organization, and diversity of local communities. Habitat parameters comprised abiotic (e.g., temperature regimes, soil parameters) as well as biotic variables (e.g., structure and diversity of the underlying vegetation).

Multidimensional statistics were applied to reveal which environmental parameters are important in structuring these communities (Wells et al. 2006b, Pfeiffer, 2003; Wells et al. 2004b). I deduced functional traits of the species that are essential for their specific occurrence patterns as well as their role within assemblages. Traits included preferences in terms of local habitat structure (Wells et al. 2004b), environmental parameters like temperature (Pfeiffer et al. 2003), morphological features, as well as behavioral traits such as foraging and movement activities, and nest-building behavior (Wells et al. 2006a).

Study sites were situated in different biomes on a global scale, including ant studies in Peninsular Malaysia, Borneo, Mongolia (Pfeiffer et al. 2003; Pfeiffer et al. in press; Pfeiffer et al. 2006), and Iran (Paknia et al. submitted). Some studies took place at a more regional scale, e. g., when anthropogenic habitat changes were considered (Wells et al. 2007a), and they could even be located in the same area where we compared different habitat layers (Wells et al. 2004b). The comparison of local and regional species pools was an important method in understanding community patterns and the forces that structure local communities. This was especially true for the rainforest habitat, helping to account for how its great structural heterogeneity leads to locally high community differences among small mammal assemblages.

Taken together, most of our current results are consistent with the niche model, that is supported also for species-rich tropical communities of both ants and small mammals. Only the food-choice experiment with seed-foraging ants (Chapter 3) gave some hints of a structuring of the ant assemblages by non-equilibrium models.

INTERNET-BASED ANT TAXONOMY AND BIODIVERSITY INFORMATICS

The American biologist E.O. Wilson of Harvard University has recently delineated the future of biological taxonomy in a widely regarded article: "Imagine an electronic page for each species of organism on Earth, available everywhere by single access on command" (Wilson 2003a). In this context, the Museum of Comparative Zoology at Harvard University has started an "E-type initiative", with the ultimate aim of putting detailed pictures of 50% of all species on Earth on the internet (http://insects.oeb.harvard.edu/etypes/about.htm). Currently, the debate about the impact of the internet on taxonomy is in full swing (Andersen 2003; Bisby et al. 2002; Blake and Bult 1996; Farr 2006; Godfray 2004; Godfray and Knapp 2004; Gotelli 2004; Guralnick et al. 2007; Huang 2003; Johnson 2007; Lee 2002; Patterson 2003; Scoble 1997; Scoble 2004), and many initiatives have been started. In order to use the opportunities provided by the World Wide Web for taxonomy, ecology and the study of biodiversity, web-based electronic databases on different taxa have been created. International institutions like the Global Biodiversity Information Facility (GBIF) and the Global Taxonomic Initiative (GTI) coordinate the national efforts of museums and universities, and aim at cross-netting and provision of data on species from all over the world. The challenge is immense: currently more than 1.7 million species are described and more than 1.5 billion specimens are housed in the museums of natural history (http://www.gbif.de). The specimen labels, on which their metadata are recorded, comprise a tremendous source of knowledge that document much of what is known about diversity, geographic distribution and phenology of organisms all over the world. Yet most of this knowledge is hardly accessible for researchers, because data are provided on media that are out of reach for the general community and mostly restricted to taxonomists. With the development of biodiversity informatics a new suite of tools is now available that can effectively address these limitations and enlarge the group of potential users (Johnson 2007). Community ecologists will benefit most directly from better access to taxonomic data (Gotelli 2004).

However, the majority of species on Earth are still undescribed and even the total number of species on earth cannot be estimated (Heywood and Watson 1995). On the other hand, habitat destruction and the resulting species loss proceed with great speed on a global scale, especially due to fragmentation and conversion of the tropical rainforests that provide a high percentage of the world's biodiversity (Laurance 1997; Turner 1996; Wilson 1992; Wilson and Peter 1988). Ecologists are trying hard to understand the consequences of these losses, but their work is hampered because taxonomic data are often sparse for those taxa that are assigned to ecological key positions, like pollination or seed dispersal. Proper identification of species, however, is the starting point for effective analyses of animal communities and for a scientific discussion about the ecological role of certain species. In the tropics especially, better knowledge of the species involved is necessary, e.g. for the comparison of species richness between tropical forest sites. In tropical insects the high number of unknown species currently results in the use of "morphospecies". However, those species lists do not allow a comparison of different study sites and a reliable calculation of beta diversity indices (Pfeiffer 2007). Thus comprehensive access by scientists to all available taxonomic descriptions and keys, and the consequent and rapid development and provision of these tools, cover a basic need of biodiversity research in order to keep pace with the rapid destruction of natural environments all over the world (Agosti and Johnson 2002).

In this context the identification of ants may be an especially important element. They play a major role in most terrestrial ecosystems and in different trophic layers, they are taxonomically well studied, easy to catch and - down to genus level - easy to identify; thus they are especially well suited for biodiversity studies (Alonso and Agosti 2000). Together with termites, they dominate all strata of tropical forests and many other habitats in terms of abundance and biomass (Fittkau and Klinge 1973). Ants have special functions as bio-indicators (e.g., Andersen & Majer 2004), and some are efficient invaders of new habitats (Holway et al. 2002). Due to these ecological key functions, ants are increasingly used for biodiversity assessment, and for the comparison of habitats and ecosystems (Agosti et al. 2000; Andersen and Majer 2004; Dunn et al. accepted). A major precondition for this was the comprehensive taxonomic evaluation and cataloguing of the ant fauna, which has made great progress in recent years, resulting in the high number of 12,032 species that are currently described in the Formicidae[3] (Bolton 1994; Bolton 1995; Bolton 2000; Bolton 2003; Bolton et al. 2006). At the same time the availability of taxonomic literature on ants was much improved by an internet portal (www.antbase.org) and the first photo databases on ants that were developed in Japan (http://ant.edb.miyakyo-u.ac.jp/E/index.html) and the USA (www.antweb.org). These databases show the most important taxonomic features of ants in detailed photographs and aim at permitting reliable species identification without the need to use voucher specimens.

A TAXONOMIC ANT DATABASE

In an attempt to contribute to these ongoing efforts, in 2003 the author started a taxonomic photo database (www.antbase.de), dealing with the taxonomy and ecology of ants in a particularly neglected region from which little information on ant taxonomy had been available, seriously hampering scientific research. The major aims of the ANTBASE project are: 1) provision of a source of reliable taxonomic data for the ecological projects in that area; 2) documentation of the overwhelming ant species richness of the Southeast Asian region, and 3) improvement of international cooperation among ant researchers. This virtual museum is based on the large ant collection of the University of Würzburg that houses the specimens of more than 10 years of field work in the primary rain forests of Kinabalu National Park on Borneo, a famous hot spot of diversity (Luping et al. 1978), below the summit of the highest mountain in Southeast Asia (e.g., Aug 1995; Brühl 1996; Floren 1995; Götzke 1994; Malsch 2002; Pfeiffer 1996). The area near the small village of Poring contains, according to current knowledge, the highest species richness of ants on Earth (Brühl et al. 1998)[4].

In many Asian countries, museums of natural history are mostly in the developing phase; taxonomists are rare, and the same is true for scientifically sound identification manuals. This lack of essential scientific infrastructure is also reflected in the number of described insect species, which is clearly below that of the Neotropics (M. Verhaagh, personal communication). In order to strengthen communication and to improve capacity-building, ant researchers have formed a cooperation group ANeT, the international network for ant research in Asia, which is funded by the Japanese Ministry for Cooperation. Besides conducting yearly congresses in different Asian countries, the initiative recently published the first issue of a scientific journal named ASIAN MYRMECOLOGY , which is co-edited by the author.

ANeT is the basis for the cooperation of scientists from 18 countries who are devoted to research on Asian Formicidae (see Fig. 2). This research initiative is supported by the myrmecological site www.antbase.de. The positive impact of this website on Asian ant research has been asserted by several authors who have included the site in their reviews (Agosti 2005; Klingenberg and Verhaagh 2005).

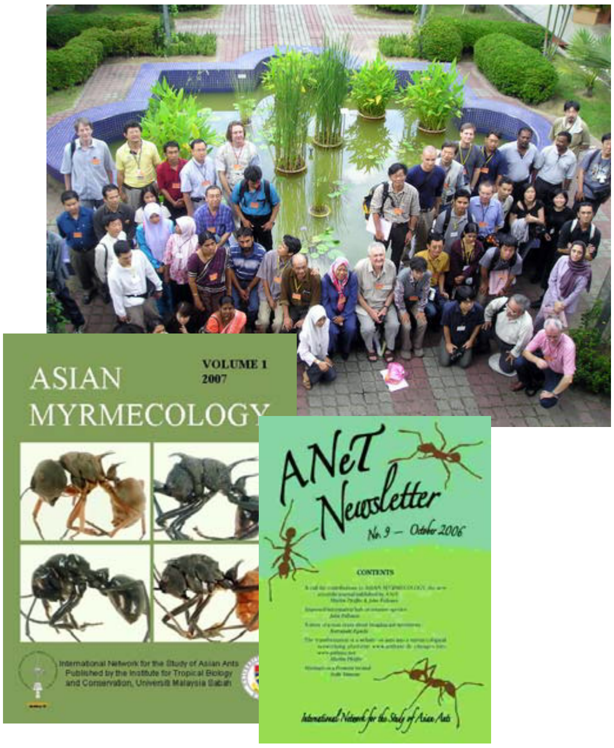

Fig. 2 Above: Members of ANeT at their annual meeting 2006 in Kuala Lumpur. Below: Titles of ANeT publications.

Starting in July 2006, www.antbase.de is now funded by DFG - Scientific Library Services and Information Systems (LIS) within the framework of the Thematic Information Networks program of the German Research Foundation (DFG). This program specifically targets the development of efficient information services and information infrastructures that are essential for the growing demand of the research community for easily accessible information. Since then, the site has been relaunched and renamed as www.antbase.net.

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* A pdf of this chapter with active hyperlinks is available at www.antbase.net.

[3] Number downloaded on 31.08.2007 at http://atbi.biosci.ohio-state.edu:210/hymenoptera/tsa.sppcount?the_taxon=Formicidae

[4] A continually updated species list is available at www.antbase.net in pdf format.

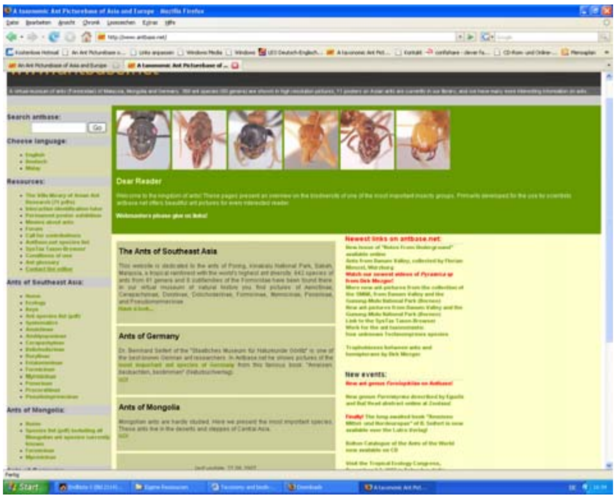


Fig. 3 Screenshot of the front page of www.antbase.net

This recent development and acceptance shows that the website is developing into a myrmecological networking platform (Fig. 3) that includes a much improved photo database, with most species being shown in high-resolution photographs (Fig. 4, 8), and a link to taxonomic information on the species from the Bill Brown Memorial Digital Library (via www.antbase.org) (see Fig. 5). The website is linked to the SysTax database system that is situated at the University of Ulm (AG Jürgen Hoppe) and is the German provider for GBIF, the international network on biodiversity data. All species pages of www.antbase.net are generated from the SysTax database, and most biodiversity and taxonomical data included in SysTax will soon be available, also through the GBIF sites.

Any user with Internet connectivity can utilize this global biodiversity data service and access the GBIF online resources (Edwards 2004). As of April 2007, the GIBIF data portal mediates access to approximately 120 million species-occurrence records from over 1000 collections housed in c. 200 institutions in c. 34 countries (Guralnick et al. 2007). However, a megadata-base like GBIF does not include the benefits of a taxon-specific database like www.antbase.net that provides a better overwiew, additional data sets and information, faster queryable data, quicker updates, and photographs of higher resolution. Moreover, access is planned to all data on ants from GBIF via a portal directly on www.antbase.net. The distribution data may be visualized by "mash-up" information onto Google Earth (Butler 2006), a service already provided at the SysTax portal.

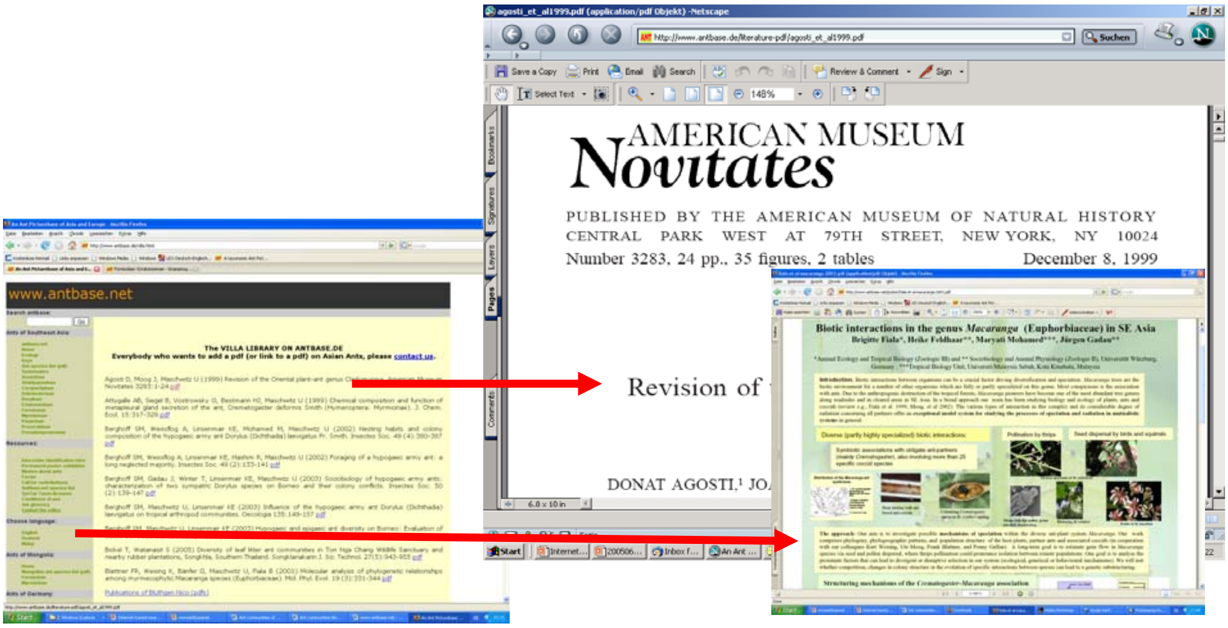
Additional features of our trilingual website (English, German, and Malay) are a web-based pdf library on Asian ants, taxonomic keys for the ant fauna of Borneo (provided by Yoshiaki Hashimoto, University of Hyogo, Japan, see Fig. 6), overview articles on the ecology of Bornean ant species, an exhibition of scientific posters, and a collection of ant videos.

Each specimen is shown in three photographs (frontal, from above, and from the side), and additionally the label is presented (see Fig. 8). Most of the pictures are automontage photographs, consisting of up to 80 single pictures that had been taken with a Leica® camera and processed by the automontage® software (Leica/Synchroscopy) in order to obtain a single high-resolution picture, with an "ultimate depth of field". As the morphology of the specimen is shown on a single picture down to the finest details, the picture provides more information at one glance than the specimen by itself, which in traditional analysis has to be explored by focussing on the different details of the reference specimen with a microscope. Thanks to this outstanding technology, species identification is possible in most cases without the study of the irreplaceable specimens, which can stay in their respective museums without the need for risky journeys to the research lab. Instead of specimens, the ant identifier will study the high-resolution pictures that are freely available via the World Wide Web. This new technique saves much work, time, and the cost of the international lending networking between museums, and allows more people to access specimens at the same time. Although the expertise of the identifier is still needed for the proper identification of the entomological material, the provision of keys and voucher specimens via internet allows us to significantly shorten the processing time.

To overcome the problem of morphospecies during the identification process, standard morphospecies numbers for common Asian species will be provisionally classified by ant experts organized in ANeT. This will be especially valuable in those groups where revisions are overdue and are not likely in the near future (e.g., the extremely species-rich genus *Camponotus*). The "ANeT numbers" will be presented in www.antbase.net and its later use will allow large-scale comparisons of the species data of different researcher groups.

A major step towards the development of a comprehensive web portal for the study of ants will be the inclusion of the FoCol data into the photo database. This data set has been established by Manfred Verhaagh and Christiana Klingenberg of the Natural History Museum of Karlsruhe and includes automontage photographs of all type specimens of ant species that have been deposited in German museums (www.anttypes.org).

Fig. 4 The three-level photodata base on www.antbase.net provides screen-filling ant pictures.


agosti_et_al1999.pdf (application/pdf Objekt) -Netscape

http://www.antbase.de/literature-pdf/agosti_et_al1999.pdf

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3283, 24 pp., 35 figures, 2 tables December 8, 1999

Revision of

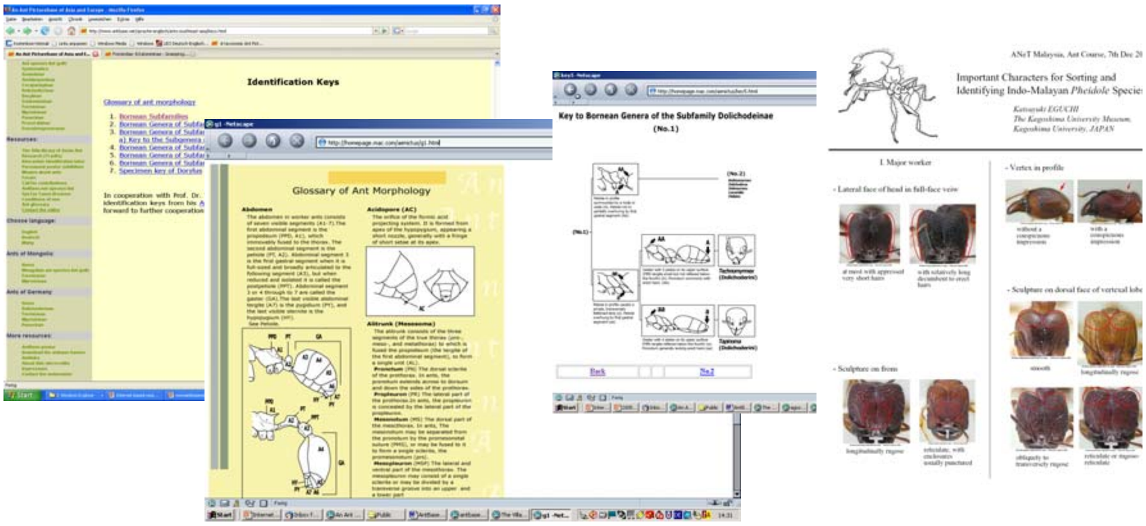
DONAT AGOSTI,¹ JO

www.antbase.net

The VILLA LIBRARY ON ANTBASE.DE
Everybody who wants to add a pdf (or link to a pdf) on Asian Ants, please contact us.

Biotic interactions in the genus *Macaranga* (Euphorbiaceae) in SE Asia

Fig. 5 The “Villa library of Asian Ant Research” provides links to pdfs of original articles. A permanent poster exhibition shows posters by different authors from long-ago conferences.


Identification Keys

Glossary of ant morphology

Glossary of Ant Morphology

Key to Bornean Genera of the Subfamily Dolichoderinae (No.1)

Important Characters for Sorting and Identifying Indo-Malayan *Pheidole* Species

Fig. 6 The keys to subfamilies and genera of Bornean ants are provided by Yoshiaki Hashimoto, University of Hyogo, Japan and are continually updated.

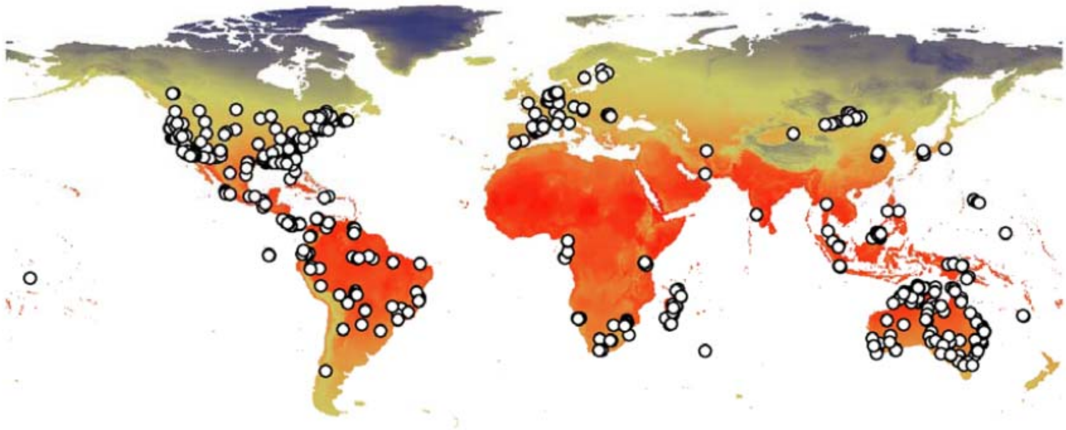


Fig. 7 Location of sites in the Global Ant Database to date. Coloration of the continents reflects mean annual temperatures, with the warmer colors reflecting warmer sites (e.g., red = hot). Data from Mongolia (Pfeiffer et al. 2003) and from Borneo (Pfeiffer et al. 2006) are included in these records. Cited from (Dunn et al. accepted) with permission.

The dataset will be available by the start of 2008 in the SysTax datasystem and comprise more than 2900 type specimens of ants from all over the world that will be available via www.antbase.net.

Following this, the original focus of www.antbase.net, which currently provides data on more than 400 ant species, including about 1200 photographs of Southeast-Asian ants, a complete photographical record of the ant fauna of Mongolia and a set of field photos of many German ant species taken by Bernhard Seifert, will be much expanded. The next steps will include the provision of photographs of the ant fauna of Iran (collaboration with Omid Paknia, University of Ulm), Kyrgyzstan (Kirgiziya) (by Roland Schultz, Zoological Institute & Museum, University of Greifswald), and the "Ants of Central Europe" (in cooperation with Berhard Seifert, Museum of Natural History in Görlitz)[5]. In addition we will provide homepages for all ant researchers cooperating in ANeT and also a database on ant collections in various Asian museums of natural history.

While much more information could have been included in this overview on the activities of www.antbase.net, the only way to truly access the possibilities of this new medium is to visit the myrmecological networking platform in the Internet.

INFRASTRUCTURE FOR GLOBAL ANT DIVERSITY ASSESSMENTS

The meta-analysis of ant distribution data provides new results on the global distribution of ants. Rob Dunn and co-workers have set up a Global Ant Database that also contains some of my data from Borneo and Mongolia (Dunn et al. accepted). Currently 27 scientists are cooperating in this attempt to use standardized data for an assessment of Formicidae global distribution patterns and are publishing their data together (see Fig. 7). The near future will bring some new insights in the global pattern of ant diversity since the database allows the testing of general macroecological theory.

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[5] A more detailed outline of the working program of www.antbase.net is given in Pfeiffer, M. 2006. The transformation of a website on ants into a myrmecological networking platform: www.antbase.de changes into www.antbase.net. ANeT newsletter 9(11-14) which is available at http://homepage.mac.com/dorylus/Resources/No.9.pdf

Anochetus sp. 5
near tua
Brown

det. K. Rościszewski

Malaysia, Negeri Sembilan
2° 59' N, 102° 19' E
Pasoh Forest Reserve
Tropical rain forest
29.1.1992 Rościszewski

AntBase.de No. 00358

SMNK 122
FN 2367
Nest flach im der
Erde
leg. K. Rościszewski

Fig. 8 A set of automontage photographs from www.antbase.net. These pictures have an ultimate depth of field. Shown are the views from the front, above, and the side plus the specimen label. The "antbase number" is an additional label that is attached to the specimen after photographing.

ANT DIVERSITY GRADIENTS AND FAUNISTIC INVENTORY

Biologists have been interested in large-scale patterns of species distribution ever since the great natural history explorations of the Earth in the 18th and 19th centuries (e.g., Humboldt 1997). Documenting and understanding the pattern of species richness has been a central aim of community ecology in recent decades (Brown 1995; MacArthur 1972b; Ricklefs and Schluter 1993; Rosenzweig 1995). Studying the species richness of animals and plants within the context of abiotic environmental gradients contributes to our knowledge of the factors governing and maintaining species diversity, and can illuminate the functional traits of the species (McGill et al. 2006).

However, a detailed faunistic knowledge of the examined habitats is the foundation for a profounder understanding of community patterns.

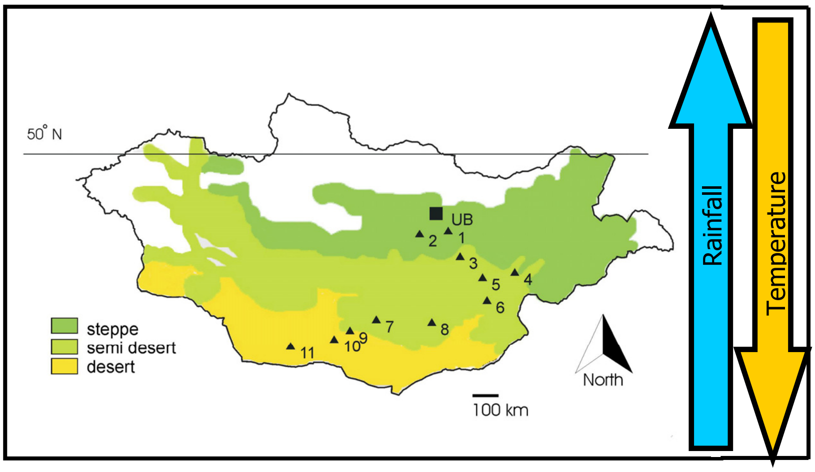


Fig. 9 A map of Mongolia. Given are the capital Ulaanbaatar and the positions of our study sites. The numbers indicate the following points from north to south: (1) Maant, (2) Zorgol, (3) Choir, (4) Delgerekh, (5) Char Airag (6) Saynshand, (7) Bayan-Zag, (8) Manlai, (9) Hongoryn Els, (10) Nemegt, (11) Ekhin Gol. Arrows symbolize the opposing gradients of temperature and precipitation along the transect.

If the species list of the regional fauna is still incomplete, a description of the local ant community is seriously hampered. In many countries of the world ant species lists have yet to be established or updated. This chapter deals with our attempts to do both: comparative community ecology and faunistic inventories of ants.

ANT RESEARCH IN MONGOLIA

The influence of environmental gradients on ant communities has been studied along both rising elevation (Brühl et al. 1999; Fisher 1998; Malsch 2002; Olson 1994; Sanders 2002) and geographical scales (Bestelmeyer and Wiens 2001; Davidson 1977; Marsh 1986; Ward 2000). In general, ant diversity was found to be correlated with net primary productivity (NPP) (Davidson 1977; Kaspari et al. 2000a; Kaspari et al. 2000b,), which is effected by temperature and precipitation. This may lead to hump-shaped patterns of diversity when both gradients run in opposing directions (Sanders 2002; Sanders et al. 2003b).

For this study of ant diversity, we chose a system with strong ecological gradients at the lower end of the productivity scale in order to compare plots with relatively low species richness. In the large Central-Asian cold deserts and steppes, strongly opposing gradients have been found for rainfall and temperature. We recorded ant distribution patterns at 11 study sites during two expeditions along a north-south transect in the Gobi Desert (Fig. 9, 10) and considered the impact of climate and plant cover on ant community structure and diversity.

Although ant community patterns in Mongolia were strongly influenced by climatic parameters, ant diversity was not correlated with plant diversity nor with any measurement of temperature or precipitation (Pfeiffer et al. 2003). Moreover, ant communities differed strongly in terms of feeding guilds and functional groups from those in the hot deserts where much research on ant communities had been conducted previously (Chew and De Vita 1980; Davidson 1977; Marsh 1985; Rojas and Fragoso 2000; Whitford 1978). These results point towards an influence of the harsh climate conditions that prevail in Mongolia.

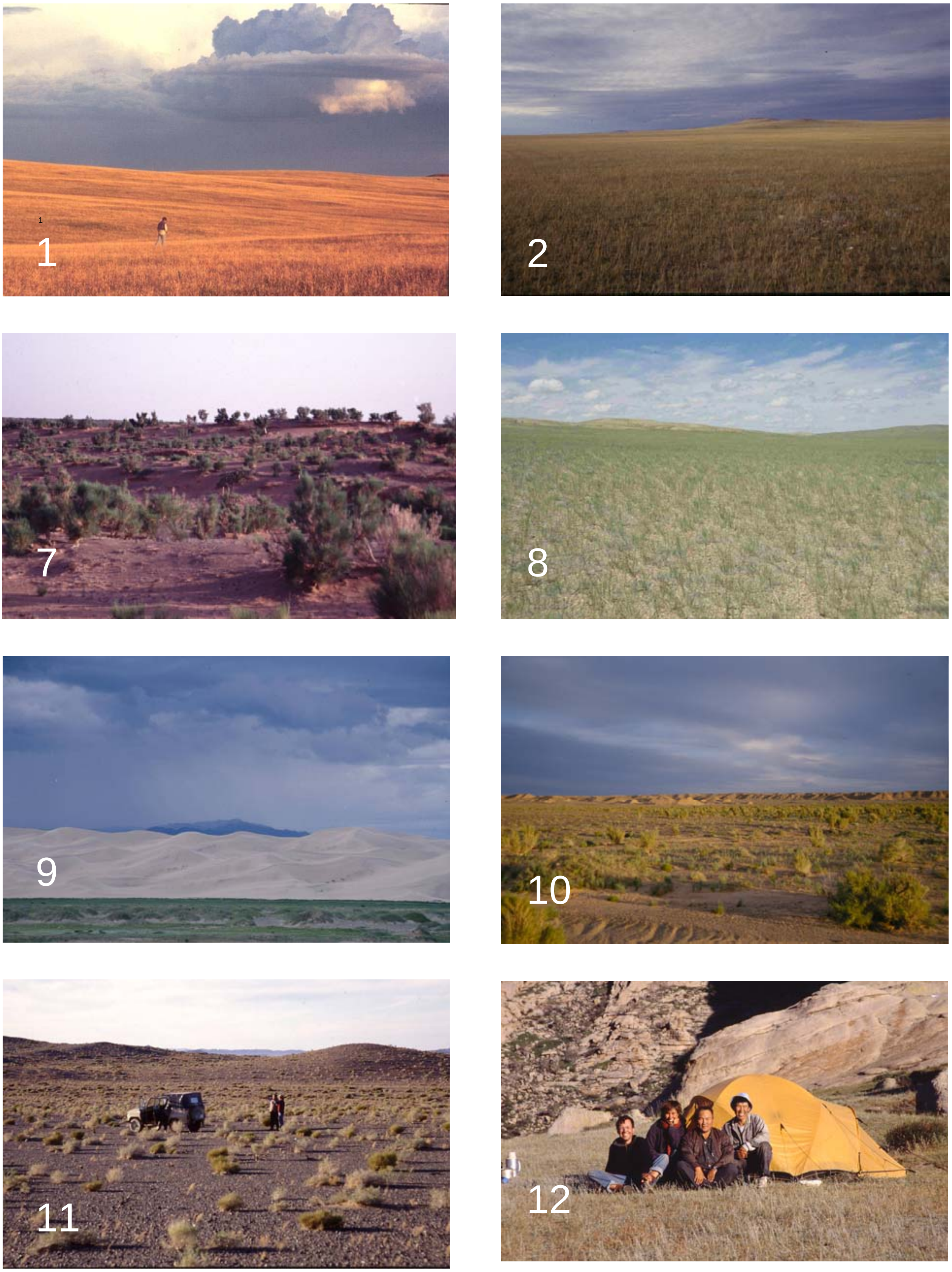


Fig. 10 Study sites along the environmental gradient. Some of the numbers correspond to the map in Fig. 9. (1) Maant, (2) Zorgol, (7) Bayan-Zag, (8) Manlai, (9) Hongoryn Els, (10) Nemegt, (11) Ekhin Gol (12) Members of the first expedition 1997 after finishing their work.

While ant species richness in the plots was not correlated with any environmental data on the studied scale (biomes), the data fit well in a correlation on a global scale that was recently calculated from data of the Global Ant Data Base (Dunn et al. in prep.). This result corroborates the need to study ecosystems on different scales to fully understand the observed patterns.

During the evaluation of the data we faced serious taxonomical problems, although the Mongolian ant species had been sampled intensively by the Hungarian entomologist Z. Kaszab during his extensive travels through the country about 40 years ago (Dlussky 1965; Dlussky and Pisarski 1970; Kaszab 1969; Pisarski 1969; Pisarski and Krzysztofiak 1981). In order to compare species at a regional scale we had to clarify the taxonomic status of many of the species, and so compiled a catalogue of Mongolian ant species. Our critical species list contained 68 ant species in 17 genera within the current borders of the country, including 6 species that were new to the Mongolian fauna (Pfeiffer et al. 2007). Such an extensive faunal study that compares collections housed in different museums, and combines the efforts of ecologists and taxonomists of several countries, is necessary to provide a proper basis for further studies of ant biodiversity and community ecology in this remote region.

Further ecological studies in Mongolia should focus on niche patterns of co-existing species and comprise ant activity patterns, thermal preferences, morphology, nest densities, and food choice. Further assessing the impact of scale effects will be another interesting aspect of studies.

Fig. 11 Field work in the Caspian forest. Extraction of soil samples with Winkler bags. Left: Omid Paknia.

RECORDING THE ANTS OF IRAN

While the project in Mongolia is still ongoing, a comparable project has been started in Iran. For the first time we conducted an inventory of the ant fauna of the country that included an intensive study of museum specimens and a review of the complete literature on the Iranian ant fauna. As a result we recorded 120 ant species for the Iranian fauna, while we found ten species that were new records for the country (Paknia et al. submitted). This preliminary species list is the starting point for the more detailed PhD study of ant community patterns within different habitats in Iran (Fig. 11). As the country is located between three biogeographic realms, the Palearctic, the Afroethiopian, and the Indo-Malayan, we expect to find many new species.

In 2007 our field study was conducted at 10 sample sites along a transect of 1600 km from the north to the south of Iran, across three main biomes (temperate broadleaf and mixed forests, temperate coniferous forests, and desert and xeric shrublands) (Fig. 12), and five main ecoregions (Caspian Hyrcanian mixed forests, Elburz Range forest steppe, Central Persian desert basins, Zagros Mountains forest steppe, and South Iran Nubo Sindian desert and semi-desert). We started field work with a survey of the ants of the Caspian forests, and all sampling sites have now been collected once. Since we are sampling not only the north-south gradient, but also local altitudinal gradients, we expect a lot of new results on ant species niche patterns, and on the effects of scale (extent and grain size) on ant diversity patterns.

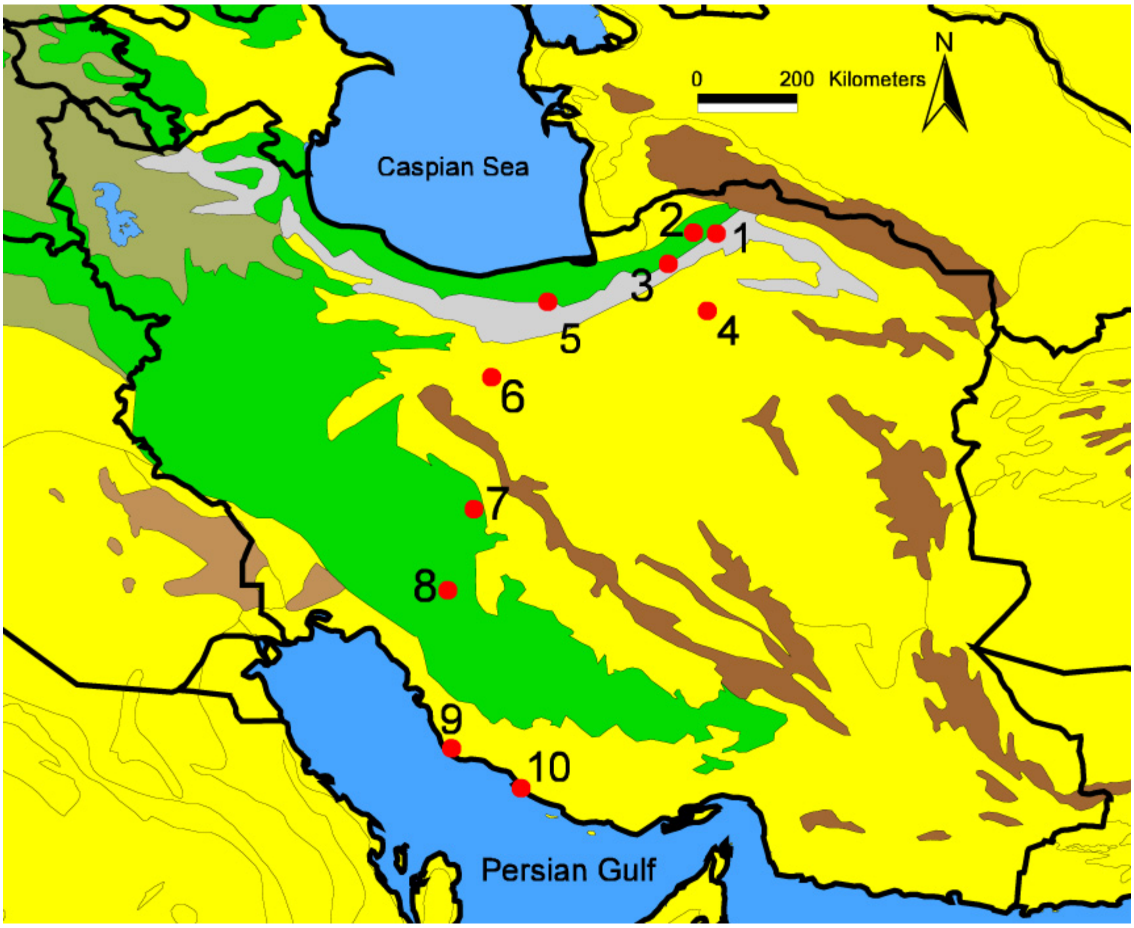


Fig. 12 Map of biomes of Iran: three main biomes were sampled along transects (green: temperate broadleaf and mixed forests, gray: temperate coniferous forests, and yellow: desert and xeric shrublands). Red points shows the sample sites (1- Mirzabilu steppe, 2- Golestan forest, 3- Khoshyelagh steppe, 4- Turan arid area, 5- Farim forest, 6- Kavir arid area, 7- Kolah ghazi arid area, 8- Dena semi-arid area, 9- Mond arid area, 10- Naiband arid area) (Cited from Paknia and Pfeiffer 2007).

NULL MODEL STUDIES OF INTERSPECIFIC INTERACTIONS: COMMUNITY STRUCTURE OF MALAYSIAN ANTS

While analyzing community patterns along an environmental gradient may be help to identify functional traits of the species that act during habitat selection, the appraisal of interspecific interactions is necessary to gain information about the processes that regulate the coexistence of species in local communities.

For an assessment of local community patterns, null models have been widely applied by ecologists and biogeographers (Dunn et al. 2007; Gotelli and McCabe 2002; Jetz and Rahbek 2001; Sanders et al. 2003a; Silvertown et al. 2001). Null models are pattern-generating models that by design exclude a mechanism of interest, and allow for randomization tests (Gotelli 2001). Thus the actual structure (of communities) is compared to a randomized pattern. This kind of statistical tool has also been used in some of my studies that were aimed at identifying the interspecific processes that structure ant communities (Pfeiffer et al. in press; Pfeiffer et al. 2006).

ARBOREAL ANT MOSAICS IN OIL PALM PLANTATIONS

The concept of “ant mosaics” arose when entomologists studied hierarchies within ant communities in different crop plantations in various parts of the world in order to get more information about the use of ants for biological control (e.g., Dejean and Corbara 2003; Leston 1973). Ant mosaics are patchworks of (arboreal) ant territories, each dominated by different species, mutually excluding each other from distinct canopy areas (Blüthgen et al. 2003; Dejean et al. 1994; Dejean et al. 1999; Dejean et al. 1997b; Jackson 1984).

Dominant ant colonies sustain themselves on honeydew from associated trophobionts and can reach very high populations with territories that comprise up to several palm trees and are defended against other dominant species (Fig. 13), while non-dominant ants are tolerated in the territories (Fig. 14). The understanding of ant mosaics is essential for ecological agriculture, as structure and composition of the mosaics have a strong influence on invertebrate communities within the crops (Leston 1973; Majer 1993) and manipulation of ant mosaics may be an effective method of biological control (Ho 1994).

Fig. 13 Dominant ants are characterized by a) polydomous nests (here a tiny nest of *Technomyrmex albipes*); b) absolute territories (*Oecophylla smaragdina* workers have spreadeagled a forager of *Camponotus* sp.); c) association with trophobionts that provide highly energetic honeydew (*Oecophylla smaragdina* at a scale insect).

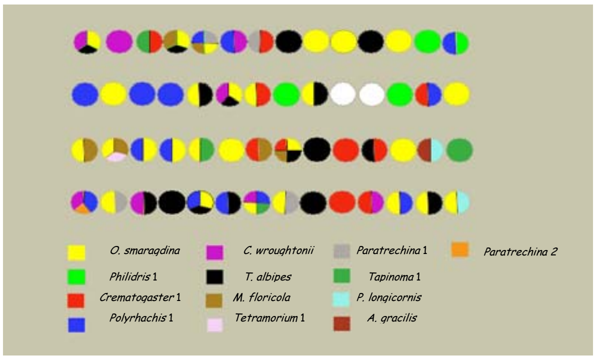


Fig. 14 Mapping of ant assemblages on oil palms. Each circle represents one palm and the different colors represent the different ant species.

Fig. 15 Malaysian oil palm plantations provide huge areas of uniform plant structures that are well suited for the test of ecological theories, but house a less diverse ant fauna.

In close interaction with Golden Hope Plantations Berhad, a Malaysian palm oil company, we studied arboreal ant mosaics in two oil palm plantations in Peninsular Malaysia and on Borneo (Fig. 15), obtaining one of the largest data sets from tropical plantations worldwide (c.f., Pfeiffer et al. in press; Sanders et al. 2007). Due to their large size and uniform plant structure, crop plantations are ideally suited for a null model study. We were able to confirm the value of the ant mosaic model for the detailed description of ant communities in crop plantations by stepwise use of null models for the first time (Pfeiffer et al. in press).

At the same time, we studied ant diversity patterns within the plantations in order to obtain reliable data for the ongoing discussion on the loss of biodiversity caused by the huge agro-forestry areas (Donald 2004). Oil palm plantations covered 4 million ha in Malaysia by 2005 (Wahid 2006) and will be further enlarged. Apart from the expected low species richness in the plantations, we found an alarming influence of invasive ant species (see Fig. 16): more than half of all species occurrences were of tramp ants (Pfeiffer et al. in press). These data highlight the problems of ant species invasions (Holway et al. 2002; McGlynn 1999) that go hand in hand with a loss of diversity (Kennedy et al. 2002), endanger natural ant communities (Sanders et al. 2003a), disrupt plant reproductive mutualisms (Ness et al. 2004; Traveset and Richardson 2006), and hamper ecosystem functioning (Bond and Slingsby 1984; Lester and Tavite 2004).

Further research in the oil palm plantations comprised the sampling of the ground ant community and the evaluation of focus species for biological control (Pfeiffer, unpublished data, Fig. 17).

Fig. 16 Some of the ant species found in oil palm plantations. From top left to down right: *Pristomyrmex pungens*, *Philidris* sp., *Technomyrmex albipes* (i), *Oecophylla smaragdina*, *Anoplolepis gracilipes* (i), *Polyrhachis bicolor*, *Monomorium floricola* (t), *Cardiocondyla wroughtonii* (t). Species marked with (i) are invasives; those with (t) are tramp species.

Fig. 17 *Oecophylla* workers attacking a nettle caterpillar, *Setothosea assigna*, a common oil palm pest.

FOOD CHOICE IN GRANIVOROUS RAIN FOREST ANTS

Resource partitioning of species is a well-known mechanism to reduce diatary overlap and interspecific competition in ants (Hölldobler and Wilson 1990; Simberloff and Dayan 1991). In the southwest desert regions of the USA, granviorous ant species with different body sizes use seeds of different sizes in their diet (Davidson 1977). This interaction has been widely used as an example of resource partitioning. Little, however, is known about seed use of ants in rainforest habitats (Kaspari 1993; Kaspari 1996), although ants may negatively affect seedling establishment in different strata of the forest (Laman 1996).

Seeds are abundant on the forest floor of the Bornean rainforests, and are used by many ant species as a food resource (MP, personal observations), so we investigated the ensembles of those ants that feed on seeds and the patterns of resource-portioning among species. We were surprised to find many of the tiniest ant species at our seed baits (Fig. 18), which attracted a wide range of ground ant species, including *Pheidole* species that are well known for their species richness in Bornean habitats (Eguchi 2001). We used a null model to assess the relationship between food use and body size of ground-dwelling ant species in three rainforests on Borneo island (Pfeiffer et al. 2006). We found a "size matching" of ant species with their load, but no resource partitioning within the three ant ensembles that contrarily showed a significant species overlap in their food-size use. As most ants may have been omnivorous species rather than true seed specialists, our results may describe all kinds of food choice by ants in species-rich habitats.

Fig. 18 A seed bait with a tiny *Oligomyrmex* ant.

THE SARAWAK SOIL ANT PROJECT: NICHES, TROPHIC LEVELS, AND COMMUNITY PATTERNS IN RAINFOREST ANTS

Little is known about the food webs of tropical soils and the role of the different taxonomic groups within them. Ants play an important role in these interactions, not only because of their high abundance and steady presence within all layers of tropical habitats, but also because of their different herbivore, carnivore, and detrivore food spectra (Agosti et al. 2000). The large radiation of certain ant genera (Bolton 2000; Eguchi 2001; Wilson 2003b), and the high diversity of the epigeic and hypogeic ant communities (e.g., Brühl 2001; Brühl et al. 2003; Brühl et al. 1999; Malsch 2002) are recognized, but the reasons for these diversifications are still unknown.

In our ongoing project in Gunung Mulu National Park Sarawak/ Malaysia, we are investigating soil ant communities in four types of tropical rainforest that differ in soil conditions and vegetation structure: alluvial forest, dipterocarp forest, limestone forest, and *kerangas* (Fig. 19).

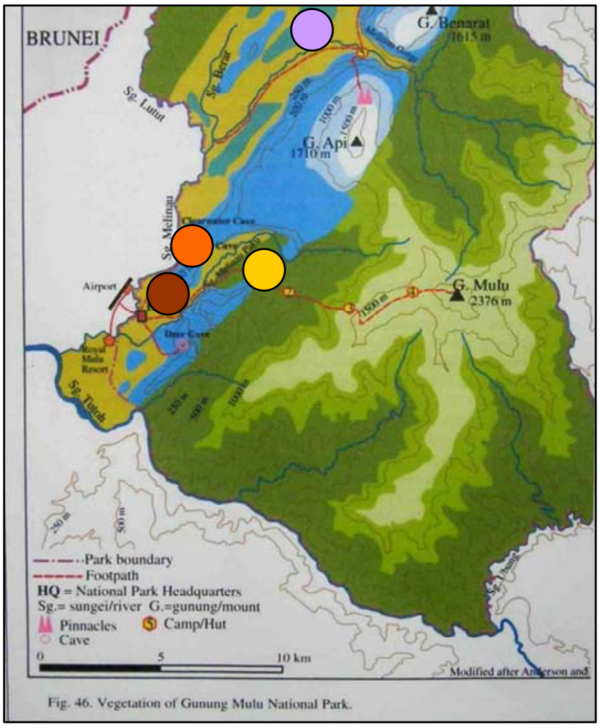


Fig. 19 Our study areas in different parts of the Gunung Mulu National Park in Sarawak, famous for the different forest types that are situated close together ● Alluvial forest, ● Limestone forest, ● Dipterocarp forest, ● Kerangas.

Fig. 20 Sampling ants from the leaf litter is team work under hard conditions. Right side: Dirk Mezger

We study diversity and species structure of communities according to the ALL protocol that investigates soil fauna using Winkler extraction and pitfall traps (Agosti and Alonso 2000)(Fig. 20). In addition, we examine the status and function of ants within the soil food web by analyzing stable isotope (δ 13C und δ 15N) ratios in the macro- and mesofauna of the soil, and we also explore ants niche parameters (temperature and humidity preferences of the different ant species), territorial behavior, and food spectra.The outcome of this study is expected to serve as a basis for establishing a model of the niche patterns of ant species that will be compared with the actual species composition within the plots. Then we can evaluate whether the structure of ant assemblages in the soil is influenced by niche or random processes, and how interspecific interaction is involved in structuring the communities. The results of the study might provide an explanation for why so many species of ants coexist in tropical soil and leaf litter habitats.

While fieldwork is still ongoing, we here present a few preliminary results of this study to illustrate our research approach (Mezger & Pfeiffer unpublished data).

DIVERSITY OF SOIL ANTS

After examination of 11 and 12 Winkler samples for alluvial, respective limestone forest. we found 68 species of ants in the alluvial forest and 84 species in the limestone forest. Species rarefaction curves indicate that species saturation is still not reached (Fig. 21).

TEMPERATURE NICHES OF ANT SPECIES

We measured temperature preferences of soil ant colonies in our lab in Gunung Mulu National Park (Fig. 23) in a “temperature organ”, an apparatus that allows the establishment of a temperature gradient in the laboratory. Complete colonies of tiny ant species (body size < 5 mm) were removed from their nests and put into the temperature organ for 24 hours, where they settled their eggs and larvae at a point along the gradient. Preferred temperatures of ant species differed among nest types and genera (Fig. 22). These first results strengthen the hypothesis that soil ant communities are structured along a temperature gradient.

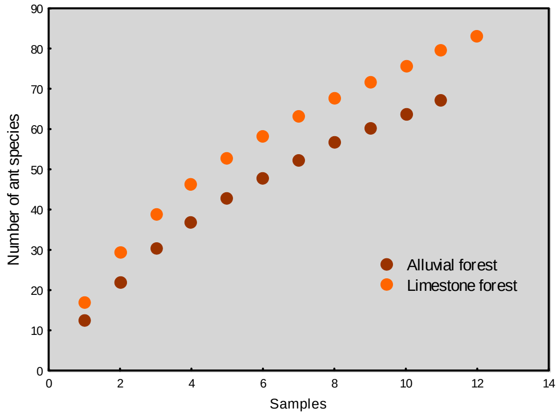


Fig. 21 Preliminary rarefaction plot of alluvial and limestone forest in Gunung Mulu NP, the graphs are still ascending, indicating that species saturation is still not reached and further samples have to be evaluated.

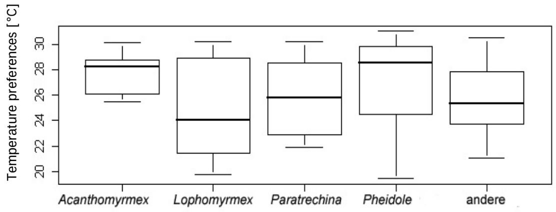


Fig. 22 Temperature preferences of different ant genera.

Fig. 23 A view to the lab in Gunung Mulu National Park.

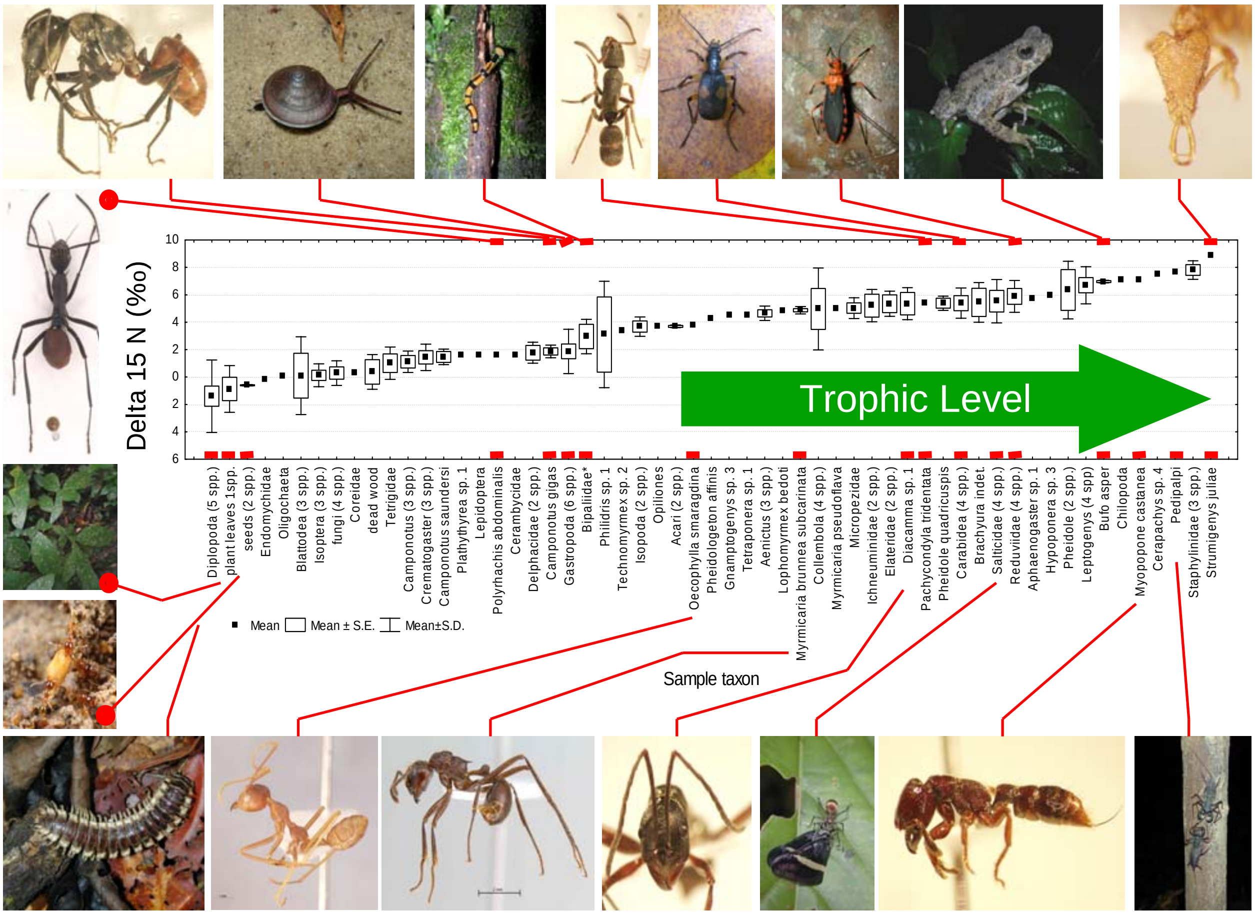
STATUS OF DIFFERENT ANT SPECIES IN THE SOIL FOOD WEB

Based on the evaluation of 140 samples of ants (nest samples) and other materials (plant and animal tissue) we analyzed the food web of the alluvial forest. The 15N/14N ratios of the soil animals in the alluvial forest varied strongly, spanning nearly 15 δ15N units (-5.8 to 8.8 ‰ δ15N). However, the great majority of the species studied varied only between -1.4 and +8.8 ‰δ 15 N units. As trophic levels differ by 3.4 δ 15N units on average (Minagawa & Wada 1985), we can conclude that the soil food web in the alluvial forest of Gunung Mulu NP may span at least 3 trophic levels. Ants were present in each of the levels; they comprise primary consumers (possibly via honeydew from trophobionts) as well as top predators (Fig. 24). Our data corroborate the idea that ants occupy a wide range of trophic positions in the soil food web and thus are crucial for ecosystem functioning in tropical forests.

Next page:

Fig. 24 (above) Measurements of 15N/14N ratios of animals and resources of the soil food web of the alluvial forest at Gunung Mulu, Borneo (see Fig. 25). Red lines connect the data to the corresponding photographs of the species. Ants comprised members of three trophic levels (Photos Mezger & Pfeiffer).

Fig. 25 (below) A view inside the alluvial forest.


Delta 15 N (‰)
10
8
6
4
2
0
2
4
6
Trophic Level
Diplopoda (5 spp.)
plant leaves 1spp.
seeds (2 spp.)
Endomychidae
Oligochaeta
Blattodea (3 spp.)
Isoptera (3 spp.)
fungi (4 spp.)
Coreidae
dead wood
Tetrigidae
Camponotus (3 spp.)
Crematogaster (3 spp.)
Camponotus saundersi
Plathythyrea sp. 1
Lepidoptera
Polyrhachis abdominalis
Cerambycidae
Delphacidae (2 spp.)
Camponotus gigas
Gastropoda (6 spp.)
Bipaliidae*
Philidris sp. 1
Technomyrmex sp. 2
Isopoda (2 spp.)
Opiliones
Acari (2 spp.)
Oecophylla smaragdina
Pheidologeton affinis
Gnamptogenys sp. 3
Tetraponera sp. 1
Aenictus (3 spp.)
Lophomyrmex bedoti
Myrmicaria brunnea subcarinata
Collembola (4 spp.)
Myrmicaria pseudoflava
Micropezidae
Ichneuminidae (2 spp.)
Elateridae (2 spp.)
Diacamma sp. 1
Pachycondyla tridentata
Pheidole quadricuspis
Carabidea (4 spp.)
Brachyura indet.
Salticidae (4 spp.)
Reduviidae (4 spp.)
Aphaenogaster sp. 1
Hypoponera sp. 3
Pheidole (2 spp.)
Leptogenys (4 spp)
Bufo asper
Chilopoda
Myopopone castanea
Cerapachys sp. 4
Pedipalpi
Staphylinidae (3 spp.)
Strumigenys juliae
Mean
Mean ± S.E.
Mean±S.D.
Sample taxon

ANT- PLANT MUTUALISM: MYRMECOCHORY - SEED DISPERSAL BY ANTS

It was the Swedish botanist Sernander who, about a hundred years ago, laid the foundation for the study of myrmecochory, seed dispersal by ants, with his voluminous book "Outline of a monograph of the European myrmecochores" (Sernander 1906). Since that time seed dispersal by ants has been studied in different ecosystems and continents (Beattie and Culver 1981; Berg 1975; Buckley 1982; Higashi et al. 1989; Horvitz and Beattie 1980; Rice and Westoby 1981; Ulbrich 1919). In the meantime more than 3000 plant species have been identified as "myrmecochores" - predominantly ant-dispersed plants (Beattie 1983; Beattie and Hughes 2002; Berg 1975; Hughes and Westoby 1992; Ohkawara et al. 1996).

Myrmecochory has formed in a co-evolution of ants and plants (Buckley 1982; Jolivet 1996; McKey 1975). Myrmecochorous seeds generally bear a nutrient-rich appendage, the elaiosome (Fig. 26), which induces some ant species to carry the whole diaspore (seed with elaiosome) back to the nest, where the elaiosome is consumed and the seed ultimately is discharged unharmed (Culver and Beattie 1980; Handel and Beattie 1990; Hughes and Westoby 1992; Ulbrich 1919) (Fig. 27). Four of the seven ant families disperse myrmecochorous seeds (Sheridan et al. 1996).

The benefits of myrmecochory to plants have been investigated in detail. As the seeds are taken to the often subterranean ant nest, they escape from predators and fires (Bond and Breytenbach 1985; Handel and Beattie 1990; Heithaus 1981; Ohkawara et al. 1996) and from the increased competition between seedlings near the mother plant (Gorb and Gorb 1997). Soils in ant nest soils have higher nutrient contents, which may increase germination rates as well as seedling survival and growth (Andersen 1988b; Beattie and Culver 1983; Horvitz and Schemske 1986). Dispersal costs for plants are relatively low (Hughes et al. 1993), however dispersal distances are shorter than those of other dispersal modes (Willson and Traveset 2000), though they can reach up to 77 m (Andersen 1988a; Gomez and Espadaler 1998).

Fig. 26 Diaspore of *Helleborus foetidus*, note the large, whitish elaiosome.

Ants benefit from myrmecochorous interactions by consuming the nutrient-rich elaiosome (Edwards et al. 2006). It is also called "ant fruit" and resembles an insect larva in its size, the often whitish color, and its chemical composition (Hughes et al. 1994). Elaiosomes provide for the ants a resource with high concentrations of proteins, lipids, and carbohydrates (Bresinsky 1963; Hughes et al. 1994; Lanza et al. 1992; Marshall et al. 1979; Morrone et al. 2000; Soukup and Holman 1987). Additionally, elaiosomes offer essential nutrients that the ants cannot synthesize themselves: unsaturated fatty acids and sterols, including cholesterol and β-sitosterol (Boulay et al. 2006; Brew et al. 1989; Gammans et al. 2005; Soukup and Holman 1987). Several studies have confirmed that ant colony size and/or reproductive output are enhanced by the consumption of seed elaiosomes (Fischer et al. 2005; Gammans et al. 2005; Morales and Heithaus 1998).

Seed-carrying behavior in ants is influenced by the fatty acid composition of the elaiosome (Boulay et al. 2006; Brew et al. 1989; Hughes et al. 1994; Marshall et al. 1979; Skidmore and Heithaus 1988). The diglycerid 1-2-diolein, which consists of two molecules of oleic acid, was found to elicit seed-removal behavior in ants for *Viola odorata* (Marshall et al. 1979). Other studies confirmed the importance of oleic acid in its free form, or as di- or triglyceride, for the induction of seed transport to the nest (Boulay et al. 2006; Brew et al. 1989; Hughes et al. 1994). Similarly, seeds adapted to dispersal by birds may also attract ants and induce seed-transport behavior in relation to size and lipid-content of their arils (Pizo and Oliveira 2001). Oleic acid is also known as a chemical releaser of necrophoric behavior in ants and has been reported to induce transport of dead nestmates to the nest middens (Wilson et al. 1958).

Fig. 27 ***Formica polyctena*** **with a diaspore of** ***Asarum europaeum*** **(Photo: S. Thamm).**

STUDYING SERNANDER'S TYPES OF MYRMECOCHORES

Sernander (1906) developed a typology of ant-dispersed diaspores and classified 15 types of myrmecochores, based on the morphology and phylogenetic origin of the elaiosome (see Fig. 28). However, almost all of these studies on myrmecochory focussed on the "*Viola odorata*-type" of diaspores, with seeds that have a large and clearly separated elaiosome that originates from the ovule (Bresinsky 1963).

A first attempt at a detailed study of the other elaiosome types was made by the author and co-workers, who studied diaspore removal in different types of myrmecochorous and non-myrmecochorous plants by a colony of *Formica polyctena* (Fig. 27) (Pfeiffer et al. manuscript). They compared diaspores of the *Viola odorata* type to those of the *Puschkinia* and *Hepatica* type among ten plant species. The latter comprised three species of the Ranunculaceae that were compared with morphologically very similar non-myrmecochorous diaspores of the same family (Fig. 28). Across the studied plant species, removal rates of ants were significantly influenced by the fatty acid content of the diaspores and were higher in myrmecochorous types than in non-myrmecochorous diaspores. While morphological differences of the diaspores influenced removal rates significantly, oleic acid was the trigger of the removal behavior, as shown by dummy experiments and discriminant analysis of the fatty acids. Authors confirmed the typology of Sernander (1906) by a PCA of the diaspore characteristics (see Fig. 10, in Pfeiffer et al. manuscript).

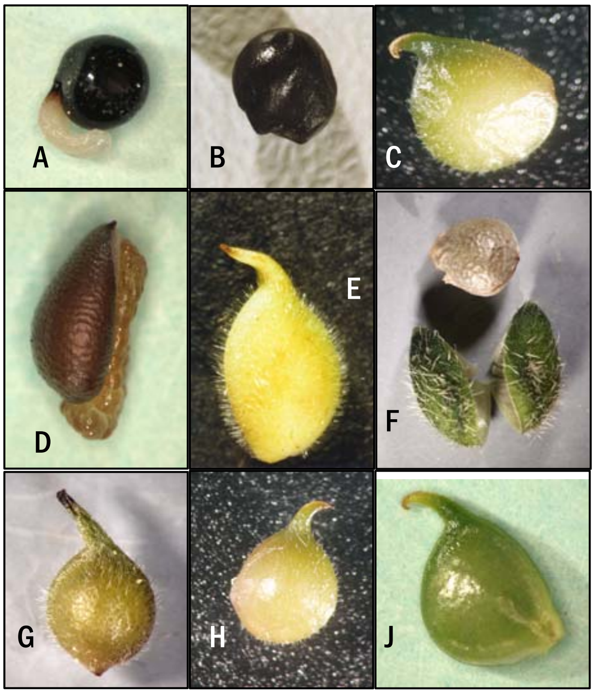


Fig. 28 Different types of diaspores according to Sernander (1906) compared with non-myrmecochorous diaspores. Viola type: A ***Corydalis cava*****, D** ***Asarum europaeum*****. Puschkina type: B** ***Allium ursinum*****, F** ***Mercurialis perennis*****. Hepatica type: C** ***Ranunculus auricomus*****, E** ***Anemone nemorosa*****, G** ***Anemone ranunculoides*****. Non myrmecochorous: H** ***Ranunculus acris*****, J** ***Ranunculus lanuginosus*****. (Photos: H. Huttenlocher).**

This study raises the question of whether ant-seed interactions are true mutualisms in any case. Ants are not able to remove the elaiosome from the seed in both the *Hepatica* and the *Puschkina* type of diaspores, and thus gain no reward for their dispersal. However, as our experiments have demonstrated, diaspore removal rates by ants were only slightly lower than in *Viola*-type diaspores. Thus, in this case ants are led by chemical cues to serve the plants' interests without receiving a proper reward. These results open a new chapter in the study of the evolution of these interesting interactions between ants and plant diaspores.

MYRMECOCHORY IN TROPICAL RAINFORESTS

Most of the studies on myrmecochory have been conducted in the temperate forests of Europe and the USA, and in the arid environments of Australia and southern Europe. Little, however, is known about one of the richest floral zones of the world that is at the same time the hotspot of ant diversity, the tropical rainforest. Beattie (1983), who reviewed the distribution of ant-dispersed plants, proposed that the species richness and abundance of both myrmecochores and diaspore-dispersing ants increases with decreasing latitude and predicted a greater variety of ant-dispersal systems in the tropics, in particular favored by poor soils that should force plants to evolve less costly modes of seed dispersal. However, so far few myrmecochores have been described in tropical forests (Horvitz and Beattie 1980), and especially few of them in the Paleotropics (Kaufmann 2002).

Fig. 29 A worker of *Polyrhachis ypsilon* is harvesting a seed of *Globba propinqua* directly from the plant.

The majority of myrmecochores described from tropical forest ecosystems are epiphytes growing in “antgardens”, which are known from the Neotropis (e.g. Corbara et al. 1999; Dejean et al. 1997a; Orivel and Dejean 1999; Ule 1908) and from the Southeast Asian rainforests (Kaufmann 2002; Kaufmann et al. 2001). In these close ant-plant interactions, ants place the seeds of certain epiphyte species into the carton walls of their nests. When the plants grow, their roots stabilize the nest walls and also act as water pumps that drain the nest after heavy rains (Yu 1994). Plants get their nutrients from the organic detritus in the nest middens situated within the nest, while ants feed on extrafloral nectaries and elaiosomes of the ant-garden myrmecochores (Davidson 1988). Ants recognize the propagules of their symbiotic plants by chemical cues (Seidel et al. 1990). Most diaspores, however, will fall to the forest floor. Dispersal of seeds by ground-living ants has been reported from the Atlantic forest of southeastern Brazil, where ants are attracted to lipid-rich diaspores that are not adapted for dispersal by ants but may occasionally benefit from this interaction (Pizo and Oliveira 2000; Pizo and Oliveira 2001). While it is unclear whether these often arrilated seeds have not really co-evolved with ants, the Neotropical herbs *Calathea microcephala* and *C. ovandensis* (Marantaceae) have been reported to be true myrmecochores (Horvitz and Beattie 1980).

A second case of true myrmecochory in rainforest herbs has been found in Borneo. *Globba* species are plants of the shady primary forest that grow in moist places along streams and waterfalls (Weber 1995). The slender herbs are up to 0.5 –1 m high, with the delicate small, yellow, white, or violet inflorescence on the top of the shoots. We studied three species, *Globba franciscii*, *G. propinqua*, and *G. pendula* with respect to their dispersal mode and distances (Pfeiffer et al. 2004). We found 21 species of ants that fed on the seed arils of the examined *Globba* species. Diaspores were either collected directly from the burst-open fruit capsules (Fig. 29) or from the forest floor. While some smaller ant species fed on the elaiosomes on the spot, larger species transported the diaspores to their nest, thereby achieving dispersal distances of up to 8 m (Fig. 30).

Fig. 30 Workers of *Oecophylla smaragdina* are carrying a seed of *G. franciscii*.

SPATIAL ORGANIZATION IN BORNEAN SMALL MAMMAL ASSEMBLAGES

Southeast-Asian rainforests are well known for their high mammal species richness (Harrison 1964; Lim and Muul 1978; Payne 1996; Payne et al. 1985). However, small mammals had been rarely studied in detail when we started our project in 2002, and little was known about specific life histories, habitat use, and the organization of non-volant small mammal assemblages in that region (Harrison 1969; Lakim 1998; Zubaid and Ariffin 1997). In particular, the habitat use and niche separation of small mammal species across the vertical dimension in the complex, multilayered tropical forests leave many questions open (Harrison 1962). In both Neotropical and Paleotropical forest sites, arboreal small mammal assemblages are estimated to comprise as many species as the terrestrial assemblages (Emmons 1995; Harrison 1962; Kays and Allison 2001; Malcolm 1995; Malcolm 2000). This rich arboreal fauna has been attributed to a structurally more complex habitat and abundant food resources, particularly the wealth and variety of fruits that occur at different seasons (Fleming 1979, Emmons 1980, August 1983). However, the arboreal strata is also a very constraining habitat due to: 1) its structure, which requires adaptations of animals for climbing or jumping that have been evolved by small mammals to different degrees, and 2) because changes of precipitation and solar radiation during the day result in strongly fluctuating regimes of temperature and humidity and generally more extreme climatic conditions (Wells et al. 2006a).

Small mammals are characterized by their high mobility, allowing the exploitation of heterogeneous environments. At the same time their relatively small size allows habitat segregation on various spatial and temporal scales. In this chapter I introduce two studies that were performed in the course of a diploma thesis that I had initiated and supervised (Wells 2002). Both papers are concerned with the spatial use of small mammal species. A third paper, from the results of the following PhD thesis (Wells 2005, see also next chapter), treats the construction of nest sites by Bornean rodents and tree shrews, which are the bases from which animals explore the surrounding space.

Fig. 31 Proper and permanent identification of small mammals in mark-recapture studies requires the use of transponders. After measuring the anesthetized animal, Konstans Wells will mark it with a subcutaneously-placed microchip.

COMPARING THE ORGANIZATION AND DIVERSITY OF SMALL MAMMAL ASSEMBLAGES IN DIFFERENT RAINFOREST STRATA

In our studies we compared the arboreal and terrestrial assemblages of small mammals in two sites in the tropical forest of Poring, Kinabalu National Park, Borneo by mark-recapture (Fig. 31) (Wells and Pfeiffer 2004) and studied the influence of habitat on small mammal distribution. We encountered one of the most species-rich small mammal communities sampled within "live" trapping studies up to now (Wells et al. 2004b): twenty different species were captured, from the six families Muridae, Sciuridae, Hystericidae, Tupaiidae, Viverridae, and Lorisidae (Fig. 32). Only a few species were constrained to one habitat layer. Spatial ecological separation as measured by different microhabitat parameters (tree heights and diameters, tree density, tree connections, bark structure, etc.) at different capture sites was stronger in the more diverse terrestrial habitat, although habitat variability was not sufficient to explain the variability between local species assemblages. Community composition was dominated by mobile species with low persistence rates (Wells et al. 2004b).

Fig. 32 Bornean small mammal species. From left to right: *Tupaia minor*, *Chiropodomys major*, *Nycticebus menagensis*, *Leopoldamys sabanus*, *Tarsius bancanus*, *Niviventer cremoriventer*, *Echinosorex gymnura*, *Maxomys surifer*, *Tupaia longipes*, *Viverra tangalunga* (Photos: K. Wells).

ARBOREAL SPACING PATTERN IN *CHIROPODOMYS MAJOR*

Chiropodomys major Thomas, 1893, the large pencil-tailed tree mouse, was by far the most abundant species in the rainforest canopy of Poring, Kinabalu National Park. It had a high persistence rate and was found in almost all of our arboreal traps (Wells et al. 2004b), thus it was the ideal focus animal for a detailed study of its spatial distribution. There was little information on this nocturnal rodent (Fig. 33) that is a common inhabitant of the tree canopies (Jenkins and Hill 1982; Musser 1979). In our study we explored the spacing patterns and microhabitat use of *C. major* in the subcanopy by live trapping with arboreal cage traps (Fig. 34). Home range size varied between the sexes (with males having home range sizes almost double those of females) and overlapped between individuals of both sexes; analysis of microhabitat preferences suggest that the activity of the rodent was positively associated with tree connections and the presence of lianas and gaps (Wells et al. 2004a).

Fig. 33 *Chiropodomys major* foraging in the canopy (Photo: K. Wells).

Fig. 34 Installing arboreal cage traps in the canopy. Mean height of traps was about 14 m.

NEST SITES OF RODENTS AND TREE SHREWS IN BORNEO

The structure and location of nests are of key importance in many aspects of an animal's life. For small mammals, nests have distinct ecological and social functions, comprising protection from enemies and adverse climate conditions (Kolbe and Janzen 2002), shelter for social interactions and raising of offspring, a larder for storage of food and prey, as well as a place for the transmission of parasites and diseases (Beaucournu and Wells 2004; Gettinger and Ernest 1995; Roper et al. 2002; Wells et al. 2007b). While nests of a few species of tree shrews were already known (Emmons 2000), no details were available on the nests of Bornean rodents. Nest locating can be difficult, especially in the multilayered tropical rainforest. The use of a spool-and-line technique proved to be a powerful tool to locate nests otherwise undetectable to the observer (Boonstra and Craine 1986; Briani et al. 2001; Miles et al. 1981). We used spool-and-line-technique as well as radio-tracking for the localization of 83 nests of seven species of non-volant small mammals (Wells et al. accepted; Wells et al. 2006b) and found that the species used different nest types. We were able to distinguish five types of nest: 1) subterranean burrows made by the animal itself, 2) ground cavities with natural entrances, 3) nests under accumulations of woody debris, 4) tree cavities, and 5) above-ground nests of woody fibers or leaves (Wells et al. 2006a).

RAINFOREST LOGGING IN BORNEO: IMPACTS ON NON-VOLANT SMALL MAMMAL ASSEMBLAGES

With more than 3000 tree species recorded on the island, Borneo is a hotspot of biodiversity (MacKinnon et al. 1996; Myers et al. 2000). However, forest destruction and loss of biodiversity in the species-rich dipterocarp rainforests of Southeast Asia, including the island of Borneo, are especially high (Curran et al. 2004; Sodhi et al. 2004). In the Malaysian state of Sabah, already 90 % of the primary rainforest has been lost or converted to secondary forest (Sabah State Government and Environmental and Conservation workgroup 2001) (Fig. 35). These losses of habitat integrity go hand in hand with a dramatic loss of the region's biodiversity (Brook et al. 2003). Projects like the WWF-initiated "Heart of Borneo Initiative"[6] attempt to conserve a considerable part of area, but even this project will include a large set of degraded areas that may differ in their ecological functions and value as habitat for various species (Rautner et al. 2005).


Fig. 35 Virgin forest and logged disturbed forest in Sabah, Malaysia (northern Borneo) 1970-95, each map showing the development over 5 years (from Sabah State Government 2001).

"Logging" is here defined as large-scale cutting of trees with heavy machinery that results in long-lasting damage to soil and forest structure. In our study, canopy height in forest that had been logged 15-25 years ago was only 25-30 m, and 50 % of the original stands appeared to be damaged, while in primary dipterocarp forests emergent trees rose to 60 m (Fig. 36).


Fig. 36 Logged forest (Photo: K. Wells).

For the better protection of tropical rainforest it is necessary to assess the conservation value of secondary forests and degraded areas in detail (e.g., Cannon et al. 1998), especially as areas that had been once logged are easily prone to further degradation and conversion to plantations of oil palms or *Acacias*[7]. The current state of forest in Sabah, with the presence of forest remnants of various sizes, disturbance regimes and histories, provides a suitable experimental setting for studies on resilience and resistance of rainforest communities following anthropogenic disturbance. In Sabah, species loss due to habitat conversion and disturbance has been already demonstrated for ants (Bickel et al. 2006; Brühl 2001; Brühl et al. 2003; Floren and Linsenmair 2001; Pfeiffer et al. in press). Similarly, rising species loss and "community alteration" has also been reported in Malaysian mammal species (Laidlaw 2000; Zubaid 1993; Zubaid and Ariffin 1997).

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[6] http://www.panda.org/about_wwf/where_we_work/asia_pacific/our_solutions/borneo_forests/index.cfm

[7] Indonesia has launched a particularly ambitious biofuels expansion program, which aims to source 17 percent of its energy needs from renewable sources by 2025. For this program, 14.5 million hectares of "degraded" land will be planted with oil palms. In Kalimantan, the Indonesian part of Borneo island, about 5.5 million hectares are available for use – an area far larger than Denmark. (www.naturealert.org Samantha Brown AFP, JAKARTA Saturday, Sep 15, 2007, Page 9.). Similarly, an area of 490,000 hectares of secondary forest will be converted to *Acacia* plantations in Sarawak (see Cyranoski D, 2007. Biodiversity: Logging: the new conservation. *Nature* 446:608-610).

Non-volant small mammals may have a high impact on rainforest regeneration, due to seed predation and consumption of seedlings and herbivores (Asquith et al. 1997; Blate et al. 1998; Corlett 1998; Curran and Webb 2000; Struhsaker 1997)(Fig. 37). On the other hand, small mammal populations are regulated by the availability of fruit and plant material (Adler 1998). The nutritious seeds of the Dipterocarpaceae, for instance, represent for rats and other vertebrates a key resource in Southeast-Asian forests (Curran and Webb 2000; Wells and Bagchi 2005).

Although the effects of rainforest degradation and fragmentation on small mammal communities are being increasingly investigated (Ganzhorn et al. 2000; Gascon et al. 1999; Goodman and Rakotondravony 2000; Lambert et al. 2006; Laurance 1997; Laurance and Bierregaard 1997; Lynam 1997), few studies have addressed the impact of logging on small mammal communities in Malaysia (Bernard 2004; Laidlaw 2000; Yasuda et al. 2003; Zubaid and Ariffin 1997). These studies compared disturbed versus undisturbed habitats and provided little information on the life history or spacing patterns of the particular species. Due to methodological and logistical problems, most of them included only two sites and a short-term trapping effort.

For a comprehensive study of species diversity in tropical rainforests, however, the role of local versus regional patterns is an essential aspect (Condit et al. 2000; Hill and Hamer 2004).In pristine rainforest, habitat complexity and the large spatio-temporal variability of resource availability lead to brief aggregations of animals in favorable habitat patches (Morales and Carlo 2006; Morris 2003). Therefore the influence of patch dynamics (that are frequently affected by stochastic events such as treefalls) has to be considered when assessing the effect of habitat conversion on species assemblages.

The impact of logging on the non-volant small mammal fauna of Sabah, Borneo, was studied in a PhD project that had been supervised by the author (Wells 2005). To take spatial and temporal habitat patchiness into account we monitored small mammal assemblages in three primary and three secondary forest areas from different parts of the country over two years. Here I present a set of papers that deal with following questions:

- Do species diversity, species composition, or variability of small mammal communities differ between pristine and logged rainforests?
- Do logging-induced habitat differences influence spatial use and movement trajectories of common small mammals?

Fig. 37 Seed dispersal in tropical forests is facilitated by a diverse array of small mammals. We examined seed contents in more than 500 faecal samples of small mammals from Bornean logged and unlogged rain forests. Seeds were found in ca. 20 % of samples gathered from rats and squirrels (six species) and ca. 15 % of samples from tree shrews (three species) (Wells & Pfeiffer, unpublished data). Apart from fig seeds, seed identification was not possible, indicating a gap in our knowledge of Asian forests that hampers the investigation of the vital role of small mammals as seed dispersers and forest regenerators. The picture shows the most commonly encountered morphotype of seed that was found in samples of all commonly caught small mammal species, except the tree shrew *Tupaia minor*. (Photo K. Wells).

- What are the characteristics of movement and ranging patterns of the giant rat *Leopoldamys sabanus* in forest types with different degrees of disturbance? Do these movement paths differ with scale?
- Do prevalence and richness of parasitic helminth worms differ in common small mammals? Are these helminth assemblages affected by logging?

LOGGING IMPACT ON SMALL MAMMAL SPECIES RICHNESS

We captured small mammals in three logged and three unlogged habitats in Sabah, Borneo, over two years. We found that species richness and diversity of small mammals were significantly higher in unlogged forests (27 species) than in logged forest (17 species). However, the common species that accounted for 95% of all captures were found in both habitats, with similar patterns of dominance, evenness, and fluctuations of abundance (Wells et al. 2007a). Multiple comparisons of replicates within and between sites have revealed that fluctuations in abundance and assemblage variability appear to be little affected by logging. Effects of forest modification on the assemblages did not differ extensively from a local to a regional scale, but were pronounced with regard to rare species. Our results emphasize the conservation value of logged forest stands (see also Meijaard and Sheil 2007), but also show that large primary forests are necessary to preserve the entire species assemblage of the region (Turner and Corlett 1996).

Fig. 38 *Tupaia tana* wearing a spool-and-line-device (Photo K. Wells).

COMPARING MOVEMENT TRAJECTORIES OF BORNEAN SMALL MAMMALS

Niche partitioning of small mammals in tropical assemblages along vertical structure and/or body size may favor coexistence in species-rich communities (Bakker and Kelt 2000; Charles-Dominique et al. 1981; Cunha and Vieira 2002; Voss and Emmons 1996). We used spool-and-line tracking (Fig. 38, 39) to compare movement paths and habitat segregation of eight species of small mammals between logged and unlogged forests. All species were affected in their movement patterns by altered forest structure in logged forests. Convergent species that are similar in their habitus and ecological needs, such as the rats *Maxomis surifer* and *M. rajah*, as well as the tree shrews *Tupaia longipes* and *T. tana*, showed contrasting responses in their movement to habitat differences, suggesting that each species was affected uniquely in its movement trajectories by multiple environmental and intrinsic features (Wells et al. 2006b). Our results highlight the impact of qualitative habitat alterations caused by logging for small forest-dwelling mammals. While our paper focussed on the more commonly captured species that were able to persist in altered habitats, other studies have shown that more specialized species may react negatively to habitat change and are thus threatened by extinction in areas of forest conversion (Henein et al. 1998; Purvis and Hector 2000; Wells et al. 2007a).

Fig. 39 Measurement of habitat parameters in dense underwood (Photo K. Wells).

EFFECTS OF LOGGING ON MOVEMENT AND RANGING OF THE GIANT RAT

Due to the extraction of large trees of commercially valuable species, logged tropical rainforests differ from primary rainforests in terms of floral composition, and in type and scale of habitat heterogeneity (Cannon et al. 1998). Animal movement in both forest types is likely to be influenced by different vegetation structure and resource patterns (DeWalt et al. 2003). We compared movement and ranging patterns of the generalist long-tailed giant rat *Leopoldamys sabanus* in logged vs. unlogged forests on two different scales (Wells et al. accepted). On a small scale (paths of 55.2 ± 20.7 m: lengths of directed walks that were aimed mainly at the burrow), recorded by spool-and-line tracks. The paths were relatively straightforward with shorter straight-line sections (step lengths) in logged than in unlogged forest. On the larger scale, as revealed by radio tracking of foraging activity, the rats showed a high individual variability in movement and searching behavior and moved with similar speed through both forest types (Wells et al. accepted). These results emphasize the behavioral plasticity of *L. sabanus* as a prerequisite for survival in an anthropogenically altered landscape and add to the perception that most of the common small mammals are able to persist even in logged forests (Lambert et al. 2005; Wells et al. 2007a).

LOGGING IMPACT ON PARASITIC HELMINTHS

The parasite load of animals reflects their life histories, which have a major influence on infection rates and composition of endoparasite assemblages (Altizer et al. 2003b). We predicted that endoparasite infection patterns within small mammal populations in Borneo would be influenced by habitat disturbance in secondary forests, since the resulting habitat differences influence resource use and behavior of small mammal and thus the transmission of parasites. Changes in habitat conditions or host densities may influence parasite transmission and infection rates, while environmental stress may reduce host immune defence and therefore increase host susceptibility to diseases (Altizer et al. 2003a; Lafferty and Holt 2003; Lenz et al. manuscript; Ostfeld and Holt 2004). We compared patterns of helminth species assemblage in two species of rats and two species of tree shrews in logged and unlogged forest sites and found that species composition and abundance patterns of endoparasite assemblages were significantly influenced by logging, with contrasting changes in infection patterns in unlogged vs. logged forests among different host species (Wells et al. 2007b). Changes in nutritional condition in logged and fragmented forests have also been thought to increase parasite abundance and richness in other mammal species in Africa and Brazil (Gillespie et al. 2005; Püttker et al. 2007).

CONCLUSIONS

In summary, our results emphasize the importance of local ecological interactions and within-habitat dynamics on diversity, community structure, habitat use, and parasitation of small mammal assemblages in dipterocarp rainforests. Given the large diversity of trees and resources that are heterogeneously distributed in the forest matrix, small mammals living in tropical rainforests face natural mosaics of habitat patches on multiple scales. Our results add to the notion that such variability is of key importance for both, 1) the plasticity of species behavior and habitat use, and 2) the occurrence of species in the assemblages of different habitats. As a result, within-habitat variability in species occurrence and animal activity complicates the predicting of the consequences of logging on community patterns, movement trajectories, and parasitation of small mammal species. General predictions of logging effects on assemblages are even more difficult, as our results suggest that even ecologically similar species are uniquely, species-specifically affected in their movement behavior and parasitic load. Because the detailed behavioral data that we recorded all stem from those species that were most commonly trapped at all sites in logged as well as unlogged forest habitats, the role of the rare species remained elusive. However, the reduced species richness found in logged habitats confirms the vulnerability of certain species to severe population reduction or extinction by logging-induced changes.

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RESEARCH ARTICLES BELONGING TO CHAPTER 3

Pfeiffer M, Chimedregzen L, Ulykpan K (2003) Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. *Journal of Biogeography* 30:1921-1935

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Journal of Biogeography, **30**, 1921–1935

Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert

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Abstract

Aim Ants (Hymenoptera/Formicidae) have strong influences on ecosystems especially in arid regions. However, little is known about ants of the vast steppe and desert regions of Central Asia. Here we provide the first comprehensive study of ant communities in Mongolia, conducted along a north-to-south gradient in climate. We examined ants' distribution patterns, assessed the impact of climatic parameters on community structure and species diversity and investigated the influence of the corresponding communities of plants.

Location Mongolia (Central Asia).

Methods We observed 31,956 ants at seed baits at 11 study sites along a transect from steppe to Gobi desert for which we attained meteorological data (mean yearly precipitation: 197 to 84 mm). Extra sampling was conducted at sugar and protein baits and by the inspection of different microhabitats. Vegetation patterns of each plot were recorded. Statistical evaluation comprised ordination and correlation.

Results We observed 15 species of ants at seed baits. Three faunal complexes of ants could be distinguished by detrended correspondence analysis (DCA): (1) in steppe baits were dominated by *Formica*- and *Myrmica*-species, (2) in semi desert we found mostly species of *Tetramorium*, *Myrmica*, *Proformica*, *Plagiolepis*, and *Leptothorax*, and (3) in desert *Cataglyphis aenescens* and *Messor aciculatus* dominated, and *Lasius* was exclusively found there. Another 11 rare ant species were sampled by hand and at sugar baits. Altogether five ant species were new to the Mongolian fauna: *Cardiocondyla koshewnikovi*, *Myrmica koreana*, *Myrmica pisarskii*, *Polyergus nigerrimus*, and *Proformica kaszabi*. Assignment of taxa to functional groups showed that in steppe cold climate specialists dominated, in semi desert we found mainly opportunists, and in desert hot climate specialists. Several functional groups know from arid zones in other parts of the world were missing. In desert certain species were highly dominant. First DCA scores of ant- and plant-communities were highly correlated with each other and with climatic parameters. While plant species diversity was positively correlated with increasing northern latitude, ant diversity and ant species richness were not correlated with latitude and responded neither to precipitation, nor to any other climatic parameter. Semi desert was a transition zone between steppe and desert, with high species richness. Ant genus composition of the ecotone overlapped with both other regions. However, beta diversity between pairs of plots within this zone was low, indicating a small-scale mosaic pattern.

This paper is dedicated to our friend and co-author, the Mongolian botanist Dr Losol Chimedregzen, who tragically died in 1998.

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Main conclusions The ant communities in the Mongolian steppe and desert zones were strongly influenced by low temperatures and differed in many aspects from the ant fauna in other arid ecosystems, especially in terms of species richness, diversity of feeding guilds, and richness of functional groups.

Keywords
Ants, Formicidae, functional groups, species diversity, detrended correspondence analysis, climate, cold desert, semi desert, Central Asia.

INTRODUCTION

Ants of most arid zones of the world have been extensively studied, in America (e.g. Davidson, 1977; Medel & Vásquez, 1994; Whitford *et al.*, 1999; Rojas & Fragoso, 2000; Bestelmeyer & Wiens, 2001; Sanders *et al.*, 2003), Australia (e.g. Andersen, 1995), Africa (e.g. Marsh, 1986; Lindsey & Skinner, 2001), and Europe (e.g. Cerda *et al.*, 1997). In Central Asia, however, where desert and steppe ecosystems are covering large areas, little is known about the ecology of ant communities (e.g. Reznikova, 1980).

Previous ant collections of Mongolia, gathered by famous entomologist Dr Z. Kaszab, were determined by Pisarski (1969a,b; Pisarski & Krzysztofiak, 1981), others by Dlussky (1965; Dlussky & Pisarski, 1970). Although our faunistic and systematic knowledge of ants of the eastern Palearctic region has been greatly improved since that time (e.g. Arnoldi, 1977; Radchenko, 1995; Seifert, 2000; Schultz, 2001; Chang & He, 2002a,b) and interesting details about the behaviour of some of the Central Asian desert ant species have been published from studies in other places (e.g. Onoyama, 1982; Yamaguchi, 1995), a survey of the ant communities of the Mongolian steppe and desert zones was still missing.

Arid regions of Mongolia are characterized by a steep climatic gradient from North to South that shapes the vegetation sequence of steppe, semi desert, and desert. In this paper we examine the structure of the Mongolian ant communities and vegetation patterns along a transect from steppe to Gobi desert. Mongolia's arid zones differ in many aspects from dry regions elsewhere, because of the strong influence of low temperatures on plant and animal life. In hot arid sites, where most previous desert ant studies have been conducted, species richness of ants is often correlated with the rainfall gradient, as productivity in these regions is coupled to precipitation (e.g. Davidson, 1977; Marsh, 1986). The Gobi desert, however, is a typical cold desert, intensively influenced by frost during long winters. As in Mongolia gradients of precipitation and temperature show opposing trends and run contrary from North to South we expected no direct correlation of rainfall and ant diversity patterns.

Besides diversity pattern ant assemblages of different continents may also differ in their guild composition, community structure, and evolutionary history. Form North American desert ant communities a strong influence of seed-harvester ants has been reported (e.g. Johnson, 2001), particularly because of abundant resources of seeds from annuals (Brown *et al.*, 1979). In Gobi desert spring ephemerals that contribute to seed abundance in other arid places (e.g. in the deserts of western Asia) are missing, because the rainfall pattern is governed by Pacific Monsoon with most precipitation occurring in summer (Breckle *et al.*, 1994). This should have strong influence on guild structure in Gobi's ants, by reducing impact of granivores. Thus we expected less diverse granivorous guilds. Generally, however, the guild concept is unsuitable for detailed studies on ant communities, because interference competition in ants cuts across guild boundaries (Greenslade & Halliday, 1983; Andersen, 1991). An appropriate basis for comparisons of ant communities can be obtained by the use of Andersen's functional group scheme (Andersen, 1995, 1997) that we employ in this study.

Few studies compared ant community composition across biome transitions and ecotones (e.g. Bestelmeyer & Wiens, 2001). Here we scrutinize a large environmental gradient and ask whether the semi desert represents a transition zone between ant communities of the steppe in the North and Gobi desert in the South of Mongolia.

MATERIAL AND METHODS

Study area

Mongolia occupies an ecological transition zone where the Siberian taiga forest meets the Central Asian Steppe and the Gobi desert. Located in the center of the Asian continent (see Fig. 1), Mongolia has a position leading to an extreme continental climate with very low precipitation. Temperature fluctuations are enormous, both daily and annually. Absolute temperatures vary from −49 °C in winter to +40 °C in summer. From North to South mean annual temperatures rise, e.g., from −1.1 °C in Ulaanbaatar (UB, N 47° 56′, O 106° 59′) to 4.3 °C in Dalanzadgad (DG, N 43° 35′, O 104° 25′). At the same time mean annual precipitation decreases steadily, ranging from, e.g. 257 mm in UB to 125 mm in DG and to < 50 mm in the Transaltai Gobi. Most of the precipitation falls in summer. This gradient of temperature and moisture in combination with different soil conditions and altitudinal changes results in a mosaic of different vegetation types (see Hilbig, 1995, 2000): north of Ulaanbaatar vegetation consists of forest and

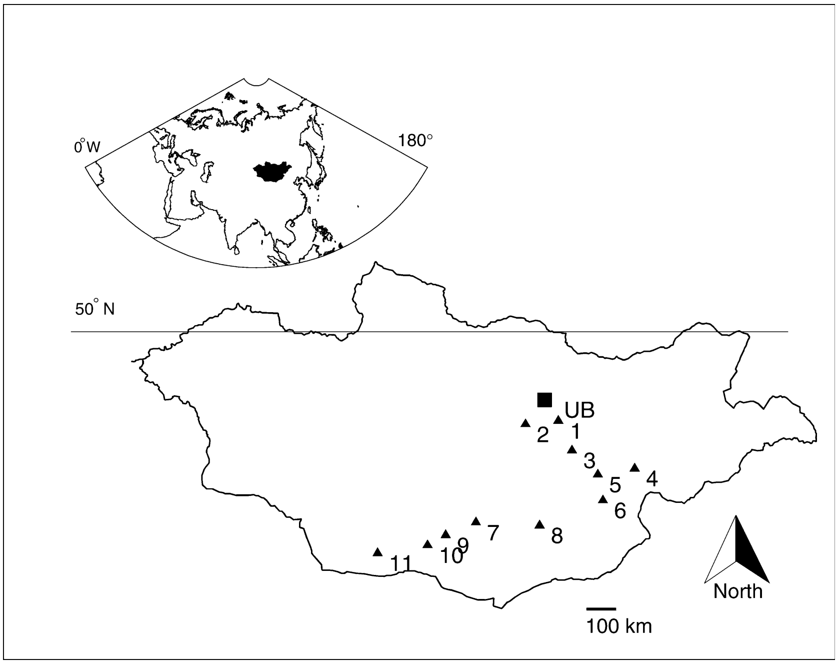

Figure 1 A map of Mongolia. Given are the capital Ulaanbaatar and the positions of our study sites. The numbers indicate the following points: (1) Maant, (2) Zorgol, (3) Choir, (4) Delgerekh, (5) Char Airag (6) Saynshand, (7) Bayan-Zag, (8) Manlai, (9) Hongoryn Els, (10) Nemegt, (11) Ekhin Gol. The world map in the upper right corner shows the geographical position of Mongolia (black) in the centre of Asia.

mountain steppe, south of N 48° latitude a patchy steppe – semidesert (steppe-desert) – desert continuum extends up to the Chinese border (Breckle *et al.*, 1994).

Generally vegetation zones in Mongolia correspond well with the distribution of precipitation. Short bunch grasses are dominant in steppe zone (Lavrenko & Karamysheva, 1993). Semi-deserts are either dominated by *Stipa-Allium* communities (desert steppe) or by shrubs and dwarf shrubs (shrub desert steppe), e.g. *Caragana*, *Artemisia* (Yunatov, 1950). In the desert zone vegetation cover generally reaches values of < 10%, often only 1–2% (Walter *et al.*, 1983). Important components of the desert vegetation are low shrubs and semi-shrubs of the Chenopodiaceae, Tamaricaceae, Zygophyllaceae, Asteraceae, and others (Pyankov *et al.*, 2000). Large herbivores, like Mongolian gazelle (*Procarpa gutturosa*) and Asian wild Ass (*Equus hemionus*) share the pastures with the livestock of nomadic herders (Schaller, 1998). Ants (Formicidae) and darkling beetles (Tenebrionidae) (Medvedev, 1990) are dominant groups of the ground-dwelling insect fauna in these habitats.

Study sites

Ants were collected during two expeditions to the Gobi desert and its adjacent steppe zones from July to September 1997 and in July/August 1999. Study areas, which should represent the typical vegetation zones and follow a gradient of precipitation, were selected on the basis of precipitation records of the Mongolian Ministry of Nature and Environment that we received by the Deutscher Wetterdienst. In the field we chose sampling sites depending on vegetation structure. We tried to compare characteristic, intact, natural plant communities and to avoid overgrazed regions. This resulted in 11 plots that were situated in mean 85 km (SD = 74.8 km) from the corresponding weather stations.

Study sites' coordinates were determined by GPS (Garmin GPS 12 XL) and are mapped in Fig. 1, geographical and climatic details are given in Table 1. From North to South we investigated following places (named to the geographical place next to them):

1. Maant. A site of the dry steppe zone near to Ulaanbaatar dominated by *Artemisia adamsii* Bess., *Leymus chinensis* Tzvel., and *Carex duriuscula* CA Mey. This plot was partly affected by nests of the common vole *Microtus brandti* Radde.
2. Zorgol. Laying below of Zorgol Khayrkhan Mountain this typical desert steppe plot was dominated by the peashrub *Caragana microphylla* Lam., the Dzungarian Bridlegrass *Cleistogenes squarrosa* (T.), and *Stipa krylovii* Roshev.
3. Choir. Desert steppe dominated by drought-resistant *Cleistogenes squarrosa* and *Carex duriuscula*, and dwarf shrubs *Caragana microphylla* Lam., *C. leucophloea* Pojark., and *C. stenophylla* Pojark.
4. Delgerekh. This site was a meadow near a brook with the highest species richness of our plots and more than 30 plant species, dominated by the Jiji grass *Achnatherum splendens* Trin., Gobi feather grass *Stipa gobica* Roshev., and a *Kochia* species.
5. Char Airag. Desert steppe dominated by the caespitose grasses *Cleistogenes soongorica* (Roshev.) Ohwi and *Stipa glareosa* P. Smirn., and semi-shrub *Caragana pygmaea* (L.) DC.
6. Saynshand. A semi desert plot: the rocky slope of a hill dominated by *Cleistogenes soongorica*, *Allium*

Table 1 Description of our study plots. Given are location, botanical–geographical region, latitude, longitude, annual rainfall, annual mean temperature and mean maxima of daily air temperature, the De Martonne aridity index, and total plant cover

Plot no.	Location	Botanical–geographical region (Grubov, 1982)	North	East	Precipitation (mm)*year^{-1}	Mean daily Air Temp (°C)*year^{-1}	Max. daily Air Temp (°C)*year^{-1}	Aridity index	Total plant cover (%)
1	Maant	Middle Khalkha	N 47°17′	E 107°38′	196	−2.2	5.7	25.13	40
2	Zorgol	Mongol. Dauria	N 47°10′	E 106°04′	196	−2.2	5.7	25.13	52
3	Choir	Middle Khalkha	N 46°22′	E 108°17′	179	0.2	7	17.55	40
4	Delgerekh	Middle Khalkha	N 45°49′	E 111°15′	197	1.4	8	17.28	43
5	Char Airag	Middle Khalkha	N 45°38′	E 109°30′	149	1.2	8.5	13.30	27
6	Saynshand	East-Gobi	N 44°51′	E 109°45′	112	3.7	10.7	8.18	30
7	Bayan-Zag	East-Gobi	N 44°10′	E 103°42′	125	4.3	11.4	8.74	16
8	Manlai	East-Gobi	N 44°05′	E 106°44′	99	3.6	10.9	7.28	30
9	Hongoryn Els	Gobi-Altai	N 43°47′	E 102°16′	125	4.3	11.4	8.74	56
10	Nemegt	Gobi-Altai	N 43°28′	E 101°24′	84	4.96	11.4	5.61	22
11	Ekhin Gol	Transaltai-Gobi	N 43°14′	E 99°01′	115	9.24	11.4	5.98	14

mongolicum Regel., and gray sage bush *Artemisia xerophytica* Krasch.

7. Bayan-Zag. A saksa'ul (*Haloxylon ammodendron*) forest near Bulgan, co-dominated of *Bassia dasyphylla* (Fisch. & C.A. Mey.) Kuntze and *Setaria viridis* P. Beauv. partly with sandy dunes. The best examined plot of our study.
8. Manlai. This place was heavily overgrazed when we visited it the second time in 1999. It was dominated by *Stipa glareosa*, and semi-shrubs of *Artemisia pectinata* Pall. and *Artemisia frigida* Willd.
9. Hongoryn Els. This plot was a sandy place near the big dune of Hongoryn Els, about 1 km away from a small river. A mosaic of bare soil and densely covered hillocks, mainly with Nitre *Nitraria sibirica* Paul., *Bassia dasyphylla*, and *H. ammodendron*.
10. Nemegt. A true desert plot in the Gobi Altai that laid at the foot of Nemegt mountain. The rich flora of this site was dominated by *H. ammodendron* and the forbs *Artemisia caespitosa* Ledeb. and *Reaumuria soongorica* Pall.
11. Ekhin Gol. A stony plot outside the oasis of Ekhin Gol that bore merely two plant species: *H. ammodendron* and *R. soongorica*.

Five of these plots (Maant, Zorgol, Manlai, Saynshand and Bayan-Zag) were censused in both years. However, in Manlai, where we had recorded low ant abundance during our first stay, we found no ants at all during our second examination.

Data collection

On each of the sampling sites we placed 75 petri dishes in a 5 × 15 bait grid with approximately 5 m spacing. Petri dishes were dug into the soil so that their edges were flush with the ground to allow easy access by ants. As a bait we used a mixture of barley and millet seeds that were partly ground in a grain mill to produce a variety of particle sizes ranging from whole seeds to floor. This standard procedure was originally used by Davidson (1977) for the study of harvester ants and has been copied in many studies on granivorous ants (e.g. Medel, 1995; Kaspari, 1996). However, we found that partly ground commercial grain attracts not only harvester ants, but that a wide range of non-granivorous ants also takes seed fragments, just as they take bread crumbs. As ground seeds are much softer than whole seeds they attract species that normally do not forage on naturally occurring seeds and are therefore well suited for an assessment of whole ant communities (A. Radchenko & B. Seifert, Pers. comm.). Sanders & Gordon (2003) who studied the organization of North American desert ant assemblages by pitfall traps, seed baits, and protein baits found that dominance pattern at different baits changed, however, seed baits attracted more species than protein baits, including even honeydew feeders (*Myrmecocystus* spp.).

Baits were monitored every 2 h, when we counted the number of ants during a 60-s observation period. Counting took place at least for a full circle of diurnal and nocturnal surface temperatures. Surface temperature was measured hourly with *Prima long* digital thermometers. Air temperature and humidity were recorded with *Hobo* data loggers (Onset, ONS-H08-032-08).

Ants were counted continuously at the baits. We took several samples of every ant species of each transect. To obtain more data on ants, we offered extra baits outside the plots: sugar water, cheese, and small pieces of meat. Additionally, in each area ants were sampled opportunistically with forceps and aspirator by inspecting different microhabitats for at least 1 h. Samples were preserved in 75% ethanol and returned to laboratory for identification. Vouchers of all specimen will be deposited in the collection of the Department of Ecology of the University of Ulaanbaatar.

Plant diversity within the grids was measured by plant cover estimates of all species. We included all vascular plant species, which were identified according to Gubanov (1996) and Grubov (1982). On each location 10 squares were mapped. Single square size depended on the scale of the vegetation and was 1 m^2 in the steppe zone, 10 m^2 in semi-desert zone, and 20 m^2 in desert vegetation.

We used a set of environmental parameters (EPs), derived from weather data of the Deutscher Wetterdienst and local weather stations, to compare climatic variation of the plots. We used mean precipitation, mean daily air temperature, mean daily maxima and minima of air temperature, total yearly maxima and minima of air temperature, mean daily air temperature in July, mean wind speed, mean steam pressure, and number of days with frost and with more than 1 mm precipitation, respectively. These data were normalized (mostly by log-transformation) if deviating from normal distribution or only used in non-parametric calculations. For each plot we calculated the De Martonne aridity index $I_a = P/T + 10$, with P is annual precipitation (mm) and T = average annual temperature (°C) (De Martonne, 1927).

Statistical analysis of community structures

Most calculations were based only on the species gathered at the seed baits in our grids, ant species that we collected by hand sampling and sugar baits were only included in the analysis of the beta diversity and functional groups (see below). Data analysis was conducted on species frequency data at our baits. Species richness of ants per site was estimated with the program 'Estimate S' Version 6B1a (Colwell, 2000; for details of the program and estimators, see Colwell & Coddington, 1994; Longino *et al.*, 2002). For rarefaction and diversity analysis we pooled all data gathered at one plot during different sample times. Rarefaction plots were plotted not with the number of samples, but with the number of occurrences on the abscissa (see Gotelli & Colwell, 2001; Longino *et al.*, 2002). Species richness was estimated by Michaelis Menten estimates, calculated from the smoothed species accumulation curves (MMMeans). Rarefaction results for plants are not shown, however, they confirmed sufficient sampling and allowed further calculation of species diversity.

For comparison of plots we calculated species richness (CSR) and a set of alpha-diversity indices using 'Estimate S'. As observed species richness depends strongly upon sample size, direct comparisons among communities that differ in the number of samples are not valid (Magurran, 1988, Lande *et al.*, 2000). Sample sizes differed greatly at our sites. To allow standardization at equivalent number of samples for each plot, we pooled ant data of all censuses and randomized orders of samples 100 times to get random order species accumulation curves. We cut these curves at 33 samples (minimum common sample size after exclusion of Manlai, see Results) and computed 'calculated species richness' and diversity indices on this basis. Plant diversity was also evaluated on the basis of individuals to avoid problems associated with different plot sizes and plant densities (Cannon *et al.*, 1998; Gotelli & Colwell, 2001). CSR and species diversity of plants was calculated on the basis of 237 individuals (= no. of plant individuals found in Ekhin-gol) by use of Ecosim 7.44 (Gotelli & Entsminger, 2001).

To analyse species assemblages at different plots we used detrended correspondence analysis (DCA, with the program PC-ORD 4.0, McCune & Mefford, 1999), an eigenvalue based technique that is particularly suitable for community data gathered at long gradients (Ter Braak, 1995). For analysis we pooled data for each plot and standardized it to equal sample size. Only species with at least three occurrences in all were included in the analysis to avoid accidental records biasing the results. Distances between the 11 plots were calculated with values of the first two DCA axes multiplicated with the corresponding eigenvalues, arranged in matrices, and tested for spatial dependence with Mantel tests (see Sokal & Rohlf, 1995).

The DCA extracts theoretical environmental gradients from the species composition data, thus monotonic relations between ordination axes and EPs are to be expected (Ter Braak, 1995). In indirect gradient analysis (Ter Braak, 1989) we correlated the DCA site scores of the first ordination axis with the EPs to evaluate the influence of EPs on community patterns. To overcome the problem of partial correlation of the EPs we (a) eliminated those parameters that were highly correlated to others, and (b) we used principal component analysis (PC-ORD 4.0) to reduce the set of EPs to three PCA axes.

Generally statistics were computed with program STATISTICA 6.0 (StatSoft, 2001). To evaluate the distribution of single ant species along the gradient, we used multiple logistic regression (lost function: Max-Likelihood) and regressed present absence data of the single species with the first three PCA axes of the EPs.

Assignment of taxa to functional groups

In the recent years Andersen (1991, 1995, 1997) has developed a functional group scheme, which allows a comparison of ant communities along our transect. Based on the abundance of ants at our baited grids and the additional records of nests and hand sampled ants, we assigned the Mongolian ant taxa to functional groups. For species that were only hand sampled we took the number of nests that we found at the different sites as an equivalence for the number of baits that were counted in the other species. Only species which occurred at least two times were included in this analysis.

Analysis of beta diversity pattern

We measured ant species overlap at the baited grids with the quantitative Morisita index (MI) (Magurran, 1988) and used Krebs' 'Program for Ecological Methodology' to calculate it (Kennedy & Krebs, 1998). To monitor similarity between ant communities at different sites by present/absence data of all ant species that we found at the sites (see Appendix) we used the formula of the qualitative Sørensen Index:

$$\text{Coefficient of similarity } = \frac{2w}{a+b},$$

where w is the number of species common to both communities and a and b are the numbers of species in each of two communities.

RESULTS

Climatic gradients

To analyse climatic gradients along our transect we used PCA to reduce all eleven EP to three PCA axes that were responsible for 93.5% of all variance. After Bonferoni correction (aBc) only the first PCA axis showed significant correlations (all $P < 0.05$) to single EPs, e.g., yearly precipitation ($r = 0.90$), mean daily air temperature ($r = 0.94$), etc., as well as to the aridity index ($r = -0.99$), confirming that variation along PCA1 followed a regime of temperature and precipitation. As PCA1 was highly significant correlated with the degrees of latitude ($r = -0.92$, $P < 0.001$), it thus corroborated that our North–South transect was strongly influenced by climate. Degrees of latitude of plots were negatively correlated with mean daily temperature ($r = -0.91$, $P < 0.001$) and positively with precipitation ($r = 0.90$, $P < 0.001$), thus confirming the steepness of the climatic gradient. As our transect points were not arranged along a straight line but followed the distribution of meteorological stations, we also tested for environmental variation along the West–East gradient, but found no significant correlation (e.g. PCA1 vs. degrees of longitude, $r = -0.04$, ns).

Species richness and abundance

Inside our grids we observed 31,956 individuals of 15 ant species at seed baits, furthermore 11 species of ants were caught at sugar baits or at other occasions during our field work (see species list in the Appendix). Plant communities consisted of a total of 91 species.

Species numbers of ants at the baits in our plots ranged from three to seven species (mean = 4.3, SD = 1.2, $n = 11$) (Table 2). Rarefaction curves of most sites quickly reached an asymptote confirming that species sampling was representative (Fig. 2). The slope of the rarefaction curves was steeper in plots where we found more than one local unique species (gathered at only one bait, see Table 2). The number of expected and observed species differed on average only by 0.44 species, however, in the Char Airag and Manlai sites by two species. Char Airag was sampled well, therefore missing species seemed to be rare, however, the Manlai plot yielded only nine samples, so missing species might be more important there. Therefore we omitted Manlai from further diversity analyses.

Patterns of species richness and diversity

We used CSR (see Methods) to check for geographical and climatic patterns of diversity using Pearson's correlations coefficient. While ants' CSR was not affected by northern latitude of plot site ($r = -0.18$, ns, see Fig. 3), CSR of plants showed a clear increase towards North ($r = 0.66$, $P < 0.05$).

For ants, we found no significant correlation of any index of diversity with annual precipitation (e.g. Shannon's H, $r = 0.15$, ns), nor with any of the other climatic parameters (including PCA scores). In plant communities alpha diversity patterns were also not significantly correlated with yearly precipitation (plants: $r = 0.49$, ns). Shannon's diversity index for plants was correlated with PCA2 ($r = -0{,}63$, $P < 0.04$, ns aBc), however, also not significant aBc.

When correlating ant diversity pattern with EPs, we checked whether high ant diversity at Delgerekh, a place with a brook nearby, would alter the results. In that case a local parameter might have changed large-scale trends. However, we found no noteworthy differences with and without this plot, thus we included it in our calculations.

Table 2 Summary statistic for ants at the baits of our plots (sorted from North to South). The table shows the total no. of samples of all investigations, the no. of species occurrences found in these samples, the observed no. of species, the no. of common species, the no. of species found only with one occurrence: the asymptote of the Michaelis–Menten equation (MMMeans) fit to the species accumulation curve, as a species richness estimator, species richness calculated on the basis of 33 samples (CSR), and Shannon's H indices of diversity of ants. For Manlai we did not calculate any diversity index, because the number of samples was too low for comparison

	No. of samples	No. of species 'occurrences'	No. of species at the baits	No. of common* species at the baits	No. of local uniques	MMMeans (max. samples)	Calculated species richness (33 samples)	Shannon (H)Index (33 samples)
Maant	91	146	3	2	0	3	3	0.89
Zorgol	33	34	3	1	0	3	3	0.83
Choir	44	52	4	3	0	4	4	1.31
Delgerekh	55	82	7	3	0	8	7	1.48
Char Airag	62	93	5	2	2	5	4	0.97
Saynshand	48	49	3	2	1	3	3	0.46
Bayan-Zag	186	382	5	4	1	5	4	1.23
Manlai	9	10	4	0	2	6	–	–
Hongoryn Els	58	74	4	2	0	4	4	0.76
Nemegt	74	143	5	4	0	5	5	1.26
Ekhin-gol	63	79	4	2	0	4	5	0.69

*Those species occurring at 10% or more of the baits.
CSR, calculated species richness.

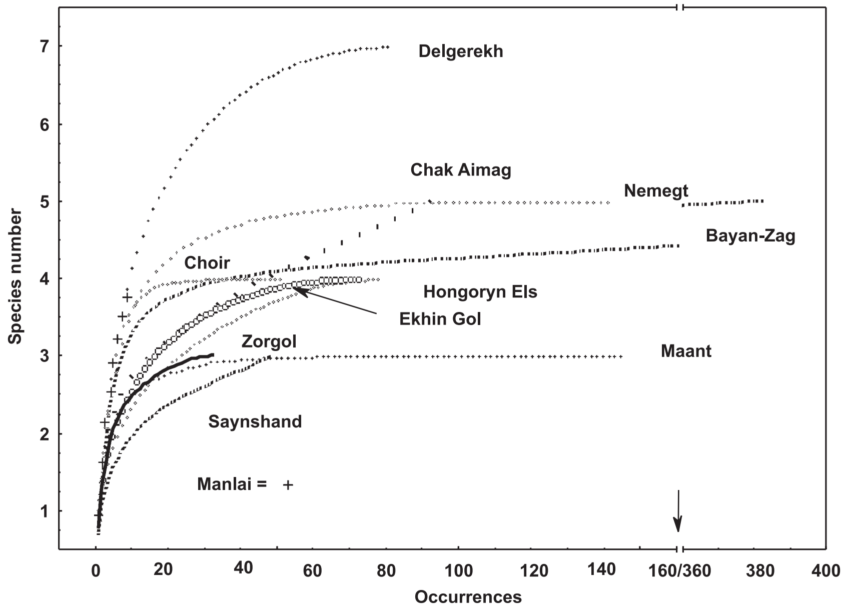

Figure 2 Sample based rarefaction curves of the ant fauna found at seed baits in the different plots. The units of the abscissa are number of 'occurrences' (see Methods, Statistical analysis of community structure). Samples of different investigation times are pooled and Maanit, Saynshand, and Zorgol were censused two times, Bayan-Zag was investigated three times, all other plots only once. Note the scale break at 160 occurrences that cut the graph of Bayan-Zag, which had a total of 382 occurrences and five species of ants.

Community patterns and indirect gradient analysis

Community composition was compared among study plots by multivariate analysis with DCA. For ants, total variance (inertia) in the species data was 3.02, eigenvalues[1] of the three axes were 0.89 (first axis), 0.55 (second axis), and 0.16 (third axis), the corresponding lengths of the gradients[2] were 5.62 SD (first axis), 3.67 SD (second axis), and 2.27 SD (third axis). Three faunal complexes of granivorous ants could be distinguished along the first DCA axis that roughly followed a gradient from South to North along our transect (Fig. 4): (1) the complex of desert ants found in the Gobi plots, (2) the group of semi-desert ants belonging mostly to plots of the Middle Khalkha, and (3) the steppe ants complex of the two northernmost plots. Actually, Manlai is 5′ south of Bayan-Zag, but because of species composition DCA arranged it to the Semi desert plots – a result that matched with the plants' community pattern. For plants total variance in the DCA was 5.9, eigenvalues and associated gradient lengths of the axes were 0.98 with 11.98 SD (first), 0.65 with 3.39 SD (second), and 0.35 with 2.70 SD (third axis). In all groups eigenvalues and gradient lengths of the first and second DCA axes showed high values indicating a good separation of species along the first and second axis.

In order to analyse whether changes in ant- and plant-communities were correlated, we compared distance matrices of the DCAs of the concerning groups. Distances between the 11 different sites in the communities of ants and plants were highly significantly correlated even aBc [Mantel test using Mantel's asymptotic approximation (MAA) for all groups: $P < 0.001$]: for ant vs. plant communities $r_M = 0.90$ ($t = 5.22$).

We used Mantel statistics (with MAA) to further evaluate the relations of distances between single DCA-scores of ant and plant communities with spatial distances: distances calculated between communities of all organisms were highly significantly correlated with distances measured in minutes of longitude between plots (plants: $r_M = 0.86$, ants: $r_M = 0.83$, for all groups $P < 0.001$ aBc), showing that changes within the communities were correlated with distances between plots.

In indirect gradient analysis DCA1 (= first axis) scores obtained for ants ($r = 0.90$) and plants ($r = 0.89$) were highly correlated with the PCA1 (= first axis) of the EPs ($P < 0.01$ aBc) confirming that changes along our transect followed a climatic gradient. In a second approach we looked for correlations of single EPs to the DCA scores: DCA1s of all groups were significantly correlated ($P < 0.01$ aBc for all variables) with mean daily temperature, daily maxima of temperature, number of days below 0 °C, and yearly precipitation, DCA2 for ants was correlated with wind speed ($P < 0.01$ aBc) (correlation coefficients in Table 3). High wind speeds are characteristic for spring and summer in the Mongolian desert-steppe regions (Lavrenko & Karamysheva, 1993).

Ant genera composition and species distribution

Ant genera composition of the three geographical zones differed significantly (Chi square test: $\mathrm{Chi}^2 = 241.6$, $P < 0.01$, Fig. 5). Eight ant genera were found at the baits in the semi desert zone, while the desert zone was

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[1] In DCA eigenvalues measure the importance of each of the axes (values between 0 and 1), but cannot be interpreted directly as proportions of variance explained; values over 0.5 often denote a good separation of species along the axis (Ter Braak, 1995).

[2] The length of the gradient is expressed in standard deviation units of species turnover (SD).

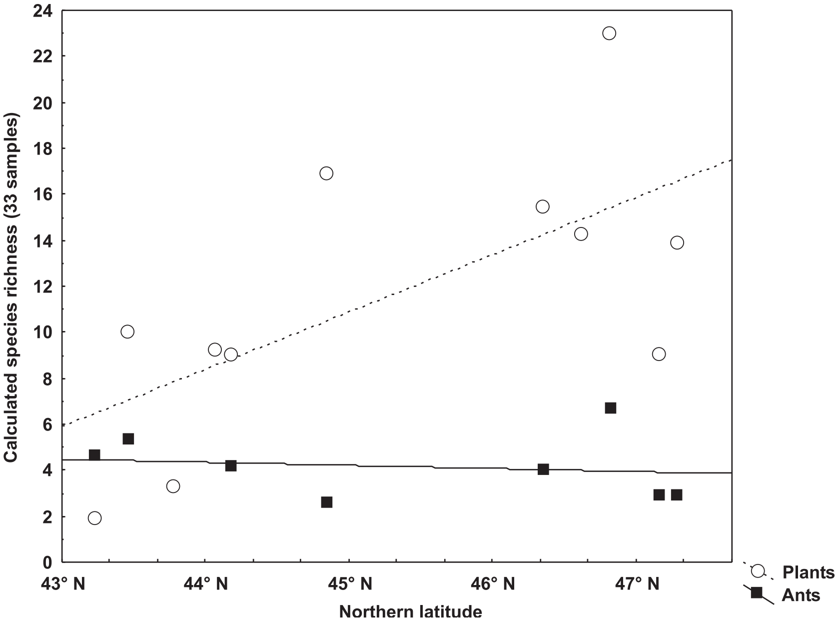

Figure 3 Calculated species richness of granivorous ants and plants plotted against northern latitude. For easy interpretation we show the regression lines of these correlations between diversity and latitude: simple line = ants, dotted line = plants.

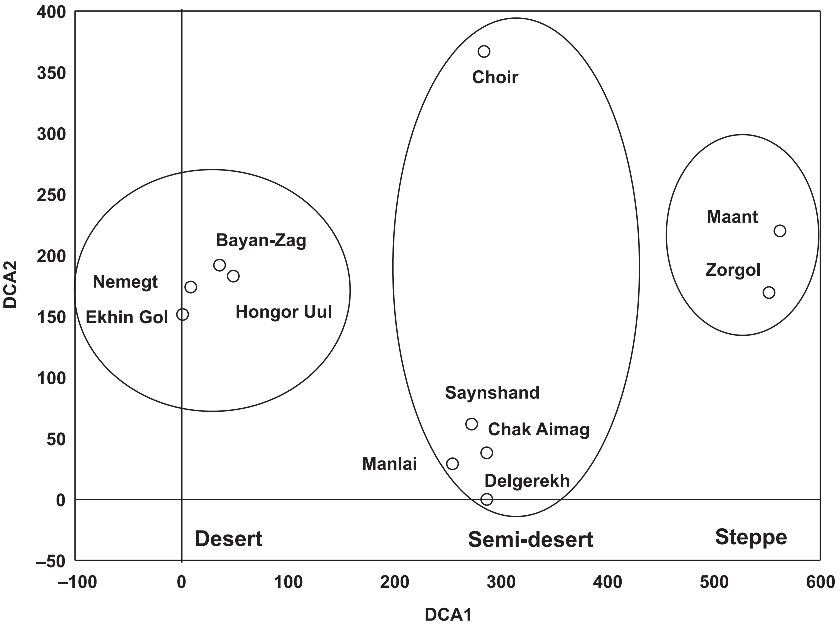

Figure 4 Detrended correspondence analysis (DCA) of the ant assemblages at different sites of our transect. Plots are arranged from South to North along the first DCA axis, starting with Ekhin Gol as the southernmost site. Ant communities were organized in three groups that are marked by circles (from left to right): desert ants, semi-desert ants (divided in two groups by DCA2), and steppe ants.

inhabited by seven, and the steppe zone by only three genera. Baits in steppe zone were dominated by *Formica*- and *Myrmica*-species. *Formica* disappeared from the baits to a large extent in semi-desert zone. *Proformica*, *Tetramorium*, *Myrmica*, and *Plagiolepis* showed their main distribution within semi-desert and *Leptothorax* was found only there, but semi-desert also harbored ant genera that had their main abundance in the two other zones (*Cataglyphis*, *Messor*, *Formica*). In desert zone *Messor* was more abundant, however, most baits were dominated by a single *Cataglyphis* species (*C. aenescens*). Abundance of *Proformica*-, *Formica*-, and *Tetramorium* species was reduced in desert as compared with semi desert zone. Extra sampling yield two more ant genera in the steppe (*Camponotus*, *Polyergus*) and three in the desert (*Camponotus*, *Cardiocondyla*, *Plagiolepis*).

Multiple logistic regression of individual species with the three PCI axes showed that nine of 19 ant species depended significantly in their distribution on environmental factors (see Appendix). This included the two dominant species of the desert *C. aenescens* and *M. aciculatus*, as well as species of *Proformica*, *Tetramorium*, and others.

Table 3 Pearson correlation coefficients for all significant correlations ($P < 0.01$ aBc) of single environmental parameters with the detrended correspondence analysis (DCA) scores of ants and plants

	Daily mean temp.	Mean daily max. temp	No. of days below 0 °C	Precipitation	Wind speed
DCA1 ants	−0.90	−0.90	0.94	0.74	–
DCA2 ants	–	–	–	–	−0.85
DCA1 plants	0.86	0.95	−0.87	−0.84	–

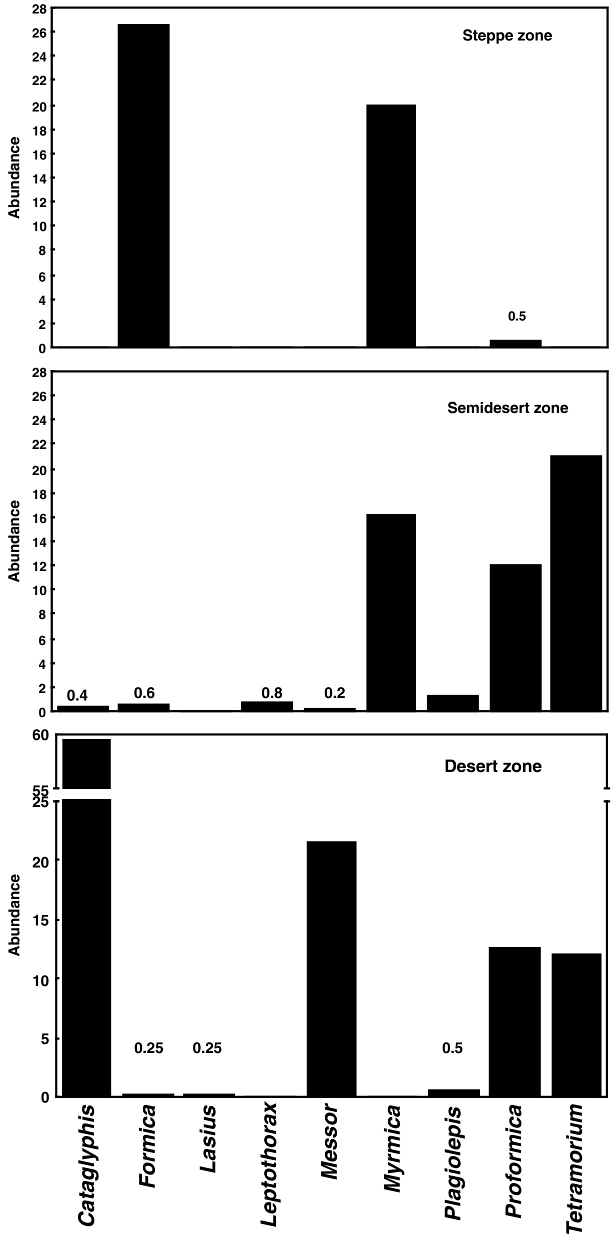

Figure 5 The mean abundance of ant genera per plot of the different climatic zones. Abundance numbers below one are given in digits. Mind different scaling and scale break of the Y-axes in the lowermost figure. The abundance of ants in plots of different zones did not differ significantly (ANOVA $F(2,8) = 3.1$; $P = 0.1$, ns).

Biogeographical patterns of functional groups composition

For a comparison of ant community composition along the environmental gradient we used Andersen's (1997) functional group scheme and assigned most species to functional groups. Only some very rare species, e.g. *Cardiocondyla koshewnikovi*, were not included in the analysis, because our knowledge about them was not sufficient for that. Following groups were separated (see also Appendix):

Cold climate specialists

The Mongolian taxa belonging here have distributions centred in the steppe region. They include the dominant holarctic *F. transkaucasica* and the temporary social parasite and slave-maker *F. sanguinea* that occurred frequently in the same nests (see Kutter, 1969). Ants of the *Formica exsecta* group that we found in some steppe localities, but not in our transects (M. Pfeiffer, Unpubl. observations) may also contribute to this group. We assigned *Myrmica pisarskii* as a cold climate specialist, too, because this mostly night-active ant was found only in the northern plots of our transect.

Hot climate specialists

The most dominant hot climate specialist was *Cataglyphis aenescens* that occurred all over the desert region and was observed to forage at surface temperatures up to 55 °C. *Messor aciculatus* was also a dominant species, merely found in the South and we counted it to this group, although the species was mainly night active.

Subordinate Camponotini

We only found one species *Camponotus turkestanus* that occurred at the desert sites. Existing mostly on phloem sap (M. Pfeiffer, Pers. observation) this night active species never fed at the seed baits.

Cryptic species

The only cryptic species in our plots was *Plagiolepis manczshurica*.

Opportunists

These taxa are defined by their wide geographical ranges, broad habitat distribution, unspecialized diets, and poor competitive ability. Here we put *Tetramorium*, *Proformica*, *Leptothorax*, and *Myrmica* (others than *M. pisarskii*), as well as some rare *Formica* species.

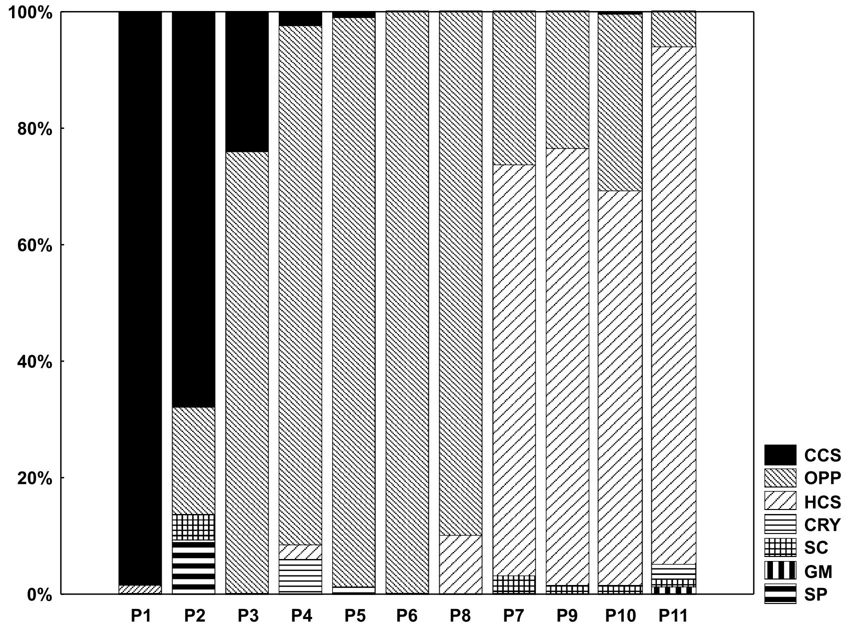

Figure 6 Functional group composition along the north–south transect. The functional groups are: CSS, Cold Climate Specialists; OPP, Opportunists; HCS, Hot Climate Specialists; CRY, Cryptic species; SC, Subordinate Camponotini; SP, Specialist Predators; GM, Generalized Myrmicinae; P1–P2, steppe; P3–P6, P8, semi desert; P7, P9–P11, desert.

Table 4 Beta-diversity between our plots (excluded Manlai) as measured by the Morisita Index calculated for ants at the baits inside the grids (above diagonal) and Sørensen qualitative Index calculated for all ant species found at the sites (below diagonal). Morisita indices of ant communities in pairs of plots along the transect are shown in bold numbers

	Maant	Zorgol	Choir	Delgerekh	Char Airag	Saynshand	Bayan-Zag	Hongoryn Els	Nemegt	Ekhin Gol
Maant		**0.98**	0.30	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Zorgol	0.55		**0.20**	0.09	0.13	0.00	0.00	0.00	0.00	0.00
Choir	0.40	0.31		**0.00**	0.02	0.03	0.24	0.16	0.10	0.00
Delgerekh	0.31	0.50	0.27		**0.95**	0.77	0.15	0.07	0.07	0.05
Char Airag	0.20	0.15	0.17	0.53		**0.71**	0.08	0.01	0.00	0.00
Saynshand	0.00	0.20	0.22	0.50	0.44		**0.10**	0.01	0.05	0.00
Bayan-Zag	0.00	0.14	0.15	0.25	0.15	0.20		**0.74**	0.85	0.77
Hongoryn Els	0.00	0.31	0.33	0.27	0.17	0.44	0.62		**0.74**	0.96
Nemegt	0.17	0.27	0.29	0.24	0.14	0.18	0.53	0.71		**0.76**
Ekhin Gol	0.00	0.12	0.00	0.21	0.13	0.00	0.35	0.38	0.56	

Generalized Myrmicinae

According to Andersen, taxa belonging to here are dominant ants that are abundant in warmer regions. However, in Mongolia we found only one ant species that fits to this pattern, *Crematogaster subdentata*, occurring in the most southern plot of Ekhin-gol.

Specialist predators

The only specialist predator in our records was *Polyergus nigerrimus*, an obligate slave-maker with highly specialized mandibles that forages exclusively for the brood of other ants.

As we found no ants belonging to the subfamily Dolichoderinae the functional group 'Dominant Dolichoderinae', which is most dominant in Australia (Andersen, 1997), could not be assigned.

Functional group composition varied systematically along our N-S transect (see Fig. 6): In steppe (P1–P2) cold climate specialists dominated, while in semi desert (P3–P6, P8) we found mostly opportunists. Desert sites (P7, P9–P11) were clearly distinguished by high abundances of hot climate specialists. Most other functional groups were rare.

Ant species turnover

We checked for similarity of ant communities in our plots with the MI (Magurran, 1988) by using quantitative data (see Table 4). Morisita indices were significantly negatively correlated with distance between compared plots, measured either in km ($r = -0.57$, $P < 0.001$ aBc) or in degrees of longitude ($r = -0.55$, $P < 0.001$ aBc). Similarity of plots within one of the three geographical regions detected by

DCA was significantly higher (MI = 0.64, SD = 0.36, $n = 13$) than in comparisons between plots of different groups [MI = 0.06, SD = 0.07, $n = 32$, Mantel test: Monte Carlo method (MCm), 1000 runs, $r = 0.92$, obs. $Z = 290$, $P < 0.001$].

Morisita indices of pairs of plots succeeding from North to South along our transect were subjected to sudden changes (Table 4). We identified three breaks in species composition within the N-S sequence of locations: site-pairs Zorgol–Choir, Choir–Delgerekh, and Saynshand–Bayan–Zag had significantly less similarity (0.1, SD = 0.1, $n = 3$) than the rest of the pairs [0.81, SD = 0.12, $n = 6$, Mantel test (MCm), 1000 runs, $r = 0.81$, obs. $Z = 290$, $P < 0.001$], thus splitting up the transect in four groups and corroborating the results of the DCA analysis, where Choir site was separated from the other semi-desert plots by the DCA2 axis.

Ant beta-diversity was further assessed by qualitative Sørensen Index (QSI) calculated for all species that we found using different methods of ant collection: steppe and semi-desert had a QSI of 0.50 [for ant species only found at the baits (asb) QSI = 0.55], semi-desert and desert had a QSI of 0.48 (asb: QSI = 0.61), and similarity of steppe and desert was lowest with only 0.24 (asb: QSI = 0.27). Again, semi desert appeared as an intermediate zone with the highest species overlap. However, species richness of ants was highest in desert with 17 species (asb = 10), whereas in semidesert we found 16 species (asb = 13), and in steppe only eight (asb = 5).

We used the QSI further to evaluate similarity of ant communities between single sites within geographical regions (Table 4). Mean within-β-diversity in semi desert and desert plots differed significantly [semi desert QSI = 0.36, $n = 6$; SD = 0.16; desert QSI = 0.52, $n = 6$; SD = 0.14, Mantel test of dissimilarity matrices (MCm), 1000 runs, $r = 0.84$, obs. $Z = 99$, $P < 0.05$], the low QSI values confirming the patchiness of the semi desert. QSI for the two steppe plots was 0.55, mean QSI for all plots ($n = 45$) was 0.27 (SD = 0.18).

DISCUSSION

Mongolia's ant communities changed considerably along the environmental gradient from steppe to Gobi desert as proven by correspondence analysis. While the steppe was dominated by cold resistant species of *Formica* and *Myrmica* (cold climate specialists), semi desert supported mainly opportunistic genera (e.g. *Tetramorium*, *Proformica*), and desert assemblages consisted mostly of hot climate specialists, especially *C. aenescens* and *M. aciculatus*.

As we had expected, we found no direct correlation of precipitation and diversity pattern in the Mongolian ant assemblages. This may be largely a result of the gradient in temperature which runs contrarily to the rainfall gradient. Although ant diversity may be coupled to rainfall as an indirect measure of productivity in arid regions (Davidson, 1977), ants are a thermophilic taxon (Hölldobler & Wilson, 1990; Andersen, 1991), which reacts negatively to low mean annual temperatures. On the contrary, diversity pattern could be a result of the productivity of resources that are a consequence of soil texture, small-scale topography, and other mosaic-like local environmental variation. These parameters are especially important in a landscape where productivity is at its minimum. Small microclimatic benefits may decide whether a species is present or absent within a location. As a possible result of these influences ant diversity was not correlated with precipitation in Australia (Morton & Davidson, 1988), nor in South America (Medel, 1995). During our study we looked for habitats with the highest productivity within the respective zone and preferred patches with intact vegetation to the bare soil beneath them. The striking differences that we experienced – especially in the more arid regions – taught us that small scale patterns are also most important for ant life in Mongolia.

However, large scale environmental pattern may have stronger influences, because abiotic variables can restrict acess to a habitat's resources, which is be especially true for ectotherm species (Kaspari & Valone, 2002). The ample seed resources of the Mongolian steppe, e.g., are probably mostly used by homoiotherm rodents that are better suited to forage for mature seeds in the cold autumn than ants. The distribution of the granivorous ant genera *Messor* and *Tetramorium* towards North seemed to be hindered by climatic effects[3]. A parallel pattern was found by Nash *et al.* (2001) in North America who compared ant communities of a sagebrush-steppe in Idaho with those of a salt-desert shrub in Utah, both habitats similar to our sites: *Formica* and generalists inhabited the steppe region, while *Messor* and most other harvester ants were merely found in the southern desert region (actually its peak abundance in North America is in the warm deserts, particularly the Mojave). Similar in Europe harvester ants are abundant only in the Mediterranean region but not in the North.

The cold climate seems to be also a major factor working against the diversification of certain ant genera. Within the huge region of central Asia (region east from Tien-Shan – Himalaya Mts) there is only one *Messor* species – *M. aciculatus*, distributed from Kirgizia-Uzbekistan till Japan (A. Radchenko, Pers. comm.), the same is true for *Cataglyphis aenescens*, while other *Cataglyphis* species are reported only far more in the South (Chang & He, 2002b). The extremely harsh and fluctuating climatic conditions within this region might reduce the number of competing species and/or allow larger ranges for those species adapted to it. The extensive distribution of *M. aciculatus* and *C. aenescens* in Gobi desert coincides with an impoverished fauna and may be an example of the dominance-impoverishment rule (Hölldobler & Wilson, 1990).

Productivity of resources is also linked to functional types (life forms) of plants. Grasses have limited access to water resources, compared with forbs and shrubs. Mongolia's desert vegetation is dominated by woody plants with deep reaching roots, e.g., the saksa'ul (*Haloxylon ammodendron*)

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[3] A. Radchenko (Pers. comm.) also looked in vain for nests of *Messor* in steppe zone, but found some *Messor* ants in the stomach of resident birds.

that has a high productivity (Slemnev *et al.*, 1999). Due to the missing rain in springtime desert annuals are scarce and most of the ant's resources originate from shrubs and dwarf shrubs. These plants contribute not only seeds but also nectar and phloem fluids to the ants, a factor with strong influence on Mongolian ant communities that were dominated by omnivores, not by granivores.

Although we had no time for a detailed analysis of feeding strategies, our observations (M. Pfeiffer, Unpubl. results) show that most Mongolian ant species were opportunists, feeding on different matters, including phloem sap from plant wounds, insect corpses, fruits and seeds, etc. Although most species were attracted to our seed baits, specialist granivores were rare, only the genera of *Messor* and *Tetramorium* include well known harvester ant species, with a substantial reliance on seeds (Marsh, 1987; Hölldobler & Wilson, 1990). This resembles ant communities in deserts of South America, where generalist ants comprised seven of 11 genera at baits of crushed seeds (Medel & Vásquez, 1994; Medel, 1995), or in Namib desert, where all ant species are highly opportunistic (Marsh, 1985). In North American deserts Sanders & Gordon (2003) found a rich assemblage of ants at seed baits, including also omnivores, insectivores, and nectarivores species, but generally seed baits were dominated by a large guild of ant granivores (see also Davidson, 1977), for which we found no equivalent in Gobi desert.

However, for comparisons of ant communities across regions and continents the use of Andersen's functional group scheme provides an appropriate basis that is better suited than a discussion on the basis of feeding guilds. Along our transect we found a clear North–South sequence of cold climate specialists, opportunists, and hot climate specialists, while all other groups had minor influence. Compared with North America and Australia (Andersen, 1997) several functional groups were absent, or sparsely casted, however, this paper deals only with ants along a limited transect, not with whole continent assemblages. Nevertheless, if we restrict comparison with the functional groups which we can expect in a steppe-desert continuum, we see that Dolichoderinae that are dominating in Australia and also some of the hot habitats of North America are absent in Mongolia at all and that 'Generalized Myrmicinae' a functional group containing species of *Pheidole*, *Crematogaster*, and *Monomorium*, is hardly represented, with the exception of a single record of *Crematogaster subdentata* in the most southern plot. Although our records may not be complete, we exclude a strong influence of these groups on the Mongolian fauna on the basis of older species lists (Dlussky, 1965; Pisarski, 1969a,b; Dlussky & Pisarski, 1970; Pisarski & Krzysztofiak, 1981). Chang & He (2002a), who sampled the ant fauna in Northwest China (34°N–41°N) found Dolichoderinae (*Tapinoma*, *Limetopum*) occurring mostly in humid forest sites in China, with the exception of *Tapinoma rectinotum*, the only species reported from grasslands in the Qinghai-Xizang region. But 'Generalized Myrmicinae' seem to be missing also far more South. So it seems that the organization of ant communities in Central Asia differs considerably from those in North America and Australia. Yet it has to be stated that this paper is only a first access to this problem and that a more intensive study, including other Mongolian regions, as well as other sampling methods (e.g. pitfall traps), has to be conducted before conclusions can be finalized.

Along our transect we distinguished three different ant assemblages in steppe, semi desert, and desert. If we compare β-diversity and species richness of the three geographical zones, it becomes clear that the semi desert as a whole is a transition zone where species of both other regions overlap in their ranges. But overlap on regional scale does not certainly imply local co-occurrence of species. On a local scale species inventories of single plots differed largely from each other. On this sampling level the semi desert appeared to be an especially patchy, mosaic-like region with low species overlap between the sites. The large regional species pool led to low local β-diversity, probably because competition for resources prohibited coexistence of all species. Beta diversity varied along the spatial North–South sequence of our whole transect as well, as shown by Morisita indices.

Bestelmeyer & Wiens (2001) studied a biome transition between shortgrass steppe and Chiahuahuan desert vegetation on a local scale and found no intermediate ant species community composition within the phytogeographical transition zone, while diversity occurring within the biome transition (in matched habitats types) was lower than outside. Like those authors, we found small values of ant species overlap on a local scale and along our transect. However, on a regional scale ant species composition in semi desert was intermediate, and changes of ant and plant communities were well correlated within the whole transect (as proven by distant values of DCA1 scores). These results illustrate a reliance of species turnover on survey extent and 'grain size', that was also found in other studies (Williams, 1996).

Taken together, our results show that Mongolian ant communities differ in many aspects from ant communities in the deserts of America and Australia, especially in terms of species richness, diversity of feeding guilds, and richness of functional groups. Cold deserts seems to be governed by other factors than hot deserts and local selection pressures on the structures of ant assemblages differ widely. More research is urgently needed for a better understanding of the crucial differences between cold and hot desert ecosystems.

ACKNOWLEDGMENTS

We are grateful to our friend and driver Dorgiin Oldokh and our Mongolian translator Odna Odonchimeg for their help during field work. We thank all our Mongolian friends and especially the herders of the Gobi for their hospitality, that made our research much more comfortable. We also owe special gratitude to Prof. Dr K. Eduard Linsenmair, University of Würzburg, for constant support during our study and to Prof. Dr Michael Stubbe, University of Halle, for important tips at the start of our enterprise. We are indebted to Dr Bernhard Seifert, Staatliches Museum für Naturkunde, Görlitz, and Dr Alexander Radchenko, Institute of Zoology of the Ukrainian National Academy of Science, Kiev, for the identification of ants. We thank especially Dr Nico Blüthgen, Dr Andreas Floren, Dr Marco Tschapka and our referees for their critical comments on earlier versions of the manuscript. One of us, M. P., wants also to express his deepest gratitude to his friends and coauthors Prof. Dr Kaman Ulykpan and Dr Losol Chimedregzen, and to the whole staff of the Mongolian National University. Likewise he wants to thank his wife Irmi Pfeiffer who contributed more than any other person to this project. In 1999 our expedition was generously funded by the 'Arthur-von-Gwinner-Stiftung für naturwissenschaftliche Forschungsreisen'.

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Appendix Ant species composition at the different study sites (site numbers as in Table 1). Species that were new to the Mongolian fauna (not listed in the cited literature) are marked with *. Ant species gathered at our baits are given with bold letters and with standardized abundance numbers. Additional species that we collected at sugar baits and by hand sampling and that were not included in quantitative calculations are indicated with x. Generally, these species were rare, only the nocturnal *Camponotus turkestanus* was frequently found at the desert sites. Most additional species were collected in Ekhin Gol (site11), where desert plus oasis were hand sampled. For species that distributions were found to be significantly correlated with environmental parameters the chi^2 values of a logistic regression are given (for details see Material & Methods). Mind that site 8 (Manlai) is shifted to the semi desert sites

Ant species	Subfamily	Functional group	Steppe			Semi-desert				Desert				Chi^2 value of significant logistic regressions
			1	2	3	4	5	6	8	7	9	10	11	
Camponotus turkestanus Andre	For.	SC	–	x	–	–	–	–	–	x	x	x	x	
Cardiocondyla koshewnikovi Ruzsky*	Myr.	–	–	–	–	–	–	–	–	–	–	–	x	
Cataglyphis aenescens *Nylander*	For.	HCS	–	–	–	2	–	–	–	49	55	74	59	9.92
Crematogaster subdentata Mayr	Myr.	GM	–	–	–	–	–	–	–	–	–	–	x	
Formica clara Forel	For.	OPP	–	–	–	–	–	–	–	–	–	x	x	
Formica clarissima Emery	For.	OPP	–	–	–	–	–	–	–	x	–	–	–	
Formica sanguinea L.	For.	CCS	5	–	–	–	1	–	–	–	–	–	–	
Formica transkaucasica Sensu Seifert	For.	CCS	35	10	–	2	–	–	–	–	–	x	–	15.27
Formica uralensis Ruzsky	For.	CCS	–	–	x	–	–	–	–	–	–	–	–	
Lasius obscuratus *Seifert*	For.	–	–	–	–	–	–	–	–	1	–	–	–	
Leptothorax mongolicus Pisarski	Myr.	–	–	–	–	–	x	–	–	–	–	–	–	
Leptothorax nassonovi Ruzsky	Myr.	OPP	–	–	–	4	–	–	–	–	–	–	–	10.65
Messor aciculatus F. Smith	Myr.	HCS	–	–	–	–	–	–	1	45	2	25	14	16.30
Myrmica bergi Ruzsky	Myr.	OPP	–	–	16	–	–	–	–	–	–	–	–	
Myrmica koreana Elmes, Radchenko & Kim (2001)*	Myr.	OPP	–	2	–	12	41	–	–	–	–	–	–	
Myrmica pisarskii Radchenko*	Myr.	CCS	33	5	12	–	–	–	–	–	–	–	–	16.30
Plagiolepis manczshurica Ruzsky	For.	CRY	–	–	–	5	1	–	–	–	–	–	2	
Polyergus nigerrimus Marikovsky*	For.	SP	–	x	–	–	–	–	–	–	–	–	–	
Proformica buddhaensis Dlussky	For.	OPP	x	x	x	x	–	–	–	–	–	–	–	
Proformica kaszabi Dlussky*	For.	OPP	–	–	18	–	–	–	–	26	13	11	–	15.28
Proformica mongolia Emery	For.	OPP	–	x	–	35	–	1	6	–	x	–	–	12.97
Tetramorium annectens Wheeler†	Myr.	OPP	–	–	6	x	6	3	1	–	4	4	–	
Tetramorium armatum Santschi	Myr.	OPP	–	–	–	–	–	–	–	–	–	28	2	10.81
Tetramorium concaviceps Bursakov	Myr.	OPP	–	–	–	–	–	–	–	–	–	–	x	
Tetramorium inerme Mayr	Myr.	OPP	–	–	–	–	–	–	–	–	–	–	x	
Tetramorium jacoti Wheeler	Myr.	OPP	–	–	–	22	44	21	2	8	–	–	–	13.34
Total no. of species			4	7	6	9	6	3	4	7	6	8	10	

†In Radchenko (1992) *T. annectens* was a junior synonym of *T. jacoti*, however, after examination of additional type material this author has revised his opinion, so *T. annectens* can now be considered a true species (A. Radchenko, Pers. comm.).

Bonner zoologische Beiträge | Band 55 (2006) | Heft 1 | Seiten 1–8 | Bonn, Januar 2007

A Critical Checklist of the Ants of Mongolia (Hymenoptera: Formicidae)

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Abstract. Here we present a critical species list of the ants of Mongolia, that is based on current literature, previously unpublished taxonomic changes, the unpublished records of the zoological expeditions of Japanese-Mongolian and German-Mongolian teams in the years 1997, 1999 and 2003 and the results of a four year Polish-German-Mongolian cooperation. We report on 68 species of 17 genera of ants that have been found within Mongolia: *Camponotus*, *Cardiocondyla*, *Cataglyphis*, *Crematogaster*, *Dolichoderus*, *Formica*, *Harpagoxenus*, *Lasius*, *Leptothorax*, *Messor*, *Myrmica*, *Plagiolepis*, *Polyergus*, *Proformica*, *Tapinoma*, *Temnothorax* and *Tetramorium*. Six species are new to Mongolia: *Formica pressilabris* Nylander, 1846, *Lasius gebaueri* Seifert, 1992, *Myrmica commarginata* Ruzsky, 1905, *Myrmica kamtschatica* Kupyanskaya, 1986, *Myrmica eidmanni* Menozzi, 1930 and *Myrmica taediosa* (Bolton, 1995).

Keywords. Asia, Mongolia, Formicidae, species list.

1. INTRODUCTION

Mongolia occupies several natural zones where the Siberian taiga forest meets the Central Asian steppe and the Gobi desert. Steep gradients of temperature and moisture show opposing trends and run contrary from North to South resulting in a vegetation sequence of forest, steppe, semi desert and desert that is considerably influenced by different soil conditions and altitudinal changes. This complex set of parameters, together with the large area of the country, creates a large variety of habitats and has a distinct influence on the biodiversity of the region (Emeljanov & Kerzhner 1983; Walter 1983; Breckle et al. 1994). Ants are a dominant part of the ground-dwelling Mongolian entomofauna, and form distinct communities in the different biomes and vegetation zones of this country (Pfeiffer et al. 2003).

The ant fauna of Central Asia has been studied for more than a century (e.g., Mocsáry & Szépligeti 1901), however, either these early expeditions did not occur on the territory of today's Mongolia (Ruzsky 1905; Stitz 1934; Yasumatsu 1940), or other authors had caste doubt on the validity of the determinations (e.g., Dlussky 1965 on Ruzsky 1915, and Pisarski 1969a on Forel 1904 and Mocsáry & Szépligeti 1901). Basic information on the Mongolian ant fauna has been gathered by the Hungarian entomologist Dr. Z. Kaszab, whose collections from the 1960s were identified by Dlussky (1965), Dlussky & Pisarski (1970), Pisarski (1969 a,b) and Pisarski & Krzysztofiak (1981). Dlussky (1964, 1967, 1969), Radchenko (1994b,c, 1995a, 1997a, 2005) and Seifert (2000, 2003, 2004) provided additional information on the ant species composition of the Mongolian fauna and were focused to the taxonomic editing of the species (for details see below). Pfeiffer et al. (2003, 2004) obtained the first ecological research data that revealed the biogeographical patterns of the Mongolian ant fauna. Here we present a preliminary checklist of the ants of Mongolia based on a critical evaluation of older literature and on the results of our own expeditions.

2. MATERIALS AND METHODS

Our study is based on altogether 2145 samples from 174 locations that were accumulated in Mongolia between 1997 and 2004 (Fig. 1). We collected ant specimens during several expeditions to the Gobi desert and the steppe and forest zones of this country. Additionally several hundred specimens of other collections were taxonomically evaluated by A. Radchenko and B. Seifert.

Three German Mongolian expeditions were conducted by M. Pfeiffer and K. Ulykpan: the first together with L. Chimedregdzen from July to September 1997, the second in July/August 1999 and the third together with A. Ulykpan in July/August 2003. They collected 703 samples mostly from baits at 67 locations in 1997 and 1999, including 11 sites that have been sampled most intensively (see Pfeiffer et al. 2003), and about 200 samples of a larger investigation at altogether 37 locations in 2003. All specimens were collected from several North-South transects between E95° and E118° longitude all over Mongolia. M. Woyciechowski collected 262 samples from *Myrmica* nests within four years (1999, 2000, 2001, and 2002) in the forest steppe zone in the Hentii region (North Mongolia). Ants from nests were collected in all types of vegetation (Mühlenberg et al. 2000) around and between three main locations stretched across ca 100 km along the 49th parallel: Honin Nuga Research Station (N49°04'48", E107°17'15"), Hot springs (N49°01'08", E107°32'43") and Ming River valley (N49°00'06", E108°02'36"). The Japanese-Mongolian expedition of Sk. Yamane and A. Ulykpan accumulated 2200 ant specimens from 233 samples from colonies and general collection that were sampled in June and July 2003, in Bogd Han National Park, Hustai N.P., and Terelj N.P. (all Tuv aimag); in Zamyn uud (Dornogovi aimag) and in July 2004 in Bogd Han N.P.; in Honin Nuga, and in Han Hentii Mts. (Selenge aimag). R. Schultz sampled the western part of Mongolia in July and August 2003 on an expedition from Ulaanbaatar through Hangai Mts. to Hovd and the Mongolian Altai (Hovd aimag) and examined 255 nest samples collected from 47 sites. He added more data to our list by the evaluation of 1) the collection of the University of Halle (77 samples from 7 locations), which was mainly due to the work of Mrs. Dr. A. Stubbe and 2) of the diploma thesis of A.-L. Lucau (2004), who collected 145 samples of the same three sites that had also been collected by M. Woyciechowski (Honin Nuga Research Station, Hot springs and Ming River valley) and was supervised by Prof. Dr. M. Mühlenberg, University of Göttingen.

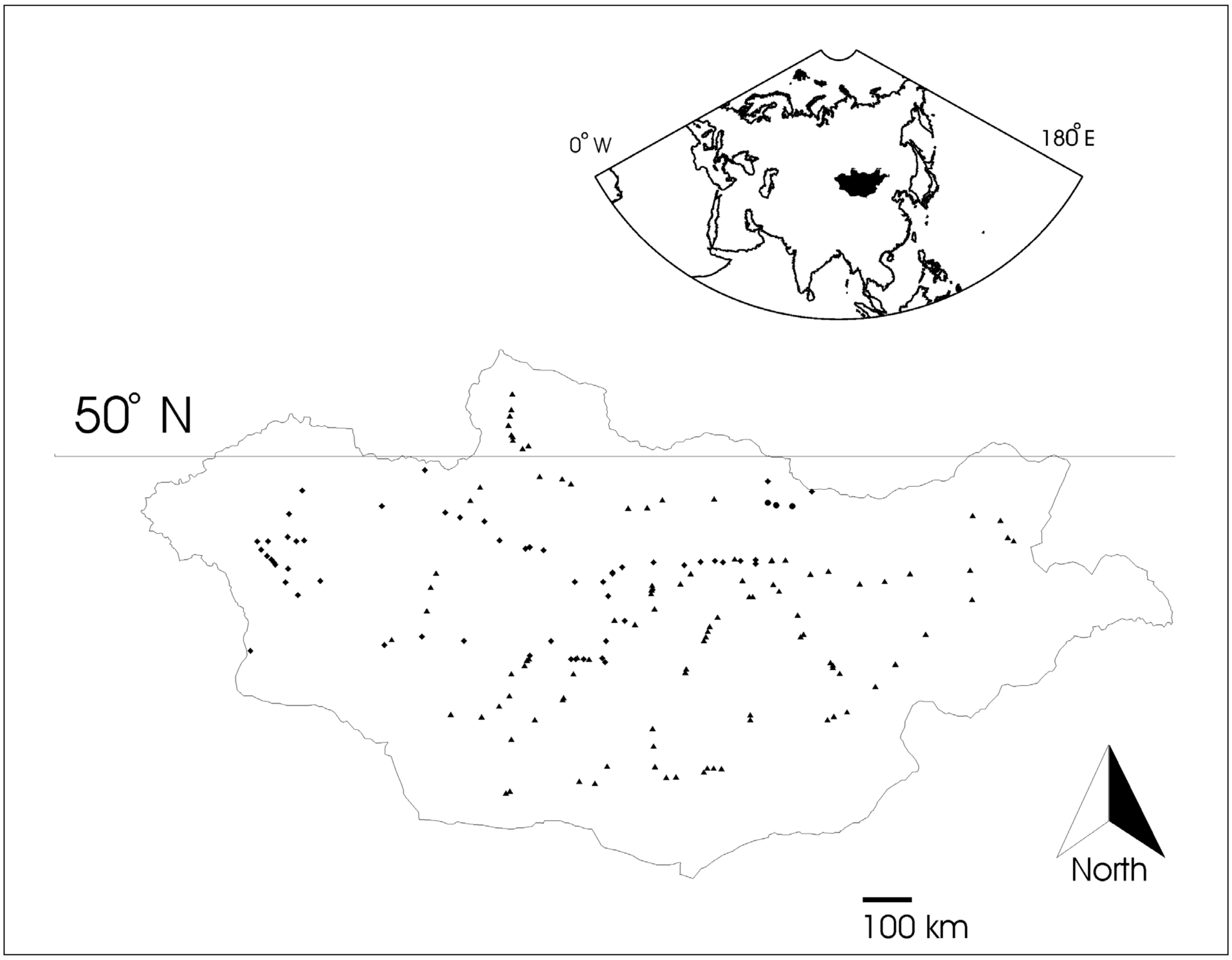

Fig. 1. Map of Mongolia. Given are the positions of our sample sites. The world map in the upper right corner shows the geographical position of Mongolia (black) in the centre of Asia.

If not explicitly stated otherwise, the material that we have collected during these journeys was identified by Alexander Radchenko (genera *Camponotus*, *Cataglyphis*, *Crematogaster*, *Messor*, *Myrmica*, *Plagiolepis*, *Proformica* and *Temnothorax*), Bernhard Seifert (genera *Cardiocondyla*, *Formica*, *Lasius* and *Polyergus*), Graham-W. Elmes (*Myrmica*) and the other authors. Collection details and localities for all species will be given in future publications, in which we plan to map the distribution patterns of the main species.

To compile the species list we compared our data with that in the literature (see Table 1 and references). These references were critically scrutinized by our taxonomic experts (B. Seifert, A. Radchenko) and the validity of the nomenclature was checked by evaluating the latest taxonomic publications (BOLTON 1995, 2003; RADCHENKO 1994a,b, 1995b,c, 1997a,b; RADCHENKO et al. 2002; SEIFERT 1992, 2000, 2003, 2004).

3. RESULTS

The resulting list of the Mongolian fauna comprises 68 species of ants of 17 genera (Table 1). After cross checking of literature we conclude that six species are new to the Mongolian fauna (R. Schultz, Sk. Yamane & M. Woyciechowski, unpubl. results):

***Formica pressilabris* Nylander, 1846**
Hangai mountain region, Arhangai aimag (province), Tsetserleg soum, ca. 12 km west of Tsetserleg, 1886 m, leg. R. Schultz, 02.08.2003, det. B. Seifert.

***Lasius gebaueri* Seifert, 1992**
Tuv aimag: Bogd Han N.P., 1550 m, leg. Sk. Yamane, 27.06.2003, det. B. Seifert.

Mongolian Altay, Hovd aimag, ca. 8 km south of Hovd, ca. 20 km west of Hovd, 2021 m, leg. R. Schultz, 08.08.2003, det. B. Seifert.

***Myrmica commarginata* Ruzsky, 1905**
Hovd aimag, Durgun soum, Chonoharaihiin gol, Derris, 1154 m, leg. A. Stubbe, 27.08.2003, det. R. Schultz & A. Radchenko.

***Myrmica eidmanni* Menozzi, 1930**
Selenge aimag, western Han Hentii Mts, 3 km SW from Honin Nuga Research Station, near Eruu River (N49°03.81', E107°16.14'), 930 m, 06.08.1999 and 8 km E from Honin Nuga Research Station, near Sharlan River (N48°57.70', E107°04.26'), 970 m, 23.07.2000, both leg. M. Woyciechowski, det. G. W. Elmes & A. Radchenko.

Selenge aimag, western Han Hentii Mts, Sharlan River, near Honin Nuga research station, 1000 m, leg. A.-L. Lucau, July 2001, det. A. Radchenko.

Selenge aimag, western Han Hentii Mts, Sharlan River, near Honin Nuga research station, leg. Sk. Yamane, July 2004, det. Sk. Yamane.

***Myrmica kamtschatica* Kupyanskaya, 1986**
Selenge aimag, western Han Hentii Mts, 8 km E from Honin Nuga Research Station, near Sharlan River (N48°57.70', E107°04.26'), 970 m, leg. M. Woyciechowski, 23.07.2000 and the same location on 6.07.2001, det. G. W. Elmes & A. Radchenko.

***Myrmica taediosa* (Bolton, 1995)**
Selenge aimag, western Han Hentii Mts, 9 km SW from Honin Nuga Research Station, near Eruu River (N49°02.39', E107°11.62'), 1045 m, leg. M. Woyciechowski, 28.07.2002, det. G. W. Elmes & A. Radchenko.

Due to taxonomic changes and to our critical evaluation of the species lists that have been previously published, this first comprehensive list of the Mongolian ant fauna contains a changed species spectrum compared to the older literature. For example *Lasius alienus* (Förster, 1850) has been reported from Mongolia in four publications (DLUSSKY & PISARSKI 1970; PISARSKI 1969a,b; PISARSKI & KRZYSZTOFIAK 1981), however, regarding to SEIFERT (1992), this species is constricted to Europe, so the taxonomic position of these samples was doubtful. A rechecking of these specimens that had been collected by Kaszab and are housed in the Hungarian National Museum showed that they were most possibly specimens of *Lasius* cf. *obscuratus*, but definitively not of *Lasius alienus* (Sándor Csõsz, Budapest, pers. comm. 2005). *Lasius* cf. *obscuratus* has been also sampled by PFEIFFER (2003) but due to the low number of specimens this determination is still uncertain and needs to be confirmed.

Other records that have been previously published are also uncertain and may be a result of misidentifications (unpublished results A. Radchenko): e.g., *Camponotus herculeanus herculeanus* Linnaeus, 1758 (in DLUSSKY & PISARSKI 1970), *Cardiocondyla stambuloffi* Forel, 1892 (in PISARSKI 1969b; PISARSKI & KRZYSZTOFIAK 1981, but see RADCHENKO 1995c and SEIFERT 2003), *Myrmica bergi* Ruzsky 1902 that was confirmed to be *Myrmica divergens* Karavaiev, 1931 (in PFEIFFER et. al. 2003, but see RADCHENKO et al. 2002), *Myrmica saposhnikovi* Ruzsky, 1903 (in PISARSKI 1969a,b, PISARSKI & KRZYSZTOFIAK 1981), that was proved to be *M. pisarskii* Radchenko, 1994 (see RADCHENKO 1994b, 1995b), and *Myrmica schencki* Viereck, 1903 (in PISARSKI & KRZYSZTOFIAK 1981), which

Table 1. A critical list of the ant species that have been found in Mongolia, according to literature, to our expeditions and the expertise of our taxonomic experts A. Radchenko and B. Seifert. a = Stitz (1934), b = Holgersen (1943), c = Dlussky & Pisarki (1970), d = Dlussky 1965, e = Pisarski (1969a), f = Pisarski (1969b), g = Pisarski & Krzysztofiak (1981), h = Radchenko (1994b), j = Radchenko (1994c), k = Radchenko (1995a), l = Bolton (1995), m = German-Mongolian expedition 1997; 1999 (collection M. Pfeiffer, unpublished), n = collection of Kawaguchi, o = Radchenko (1997a), p= Dubatolov (1998), q = collection of M. Woyciechwski (1999–2004), r = collection of R. Schultz (leg. A.-L. Lucau 2001, 2003), s= collection of R. Schultz (leg. University of Halle, Germany), t = Imai et al. (2003), u= Pfeiffer et al. (2003), v = German-Mongolian expedition 2003 (M. Pfeiffer), w = German-Mongolian expedition 2003 (R. Schultz), x = Seifert 2003, y = Japanese-Mongolian expedition 2003 (Sk. Yamane), z = Japanese-Mongolian expedition 2004 (Sk. Yamane), 1 = Seifert (2004), 2 = Radchenko (2005), 3 = Personal collection A. Ulykpan. Valid scientific names were obtained from Bolton 1995, 2003; Radchenko 1994 a,b, 1995b,c, 1997 a,b; Radchenko et al. 2002 and Seifert 2000, 2003, 2004.

Scientific name	References
Camponotus japonicus Mayr, 1866	b,c,e,f,g,s,y,z,3
Camponotus herculeanus sachalinensis Forel, 1904	c,e,f,g,w,y,z,3
Camponotus saxatilis Ruzsky, 1895	m,o,w,z,
Camponotus turkestanus André, 1882	f,g,s,u,v
Cardiocondyla koshewnikovi Ruzsky, 1902	u,w,x
Cataglyphis aenescens (Nylander, 1849)	c,e,f,g,s,u,v,w
Crematogaster subdentata Mayr, 1877	g,u
Dolichoderus sibiricus Emery, 1889	2
Formica aquilonia Yarrow, 1955	e,n,v,y, z
Formica candida Smith, 1878	c,d,e,f,g,n,r,s,u,v,w,y,z,1,3,
Formica clara Forel, 1886	c,f,u,v,y
Formica clarissima Emery, 1925	s,u,w
Formica cunicularia Latreille, 1798	c,f,g,3
Formica exsecta Nylander, 1846	d,m,w,y,z
Formica forsslundi Lohmander, 1949	c,e,f,g,w,3
Formica japonica Motschoulsky, 1866	t
Formica kozlovi Dlussky, 1965	d,e,f,g,m,w,y,3
Formica lemani Bondroit, 1917	c,d,f,g,m,w,y,z,3
Formica lugubris Zetterstedt, 1838	f,w,y z,
Formica manchu Wheeler, 1929	c,d,e,f,g,l,m,n,s,w,y,z,3
Formica pisarskii Dlussky, 1964	d,e,f,g,v,w,y,3
Formica pratensis Retzius, 1783	c,d,f,s,3
Formica pressilabris Nylander, 1846	w
Formica sanguinea Latreille, 1798	c,d,e,f,g,s,u,y,z,3
Formica truncorum Fabricius, 1804	c,d,f,3
Formica uralensis Ruzsky, 1895	c,d,e,f,g,u,w,y,3
Harpagoxenus zaisanicus Pisarski, 1963[1]	e,f,g,3
Lasius distinguendus (Emery, 1916)	e,f,3
Lasius flavus (Fabricius, 1781)	b
Lasius gebaueri Seifert, 1992	w,y,z,3
Lasius niger (Linnaeus, 1758)	b,c,f,g
Lasius przewalskii Ruzsky, 1915	g,w,y,z,3
Leptothorax acervorum (Fabricius, 1793)	e,f,g,w,3
Leptothorax muscorum (Nylander, 1846)	c,e,f,g,y,3
Messor aciculatus (Smith, 1874)	e,f,u,y
Messor excursionis Ruzsky, 1905	g
Myrmica angulinodis Ruzsky, 1905	c,e,f,g,r,w,q,y,z,3
Myrmica arnoldii Dlussky, 1963	c,e,g,r,q,y,z,3
Myrmica commarginata Ruzsky, 1905	s
Myrmica divergens Karavaiev, 1931	c,e,g,w,q,y,z,3
Myrmica eidmanni Menozzi, 1930	q,r,z

Myrmica forcipata Karavaiev, 1931	e,f,g,r,w,q,3
Myrmica kamtschatica Kupyanskaya, 1986	q
Myrmica kasczenkoi Ruzsky, 1905	c,e,f,g,v,w,y,3
Myrmica koreana Elmes, Radchenko & Kim 2001	u,q
Myrmica pisarskii Radchenko, 1994	h,s,u,w,q,y,3
Myrmica rubra (Linnaeus, 1758)	b,k
Myrmica ruginodis Nylander, 1846	k,q
Myrmica sulcinodis Nylander, 1846	e,f,r,q,3
Myrmica taediosa Bolton, 1995	q
Plagiolepis manczshurica Ruzsky, 1905	e,f,g,u
Polyergus nigerrimus Marikovsky, 1963	p,u
Proformica buddhaensis Ruzsky, 1915	f,g,u
Proformica coriacea Kuznetsov-Ugamsky, 1927	f
Proformica jacoti (Wheeler, 1923)	g,w
Proformica kaszabi Dlussky, 1969	u
Proformica mongolica (Emery, 1901)	c,e,f,g,u,w
Tapinoma orthocephalum Stitz, 1934[2]	a
Tapinoma sinense Emery, 1925	j
Temnothorax kaszabi (Pisarski, 1969)	f,g,3
Temnothorax melleus (Forel, 1904)	f
Temnothorax mongolicus (Pisarski, 1969)	f,u,v,z
Temnothorax nassonowi (Ruzsky, 1895)	e,f,g,u,y
Temnothorax serviculus (Ruzsky, 1902)	c,e
Tetramorium armatum Santschi, 1927	g,u
Tetramorium concaviceps Bursakov, 1984	u
Tetramorium inerme Mayr, 1877	f,u
Tetramorium tsushimae Emery, 1925	c,e,f,g,u,w,y

[1] This species is on the red list of Mongolia (http://www.redlist.org).

[2] This species has been reported from South Mongolia, but it is unclear whether this place is now in the Peoples Republic of China.

in fact is *M. koreana* Elmes, Radchenko & Kim 2001. Other mistakes seem to be most probably *T. caespitum* Linnaeus, 1758 (in Dlussky & Pisarski 1970; Pisarski 1969b), that may be *Tetramorium tsushimae* Emery, 1925 and also *Tetramorium ferox* Ruzsky, 1903 (in Pisarski & Krzysztofiak 1981). Similarly, Dlussky & Pisarski (1970) and Pisarski (1969b) reported about *Formica polyctena* Förster, 1850 to occur in Mongolia's forest steppe, however, this seems to be a misidentification of specimens of *Formica aquilonia* Yarrow, 1955 (B. Seifert, pers. obs.). Because of the cold winter the occurrence of *F. polyctena* within Mongolia should be impossible. We excluded all suspicious records from our species list.

Due to the failure to access type material of *Formica subpilosa ruzskyi* Dlussky 1965, only indirect assessment of the status of this taxon is possible. Most certainly this taxon is conspecific with *F. clarissima* Emery, 1925 because any material known from Mongolia and Tibet seems to belong to one and the same species according to structural characters. Furthermore there is no indication that those pigmentation characters proposed by the Dlussky (1965) for the differentiation of the *Formica subpilosa* subspecies *pamirica* Dlussky 1965, *clarissima* Emery 1925 (to which Dlussky applied the unnecessary replacement name *ruzskyi* Dlussky 1965) or *litoralis* Kuznetzov-Ugamsky 1926 could have any practical value. However, structural characters such as body morphometrics or setae counts computed in a discriminant analysis allow the separation of four Asian allospecies *Formica subpilosa* Ruzsky 1902, *F. clarissima* Emery 1925, *F. litoralis* Kuznetzov-Ugamsky 1926 and *F. pamirica* Dlussky 1965 (B. Seifert, unpubl. data). According to the material investigated by us only *F. clarissima* Emery 1925 could be confirmed for Mongolia. The possible occurrence of *F. subpilosa* in semideserts of S Mongolia, as extension of the population from Chinese Gobi desert, should be checked during further field studies. Similarly *Cataglyphis aenescens roickingeri* and *C. aenescens tankrei* have been synonymized with *C. aenescens* (Nylander, 1846) (Radchenko 1997b).

Table 2. Valid names of Mongolian ants and their former names or junior synonymies that have been used in the older literature.

Valid name	Former name
Cataglyphis aenescens (Nylander, 1846)	*Cataglyphis aenescens roickingeri* For
	C. aenescens tankrei For
Formica manchu Wheeler, 1929	*F. longiceps* Dlussky, 1964
F. dlusskyi Bolton, 1995	
Formica candida Smith, 1878	*F. picea* Nylander, 1846, sensu Dlussky 1967;
	sensu Dlussky & Pisarski 1971, and other authors
	F. transkaucasica Nassonov, 1889,
	sensu Collingwood 1979, and other authors
Temnothorax kaszabi (Pisarski, 1969)	*Leptothorax kaszabi* Pisarski, 1969
Temnothorax melleus (Forel, 1904)	*Leptothorax melleus* Forel, 1904
	Leptothorax melleus csikii Pisarski, 1969
Temnothorax mongolicus (Pisarski, 1969)	*Leptothorax mongolicus* Pisarski, 1969
	Leptothorax serviculus mongolicus Pisarski, 1969
Temnothorax nassonovi (Ruzsky, 1895)	*Leptothorax nassanovi* Ruzsky, 1895
Temnothorax serviculus (Ruzsky, 1902)	*Leptothorax serviculus* Ruzsky, 1902
Tetramorium tsushimae Emery, 1925	*Tetramorium annectens* Pisarski, 1969
	Tetramorium jacoti Wheeler, 1927

In several cases the names of the species have been changed since that time when Dlussky and Pisarski identified the ant species from Kaszab's rich collection of the Mongolian fauna. For example *Formica manchu* Wheeler, 1929 was formerly named *F. longiceps* Dlussky, 1964 or *F. dlusskyi* Bolton, 1995 (see Seifert 2000) or *T. tsushimae* Emery, 1925 formerly considered as *Tetramorium annectens* Pisarski, 1969 or *Tetramorium jacoti* Wheeler, 1927 (see Bolton 1995). In the case of *Formica candida* Smith, 1878 this ant taxon was divided into two different species with separate zoogeography (Seifert 2004): the western "Black Bog Ant" redescribed as *Formica picea* Nylander, 1846, and *F. candida*, which is found in East Siberia from the eastern Altai mountains up to the Russian Far East, in Tibet, Mongolia, and North Korea. With these redescriptions the older name *Formica transkauscasica* Nassonov, 1889 that has been used for *F. candida*, e.g., in Pfeiffer et al. (2003), is invalid. Similarly some species of the genus *Leptothorax* have been transferred to the genus *Temnothorax* (e.g., *Temnothorax mongolicus* (Pisarski, 1969) or *Temnothorax nassonovi* (Ruzsky, 1895) (Bolton 2003). We excluded all synonymies (see Table 2) from the list.

4. DISCUSSION

For the first time we present a critical, tentative species list of the Mongolian Formicidae that includes all previously recorded taxa. We also added six new species, *F. pressilabris*, *L. gebaueri*, *M. commarginata, M. eidmanni*, *M. kamtschatica* and *M. taediosa* to the ant species list of Mongolia. Up to now the genus *Formica* provides the highest number of species (18) in this list, while *Myrmica* is represented by 14, *Lasius, Proformica* and *Temnothorax* by five species, each. The large number of *Formica* and *Myrmica* ants, that dominate the northern parts of Mongolia, may be a hint towards the higher productivity of these regions (forest, steppe) compared to the semi deserts and deserts in the southern country. However, the study of the Mongolian Formicidae is still going on, and we are expecting that more species will be added to the list within the next years (e.g., social parasitic ants), because of new collections and/or changes in the taxonomic system.

Acknowledgements. We thank Prof. Dr. Kaman Ulykpan, Mongolian National University, Ulaanbaatar, for his kind cooperation and help during the organization of our expeditions and also for the collection of some of the ant specimens. We are indebt to Dorjiin Oldokh, Odna Odonchimeg, and to the late Dr. Losol Chimedregzen for their help during field work. We thank Ana-Lena Lucau, for the collection data of some Mongolian ant species. Prof. Dr. M. Woyciechowski's and Ana-Lena Lucau's data were collected during their stay in the Honin Nuga Research Station guided by Prof. Dr. Michael Mühlenberg, Georg-August-University, Göttingen, Germany and thanks to the financial support of Georg-August-University of Gottingen. This Station was founded thanks to the cooperation of the Georg-August-University of Gottingen and the National University of Mongolia, Ulaanbaatar. We are very grateful for this support of our study. We owe special gratitude for collection data to Assoc. Prof. Dr. Sadao Kawaguchi, Faculty of Agriculture, Kyushu University, Japan, and to Dr. Annegret Stubbe, Martin-Luther-University, Halle. We thank especially Sándor Csõsz of the Hungarian National Museum for sending an actual, tentative identification of the specimens formerly described as *Lasius alienus* and Dr. G.W. Elmes for his help during the determination of *Myrmica* species. We appreciate an anonymous referee for his helpful comments on a former version of the paper. In 1999 the German-Mongolian expedition (M.P.) was generously funded by the "Arthur-von-Gwinner-Stiftung für naturwissenschaftliche Forschungsreisen".

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Received: 06.06.2005
Revised: 17.06.2005
Accepted: 01.07.2005
Corresponding editor: D. Stüning

A Preliminary Checklist of the Ants (Hymenoptera: Formicidae) of Iran

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Abstract

The first checklist of the ants of Iran is presented in this paper. The study is based on a comprehensive review of literature (24 articles) and the examination of material from three museums in Iran and in Russia. 120 species and subspecies of ants belonging to 25 genera and the five subfamilies Formicinae, Myrmicinae, Ponerinae, Dolichoderinae and Aenictinae are recognized for the Iran. Most of the reported ants were sampled from the north of Iran, near to human settlements. Ten species, *Aphaenogaster gibbosa*, *A. kurdica*, *Camponotus aethiops*, *C. sanctus*, *Lasius illyricus*, *Messor denticulatus*, *M. minor*, *Pachycondyla nigirta*, *Ponera cf. coarctata* and *Temnothorax parvulus* are recorded for the Iranian fauna for the first time The most species rich genera are *Camponotus, Messor and Cataglyphis* with twenty two, sixteen and fifteen species, respectively. Thirteen species that were recorded in previous studies are excluded from the species list as doubtful species. Because still many parts of the country are unstudied, we believe that the species richness in Iran is higher.

Keywords: ant, Iran, checklist, new records

Introduction

So far many faunistic researches on ants have been recently carried out in several parts of Asia (e.g., East and Southeast Asia: KUPYANSKAYA 1990, WU & WANG 1995, TERAYAMA 1994, IMAI & al. 2003, RADCHENKO 2005, OGATA 2005, CHUNG & MOHAMED 1996, BHARTI 2002 a, b; central Asia: TARBINSKY 1976, DLUSSKY & al. 1990, SCHULZ & al. 2006; PFEIFFER & al. 2007), however, in the west and south west of Asia only the ant fauna of Saudi Arabia (COLLINGWOOD 1985, COLLINGWOOD & AGOSTI 1996) has been studied well. The ant fauna of other countries from the Middle East like Iran has been investigated only partly.

In Iran most of the myrmecological studies were conducted in two main periods: the first period was between 1890 and 1930, when European scientists collected ants during their expeditions in Iran and ant taxonomists studied these collections. In the earliest survey FOREL (1904a) recorded 13 species from two subfamilies, Formicinae and Myrmicinae.

These specimens had been collected by Zarudny mostly from North East and East of Iran, between 1896 and 1898. FOREL (1904b) and EMERY (1906) also described several new species from Iran. CRAWLEY (1920a, b) recorded 12 species from North West Iran including the first ponerine ant that he later described as a new species, *Anochetus evansi* Crawley, 1922 (CRAWLEY 1922). MENOZZI (1927) recorded seven species from the south of Iran. From 1930 to 1990 no myrmecological research has been preformed in Iran or at least there is no data available. The second period of ant research in Iran started in the 1990 decade and continues until now. RADCHENKO (1994a) described *Temnothorax iranicus* RADCHENKO, 1994 from Iran and later recorded further species from this country (RADCHENKO, 1994b, 1995, 1996, 1997 and 1998). SEIFERT (2003) described two species, *Cardiocondyla brachyceps* SEIFERT 2003 and *C. persiana* SEIFERT 2003 and recorded another five species from this genus *Cardiocondyla*. ARDEH (1994) recorded 13 species from two subfamilies, Formicinae and Myrmicinae from Karaj region. Alipanah and colleagues reported on the fauna of Tehran (ALIPANAH & al. 1995 & 2000), the fauna of South West of Iran (Khuzestan province) (ALIPANAH & DEZHAKAM 2000) and seven other species from different parts of country (ALIPANAH 2004). TIRGARI AND PAKNIA (2004 & 2005) recorded six species from Lar city (Fars province) in south of Iran. RADCHENKO & ALIPANAH (2004) documented the first Iranian species from the subfamily Aenictinae. PAKNIA & KAMI (2007) reported 15 species from different localities of country.
As Iranian myrmecologists have published their reports in many cases only in local journals or presented them at certain national congresses in Persian language, it is difficult to access this literature. Other problems arise from old and excursive records which had been published by scientists from other countries and need to be reconfirmed. For all of these reasons a preliminary checklist of the Iranian ants is a helpful tool for myrmecologists that are interested in Asian ants.

Material and Methods

This study is based on the review of 24 scientific papers, abstracts of congresses and thesis reports that were published inside and outside of Iran about ants. Additionally, we examined the Iranian specimens that are kept at the Plant Pests and Disease Research Institute of Iran (PPDRI), Zoological Museum of Gorgan University (ZMGU), Zoological Museum of Moscow State University (ZMMU) and Zoological Institute of Russian Academy of Sciences, St.-Petersburg (ZIN). The names of those genera, species and subspecies that have been recorded were compared to BOLTON (2005) in order to use only valid names of the species. Some of these species have been reported from several localities, but here we bring only the first location record. Altogether we included 192 records of ants. We used the software ArcView to map the distribution of collection records of the ants in Iran.

Results

After crosschecking of data, our preliminary species list of Iran comprises 120 species and subspecies of ants belonging to 25 genera and five subfamilies (Formicinae, Myrmicinae, Ponerinae, Dolichoderinae and Aenictinae) (Table 1). The subfamilies Myrmicinae and

Aenictinae with 53 and one species have the most and the least numbers in the list, respectively. Eight species and subspecies have been described from Iran during former studies (indicated by * in Table 1). Ten ant species are recorded for the first time for Iran in this paper:

Aphaenogaster gibbosa **(LATREILLE, 1798)**

Mazandaran province, Miankaleh peninsula, Plangan, in shrubs and grass habitats, 14.IV.2005, leg. Omid Paknia, det. Alexander Radchenko, material deposited in ZMGU.

Aphaenogaster kurdica **RUZSKY, 1905**

Golestan province, Aliabad, near Kabudval waterfall, in forest habitat, 17.VI.2005, leg. Omid Paknia, det. Alexander Radchenko, material deposited in ZMGU.

Camponotus aethiops **(LATREILLE, 1798)**

Golestan province, Golestan National Park, Almeh, 17-19.VII.1996, leg. V. Nazari, det. Alexander Radchenko, material deposited in PPDRI.

Camponotus sanctus **FOREL, 1904**

Hormozgan province, Minab, Rudan, 8.VI.2000, leg. V. Nazari, det. Alexander Radchenko, material deposited in PPDRI.

Lasius illyricus **ZIMMERMANN, 1937**

Mazandaran province, Ruyan, Abpari forest. 3.VI.2005, leg. Nasim Vakhideh, det. Bernhard Seifert, material deposited in ZMGU.

Messor denticulatus **SANTSCHI, 1927**

North Khorasan, Bojnurd, Mirzahasnlu village, 23.VII.2004, leg. Zahra Rahmani, det. Alexander Radchenko, material deposited in ZMGU.

Messor minor **(ANDRE, 1883)**

Hamedan province, Hamedan, 25.V.1997, leg. Peyman Moghadasi, det. Alexander Radchenko, material deposited in ZMGU.

Pachycondyla nigrita **(EMERY, 1895)**

Hormozgan province, Lavan island, 17.XI.1999, leg. M. Mofidi-Neyestanak & H. Barari, det. Helen Alipanah, material deposited in PPDRI.

Ponera cf. coarctata **(LATREILLE, 1802)**

Golestan province, 20 km East Gorgan, Tuskestan forest, 28.V.2005, leg. Omid Paknia, det. Alexander Radchenko, material deposited in ZMGU.

Temnothorax parvulus **(SCHENCK, 1852)**

Golestan province, Gorgan, Tuskestan forest, 28.V.2005, leg. Salman Shalchian, det. Alexander Radchenko, material deposited in ZMGU.

Thirty one percent of 192 records are from natural environments or human environments in Tehran province (Fig. 1, overlapped points); however, the province area is only 2% of total area of country. Almost 12% of the reports are from the Caspian area in the North of Iran that comprises 4% of country. There is not any record from the central parts of Iran, especially the central desert ecoregion (Fig. 1).

We recognized thirteen recorded species and subspecies as doubtful (Table 2). In critical view the possibility that these species really occur in Iran is low. For example the current recorded distribution of the species *Camponotus atlantis* FOREL, 1890, *Crematogaster antaris* FOREL, 1894, *C. scutellaris* (OLIVIER, 1792) and *Monomorium salomonis* (LINNAEUS, 1758) is in North Africa or southern Europe, rather than in a Middle Eastern country. *Messor capitatus* (LATREILLE, 1798) occurs in South Europe. The distribution of another group of species, *Camponotus cruentatus* (LATREILLE, 1802), *C. micans* (NYLANDER, 1856), *C. thoracicus* (FABRICIUS, 1804), *Messor barbarus* (LINNAEUS, 1767) and *M. capitatus* (LATREILLE, 1798) is in the Mediterranean region. *Camponotus maculatus* (FABRICIUS, 1782) occurs in Africa, mainly in the tropical region. *Myrmica sabuleti* MEINERT, 1861 and *Tetramorium moravicum* KRATOCHVIL, 1941 are distributed in Europe. The distribution of *P. nigrita* is Southeast Asia.

Discussion

Although the first reports of Iranian ants were published about one hundred year ago, the fauna of this family has not been completely cleared so far. Many parts of the country have not been studied up to now. There are few records especially from the West and the Northwest of the country, where mountains ranges impede the access to habitats; and also from the East and the center of Iran, with their wide desert biomes. Most of the records are from the North of Iran, but many of these samples were collected in disturbed environments near human settlements. There is no considerable report from natural habitats in the region, especially from the Caspian deciduous forests that we expect to be especially species rich due to the enormous age of these forests that are estimated to exist there from late Tertiary period (ZOHARY, 1973). This holds not only in the North, but also in other places (e.g. TIRGARI & PAKNIA 2004, 2005). Most of the recorded species in our list belong to *Camponotus, Messor* and *Cataglyphis* with 22, 16 and 15 species, respectively. The main reason for the dominance of these genera are the climate conditions of the Iran that comprises mainly arid and semi arid zones. However, another reason may be that these ants are large and easy to find. So most probably the method of collecting has influenced these results. In the majority of the current studies, "direct hand collecting" has been the main method. For this reason small sized and cryptic ant genera or subfamilies are underrepresented in the checklist (e.g. Leptanillinae ants) or only few species of a genus have been recognized (e.g. in *Solenopsis*, *Temnothorax* and *Leptothorax*). The same is true for the social parasites that are also missing in our list. Thoroughful investigations of ant diversity with standard sampling methods (see AGOSTI & al. 2000) like pitfall traps, bait trapping or soil extraction with Winkler collectors in different parts of country, especially the uninvestigated areas, are urgently needed to clear the ant fauna of Iran.

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Table 1 List of Iranian ant species according to our review of literature and the examination of material of three museums in Iran and Russia. For species that have been recorded more than one time we listed just the first record.

Scientific Name	**Locality**	**Reference**
Aenictus dlusskyi ARNOL'DI, 1968	Tehran (Tehran Province)	RADCHENKO & ALIPANAH (2004)

Anochetus evansi Crawley, 1922*	Sar-i-Pal (?)	Crawley (1922)
Aphaenogaster gibbosa (Latreille, 1798)	Miankaleh Peninsula (Mazandaran Province)	New to Iran
Aphaenogaster kurdica Ruzsky, 1905	Ali Abad (Golestan Province)	New to Iran
Aphaenogater syriaca Emery, 1908	Dezful (Khuzestan Province)	Alipanah & Dezhakam (2000)
Camponotus aethiops (Latreille, 1798)	Golestan National Park (Golestan Province)	New to Iran
Camponotus armeniacus Arnol'di, 1967	---------	Radchenko (1996, 1997)
Camponotus buddhae Forel, 1892	---------	Radchenko (1996, 1997)
Camponotus compressus (Fabricius,1787)	Bandar-e-abbas (Hormozgan Province)	Menozzi (1927)
Camponotus cecconii Emery, 1908	Tehran (Tehran Province)	Alipanah & al. (1995)
Camponotus fedtschenkoi Mayr, 1877	---------	Radchenko (1996)
Camponotus fellah Dalla Torre, 1893	Lar (Fars Province)	Tirgari & Paknia (2004)
Camponotus gestroi Emery, 1878	Tehran (Tehran Province)	Alipanah & al. (2000)
Camponotus kopetdaghensis Dlussky & Zablin, 1985	Golestan National Park (Golestan Province)	Alipanah (2004)
Camponotus libanicus Andre, 1881	Tehran (Tehran Province)	Alipanah & al. (2000)
Camponotus oasium Forel, 1890	Mashhad (Khorasan Province)	Forel (1904a)
Camponotus oertzeni Forel, 1889	---------	Radchenko (1996, 1997)
Camponotus sanctus Forel, 1904	Minab (Hormozgan Province)	New to Iran
Camponotus turkestanicus Emery, 1887	---------	Radchenko (1996, 1997)
Camponotus turkestanus Andre, 1882	---------	Radchenko (1996, 1997)
Camponotus vogti Forel, 1906	Tehran (Tehran Province)	Alipanah & al. (2000)
Camponotus xerxes Forel, 1904*	Karaj (Tehran Province)	Ardeh (1994)
Cardiocondyla brachyceps Seifert, 2003*	Shiraz 51 Km W (Fars Province)	Seifert (2003)
Cardiocondyla elegans Emery, 1869	Miankaleh peninsula (Mazandaran Province)	Seifert (2003)
Cardiocondyla fajumensis Forel, 1913	Dow Gonbadan (Kohkiluye va Boyer ahmad)	Seifert (2003)
Cardiocondyla mauritanica Forel, 1890	Basht (Fars Province)	Seifert (2003)
Cardiocondyla persiana Seifert, 2003*	Shiraz (Fars Province)	Seifert (2003)
Cardiocondyla sahlbergi Forel, 1913	Maku (East Azerbaijan Province)	Seifert (2003)
Cardiocondyla stambuloffii Forel, 1892	Khoy (East Azerbaijan Province)	Seifert (2003)
Cardiocondyla unicalis Seifert, 2003*	Ma mulan (Lorestan Province)	Seifert (2003)
Cataglyphis aenescens (Nylander, 1849)	Herirud Kiafikala (Khorasan Province)	Forel (1904a)
Cataglyphis altisquamis (Andre, 1881)	Northern Iran	Radchenko (1998)
Cataglyphis bellicosus (Karavaiev, 1924)*	Tehran (Tehran Province)	Karavaiev (1924)
Cataglyphis bucharicus Emery, 1925	North of Iran	Radchenko (1998)
Cataglyphis cuneinodis Arnol'di, 1964	---------	Radchenko (1998)
Cataglyphis emery (Karavaiev, 1911)	---------	Radchenko (1998)
Cataglyphis foreli (Ruzsky, 1903)	Mashhad (Khorasan Province)	Forel (1904a)

Cataglyphis frigidus persicus (EMERY, 1906)*	Shiraz (Fars Province)	EMERY (1906)
Cataglyphis lividus (ANDRÉ, 1881)	Zirkuch Buniabad (Khorasan Province)	FOREL (1904a)
Cataglyphis niger (ANDRÉ, 1881)	Tehran (Tehran Province)	FOREL (1904a)
Cataglyphis nigripes Arnoldi, 1964	West of Iran	RADCHENKO (1998)
Cataglyphis nodus (BRULLÉ, 1833)	Bushehr (Bushehr Province)	MENOZZI (1927)
Cataglyphis ruber (FOREL, 1903)	---------	RADCHENKO (1998)
Cataglyphis setipes (FOREL, 1894)	East of Iran	RADCHENKO (1998)
Cataglyphis viaticus (FABRICIUS, 1787)	Mashhad (Khorasan Province)	FOREL (1904a)
Crematogaster inermis MAYR, 1862	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Crematogaster sorokini RUZSKY, 1905	Hamedan (Hamedan Province)	ALIPANAH (2004)
Crematogaster subdentata MAYR, 1877	Karadj (Tehran Province)	ARDEH (1994)
Formica cunicularia LATREILLE, 1798	Tehran (Tehran Province)	ALIPANAH & al. (2000)
Formica lusatica SEIFERT, 1997	Babol Sar (Mazandaran)	PAKNIA & KAMI (2007)
Formica rufibarbis FABRICIUS, 1793	North West of Iran	CRAWLEY (1920b)
Formica sanguinea LATREILLE, 1798	Tehran (Tehran Province)	ALIPANAH & al. (2000)
Lasius alienus (FÖRSTER, 1850)	North West of Iran	CRAWLEY (1920b)
Lasius brunneus (LATREILLE, 1798)	Bandar-e-anzali (Gilan Province)	CRAWLEY (1920b)
Lasius emarginatus (OLIVIER, 1792)	North West of Iran	CRAWLEY (1920b)
Lasius illyricus ZIMMERMANN, 1937	Ruyan (Mazandaran Province)	New to Iran
Lasius lasioides (EMERY, 1869)	Miankaleh peninsula (Mazandaran Province)	PAKNIA & KAMI (2007)
Lasius neglectus VAN LOON, BOOMSMA & ANDRASFALVY,1990	Babolsar (Mazandaran Province)	PAKNIA & KAMI (2007)
Lasius platythorax SEIFERT, 1991	Dezfull (Khuzastan Province)	ALIPANAH (2004)
Lasius turcicus SANTSCHI, 1921	Tehran (Tehran Province)	ALIPANAH & al. (2000)
Lepisiota dolabellae (FOREL, 1911)	Karadj (Tehran Province)	ARDEH (1994)
Lepisiota bipartita (F. SMITH, 1861)	Kerman Bazman (Kerman Province)	FOREL (1904a)
Lepisiota semenovi (RUZSKY, 1905)	Rudan (Hormozgan province)	TAHMASEBI & ALIPANAH (2000)
Leptothorax acervorum (FABRICIUS, 1793)	Miankaleh Peninsula (Mazandaran Province)	TAYLOR (2006)
Liometopum microcephalum (PANZER, 1798)	Saghez (Kordestan Province)	PAKNIA & KAMI (2007)
Messor caducus (VICTOR, 1839)	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Messor concolor SANTSCHI, 1927	Miankaleh Peninsula (Mazandaran Province)	TAYLOR (2006)
Messor dentatus SANTSCHI, 1927	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Messor denticulatus SANTSCHI, 1927	Bojnurd (North Khorasan)	New to Iran
Messor ebeninus SANTSCHI, 1927	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Messor galla (MAYR, 1904)	Lar (Fars Province)	TIRGARI & PAKNIA (2004)
Messor incorruptus KUZNETSOV-UGAMSKY, 1929	Hamedan (Hamedan Province)	ALIPANAH (2004)
Messor intermedius SANTSCHI, 1927	Bushehr (Bushehr Province)	MENOZZI (1927)
Messor meridionalis (ANDRE, 1883)	Dezfull (Khuzastan Province)	ARDEH (1994)

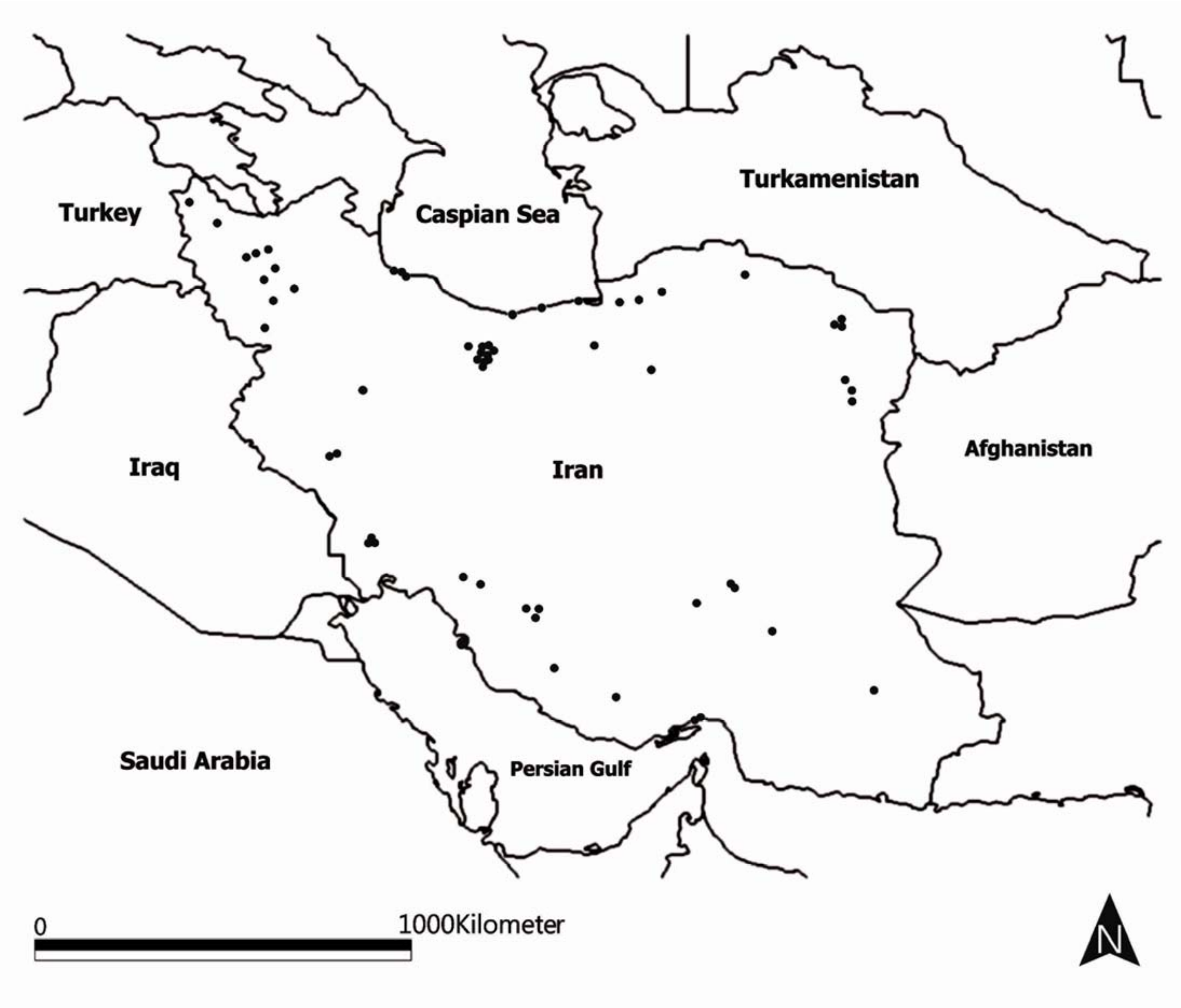
Messor minor (ANDRE, 1883)	Hamedan (Hamedan Province)	New to Iran
Messor rufotestaceus (FORSTER, 1850)	Dezful (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Messor semirufus (ANDRE, 1883)	North West of Iran	CRAWLEY (1920a)
Messor structor platyceras CRAWLEY, 1920*	North West of Iran	CRAWLEY (1920a)
Monomorium abeillei ANDRE, 1881	Dezful (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Monomorium destructor (JERDON, 1851)	Ahwaz (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Monomorium kusnezowi SANTSCHI, 1928	Mashhad (North Khorasan	ALIPANAH (2004)
Monomorium nitidiventre EMERY, 1893	Ghir Karzin (Fars Province)	TAYLOR (2006)
Monomorium pharaonis (LINNAEUS, 1758)	Bandar-e-abbas (Hormozgan Province)	MENOZZI (1927)
Myrmica bergi RUZSKY, 1902	Bandar-e-anzali (Gilan Province)	CRAWLEY (1920a)
Pachycondyla sennaarensis (MAYR, 1862)	Lar (Fars Province)	TIRGARI & PAKNIA (2005)
Paratrechina flavipes (SMITH, F., 1874)	Ahwaz (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Paratrechina longicornis (LATREILLE, 1802)	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Paratrechina vividula (NYLANDER, 1846)	Hilmend (Sistan va Baluchestan Province)	FOREL (1904a)
Pheidole pallidula (NYLANDER, 1849)	North West of Iran	CRAWLEY (1920a)
Pheidole sinaitica MAYR, 1862	Lar (Fars Province	TIRGARI & PAKNIA (2004)
Pheidole teneriffana FOREL, 1893	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Plagiolepis pallescens FOREL, 1889	Tehran (Tehran Province)	ALIPANAH & al. (2000)
Plagiolepis taurica SANTSCHI, 1920	Karadj (Tehran Province)	ARDEH (1994)
Polyrhachis lacteipennis SMITH, F. 1858	Lar (Fars Province)	TIRGARI & PAKNIA (2004)
Ponera cf. coarctata (LATREILLE, 1802)	20 km East of Goran (Golestan Province)	New to Iran
Solenopsis cf. fugax (LATREILLE, 1798)	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Solenopsis cf. latro FOREL, 1894	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Tapinoma erraticum (LATREILLE, 1798)	South West of Caspian Sea	CRAWLEY (1920a)
Tapinoma karavaievi EMERY, 1925	Ahvaz (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Tapinoma simrothi KRAUSSE, 1911	Lar (Fars Province)	TIRGARI & PAKNIA (2004)
Temnothorax iranicus (RADCHENKO, 1994*)	Tehran (Tehran Province)	RADCHENKO (1994a)
Temnothorax parvulus (SCHENCK, 1852)	20 km E. Gorgan (Golestan Province)	New to Iran
Tetramorium caespitum (LINNAEUS, 1758)	Bandar-e-anzali (Gilan Province)	CRAWLEY (1920a)
Tetramorium chefketi FOREL, 1911	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Tetramorium davidi FOREL, 1911	Tehran (Tehran Province)	ALIPANAH & al. (1995)
Tetramorium ferox RUZSKY, 1903	Lar (Fars Province)	TIRGARI & PAKNIA (2004)
Tetramorium forte FOREL, 1904	Karadj (Tehran Province)	ARDEH (1994)

Table 2. List of ant species that are doubtful for Iranian fauna. All species have been recorded from Iran only once.

Species Name	**Locality**	**Reference**
Camponotus atlantis FOREL, 1890	Karadj (Tehran Province)	ARDEH (1994)
Camponotus cruentatus (LATREILLE, 1802)	Gonbad-e-Kavoos (Golestan Province)	TAYLOR (2006)
Camponotus maculatus (FABRICIUS, 1782)	Kerman (Kerman Province)	FOREL (1904a)
Camponotus micans (NYLANDER, 1856)	Kerman (Kerman Province)	TAYLOR (2006)
Camponotus thoracicus (FABRICIUS, 1804)	Kerman, Bazman (Kerman Province)	FOREL (1904a)
Crematogaster antaris FOREL, 1894	Ahvaz (Khuzestan Province)	ALIPANAH & DEZHAKAM (2000)
Crematogaster scutellaris (OLIVIER, 1792)	Bandar-e-anzali (Gilan Province)	CRAWLEY (1920a)
Messor barbarus (LINNAEUS, 1767)	Mashhad (Khorasan Province)	FOREL (1904a)
Messor capitatus (LATREILLE, 1798)	Mashhad (Khorasan Province)	FOREL (1904a)
Monomorium salomonis (LINNAEUS, 1758)	Bushehr (Bushehr Province)	MENOZZI (1927)
Myrmica sabuleti MEINERT, 1861	Karadj (Tehran Province)	ARDEH (1994)
Pachycondyla nigrita (EMERY, 1895)	Lavan island (Hormozgan Province)	New to Iran
Tetramorium moravicum KRATOCHVIL, 1941	Tehran (Tehran Province)	ALIPANAH & al. (1995)

Figure Captions:

Fig. 1: Map of Iran including sample sites of 192 recorded ants in Iran (black points).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RESEARCH ARTICLES BELONGING TO CHAPTER 4

Pfeiffer M, Ho CT, Teh CL (in press) Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm (*Elaeis guineensis*) in Borneo and Peninsular Malaysia *Ecography*

Pfeiffer M, Nais J, Linsenmair KE (2006) Worker size and seed size selection in 'seed'-collecting ant ensembles (Hymenoptera : Formicidae) in primary rain forests on Borneo. *Journal of Tropical Ecology* 22:685-693

Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm (*Elaeis guineensis*) in Borneo and Peninsular Malaysia

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Abstract. The oil palm, *Elaeis guineensis*, is a native of West Africa and is now extensively grown in South-East Asia. In 2005, the crop covered four million ha of Malaysia. We examined the arboreal ant fauna in two oil palm plantations that had been farmed with integrated pest management practices for at least 10 years. Having cut and examined palm fronds from 595 and 503 palms in Borneo and Peninsular Malaysia respectively, we studied diversity in ant assemblages, analysed composition of ant mosaics by stepwise use of null-models, and explored the influence of exotic vs. native species on community structure. Altogether we sampled 53 species of canopy ants, of which 23 species were shared between both sites. Seventeen species in Borneo and 24 species in Peninsular Malaysia accounted for 95% of all species occurrences (SOCs). Forty six percent of all SOCs belonged to 12 tramp ant species with pan-tropical distributions. Forty percent of all SOCs were exotic ants. Six dominant species were found in Borneo, five in the Peninsula. The three most abundant species, *Anoplolepis gracilipes*, *Oecophylla smaragdina* and *Technomyrmex albipes* were dominant in both sites. Three dominants were invasive species that were found on more palms than the native group. Dominant tramp species coexisted with non-dominants more often and tolerated more species of non-dominant ants than native dominants. Null model analyses indicated that species were arranged in mosaics at both the Malaysia and Borneo sites. Dominant species showed much less co-occurrence than expected by chance, pointing towards species segregation (even in presence of introduced, invasive species). Similar results were obtained for all species. Non-dominant ants were either positively associated with their dominants, or co-occurred randomly in the presence of dominant species. In contrast, ant assemblages on palms without dominants showed species segregation.

Introduction

The spatial ecology of ant assemblages in tropical crop plantations in various parts of the world have been frequently examined, and most studies have argued that these assemblages are structured in ‘ant mosaics’ (e.g. Leston 1973, see reviews of Dejean and Corbara, 2003; Blüthgen and Stork 2007). Ant mosaics are patchworks of often arboreal ant territories, each dominated by different species, mutually excluding each other from distinct canopy areas (Jackson 1984, Majer and Camer Pesci 1991), thus showing non-random species co-occurrence patterns (Blüthgen et al. 2004). Dominant species maintain large colonies and are often characterised by behavioural dominance, polydomy and use of carbohydrate-rich homopteran exudates (Davidson 1997). Differential patterns of resource use are often the main drivers of ant community structure and territoriality among dominant species (Blüthgen et al. 2004). Ant mosaics are hierarchically structured, with each dominant species coexisting with one or more subordinate, non-dominant species (with less populous colonies and lower level of aggressiveness). Subordinant species often share the same territories and/or trails (Majer 1993, Dejean and Corbara 2003) and may be positively associated with particular dominant species (Leston 1973). Under certain conditions some non-dominant species are able to defend territories in the same way as do dominants; such species are called “sub-dominant” species (Leston 1973).

Large plantations of *Elaeis guineensis* in Malaysia (Ho and Teh 1997, Ho 2002) are intensive cultures with significant impact on the ecosystem. The initial clearing of land for planting with the non-native oil palm creates empty space for colonization by other species. These colonizing species can be native species that come from surrounding areas or they can be exotic species that are dispersed by human commerce and especially adapted to invade disturbed regions. Ants are a dominant insect group in oil palm plantations (Pfeiffer, Ho, Teh, personal observations), and non-native status of *Elaeis guineensis* in Malaysia could predispose the cultivar to support exotic ant species in its ecosystem.

In this study, we assessed ant species richness and community composition within the plantations to analyse whether and how native and introduced arboreal ant species react to the disturbance that has been created by the installation of the plantation and to the introduction of this non-native tree species. Regarding this topic our experiment included a double control: 1) the intensive studies on the arboreal ant diversity in Malaysian forests that had been conducted by canopy fogging in the last years (e.g. Floren and Linsenmair 2000, 2005) and 2) the ant species composition in African plantations of *E. guineensis,* the natural environment of this tree species (Dejean et al. 1997). Both can serve as references to which the results of our analysis can be compared.

Additionally, we studied the ant community patterns in detail to consider the impact of territoriality and to determine whether the assemblages in the plantations were structured in a mosaic model for which we expected a high influence of exotic ants. Due to the high homogeneity of their plant cover intensive plantations are the ideal model system for null models studies in spatial ecology that have been proven as useful tools for a verification of ant mosaics (Blüthgen and Stork 2007, but see Sanders et al. 2007). For example, Ribas and Schoereder (2002) recently used null model analyses to reassess several former published ‘ant mosaic’ studies and revealed that in some cases dominant ant species co-occurred randomly instead of showing a true mosaic pattern, hence pointing towards the association of ant species with certain resources and conditions. Similarly, the re-assessment of an ‘ant mosaic’ in a cocoa plantation that was invaded by *Wasmannia auropunctata* showed random co-occurrence patterns among dominant species, segregated patterns among subdominant species on trees without dominant species, and random patterns among non-dominant specices in the presence of dominant species (Sanders et al. 2007). While the reasons for the observed pattern may be manifold, invasive ants are known to disturb native ant assemblages (Sanders et al. 2003) and ecosystem functioning (Ness et al. 2004). Whereas most studies on the impacts of invasive ants have focused on mainly ground-dwelling ants, e.g. the imported fire ant and the Argentine ant (e.g. Ness et al. 2004, Sanders et al. 2003), here we present one of the rare studies that deals with arboreal invasive species and is conducted at canopy level.

We accumulated a large dataset on arboreal ant assemblages (ca. 1100 palms) at two sites with intensive oil palm cultures of South East Asia, in Borneo and Peninsular Malaysia . Specifically we investigated: 1) the diversity and structure of ant assemblages in these plantations, 2) the proportion of ants that are native, exotic, or tramp ants, 3) whether ants in these systems are assembled in mosaics, and 4) whether the species associations of dominant native species and dominant tramp ants differ. In addition, we used null model analyses to ask whether dominant species are spatially segregated, as mosaic theory predicts and whether invasive species ‘disassemble’ species co-occurrence patterns.

Methods

STUDY SITES

Ants were studied in two oil palm plantations farmed with integrated pest management practices in the Golden Hope Research Centre (GHRC) in Banting, West-Malaysia (627 ha, founded in 1955, N 02°48.15 E 101°27.67’) and in the Golden Hope Plantation (Sabah) Sdn Bhd in Tawau (GHPT) on Borneo (4331 ha, founded in 1949, N 04°22.54’ E 117° 51.31’) (Fig. 1).

The average annual rainfall at GHRC was 1735.7 mm with rainfall occurring at a mean of 126 days (January 2000 to December 2004; GHRC unpublished data), while at GHPT Borneo mean annual precipitation was 2091 mm, occurring at a mean of 138 days (January 2000 to December 2004; GHPT unpublished data).

DEFINITION OF THREE GROUPS OF NON-NATIVE ANTS

In our study, we distinguished three groups of non-native ants (see Passera 1994, McGlynn 1999, Holway et al. 2002). 1) Transferred, introduced, alien or exotic ants are collected in habitats not native to the species. 2) Tramp ants are dispersed by human commerce and have a pan-tropical or world wide distribution, but are mostly confined to human-modified habitats. 3) Invasive ants are the most successful introduced species being able to penetrate natural ecosystems (disturbed or undisturbed) and to outcompete native ants and affect other organisms. This definition is not necessarily nested, as some of the tramp species are of South-East Asian origin and are not exotic species for Malaysia.

SAMPLING TECHNIQUE

Sampling was conducted by following the harvesters that typically cut about two to three palm fronds from the palms during harvesting to access ripe palm fruit bunches. The first two cut fronds were examined for about 10 minutes and all ants found in this time period were sampled. Additional fronds surveyed generally yielded no further species (pers. obs. M. Pfeiffer). On average, about 50 randomly chosen palms were sampled per field, this number being dependent on ripe bunches available at a harvesting round. Sampling of neighbouring palms (mean distance = 8.92 m) was avoided by marking sampled palms, samples being usually drawn from palms that were about 20 m apart from each other. As dominant ants did not normally exert control over more than two neighbouring palms (pers. obs. M. Pfeiffer), this distance was enough to ensure independence of samples. In a few cases where *Anoplolepis gracilipes* controlled small groups of palms, we sampled these regions only once. Ant sampling was done with forceps and ant specimens were stored in 96% alcohol.

In Borneo, we sampled 13 fields in GHTP, totalling 595 palms (28 Sept. to 19 Oct. 2004). In West Malaysia, nine fields with 503 palms were sampled (10 to 29 Aug. 2005). In both sites we assessed fields with a large variety of age classes (three to 26 years old). Data on the history of the fields of both sites provided by Golden Hope Research Sdn. Bhd. confirmed the fields to have been free of insecticide treatments for at least eight years.

Ants were identified with the help of taxonomic experts (see acknowledgments) and in our lab at the University of Ulm, Germany, where a reference collection (voucher material) of all species from this study is kept (with pictures of most species available via Internet at http://www.antbase.net).

IDENTIFICATION OF DOMINANT ANTS

Dominant ants are characterised by extremely populous colonies, the ability to build large or polydomous nests and a highly developed territoriality (Dejean and Corbara, 2003). A high rate of carbohydrate feeding, obtained from trophobionts is another characteristic of dominant ants (Davidson, 1997, Blüthgen et al. 2004). Three terms are used in the current discussion: besides ‘numerical dominance’, or the predominance in number or biomass, there is ‘behavioural dominance’ in respect of fighting abilities, aggression level and dominance at baits and ‘ecological dominance’ that applies to invasive species (Davidson, 1998).

We classified ants as dominants if they fulfilled at least two of the following criteria: full-grown colonies with more than 5000 individuals, polydomous nests with usually more than two nests per fronds (checked during examination of the fronds, see above), dominance at tuna baits (unpublished observations), observations of territorial borders and/or territorial fights with exclusion of other dominant species from the territory and frequent high level of aggressiveness. Most of the species in our study which we identified as dominant were already known dominants from other studies (Room 1975, Majer 1993, Dejean and Corbara 2003, Abbott 2006, Blüthgen and Stork 2007), e.g. *O. smaragdina.* In other species (e.g. *Philidris* sp. 1) we tested their aggressiveness by presenting individuals and/or nests of other dominant species in their territory.

ANALYSES

For the calculations of rarefaction curves with software package EstimateS (Version 7.0, R. K. Colwell, http://viceroy.eeb.uconn.edu/EstimateS) we used the sample-based rarefaction approach (Gotelli and Colwell, 2001). Here, all ants of one (morpho-) species (group) that were collected at one palm tree were counted as one species occurrence, while a sample was comprised of all species taken at one palm. We used the Cole rarefaction to plot the rarefaction curves.

Recently, Brose and Martinez (2004) published a method to optimise the estimation of species richness by the choice of optimal species estimators. We followed their method and (1) estimated S_{true} based on all samples by a range of estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2, Bootstrap, MMMean); (2) calculated the estimated mean of sample coverage; (3) chose the most accurate estimator for sample coverage according to the tables provided by Brose and Martinez (2004) and (4) estimated species richness with this estimator and with the maximum number of occurrences per site.

Alpha diversity was assessed by computing diversity indices with EstimateS. We calculated the effective number of species (D) from the Shannon Entropie, given by the Shannon Diversity Index H, according to the formula of Jost (2006): $D = \exp(H)$. The effective number of species equals species richness if all species of a sample have the same frequency. It decreases with decreasing evenness of a sample. Simpson diversity was used as a complement to focus on the most frequent species of a sample. Beta diversity was calculated using Morisita’s Index of Similarity (Krebs 1989).

We analysed species co-occurrence patterns with software EcoSim 7.70 (Gotelli and Entsminger 2001). First, we arranged species in a species x site matrix. In these matrices columns represented the single palms at a site, and rows were all ant species that had been collected at the site. We then used the ‘C-score’ co-occurrence index of Stone and Roberts (1990) that quantifies the average number of ‘checkerboard units’ (CUs) for all species pairs within a matrix. A CU is a 2 x 2 presence-absence sub-matrix of the form 10/01 or 01/10, referring to "the way two species might colonise a pair of islands; whenever each species colonises a different island this adds 1 to the C-score" (Stone and Roberts 1990). For each species pair the number of CUs is $(R_i - S)(R_j - S)$ where S is the number of shared sites and R_i and R_j are the number of species occurrences (row totals) for species *i* and *j*. The C-score is the average of all possible checkerboard pairs, calculated for species that occur at least once in the matrix. The observed C-score was then compared to the C-scores generated from 5000 randomizations, or null communities. In a community with less pairwise species co-occurrence the C-score should be significantly higher than the C-score of the null communities, and an unusually small index, however, points towards species aggregation.

We used a fixed-equiprobable model to generate the null communities because all palms in all fields in each of the plantations were equally likely to support ant species found across all fields of this plantation. From the ant species' perspective individual oil palms are small, uniform sample plots that are equivalent to one another and are equally likely to be successfully colonised. Thus the appropriate randomisation for our data is a fixed, equiprobable algorithm in which row totals (species occurrences) are preserved, but occurrences for each species are randomly distributed among the columns (trees). This model is robust in relation to type I and type II statistical errors, taking into account ‘empty’ sample plots and allowing species number per sample plot to vary in the null models (Gotelli and Entsminger 2001).

In order to analyse the complex patterns of positive and negative associations among ant species (Blüthgen and Stork 2007), we constructed several matrices and tested at different levels of the communities: 1) the entire ant assemblages (2 matrices: 36 x 595, 39 x 503); 2) the dominant species (6 x 595, 5 x 503); 3) those assemblages on palms without dominant species (31 x 78, 34 x 165). In the fourth step we tested those ant sub-communities that co-occurred on palms together with one of the dominant ant species, thus restricting analysis to subsets of palms (columns). There was one submatrix associated with each dominant species. Each submatrix consisted only of the palms on which a dominant species was detected and those non-dominant species that were sampled at least five times (to avoid the evaluation of random aggregations). At the same time we excluded all species (rows) that had been classified as ‘dominant’ in the first steps of the analysis.

For the analysis of sub-communities as stated above we needed at least two non-dominant species as the dominant species itself was not included in the tests. Thus no results could be obtained in the case of *Pheidologeton affinis* in Banting and *Philidris* sp. 1 in Tawau. While with *P. affinis* no species co-occurred more than five times, in *Philidris* sp. 1 one non-dominant species, *Polyrhachis bicolor*, fulfilled this condition and thus these species were tested pairwise.

Pairwise C-score analysis was also used to investigate interactions between individual dominant species . Here we included all palms of one site and tested co-occurrence patterns of only two species (2 x 595, 2 x 503). To manage type I error during pairwise comparison we controlled the false discovery rate (FDR) (Benjamini and Hochberg 1995, for a detailed description of the method see Verhoeven et al. 2005), rather than use a Bonferroni-type correction. Significance thresholds corresponding to a FDR level of 0.05 were 0.0398 for Tawau and 0.0426 for Banting, respectively. We obtained similar results from a parallel set of analysis in which we used chi-square tests in combination with a control of FDR, however, these results are not given here.

To compare results across sub-communities we calculated the standardized effect size (SES) for each matrix. The SES is a measure for the number of standard deviations that the observed index is above or below the mean index of the simulated communities (Sanders *et al.*, 2003).

To test whether exotic dominant species were more often associated with non-dominant species than native dominants, we compared species occurrences of non-dominants on the palms dominated by native vs. exotic species in an U-test.

Results

DIVERSITY PATTERNS

The rarefaction curve indicated that sampling was almost complete (Fig. 2). Altogether we sampled 53 species of canopy ants, 36 species in Tawau and 39 species in Banting (see Table 1). In Borneo 17 and in Peninsular Malaysia 24 species accounted for 95% of all species occurrences. The ICE-estimator predicted a total of 38 ant species for Tawau and 41 species for Banting. Shannon Entropie H was calculated at a common sample size of 503 palms as 2.72 ± 0.02 for Tawau and 3.08 ± 0.0 for Banting, resulting in an effective number of species of 15.18 for Tawau and 21.76 for Banting (see Jost 2006). Simpson diversity was 10.77 ± 0.19 for Tawau and 16.34 ± 0.0 for Banting. We found in Tawau a mean of 1.90 ant species per palm (S.D.= 1.00, min =1, max = 7), in Banting of 2.12 species (S.D. = 1.17, min =1, max =7).

Twenty-three species were shared between both sites, resulting in moderate beta-diversity (Morisita's Index of Similarity: 0.68). *Technomyrmex albipes*, *Oecophylla smaragdina* and *Anoplolepis gracilipes* were the most abundant ant species in the palm canopy in both regions (see Table 1 for full names). We found a high prevalence of non-native ant species: 46 % of all species occurrences (SOCs) belonged to 12 tramp ant species, and at least four of these species were invasive (comprising 34% of all SOCs). At least ten species (40 % of all SOCs) were exotic ants from outside Malaysia.

ANT MOSAICS

With regard to our definition and preliminary experiments we found five dominant ant species in Banting and six in Tawau. While the three most abundant species, *A. gracilipes*, *O. smaragdina* and *T. albipes* were found to be dominant in both sites, *Paratrechina longicornis* was dominant only in Banting, while in Tawau it occurred only with few individuals on 16 palms and was therefore not included in the analysis. Similarly, *Pheidologeton affinis* occurred in Banting only on 21 palms, but was exceptionally aggressive and considered a true dominant. *Camponotus arrogans*, *Crematogaster rogenhoveri* and *Philidris* sp. 1 were dominants that only occurred at Tawau.

When we tested entire arboreal ant assemblages, we found clear evidence for species segregation in both of the plots (Tawau SES = 7.9; Banting SES = 6.5, $p_{o>e}$ for both < 0.001, details see Table 2). As predicted by ant mosaic theory, species segregation was also found when we tested species co-occurrence patterns of only the dominant ant species of both sites. The observed index was significantly larger than the simulated index in Borneo (observed C-score: 8750.9 vs. simulated C-score: 7327.2) and in the Peninsular Malaysia (observed C-score: 4585.0 vs. simulated C-score: 3688.0) (both $p_{o>e} < 0.001$, see Table 2). However, when we tested only those communities that occurred on palms without dominant species we found similarly segregated patterns. This was especially clear in Tawau 2004 (SES = 6.42 $p_{o > e} < 0.001$), but also true for Banting 2005 (SES = 2.20 $p_{o > e} < 0.01$).

Then we analysed the communities of those subordinate ants associated with a single species of dominant ant separately. In most cases the observed index did not differ from null prediction, suggesting a random structure to the sub-communities. In some cases we found an observed index that was significantly smaller than the simulated index, thus pointing towards a positive association of species that has been predicted by ant mosaic theory. These positive associations were found on palms dominated by *A. gracilipes* and *T. albipes* in Tawau (each $p_{o < e} < 0.01$) and in the case of *O. smaragdina* and its non-dominants, that obtained a significant result in Banting ($p_{o < e} < 0.001$) and showed at least a tendency to have positive species relationships in Tawau ($p_{o < e} = 0.07$) (see Table 2). As *Philidris* sp.1 was found to be positively associated with the non-dominant *Polyrhachis bicolor* in pairwise analysis, at least four of 11 dominant species showed positive associations with their non-dominants. Species combinations in communities of non-dominant species associated with certain dominants differed between plots and among species (Table 3).

In paiwise tests among the dominants, *T. albipes* was positively associated with *A. gracilipes* in both sites and with *O. smaragdina* in Tawau. Thus these species pairs were co-dominants on certain palms (Leston 1973, Dejean and Corbara 2003) (Table 4).

Of a total of eight dominant species, three were confirmed alien tramp species, and these were more frequently found on palms than the native group (667 vs. 551 SOCs). This tendency was more pronounced in the plantation in Banting, where exotic dominants colonised twice as many palms than natives (276 vs. 138 SOCs). More subordinate species were found coexisting on palms with tramp dominants than with native dominants, on average 7.6 ±2.6 species per sub-community vs. 3.8 ± 2.9 species (data from Table 3, T-test T(1, 9)= 2.2, p = 0.055). At the same time dominant tramp species were significantly more often found together with non-dominant species than native dominants (0.89 ± 1.0 vs. 0.64 ± 0.9, U-test $n_1 = 597$, $n_2 = 490$, U = 129218.9, Z = 3.31, p <0.001).

Random community patterns had been predicted as a result of community disassembly by invasive species, however, few of our results support this hypothesis. At both sites we found the invasive dominant species *A. gracilipes* and *T. albipes*, However, in both cases communities of dominants were clearly non-random and spatial segregated. Similarly, non-dominant species that co-occurred with these two species were positively associated in three of four cases, with only those sub-community associated with *T. albipes* in Banting being randomly structured. Additionally the randomly structured sub-community of the invasive *P. longicornis* in Banting pointed towards community disassembly.

Discussion

DIVERSITY PATTERNS

One aim of our study was to assess ant species richness and composition within the plantations in order to give reliable figures for the ongoing discussion on the loss of biodiversity and the impact of exotic species in agro-forests (Donald 2004). As expected for a monoculture plantation site, ant diversity in both plots was low when compared with natural rain forests. Whereas in primary forest in Sabah about 280 arboreal ant species have been collected from the Kinabalu National Park by canopy fogging (Floren and Linsenmair 2005), we found only about 40 species in Malaysian oil palm plantations, with a handful of species dominating the assemblages. Additional methods, like intensive sampling on the palm stem revealed only few further species that overlapped with the ground ant community (Pfeiffer, personal observations). However, the sampling methods and efforts used in the forest studies were different to ours and thus may affect our capability to directly compare species richness. But while our species accumulation curves were close to reaching asymptotes, those of Floren and Linsenmair (2000, 2005) were far from species saturation, thus it is most likely the case that arboreal species richness is much higher in primary forest than in the survey plantations. Similar patterns have been reported by Brühl (2001) who found 41 species of ants on the floor of oil palm plantations in East Sabah (with *A. gracilipes* and *Dolichoderus* sp. accounting for more than 50% of the SOCs). Only 13 of the 186 ground dwelling forest species collected in this region (6.9%) were also reported from oil palm estates (Brühl 2001).

In essence, Malaysian oil palm plantations are inhabited by a depauperate ant fauna dominated by certain species of ‘tramp ants’ (Table 1). Some of these species probably originated from South East Asia, like the myrmicines *Monomorium floricola* and *Cardiocondyla wroughtonii*; others are from the nearby Pacific region, e.g., the most abundant *T. albipes* (Barry Bolton, pers. comm.); while *Paratrechina longicornis* originated from Africa, and *Tetramorium simillimum* and *Hypoponera punctatissima* from Europe (McGlynn 1999). Several species are of unknown origin, e.g. *Tapinoma melanocephalum* being first reported from French Guiana or *A. gracilipes* that came most probably from tropical Africa (Passera 1994, Abbott et al. 2006). These ants may spread further and establish new territories during replanting of estates.

In the oil palm plantations in Cameroon, *Crematogaster gabonensi* and *Tetramorium aculeatum* were the most abundant species (Dejean *et al*. 1997), the number of dominants (six), was comparable to those found in Malaysia (six and five). One of the dominants in Cameroon was *Pheidole megacephala*, an invasive species that originates most probably from Africa (McGlynn 1999). Composition of ant genera, though not species, was similar in Africa to those in the Malaysian plantation.

ANT MOSAICS

Ant mosaics have been documented from a variety of plantation, secondary forest, (Dejean et al. 1994) rainforest (Blüthgen et al. 2004) ecosystems (but see Floren and Linsenmair 2000, Ribas and Schoereder 2002, Sanders et al. 2007). Mosaic theory predicts (1) species segregation of the dominant ant species, while (2) non-dominant ant species should be (partly) associated with their dominants (Leston 1973, Hölldobler and Wilson 1990). Ribas and Schoereder (2002), who tested 14 reported ant mosaics in various crop plantations with null-models whether they fit to these predictions, claimed the ant mosaic model to be valid in only about half of these cases and alternatively stressed the importance of habitat preferences and stochastic events for the structuring of arboreal ant assemblages.

In the case of arboreal ant communities of the Malaysian oil palm plantations the theoretical criteria for ant mosaics were satisfied. Firstly, we showed that the whole ant assemblage had C-scores that were significantly higher than expected, thus demonstrating spatial segregation of the species. Non-random spatial co-occurrence patterns have been found in several ant assemblages that were compared to null models (e.g., Gotelli and McCabe 2002, Badano et al. 2005 and some of the examples in Ribas and Schoereder 2002). The dominant ants found in this study were spatially segregated, as suggested to be a main criteria in mosaic formation (Leston 1973) and our results corroborated other studies of arboreal ant assemblages (Blüthgen et al. 2004, Leston 1978).

As species segregation was found even on palms without dominant species, this be a hint to the presence of “sub-dominant” species that generally act as non-dominants but which are able, under certain conditions, to defend territories in the same way as do dominants (Leston 1973). However, especially when aggressive dominant species are missing different microhabitat preferences of the species may be crucial for the explanation of the spatial structuring of ant assemblages (Ribas and Schoereder 2002). As we here merely describe spatial patterns we can not conclude which of those explanations is the right one.

In the next step we scrutinized the different dominated sub-communities of both sites, by exploring co-occurrence of subordinate ants on subsets of palms that were dominated by certain species. In at least three of eleven cases we found C-scores that were significantly lower than expected, suggesting that species were aggregated. This was also true for *Philidris* sp. 1 that was found to be associated with the non-dominant *Polyrhachis bicolor* in pairwise analysis. Thus in these cases that comprise most dominants in Tawau one of the predictions of Leston (1973) for ant mosaics - positive association of non-dominant species - was fulfilled.

However, in about 50% of our tests C-scores showed non-significant effects, so dominant ants were randomly associated with non-dominant species. In contrast, co-occurrence patterns of ants were highly non-random on palms without dominant species, suggesting that dominant ants exert influence on subordinate ant communities in one of two ways: either they were associated with a certain suite of non-dominant species (Leston 1978) or they increased the randomness in the dominated ant communities. The latter ‘disassembling’ of ant communities seems to be common in the presence of many dominant competitors, especially of invasive species (Gotelli and Arnett 2000, Sanders et al. 2003, 2007).

However, in the canopy of oil palm plantations in Peninsular Malaysia and Borneo, dominant species showed non-random spatial segregation, although three invasive species were among them. Likewise positive associations were found in three of the five sub-communities that were associated with those invasive dominants. Only in two of those assemblages of subordinated species we detected random patterns. Contrary to our results, random patterns were found at the level of dominants and on the level of the subordinate species in the arboreal ant community of a cocoa farm in Brazil that was invaded by *Wasmannia auropunctata* (this species in invasive even in its native range, see Le Breton et al. 2004) (Sanders et al. 2007). The main difference to our findings seems to be that the little fire ant *W. auropunctata* does not tolerate other species, while the Asian invasives tolerated a larger set of dominants (and non-dominants, see below).

Some dominant species tended to be aggregated:, viz. *A. gracilipes* with *T. albipes* and *T. albipes* with *O. smaragdina*. These species acted as co-dominants, as confirmed by pairwise analysis of species. Similar patterns have been reported in other ant mosaics (Dejean *et* al., 1999). As *A. gracilipes* nested in the ground and near to fruit bunches, it was more restricted to the palm trunk, while *T. albipes* built hundreds of tiny carton nests near to the centre rib of the palm fronds, thus spreading over the whole palm canopy (unpublished pers. observations). In this way both species can share arboreal space. A use of similar resources may contribute to the positive association. However, as we used presence-absence data, we cannot exclude that the co-occurrence of both species is only due to patrolling or fighting at the territorial borders where relatively few workers of one of the species may have been involved. A positive relationship between *T. albipes* and *O. smaragdina* was also found in the cocoa plantations in Papua New Guinea, where ant community composition was remarkably similar to those found in our study (Room 1975). On coconut trees in Sri Lanka *T. albipes* was associated with *Monomorium floriola* (Way et al. 1989). Generally, the results of the pairwise analysis of species co-occurrence in dominant ants support our identification criteria for the dominants, as each dominant showed significant negative interaction with most other dominants, confirming the exclusion of species from certain palms. Some cases of random interaction may be attributed to the above-mentioned mechanisms of species co-occurrence at territorial borders that may overlay species separation.

Taken together our study corroborates the ant mosaic theory for the territoriality of the dominant species and the positive association of certain non-dominants with dominant species in this system. However, the impact of natives, dominants and invasives on the non-dominants seem to be inconsistent as positive association and random interaction occurred in both groups. Analysis of the communities on palms without dominants showed species separation.

When analysing the sub-communities of the dominated ants we found that dominant tramp species coexisted more often with non-dominant ants and tolerated a larger set of species. These figures may either underline the behavioural adaptation of dominant tramp species to disturbed habitats and low cost interaction with native species or merely be a result of the short time of interaction among the species. Detailed behavioural studies are needed to learn more about the mechanisms leading to the compatibility of ant species.

IMPACT OF EXOTIC SPECIES

The strong global demand for oils and fats has caused a rapid growth of the oil palm industry in South East Asia, leading to the conversion of large areas of land to oil palm plantations that covered four million ha of the country in 2005 (Mohamad Basri Wahid, 2006). Plantations now comprise 56% of Malaysia’s forest and woodland cover (Donald 2004), and attempts to produce biofuels from palm oil may further enlarge the production. From the point of nature conservation the strong influence of exotic species in oil palm plantations is as problematic as the dramatic reduction of native biodiversity, especially given the large size of these monocultures in a former region of mega-diversity. This study has demonstrated that exotic species make up 40 % of all ant species that occur in oil palms plantations; in terms of biomass this percentage would be much higher. Exotic tramp ants dominated the plantations in both sites. Although they comprised only three of eight dominants, non-natives were more abundant in present-absence counts.

The main drivers for the establishment of invasive alien species in these areas are the complete eradication of the native fauna and flora during the establishment of plantations and the large scale planting of an exotic plant species. Tramp species are well adapted to disturbed habitats, and some can have major impacts on native communities. Invasive ants show specific traits like polygyny, intranidal mating, budding, reduced intraspecific aggression and possibly unicoloniality (e.g. Heinze *et. al.* 2006). They can outcompete native ant species, thus actively changing community patterns in large areas. For example, *A. gracilipes,* the yellow crazy ant, has invaded large parts of the rainforest on Christmas Island where it forms polygynous, uni-colonial super colonies, thereby reaching extremely high population densities of > 2000 ants per m^2 in > 2500 ha of 10,000 ha rainforest on the island (Abbott 2006). *A. gracilipes* reduced the diversity of native ant species and eliminated a keystone species of this ecosystem (O’Dowd et al. 2003). At the same time its potential for biological control is hardly documented, while it worked destructively against biological control with other ants, e.g. they displaced the beneficial *Oecophylla longinoda* in East Africa (Way and Khoo 1992). Regarding the potential dramatic influence of *A. gracilipes* on ecosystem functionality and the huge size of oil palm plantations that provide ample space for its distribution, we suggest further monitoring of the species’ activity in Malaysia. Intelligent plantation planning should aim at the establishment of sustainable and stable agro-ecosystems, and enhance/protect native biodiversity inside and outside of plantations to guarantee ecosystem services and reduce exotic invaders.

Acknowledgements

We are grateful to the Management of Golden Hope Plantations Berhad and the EPU Malaysia for research permission. We are deeply indebted to Tuan Haji Khairudin Hashim, Executive Director of Golden Hope Research Sdn. Bhd. and the Golden Hope staff of Table Estate and G HRC Banting for their hospitality and gracious support during our study. We thank especially Abdul Latif Ramlan and Faizul Ariffin for the help with the organisation of the research and Selvam Perumal for help during the collection of ants. We are much obliged to Irmi Pfeiffer for help with the logistics. We owe gratitude to Manfred Verhaagh, Museum of Natural History Karlsruhe, Bernhard Seifert, Museum of Natural History Görlitz, Katsuyuki Eguchi, University of Kagoshima, Herbert Zettel, Museum of Natural History Wien, and Barry Bolton, Museum of Natural History London for help during the identification of ants and to Karl Eduard Linsenmair, University of Würzburg for the provision of his car. This article has greatly benefited with comments on previous versions from Carsten Brühl, University of Landau, Andreas Floren, University of Würzburg, Dirk Mezger, University of Ulm, and five anonymous reviewers. Moreover we are grateful to John R Fellowes, London, and to subject editor Nathan J Sanders, University of Tennessee, for their valuable comments and language editing.

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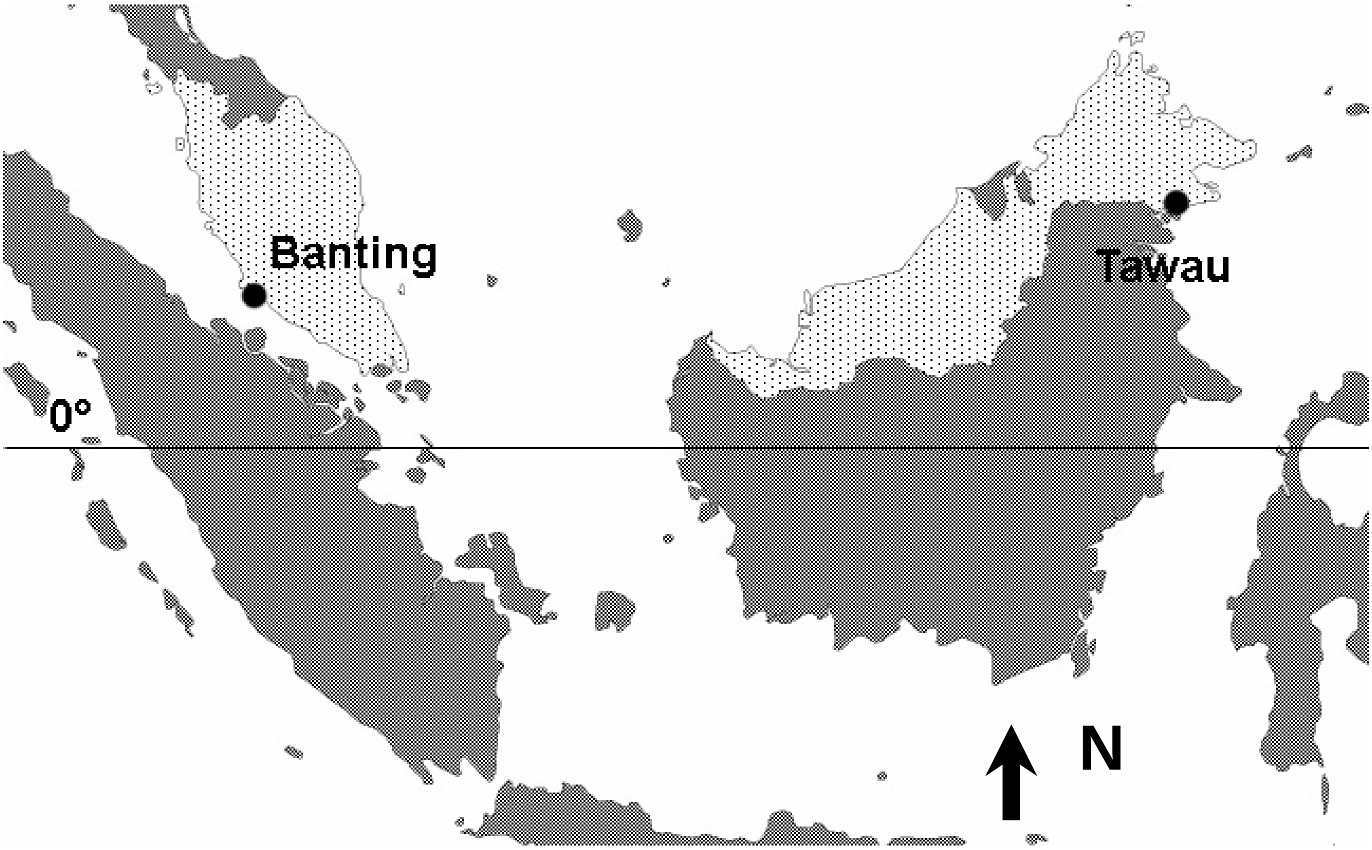
Figure Legends

Fig. 1 The sample sites in Borneo and Peninsular Malaysia lay about 1800 km apart from each other. The bright areas comprise the territory of Malaysia.

Fig. 2 Rarefaction plot of our study, confirming the low ant species richness of the oil palm plantations in Banting (Peninsula) and Tawau (Sabah, Borneo). Species saturation was reached for both sites.


Banting
Tawau
0°
N

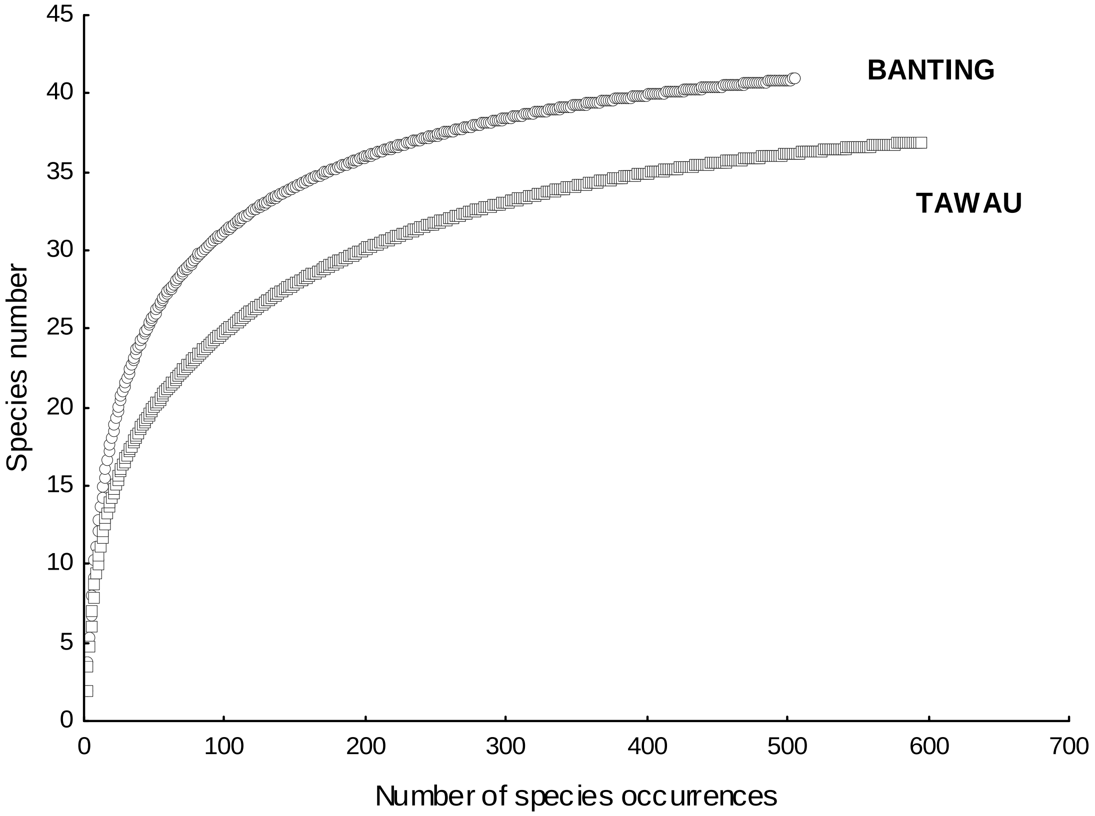

BANTING
TAWAU
Species number
Number of species occurrences
0
5
10
15
20
25
30
35
40
45
0
100
200
300
400
500
600
700

Table 1

Ant species composition in Tawau, Borneo and Banting, Peninsular Malaysia. Given are the names of the species, the number of species occurrences in the plots, the sum of both plots, a characteristic of ant species of invasive (I), tramp (T) or alien (A) species according to literature (McGlynn 1999, Pacific Invasive Ant Group 2004) and pers. com. with B. Bolton.

Species	Subfamily	Tawau	Banting	Sum	Category	Origin
Technomyrmex albipes Smith	Dol.	245	84	329	I, T, A	Pacific
Oecophylla smaragdina Fabricius	For.	179	117	296		
Anoplolepis gracilipes Smith	For.	130	150	280	I, T, A	Africa?
Tapinoma melanocephalum Fabricius	Dol.	64	70	134	I, T, A	F.Guiana?
Monomorium floricola Jerdon	Myr.	61	54	115	T	Asia
Polyrhachis bicolor Smith	For.	88	11	99		
Crematogaster rogenhoferi complex	Myr.	96	0	96		
Philidris sp. 1	Dol.	82	0	82		
Crematogaster sp. 3	Myr.	0	78	78		
Plagiolepis cf. *alluaudi* Emery	For.	63	2	65	T, A	India
Paratrechina sp. 2	For.	16	48	64		
Pheidole fervens Smith	Myr.	2	61	63		Asia
Paratrechina longicornis Latreille	For.	16	42	58	T, I, A	Africa
Camponotus arrogans Smith	For.	56	0	56		
Cardiocondyla wroughtonii Forel	Myr.	34	15	49	T	Asia
Meranoplus bicolour Guérin-Méneville	Myr.	0	48	48		
Camponotus sp. 2 (*variegatus*-complex, near '*dulcis*')	For.	0	36	36		
Polyrhachis sp. 6	For.	0	36	36		
Crematogaster sp. 5	Myr.	2	30	32		
Tetramorium tonganum Mayr	Myr.	21	11	32	A	Pacific
Camponotus sp. 3	For.	0	30	30		
Diacamma sp. 1	Pon.	1	24	25		
Pheidologeton affinis Jerdon	Myr.	0	21	21		
Crematogaster sp. 2	Myr.	0	20	20		
Tetramorium pacificum Mayr	Myr.	17	1	18	T, A	Pacific
Polyrhachis sp. 9	For.	1	16	17		
Pristomyrmex punctatus Smith	Myr.	17	0	17		
Crematogaster sp. 4	Myr.	2	13	15		
Paratrechina sp. 1	For.	14	0	14		
Iridomyrmex sp. 1	Dol.	0	11	11		
Tetramorium lanuginosum Mayr	Myr.	1	8	9	T	SEA
Tetramorium simillimum (Smith)	Myr.	4	5	9	T, A	Europe
Hypoponera cf. *punctatissima* Roger	Pon.	0	8	8	T, A	Europe
Diacamma sp. 2	Pon.	0	7	7		
Pheidole bugi Wheeler	Myr.	0	7	7		
Polyrhachis sp. 4	For.	4	3	7		
Technomyrmex sp. 4	Dol.	7	0	7		
Pheidologeton pygmaeus Emery	Myr.	6	0	6		
Technomyrmex sp. 3	Dol.	6	0	6		
Bothriomyrmex sp. 1	Dol.	5	0	5		
Pheidole plagiaria Smith	Myr.	2	3	5		
Camponotus bedoti Emery	For.	3	1	4		
Pheidole annexus Eguchi	Myr.	4	0	4		
Technomyrmex sp. 2	Dol.	4	0	4		

Tetramorium bicarinatum Nylander	Myr.	0	4	4	T	SEA
Vollenhovia sp. 1	Myr.	4	0	4		
Dolichoderus thoracicus Smith	Dol.	0	3	3	A	Sulawesi
Ochetellus sp.1	Dol.	3	0	3		
Platythyrea parallela Smith	Pon.	2	1	3		
Polyrhachis sp. 7	For.	0	3	3		
Technomyrmex elatior Forel	Dol.	0	3	3		
Tetramorium insolens Smith	Myr.	0	3	3		
SUM		1262	1088	2350		

Table 2. Results of the analysis of species co-occurrence patterns with EcoSim 7.70. Given are the tested sub-communities of ants, the standardized effect size (SES), the observed and the simulated index, the variance of the simulated index, the probability that the observed index is larger, or smaller than the mean of the simulated index and the number of species within the sub-group. The first two lines of the table show the results for the analysis for all species, followed by the analysis of only the dominant species (line 3-4) and those of the ant communities on trees without dominants (line 5-6). In each of the sites the observed index that is significantly larger than the simulated index, thus pointing towards species segregation. The rest of the table shows the results of the analysis of sub-communities that were dominated by the ant species that is given in the first column of the table. In none of these sub-communities we found an observed index significantly larger than the simulated one, while in some cases the observed index was significantly smaller than expected thus indicating a positive association of the species. The exact names of the non-dominant ant species are given in Table 3. * indicates a tendency for positive association of species; + indicates a positive association with the main non-dominant species that had been found in pairwise tests (see text).

(Sub-)community tested	**Standardized Effect Size**	**observed index**	**Mean of simulated index**	**Variance of simulated index**	**p o>e**	**p o<e**	**Number of species within subgroup**
All species 2004	7.863	617.6	568.6	38.8	0.001	n.s.	38
All species 2005	6.503	575.7	547.5	18.9	0.001	n.s.	39
2004 dominants	7.243	8750.9	7327.2	38629.3	0.001	n.s.	6
2005 dominants	6.565	4585.0	3688.0	18667.1	0.001	n.s.	5
2004 without dominants	6.42	24.4	19.4	0.75	0.001	n.s.	31
2005 without dominants	2.20	78.6	76.1	1.40	0.010	n.s.	34
2004 Tawau							
Anoplolepis gracilipes	-2.287	50.0	55.6	6.1	n.s.	0.05	7
Camponotus arrogans	0.450	42.7	39.3	54.7	n.s.	n.s.	3
Crematogaster rogenhoveri	-0.641	31.5	32.9	4.7	n.s.	n.s.	5
Oecophylla smaragdina	-1.448	119.0	126.9	29.5	n.s.	0.074*	7
Philidris sp. 1						+	1
Technomyrmex albipes	-2.159	147.0	159.0	31.4	n.s.	0.05	6
2005 Banting							
Anoplolepis gracilipes	-1.246	113.5	117.1	8.2	n.s.	n.s.	12
Oecophylla smaragdina	-2.047	49.6	54.8	6.4	n.s.	0.05	7
Paratrechina longicornis	1.013	39.8	36.1	13.5	n.s.	n.s.	5
Pheidologeton affinis							0
Technomyrmex albipes	-1.239	51.0	54.8	9.4	n.s.	n.s.	7

Table 3. Dominant ant species (bold letters) and the non-dominant ant species (normal letters) that occurred in their territories in the two observation sites. Given are only non-dominant ant species that occurred more than 5 times. Species are sorted according to their species occurrences on the palms. * indicates a non-random composition of the community (see Table 2).

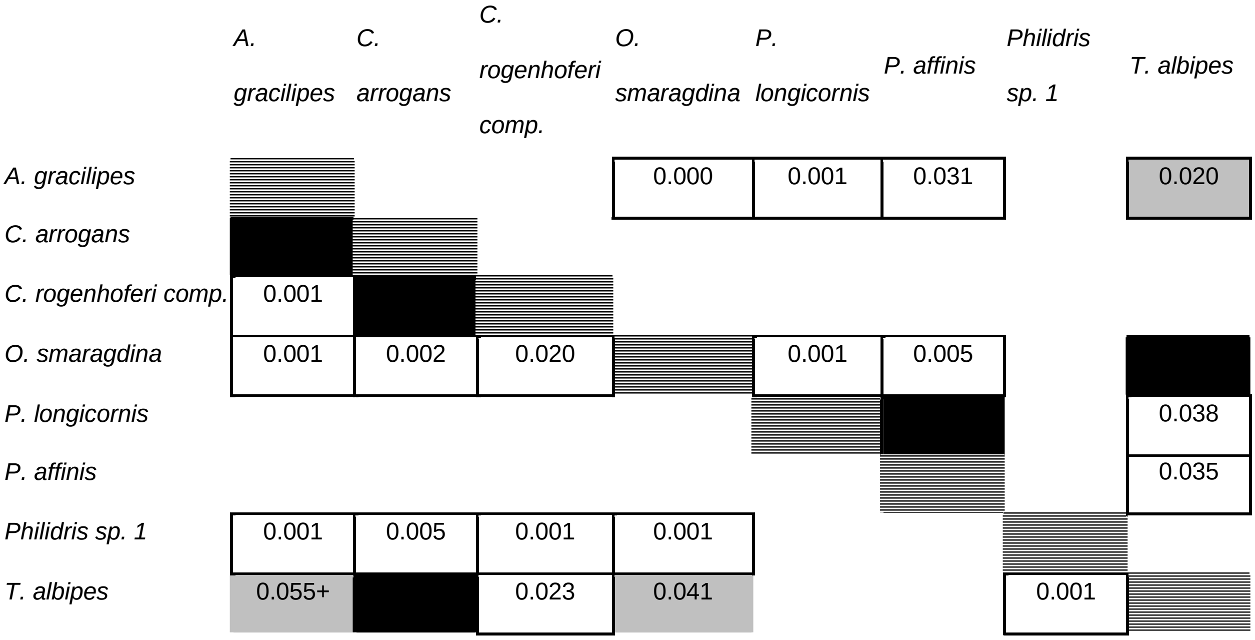
Banting

A. gracilipes	***O. smaragdina****	***P. longicornis***	***P. affinis***	***T. albipes***
Crematogaster sp. 3	*Crematogaster sp. 5*	*Crematogaster sp. 3*		*Tapinoma melanocephalum*
Tapinoma melanocephalum	*Monomorium floricola*	*Camponotus sp. 3*		*Pheidole fervens*
Monomorium floricola	*Tapinoma melanocephalum*	*Camponotus sp. 2*		*Monomorium floricola*
Pheidole fervens	*Crematogaster sp. 2*	*Polyrhachis sp. 6*		*Crematogaster sp. 5*
Paratrechina sp. 2	*Crematogaster sp. 4*	*Tapinoma melanocephalum*		*Polyrhachis sp. 6*
Crematogaster sp. 5	*Crematogaster sp. 3*			*Crematogaster sp. 3*
Meranoplus sp. bicolor	*Paratrechina sp. 2*			*Paratrechina sp. 2*
Polyrhachis sp. 6				
Cardiocondyla wroughtonii				
Diacamma sp. 1				
Polyrhachis bicolor				
Tetramorium lanuginosum				

Tawau

A. gracilipes*	***C. arrogans***	***C. rogenhoferi compl.***	***O. smaragdina(*)***	***Philidris****	***T. albipes****
Monomorium floricola	*Plagiolepis*	*Polyrhachis bicolor*	*Polyrhachis bicolor*	*Polyrhachis bicolor*	*Polyrhachis bicolor*
Polyrhachis bicolor	*Tapinoma melanocephalum*	*Tapinoma melanocephalum*	*Monomorium floricola*		*Cardiocondyla wroughtonii*
Tapinoma melanocephalum	*Monomorium floricola*	*Tetramorium tonganum*	*Tapinoma melanocephalum*		*Monomorium floricola*
Cardiocondyla wroughtonii		*Monomorium floricola*	*Cardiocondyla wroughtonii*		*Pristomyrmex punctatus*
Pristomyrmex punctatus		*Tetramorium pacificum*	*Tetramorium tonganum*		*Paratrechina sp. 1*
Paratrechina sp. 1			*Plagiolepis cf. alluaudi*		*Tetramorium pacificum*
Paratrechina sp. 2			*Tetramorium pacificum*		

Table 4. Interaction of dominant species in Banting (above diagonal) and Tawau (below diagonal) as revealed by pairwise C-score analysis. Empty fields refer to species that were absent at the respective site. White fields indicate species segregation with C-scores significantly higher than expected by chance. Grey fields point to positive species interactions, with C-scores significantly lower than expected by chance that indicate co-dominant species. Significant p values that are rounded to three digits are given inside the fields. + indicates a nearly significant value. Black fields symbolize pairwise species interactions with C-scores that did not differ from random patterns.



	A. gracilipes	*C. arrogans*	*C. rogenhoferi comp.*	*O. smaragdina*	*P. longicornis*	*P. affinis*	*Philidris sp. 1*	*T. albipes*
A. gracilipes	▤			0.000	0.001	0.031		0.020
C. arrogans	■	▤						
C. rogenhoferi comp.	0.001	■	▤					
O. smaragdina	0.001	0.002	0.020	▤	0.001	0.005		■
P. longicornis					▤	■		0.038
P. affinis						▤		0.035
Philidris sp. 1	0.001	0.005	0.001	0.001			▤	
T. albipes	0.055+	■	0.023	0.041			0.001	▤

Journal of Tropical Ecology (2006) **22**:685–693. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467406003622 Printed in the United Kingdom

Worker size and seed size selection in 'seed'-collecting ant ensembles (Hymenoptera: Formicidae) in primary rain forests on Borneo

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(*Accepted 16 June 2006*)

Abstract: 'Size matching' of forager size and prey size is an ecological mechanism that should partition diets both within ant colonies and ensembles. We studied the relationship between ant body size and food size in tropical leaf-litter ant ensembles at different levels. In three plots of primary rain forest in Sabah, Malaysia, we observed altogether 50 species of 18 genera of ants (e.g. *Pheidole*, *Recurvidris*, *Lophomyrmex*, *Paratrechina*, *Odontoponera*) that harvested seed particles from baits of milled rice of various particle size. At colony level 'size matching' of individual foragers with their load was found only in one of 12 tested species, viz. *Pheidole lucioccipitalis*. However, ant species differed considerably with respect to 'seed' size used: on average, foragers of larger species transported significantly larger 'seed' fragments. This was highly significant in a subset of ant species with at least 12 records of size choice per species. But when we investigated resource partitioning within each of the three ant ensembles with a null model, analysis proved that there was a significant overlap in seed size selection of species at two of the sites, thus indicating that food size choice of foragers had little influence on niche patterns and community structure of ants. Ant species with workers that were not matched with their seed resources (viz. *Oligomyrmex* or *Pheidologeton*) engaged in cooperative 'seed' transport, mass recruitment to and *in situ* mastication of rice fragments. Mean 'seed' transport distance was 38.4 cm.

Key Words: ant-seed interaction, community ecology, dispersal, null model, *Pheidole*, predation, resource partioning, size matching, South East Asia, tropical forest

INTRODUCTION

In tropical rain forests, ants can act positively as dispersal agents of plants, as in the case of myrmecochory (Pfeiffer *et al.* 2004), or alternatively as seed consumers with a negative effect on plant recruitment (Feldmann *et al.* 2000, Laman 1996). Both mechanisms are combined when dispersal of seeds is a byproduct of granivory (Levey & Byrne 1993). Ants can also function as secondary dispersers of seeds that have been dispersed by birds (Boehning-Gaese *et al.* 1999) or other vertebrates (Pizo & Oliveira 1999), and hence can play an important role in plant recruitment (Vander Wall *et al.* 2005). In this context seed dispersal of plants depends on specific seed-ant interactions, e.g. larger ants may disperse seeds over longer distances (Ness *et al.* 2004, Pfeiffer *et al.* 2004). 'Ensembles' (phylogenetically bounded groups of species that use a similar set of resources, *sensu* Fauth *et al.* 1996) of ants should partition resources by 'size matching' of forager size of a species and seed (prey) size (Retana & Cerdá 1994). Moreover, 'size matching' is an ecological mechanism to increase colony efficiency within species by 'optimal foraging' (Hölldobler & Wilson 1990). In neotropical rain forests seed size selection has been found to be directly linked to the body size of the foraging ant (Kaspari 1996). Recent research has shown that invasive ant species can change seed dispersal patterns in ant-seed mutualisms dramatically when their mismatching with seeds results in shorter dispersal distances (Ness *et al.* 2004). Size matching may cause a pattern of seed size selection within an ant ensemble that is more varied than expected by chance, due to the influence of interspecific competition on seed size selection. In such a situation, larger ant species are expected to forage mainly on large seeds, while smaller species should tend to predominantly harvest smaller seeds (Retana & Cerdá 1994). Such patterns have been frequently reported from different ecosystems (Davidson 1977, Kaspari 1996). However, an

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investigation of niche differentiation of ant species within an ensemble by different size choice of food is still missing, although it can easily be tested by null model analysis of niche overlap (Gotelli 2001).

We studied seed foraging of ants in tropical leaf-litter ant communities in Sabah, Malaysia, in order to obtain more information regarding ants' foraging behaviour and seed use. In this paper we describe the composition and behaviour of the ant fauna at artifical seed bait stations in the leaf litter of three Bornean lowland rain forests. In particular, we have investigated whether body size of ants is related to choice of seed size and seed transport distances. We tested two hypotheses: (1) Size matching influences the behaviour of ants on both species and colony level resulting in a relationship of the size of the removed bait and ant body size, within and among species. (2) Ant ensembles are structured by niche patterns related to food size choice of foragers. Thus at a given location ant species should differ more in their use of particle size than expected by chance. To test these assumptions, we explored seed size selection between and within ant species and tested for any overlap of seed size selection among species at distinct sites by null model analysis.

METHODS

Size matching of ants and seeds in leaf-litter ant ensembles was studied in three primary dipterocarp rain-forest sites in Sabah (Malaysia) in the north of Borneo: (1) a forest plot situated about 400 m from the forest edge in Kinabalu National Park at Poring Hot Spring (N 6°2′ E 116°42′, altitude *c.* 450 m, total size 75 400 km^2), (2) a site lying deep within the forest (43 800 ha) near the Danum Valley Field Centre (14°58′ N 117°48′ E, altitude *c.* 300 m) and (3) a plot situated about 1 km from the forest edge in Tawau Hills National Park (27 972 ha at 4°24′ N 117°54′ E, altitude *c.* 200 m). All plots were covered by dense forest and were accessed by well-established trail systems.

Field work was performed during February 2000 (Poring), February/March 2001 (Tawau) and August/September 2002 (Danum). Borneo has a humid, aseasonal climate with an average of more than 100 mm mo^{-1} rainfall and larger temperature variation within one day than within the year (Walsh & Newbery 1999). As our study was performed in periods of relatively low rainfall, climatic conditions of the different study periods are readily comparable.

Several studies on food choice in harvester ants have used milled barley baits to vary seed size at a standardized nutritional value (Davidson 1977, Kaspari 1996). However, milled barley seeds are much softer than whole seeds and may attract many ant species that normally do not forage for seeds, because they can feed on them without the need of the specialized strong mandibles that are found in typical harvester ants (Pfeiffer *et al.* 2003). Moreover, barley meal agglutinated in the high tropical humidity, an attribute that seriously hampered the pilot experiments. For these reasons, milled rice, which is much harder than barley at any particle size and does not agglutinate was selected as bait. Although it differs in chemical cues, nutrient content and other aspects from naturally occurring seeds, it proved to be a useful seed mimic. Ants were baited with milled rice that was sieved into five particle sizes: < 0.2, 0.2–0.5, 0.5–0.8, 0.8–1.5 and 1.5–2.5 mm. The five particle sizes were arranged in piles of similar grading (0.5 cm radius) on a small plastic tray (4.5 cm radius) on the forest floor to attract terrestrial ant species. This method and seed-size range were similar to those used by Kaspari (1996) for the assessment of a neotropical harvester-ant ensemble. At each station, a small shelter of plastic foil protected baits from rain.

In each forest, we set up transects composed of 30 sampling stations, 10 m apart and 2 m from the nearest trail. Seed baits were set out after dawn (07h00) and at midday (*c.* 12h00). They were permanently controlled each of these times for at least 4 h and were not moved during the day. To keep seed availability roughly constant throughout our experiments, baits were replenished when necessary. Each morning, seed baits were put several metres further into the forest to avoid re-sampling the same ant colonies. As the transect was moved into the forest day by day, we considered each bait per day as an independent sample. Each plot was sampled for 17 d. In total, we sampled ants at 1530 seed baits.

Ants that harvested the 'seeds' and transported them to their nests were collected into separate vials (with alcohol) at each station and for each particle size when they returned from the trays. In some cases, we were able to measure the distance over which the 'seeds' were transported. However, tiny ant species that fed on the rice on the spot had to be sampled at the baits. In our laboratory, specimens were sorted out into morphospecies. Further species determination was done with the help of the Zoological Collection of the Biocenter at the University of Würzburg (see http://www.antbase.net), which houses a wide range of species of leaf-litter ants from former studies of this forest stratum (Brühl *et al.* 2003, Malsch 2002). Specimens of *Pheidole* were identified by Dr Katsuyuki Eguchi, Kagoshima University, Japan, according to his latest revision (Eguchi 2001). In several cases within this genus, specimens could only be determined to species groups because of the lack of majors.

For the morphological study, the head width and tibia length of 329 ant specimens from various colonies (different baits or different days of collection) for which behavioural data had been noted were measured with an ocular micrometer mounted on a binocular microscope (Wild M5A, Switzerland). Both measures are highly correlated with ant mass (Kaspari & Weiser 1999). For the study of size matching within species, we checked the following species for which we had sampled individuals of at least nine different colonies and their 'seed' loads: *Lophomyrmex bedoti* (n = 41), *Odontoponera transversa* (n = 15), *Paratrechina* sp. 3 (n = 9), *Pheidole aristotelis* (n = 23), *P. cariniceps* (n = 9), *P. lucioccipitalis* (n = 32), *Pheidole* sp. A (n = 76), *Pheidole* sp. C (n = 15), *Pheidologeton affinis* (n = 11), *Recurvidris* sp. 1 (n = 38), *R. browni* (n = 16), *Tetramorium* cf. *zypidum* (n = 10).

In general, statistics were computed with the program STATISTICA 6.0 (STATSOFT 2001, www.statsoft.com). We calculated the correlation coefficients r or R for Pearson or non-parametric Spearman correlations, respectively, and the coefficient of determination r^2 for the regression. For the calculations of rarefaction curves with software package EstimateS (Version 7.0, R. K. Colwell, http://viceroy.eeb.uconn.edu/EstimateS) we used the sample-based rarefaction approach (Gotelli & Colwell 2001): all ants of one (morpho-)species (group) that were collected at one bait station within 1 d were counted as one species occurrence, while a sample comprised all species taken at one station per day. We calculated the estimated range of sample coverage according to Brose & Martinez (2004) as the actual number of species times 100 divided by the mean estimated species number based on a range of estimators that usually differ in their estimations (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2, Bootstrap, MMMean).

The use of a particular particle (seed) size by an ant species can be the result of competition among species, because species may differ in their use of resources in a way that reduces niche overlap. However, even in the absence of competition, species will differ in their utilization of resources. Niche overlap can be measured by different indices (Winemiller & Pianka 1990). By means of a null model we can produce a pattern (and a resulting index) as expected in the absence of competition and compare it with that found within natural ant ensembles. If niche overlap is significantly smaller in the natural ensemble than in the randomly generated community, we expect that ant species should differ in their selection behaviour as a result of competition. On the other hand a significantly larger overlap index would point towards a shared use of seed resources.

We used the niche overlap module of EcoSim 7.70 (EcoSim: Null Models Software for Ecology. Aquired Intelligence INC, & Kesey-Bear, http://www.garyentsminger.com/ecosim/index.htm) to analyse the seed size selection of the most abundant ants in the three species ensembles, to test for an influence of competition and to compare them with 1000 random matrices generated by the null model. If ant ensembles were structured by competition, we expected that this competition should work mainly on the abundant species that are more likely to interact with each other. Therefore, we excluded all species with an abundance of less than 2% of the total abundance of the respective plot (see Appendix) from the analysis of niche overlap at the particular site. From the food-choice data and the abundance of the respective ant species within the plot we calculated the observed utilization of the five particle sizes by each species (as mean number of counts). In the calculation table each row represented a different species in the ensemble, each column represented a different seed size category, and each cell represented the observed utilization of the seed size by a particular species. We calculated the overlap index of Pianka (1973) for each pair of ant species in the ensemble, for a set of seed sizes. As we offered similar amounts of seed baits of all size classes, we assumed that the different resource states were equally abundant in the environment and set the value for resource states to 'equiprobable'. We used the RA3 randomization algorithm that retains niche breadth and reshuffles niche utilization values within each row of the matrix. So the amount of specialization for each ant species was retained, but it was allowed to potentially use other seed sizes. This algorithm has been recommended by Winemiller & Pianka (1990), who have systematically compared the behaviour of different randomization algorithms used in the analysis of niche overlap. They recommended the RA3 algorithm for its good statistical properties for detecting non-random niche overlap patterns (for detailed information see EcoSim 7.70 Tutorial).

RESULTS

Species richness

In total, we found 50 species (or species-groups) of 18 genera and four subfamilies of ant. We recorded 30 species for Danum, 32 for Poring and 37 for Tawau (see Appendix). The sample-based rarefaction curves (Figure 1) were relatively flat, indicating a sufficient sampling of the communities. Sample coverages of the plots ranged from 69% to 89% of estimated species richness.

Species richness at each bait station per day was low, as we sampled ants at only 33% of all baits. In Poring we found on average a species density of 0.72 species per bait d^{-1} (SD = 1.08, max = 6), whereas in Danum we collected 0.50 species per bait d^{-1} (SD = 0.73, max = 4), and in Tawau we found only 0.40 species per bait d^{-1} (SD = 0.87, max = 5). When analysing species composition in detail, we found that the most abundant ant species was *Pheidole* sp. A (*hortensis* or *clypeocornis*), followed by *Lophomyrmex bedoti* and *Recurvidris* sp. 1 (Appendix). The composition of species ensembles differed at the sites. Whereas only 16 species were found at all sites, 18 species of ant were found at only one of the sites and

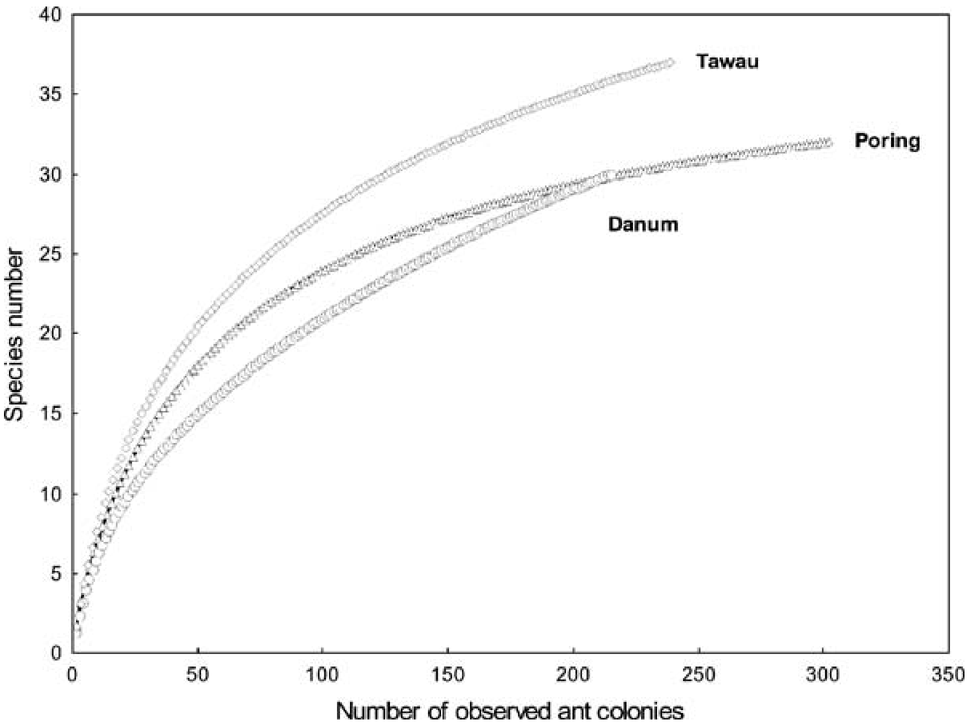

Figure 1. Randomized sample-based species accumulation curves of ant species in the three rain-forest plots. The accumulation curves of Tawau and Poring are approaching the asymptote, indicating species saturation. As ants are social insects the x-axis indicates the number of observed ant colonies (species occurrences) at the baits, rather than the number of individual foragers.

9 species were found at only one bait (Appendix). Four of the most abundant species of the whole ant ensemble were absent at no less than one of the plots, and three species, common at some of the plots, were singletons at other plots. Beta-diversity analysis by the qualitative Sørensen Index (QSI) confirmed the moderate species overlap: we found indices of 0.71 for Danum/Poring, 0.66 for Danum/Tawau and 0.64 for Poring/Tawau. The genus *Pheidole* was most abundant within the three ant ensembles with 18 seed-harvesting species (or species groups).

Size matching of ants and 'seeds'

Size matching was evaluated from 329 measurements of ants that transported seeds of known size. Within these data and across species, we found a positive correlation of seed size and head width (Spearman $R = 0.36$, $P < 0.001$) or tibia length (Spearman $R = 0.42$, $P < 0.001$). Tibia length and head width of the ants were also well correlated (Spearman $R = 0.86$, $P < 0.001$). Twelve ant species, each with observations of at least nine colonies, were tested for size matching of individual foragers with their loads within species. Only in one species, *Pheidole lucioccipitalis*, were larger foragers found to transport larger pieces of grain ($n = 32$, head width vs. grain size: Spearman $R = 0.56$, $P < 0.001$; tibia length vs. grain size: Spearman $R = 0.47$, $P < 0.05$); in all other species, correlations of grain size with head width or tibia length were not significant, with seven species being positively correlated and five negatively.

To compare overall seed use by species, we calculated a grand seed-size mean for each species. Ant species differed considerably in seed-size use: species with larger head widths transported significantly larger mean seed sizes (linear regression, $F_{1,33} = 39.1$, corr. $r^2 = 0.52$, $P > 0.0001$, Figure 2). This connection was even closer when we regressed the mean size of transported grains on mean tibia lengths of the carrying ant species: for all observed species, we found a corrected r^2 of 0.59 ($F_{1,34} = 52.4$, $P < 0.0001$) but, when we took a subset of ant species with at least 12 records of size choice per species, the coefficient of determination increased to 74% ($F_{1,10} = 32.7$, corr. $r^2 = 0.74$, $P < 0.001$), thus indicating the strong interrelation of ant size and choice of food size (see Figure 3). Regression results proved a positive correlation between seed size and ant tibia size in two tribes of the Myrmicinae (Pheidolini: $y = 0.597 + 0.520x$, $F_{1,14} = 8.02$, corr. $r^2 = 0.32$, $P < 0.05$; Solenopsidini: $y = 0.619 + 0.612x$, $F_{1,8} = 18.3$, corr. $r^2 = 0.66$, $P < 0.01$), while the low number of species in other taxa impeded their separate analysis.

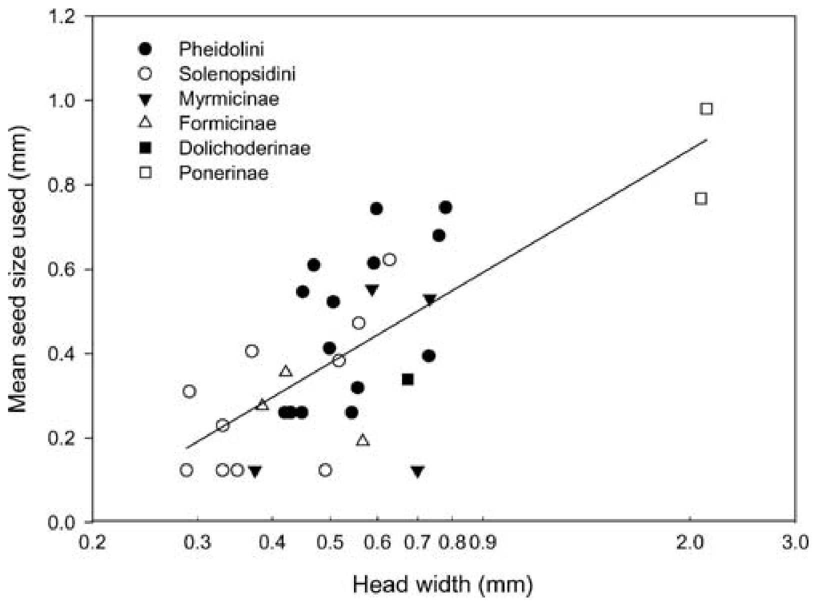

Figure 2. Mean seed size utilized as a function of the logarithm of head width of the various ant species (seed size used = 0.63 + 0.84 log(mean head width), $r^2 = 0.52$, $P < 0.001$). Symbols represent the different tribes and subfamilies (Appendix). Note the logarithmic scaling of the x-axis.

In six species, including the dominant *Pheidole* sp. A and *Recurvidris* sp. 1, we noted collective transport of the largest 'seeds' (Appendix). In another 185 cases, ants of 35 species were observed feeding on the baits without transporting the seeds to their nests. These observations comprised large ants that fed on the smallest grain fraction, and small ants, notably of the genera *Oligomyrmex*, *Cardiocondyla* and *Monomorium* that fed on

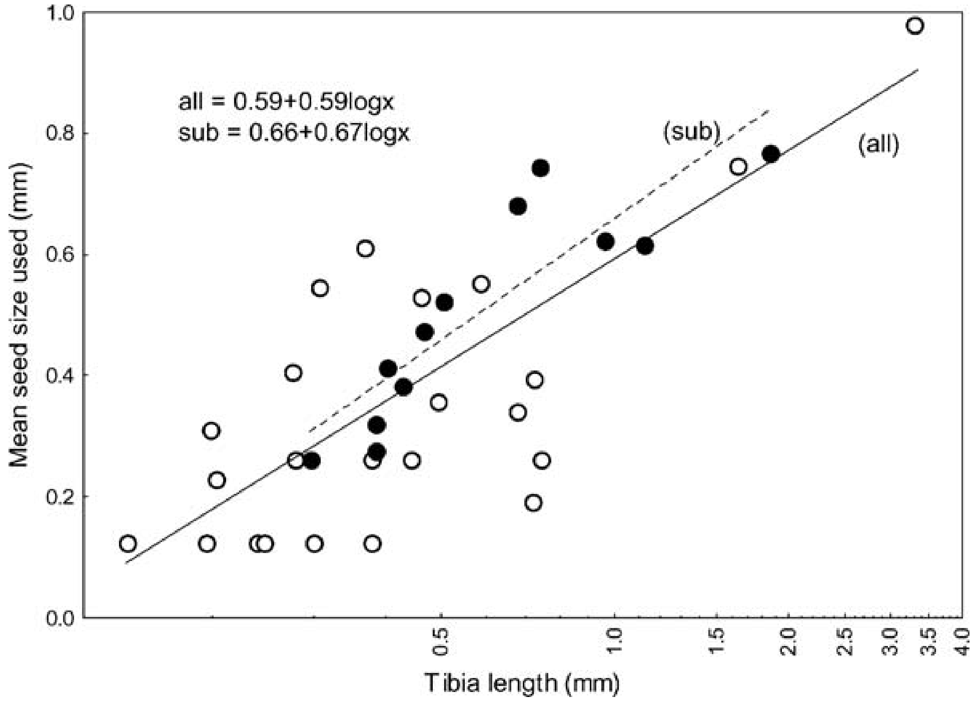

Figure 3. Relationship between size of ant species (measured as the logarithm of mean tibia length) and choice of 'seed' size. Black dots indicate a subset (sub) of ant species (n = 12) that had been sampled at least 12 times (mean = 36.3) and that showed an especially close correlation between tibia length and seed size used (seed size = 0.66 + 0.67 log(tibia length), $r^2 = 0.74$, dotted line), whereas this correlation was lower for all 36 ant species (all; seed size = 0.59 + 0.59 log(tibia length), $r^2 = 0.59$ straight line). Note the logarithmic scaling of the x-axis.

Table 1. Results of the simulation analysis with the niche overlap module of EcoSim7.70. The numbers of the most abundant species in the three plots, each with more than 2% abundance, are shown. For these species, the observed mean of overlap in seed size selection of the species, the mean simulated index and the variance of this index are given, as is the probability that the simulated index is larger or smaller than that of the observed index. If the observed mean is smaller than expected, patterns of size selection are more varied than expected by chance, while a significant larger observed mean points towards a shared utilization of seed size classes by ant species.

	Danum (n = 9)	Poring (n = 15)	Tawau (n = 16)
Observed mean	0.567	0.655	0.696
Mean of simulated index	0.534	0.487	0.542
Variance of simulated index	0.00138	0.00105	0.00057
P (observed < expected)	ns	ns	ns
P (observed > expected)	ns	0.001	0.001

rice grains that they were unable to move (Appendix). Although seed-size preferences and sizes of ant species were tightly correlated during 'seed' transport, the food choice of species was independent of food transport of individual foragers because of cooperative transport and in situ feeding on the rice fragments.

Mean seed transport length was 38.4 cm (n = 124, SD = 35.9 cm) and we found no significant correlation between ant size and transport distance (nine species with at least five measurements, Pearson correlation $r = 0.35$, $P > 0.05$), for example, we observed tiny *Oligomyrmex* ants, transporting rice fragments over about 100 cm.

Null model analysis proved that in Poring and Tawau the observed pattern of overlap in 'seed' size selection was significantly larger than expected by chance, thus indicating shared utilization of similar seed size classes by several ant species. 'Seed' size selection pattern of ants in Danum showed no significant deviation from a random distribution (Table 1).

DISCUSSION

As expected we found a close correlation between the size of the ants and the size of the collected 'seeds' at the species level, pointing towards resource partitioning, a well-known mechanism for the coexistence of species (Hölldobler & Wilson 1990). Similar results have been found in many species-rich granivorous ensembles, especially in arid regions (Davidson 1977, Retana & Cerdá 1994), and also under tropical conditions (Kaspari 1996), but have never been tested in a null model. However, our second hypothesis, that ant species should differ more in their use of particle size than expected by chance, could not be proved in any of the sites. Instead, we found a significant overlap in seed sizes used among the dominant ant species in two of the observed communities, when we applied the null model to our data. This common use of similar-sized resources may even be higher, if we take into consideration the rare ant species that have been excluded from our analysis. Moreover, we have observed several foraging mechanisms in ants enabling seed use by ant species that are not 'size-matched' to their resource, viz. in those ants that engage in cooperative seed transport, mass recruitment and in situ mastication of large seeds (a phenomenon, also observed by Kaspari 1996). Ant species of different sizes may thus compete for the same resources by the employment of these different strategies. Besides, interspecific competition for seed food is also governed by mechanical constraints imposed by seed morphology and the chemical composition of real seeds. Hence, although interspecific size-matching occurs during seed removal, it seems to be of low significance for competition and niche patterns because other mechanisms work against it and because of the large overlap in food size selection within a tropical ant ensemble.

Ant size-seed size relationships are highly important in mutualistic seed-dispersal systems, because ant body size influences seed preferences significantly (Gorb & Gorb 1995) and predicts dispersal distance of ant-adapted seeds (Ness *et al.* 2004). In myrmecochorous dispersal systems, in which small-sized invasive species replace the original ant partners but are unable to achieve the same dispersal distance for the plant seeds, plant dispersal may be seriously endangered, as recently demonstrated by Ness *et al.* (2004). This may even lead to the extinction of rare plant species (Bond & Slingsby 1984).

In a previous study of myrmecochory in the same plots in Tawau Hills National Park and Kinabalu National Park, we found a mean of 112 cm for dispersal distances of myrmecochorous *Globba* seeds that were well correlated with ant species sizes (Pfeiffer *et al.* 2004). In our present work, the much smaller ants (median tibia length 0.41 mm vs. 2.1 mm) have been observed to transport food particles over a mean distance of only 38 cm and we have found no correlation of transport distance to the body size of the ant species. This indicates that in a small-sized ant ensemble, where species differ little in their foraging ranges, distance to the nest entrances influences transport distance more than body size does (Gomez & Espadaler 1998).

At the colony level, we found intra-colony size matching of forager size and 'seed' size in only one species, viz. *Pheidole lucioccipitalis*, although, this correlation was weak (Spearman r = 0.56) compared with the load-head width relationship that was found for nectar transport in giant ants *Camponotus gigas* (r = 0.73, Pfeiffer & Linsenmair 1998). One reason for this poor size matching is that a seed-transporting ant has to choose among various loads by a series of attempts, whereas a nectar-transporting ant can simply ingest the optimal load for its size.

Low regression coefficients for load-size relationships have also been found within several polymorphic Costa Rican harvester ant species (Kaspari 1996). Although size matching seems to play a major role in the foraging of leaf-cutting ants (Roces 1990), we conclude that it may be less important during seed transport in tropical ants in respect to interspecific competition and colony ergonomics. However, seed size selection of ants may be of adaptive value at least for the myrmecochorous dispersal systems within Asian forests (Pfeiffer *et al.* 2004) that have yet to be studied in more details.

Although we made an experiment on the 'seed' transport of ants, we do not want to speculate whether the species involved are granivorous or not. The size-matching of ant foragers with the items they transport is of general ecological importance. Our observations of in situ feeding on rice particles by 35 ant species indicate that seeds may be a part of an omnivorous diet in several species, but there is still a profound lack of knowledge concerning the ecology and biological role of most Bornean leaf-litter ant species (Berghoff *et al.* 2003). Further studies of the life history of particular ant species are urgently needed to ascertain their seed use.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit (EPU, Malaysia) for permission to carry out research in Borneo. We are extremely grateful to Dr Waidi Sinun of the Danum Valley Management Committee for cooperation in the Danum Valley and to the staff of Sabah Parks for providing logistic help in Kinabalu National Park and Tawau Hills National Park. We are also indebted to Dr Katsuyuki Eguchi, Kagoshima University, for the identification of the *Pheidole* specimens, Prof. Nick Gotelli, University of Vermont, and Dr Gary Entsminger for their help with the null model analysis. We show appreciation to Irmi Pfeiffer, Yvonne Ritze, Dr Konstans Wells, Ralf Lauterbach, Ellen Sperr and Matthias Hepfer for assistance during field work and/or species sorting, to Katrin Deufel for the measurement of the ants and Jakob Fahr for interesting and frequent methodological discussions. We thank Dr Robert R. Dunn and various anonymous reviewers for their valuable comments on earlier versions of the manuscript and Dr Theresa Jones for the correction of the English. This study is a part of the Royal Society SE Asia Rain Forest Programme (RS 187).

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Appendix. List of species of ants at our baits in three rain-forest locations in Sabah, Borneo. The species subfamily (D = Dolichoderinae, F = Formicinae, M = Myrmicinae, P = Ponerinae), the species names, the numbers of species occurring at the plots and in total and the cooperative seed transport of several workers (indicated by an X) are given. Feeding = number of experiments in which workers were observed to feed on the rice baits. Pictures of many of the ant species are provided at http://www.antbase.net.

Species	Danum	Poring	Tawau	Total	Cooperative 'seed' transport	Feeding
Subfamily Dolichoderinae						
Tapinoma sp. 5	0	7	0	7		
Subfamily Formicinae						
Paratrechina sp. 19	1	2	7	10		5
Paratrechina sp. 21	0	0	1	1		1
Paratrechina sp. 3	1	23	3	27		8
Paratrechina sp. 6	1	3	5	9		4
Subfamily Myrmicinae						
Cardiocondyla sp. 1	0	0	5	5		5
Leptothorax sp. 3	1	9	0	10		2
Meranoplus malaysianus Schödl	0	2	0	2		1
Proatta butteli Forel	1	3	3	7		2
Tetramorium sp. 1	1	1	2	4		1
Tetramorium cf. *zypidum*	0	11	5	16		3
Tetramorium sp. 3	2	0	1	3		1
Tetramorium sp. 4	0	1	0	1		
Subfamily Myrmicinae, Tribe Pheidolini						
Aphaenogaster sp. 1	0	3	0	3		
Pheidole acantha Eguchi	0	0	1	1		1
Pheidole aglae Forel	7	8	2	17		2
Pheidole annexus Eguchi	1	1	0	2		1
Pheidole aristotelis Forel	15	17	27	59		13
Pheidole cariniceps Eguchi	10	22	6	38	X	
Pheidole deltea Eguchi	2	0	2	4		3
Pheidole inornata Eguchi	2	0	0	2		
Pheidole lucioccipitalis Eguchi	3	21	26	50	X	10
Pheidole quadrensis Forel	0	2	0	2		1
Pheidole quadricuspis Emery	0	0	3	3		
Pheidole rabo Forel	1	0	0	1		
Pheidole sarawakana Forel	0	2	1	3		1
Pheidole sp. A (*hortensis* or *clypeocornis*)	20	83	32	135	X	35
Pheidole sp. B (*butteli* or *tawauensis*)	6	5	11	22		9
Pheidole sp. C (*sauberi* or *elisae*)	1	3	20	24		2
Pheidole sp. D (*poringensis* or *angulicollis*)	2	0	6	8		4

Appendix. Continued.

Species	Danum	Poring	Tawau	Total	Cooperative 'seed' transport	Feeding
Pheidole sp. 1	0	0	1	1		
Pheidole tjibodana Forel	0	0	1	1		
Subfamily Myrmicinae, Tribe Solenopsidini						
Lophomyrmex bedoti Emery	26	32	17	75		20
Lophomyrmex longicornis Rigato	1	5	0	6		1
Mayriella sp. 1	1	5	2	8		2
Monomorium floricola Jerdon	0	0	1	1		
Monomorium sp. 1	1	4	1	6		2
Monomorium sp. 2	1	0	1	2		
Monomorium sp. 4	0	0	2	2		2
Monomorium sp. 5	0	0	1	1		
Oligomyrmex sp. 1	0	6	3	9		6
Oligomyrmex sp. 2	0	7	4	11		6
Pheidologeton affinis Jerdon	7	5	7	19	X	3
Pheidologeton sp. 2	3	1	0	4		
Recurvidris browni Bolton	19	1	9	29		6
Recurvidris kemneri Wheeler & Wheeler	2	0	3	5		3
Recurvidris sp. 1	74	0	0	74	X	16
Subfamily Ponerinae						
Platythyrea sp. 1	0	0	0	1		
Diacamma sp. 2	2	1	0	3	X	
Odontoponera transversa Smith	0	6	16	22		3
Total	215	302	239	756		

RESEARCH ARTICLES BELONGING TO CHAPTER 6

Pfeiffer M, Huttenlocher H, Ayasse M (manuscript) Myrmecochory in spring ephemerals with different types of elaiosomes: how chemical composition of diaspores influences ant removal rates.

Pfeiffer M, Nais J, Linsenmair KE (2004) Myrmecochory in the Zingiberaceae: seed removal of *Globba franciscii* and *G. propinqua* by ants (Hymenoptera -Formicidae) in rain forests on Borneo. *Journal of Tropical Ecology* 20:705-708

Myrmecochory in spring ephemerals with different types of elaiosomes: how chemical composition of diaspores influences ant removal rates

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Abstract

About 100 years ago the Swedish botanist Sernander developed a typology of ant dispersed diaspores. Since that time the role of the elaiosome in myrmecochory has been subject to many studies. However, most of them focus on myrmecochores of the “Viola odorata-type” that show a clearly defined elaiosome. Besides these we studied diaspores of the “Puschkinia-” and “Hepatica-type” with elaiosomes that can not be separated from the seed by the ants and thus merely work by chemical cues, without any reward for the ants. We compared diaspores of eight myrmecochorous plant species with two non-myrmecochorous species of the genus *Ranunculus.* These diaspores looked very similar to the Hepatica-type diaspores of then same genus and seemed to differ mainly in their chemical composition.

To account for the different chemical and morphological cues we tested removal rates of diaspores, dummies that were prepared with seed extracts and pure fatty acids, as well as scent-standardized diaspores in a population of *Formica polyctena*. Free fatty acids of diaspores were identified by gas chromatography with a polar column.

All myrmecochorous types of diaspores were removed much quicker than the non-myrmecochorous diaspores. The Viola odorata type diaspores had the highest removal rates. Removal rates of the diaspores and dummies with seed extracts were highly correlated and significantly influenced by their fatty acid composition. As shown by multiple regression and discriminant analysis oleic acid was the main trigger substance that elicited seed removal behaviour by the ants. Experiments with dummies that were prepared with pure fatty acids showed that ants removed preferable dummies with unsaturated fatty acids. Myrmecochorous species differed significantly from non-myrmecochorous in the removal rates of their scent-standardized diaspores, thus pointing towards an impact of diaspore morphology. A factor analysis of chemical and morphological diaspore traits supported Sernander’s typology of diaspores. It is questionable whether the myrmecochores of the Hepatica and Puschkinia type can be considered as mutualists.

Key words: elaiosome types, fatty acids, oleic acid, myrmecochory, central Europe, *Formica polyctena*, spring ephemeral, Ranunculaceae,

Introduction

Ants are the major group of invertebrate seed dispersers. Worldwide more than 3000 plant species, the so called myrmecochores, are known to be predominantly ant dispersed (Beattie and Hughes 2002). In myrmecochorous diaspores seeds bear a lipid-rich appendage, the elaiosome that is an attractant for ants. In many cases the elaiosome serves as a food reward for the ants (Edwards et al. 2006) that is preferably fed to the larvae (Fischer et al. 2005; Gammans et al. 2005). For plants myrmecochory potentially provides various advantages, e.g. directed dispersal to sites with enhanced nutrient supply, escape from predators and fires, and a wide range of dispersal distances (Andersen 1988; Beattie and Culver 1982; Gorb and Gorb 1997; Heithaus 1981; Higashi et al. 1989).

The foundation for the study of myrmecochory was laid about hundred years ago by the Swedish botanist R. Sernander with his voluminous book “Outline of a monograph of the European myrmecochores” (Sernander 1906). Sernander systematically studied the European myrmecochorous plant species, tested the attractiveness of their diaspores for different ant species in numerous experiments and classified plants into different types of myrmecochores, depending on the morphology and phylogenetic origin of the elaiosome. The best known type of myrmecochorous plant is the "Viola odorata"-type, which seeds have a large and clearly separated elaiosome that originates from the ovule (Bresinsky 1963); besides Sernander (1906) found 14 other types of myrmecochores with different origin and morphology of the seed appendix. Not in every type of diaspore the elaiosome can be separated easily from the seed by the ants; in some cases ants will get no food reward for their transport effort, although the chemical cues of their load have promised compensation.

The chemical composition of elaiosomes varies among and within the different plant species (Boulay et al. 2006; Bresinsky 1963; Lanza et al. 1992). The diglycerid 1-2-diolein (consistent of two molecules of oleic acid) was identified as main attractant in seeds of *Viola odorata* (Marshall et al. 1979) and the fatty acid composition of the elaiosomes, especially the content of oleic acid, is responsible for the attraction of the ants and the release of the carrying behaviour (Brew et al. 1989; Gammans et al. 2006; Hughes et al. 1994; Lanza et al. 1992; Morrone et al. 2000; Skidmore and Heithaus 1988). A recent study on *Helleborous foetidus* stressed the importance of the free oleic acid for myrmecochory (Boulay et al. 2006).

While these and other studies (Beattie and Culver 1981; Berg 1975; Gorb and Gorb 1995; Mark and Olesen 1996; Oberrath and Boehning-Gaese 2002; Pfeiffer et al. 2004), focused on myrmecochores of the Viola odorata type, we do know only little about the dispersal of other diaspore types, although they comprise the majority of the European myrmecochores (Sernander 1906, Ulbrich 1919). Bresinsky (1963) made the last attempt to directly compare diaspores of different types; however, he restricted his study to the plants and had no access to modern methods of chemical analysis. Here we present a comparative study of 10 widespread European plant species that comprise three morphological different types of myrmecochores and two non-myrmecochorous diaspores. Six of the species are closely related members of the Ranunculaceae. We investigated diaspores' content of the four most common free fatty acids and compared fatty acid patterns and morphological traits to the removal rates of the respective diaspore species.

We hypothesised that 1) a separate elaiosome is not necessary to trigger diaspore removal; 2) removal rates are largest for the Viola odorata type diaspores that provide an ant reward; 3) free oleic acid is the main chemical attractant in all elaiosome types; 4) other free fatty acids may additionally impact removal of diaspores; 5) morphology of the diaspores will also affect myrmecochory.

Material and Methods

Study area, habitat description and time of study

Our study was conducted in a forest area near the University of Ulm, at the "Zuckerhut", a hill near the village of Bollingen, Germany. Here beech forest was mixed with patches of plantations of *Picea abies*. At a small clearing and along a forest road there were two colonies of the polydomous *Formica polyctena* with about ten nests that existed there for at least five years (unpublished observations). We performed all field tests within the territories of these ants between May and August in 2006 and 2007.

Plant species, elaiosome types and diaspore parameters

Sernander (1906) systematically studied the diaspores of the European myrmecochores and assigned them to different types, depending on the morphology and phylogenetical origin of the elaiosome. In our study we compared myrmecochores with non-myrmecochorous plant species regarding the ant removal rates of diaspores and their chemical composition. Following the nomenclature of Sernander (1906), we tested diaspores of the following types:

Viola odorata type. The most common elaiosome type, e.g. found in *Viola*, *Helleborus*, *Scilla* or *Gagea* . Large, whitish coloured and easily recognisable elaiosomes that are only weakly connected to the seed. This type of elaiosome is often developed from the raphe region of the ovule (Bresinsky 1963) and we refer here to it in short as "Viola-type".

Hepatica type. In this type of myrmecochore the elaiosome is a part of the fruit, often originated from the exocarp (Bresinsky 1963). In the case of the Ranuculaceae the swollen peduncle serves as an elaiosome, the enlarged cells of the exocarp include oily substances that work as attractant for ants. This type of diaspores can be found in species of *Anemone*, *Ranunculus* and *Fumaria*.

Puschkinia type. The Puschkinia type is also named Ornithogalum type (Ulbrich 1919). In this type seeds have no elaiosome that can be separated from the seed. However, the Sarcotesta (outer layer of the epidermis) includes oil-containing cells that attract ant species (Bresinsky 1963). Besides being present in the name giving plant genera this elaiosome type is also found in several species of *Mercurialis*, *Allium*, and *Iris*. The Puschkinia type is often developed in diplochores, e.g. in *M. perennis* and *A. ursinum*, the species we have tested in this study.

Both latter types of elaiosomes can not be separated from the seeds by the ants, and thus they provide no food for the ants. This means that ants get no reward for their dispersal services by the plants.

In our study we compared seeds of eight myrmecochorous plant species of different elaiosomes types with two non myrmecochorous species of the genus *Ranunculus* (see Tab. 1; Fig. 1). These diaspores look very similar to the myrmecochorous species of the genera and seemed to differ mainly in their chemical composition.

At the time of seed ripening diaspores of the different plant species were collected in the surrounding of Ulm in the Swabian Mountains. To obtain seed mass we weighted ten piles of five seeds of each species (Sartorius 2004 MP6) and calculated the mean weight of one seed.

Preparation of scent-standardized seeds and seed dummies

To test for the influence of chemical ingredients of the seeds (e.g. free fatty acids) we used dummies that were treated with seed extracts or pure fatty acids. The inert dummies we made from perlite (Knauf, Neuburg an der Donau) a very light and porous granulate material from aluminium silicate. This material is able to incorporate plant extracts and can be easily handled by ants due to its coarse surface texture.

For the preparation of the dummies we made ten samples per species. For each sample 20 diaspores were extracted in 1 ml pentane for 40 hours in a clean glass vial. Extracts were concentrated to 50 µl in a water quench at 40°C using nitrogen scavenging. To account for losses during dummy preparation, each of the extracts, corresponding to 20 seed equivalents was reallocated on 10 dummies with an injection syringe. Controls were prepared by treating each perlite with 5 µl pentane.

We also prepared dummies with oleic acid, linoleic acid, and linolenic acid, by dispensing a drop of a solution of 70 µl of one these fatty acids and 700 µl pentane. For the preparation of dummies with stearic and palmitic acid, we soaked the dummies in a saturated hot solution of fatty acid and pentane. We used 0.179g palmitic acid and 210 µl pentane and 0.189g stearic acid and 210 µl pentane, respectively. As the boiling point of pentane is only 37°C we always put so much fatty acid into the solution that its volume was constant during the preparation of 100 dummies. For each kind of dummy 10 dummies were put in aluminium foil at each time and were cooled (8°C) until they were used in the experiments.

To test for differences in removal rates due to seed morphology we used scent-standardized diaspores of all species. Diaspores were extracted for 24 hours in a Soxleth-apparatus at 60°C. For each species about 250 diaspores were extracted in 250 ml pentane. After extraction seeds were dried in the flue for several hours until the pentane was completely evaporated. As these diaspores were completely free from all chemical substances of content they would not have attracted ants, this leading to removal rates so low that significant results would not have been obtained. In order to increase their attractiveness for the ants we dropped 0.8 µl of a 7µl oleic acid /70µl pentane solution on each of 100 soxleth-extracted diaspores.

Experimental determination of ants' removal rates

To obtain removal rates we offered 10 items in three test series: 1) diaspores, 2) dummies or 3) scent-standardized diaspores, as described above. In each test the items were offered on wooden trays (10 x 10 cm) that had a round deepening of ca 2 mm depth and 4.5 cm radius in the middle part to prevent diaspores from falling off the tray due to movements of ants. We placed the trays to almost the same places in the various experiments: in about 3 to 5 m distance to nests of *F. polyctena* and in about 30 cm distance to their trails. Removal of items from the trays was directly observed during the experiments that lasted one hour. After 5, 10, 15, 30, 45 and 60 minutes we noted the numbers of items (diaspores, dummies, scent-standardized seeds, etc.) that had been removed from the tray. After 45 minutes removal rates between different species of diaspores differed at most, so we took this period for evaluation. During experiments we measured air temperatures, tests were only conducted when temperatures were above 18°C and below 30°C. Trays were used only once and were cleaned with boiling water before the next use.

The immediate vicinity of an ant colony is an "urban" complex with multiple trunk roads starting at the nests and leading to the foraging areas of the ants. Between these roads there are places of lower ant activity where we placed our test trays. Ant activity at these trays plays a major role in the diaspore removal pattern of ants and is only partly influenced by the tested diaspores (Pfeiffer, personal observations). A tray that is near to a trunk road may be visited more often by ants than a tray situated in a more remote area, so more ants have the possibility to collect seeds on those trays.

To control for different ant activity during our experiments, e.g. due to different ambient temperatures and/or site preferences of the ants we used a standard that enabled us to gauge mean ant activity at the trays (see also Peters et al. (2003). As standard we took small green plastic pearls (Rayher, 2 mm) that had a hole in their middle and could be easily transported by the ants. For unknown reasons ants carried these pearls at low rates constantly from the trays, depending on their general activity in that region. Ten of those pearls were placed on the tray in each of the experiments and removal rates of the pearls were counted when we checked the removal of the other items.

Statistical evaluation of removal rates

To check the influence of different ant activity at the trays we regressed sums of removed items per species on the sums of removed pearls from those trays. When the regression confirmed a significant relationship, removal rates were standardized according to the formula $R_s = R_i - R_p$, with R_s being the standardized removal rate, R_i is the removal rate of the examined item and R_p the removal rates of pearls. Taking the difference between both removal rates produced more meaningful results than taking the ratio R_i / R_p, as this formula does not account for total numbers of removed items/pearls (Peters et al. 2003).

Standardized removal rates R_s of the different species were compared with multiple U-tests. Type I error during pairwise comparison was managed by controlling the false discovery rate (FDR) (Benjamini and Hochberg 1995; for a detailed description of the methods see Verhoeven et al. 2005), rather than use a Bonferroni-type correction.

When we found no significant relation between ant activity and removal rates, we pooled original removal rates R_i of each species from all experiments and compared them by (more powerful) 2*2 tables and Fisher's exact tests, respectively chi-square tests, to check for differences between plant species or diaspore types. Type I error during pairwise comparison was managed by controlling the FDR.

For further statistic evaluation we calculated the arithmetic mean of the numbers of all removed items and conducted data presentation, multiple regression analysis and discriminant analysis on this basis.

Although we planned 10 experiments of each kind for each species of plant, some of the experiments could not be performed due to worse weather conditions (e.g., heavy rainfall), resulting in unequal Ns. Additionally we got a second set of data (n=10) for three types of diaspores (ASA, COCA, ANN) from a students' course that was included in our study.

Free fatty acid composition of the diaspores

Sample preparation

For each of the ten focus plant species we made seven extracts, each with five diaspores that were extracted in 500 µl pentane for 40 hours in a glass vial. Diaspores were divided into several pieces to improve extraction yield. Extracts were concentrated to 50 µl in a water quench at 40°C using nitrogen scavenging.

Free fatty acids were identified by gas chromatography (ThermoFinnigan GC Trace with FID-detector) with a polar column (J+W GC Column Wax2), which is especially suited for the detection of fatty acids. We used a grid of fatty acids to identify a standard (100 µl Octane acid in 1 ml hexane), and used 1 µl standard per sample. We identified the amount of palmitic acid (hexadecane acid; abbreviation: PA), oleic acid (delta9-Octadecenoic acid; OA), linoleic acid (9,12-octadecadiene acid; LL) and linolenic acid (9, 12, 15 Octadecatriene acid; LN) by comparing their peak size to that of the standard.

Gas chromatographic analyses (GC)

Samples of free fatty acids were analyzed on a Thermo Trace gas chromatograph (Thermo Electron, Waltham, USA) equipped with a DB-Wax capillary column (30m, 0.25mm i.d., J&W) and a FID. Hydrogen was used as carrier gas (2 ml min^{-1} constant flow). 1µl of the sample was injected splitless at 50°C. After one minute the split valve was opened and the oven temperature increased at 4°C min^{-1} to 310°C. for 19 minutes.

For quantitative analyses 1 µl of octanoic acid (100 µg/ml stock solution) was added as an internal standard (IS).

Gas chromatographic - mass spectrometric analyses (GC-MS)

Samples containing extracts of diaspores were analysed with a Hewlett Packard HP 6890 Series gas chromatographic – mass selective detector (GC-MS, Agilent Quadrupol 5972) to identify the chemical structures of compounds. The settings for the GC method were the same as described above. On the contrary to the GC analyses the carrier was He_2 with a flow of 1 ml/ min. For structure elucidation the Agilent MSD Enhanced ChemStation G1701DA D.01.00, the NIST library and a synthetic mixture of fatty acids were used. Identification of compounds was carried out by comparison of mass spectra and retention times of natural products with corresponding data of synthetic reference samples.

Results

Ant activity at the trays

First we wanted to check whether our test setting was appropriate for a neutral test of the influence of different morphological and chemical cues on the foraging behaviour of our focus colonies of *Formica polyctena*. In the optimal case for a test ant activity at all test trays should be equal, thus there should be no influence of ant activity patterns on the removal of items from the trays.

After our experiments we found no significant connection between ant activity at the trays as measured by removal of control pearls R_p and removal of diaspores R_i (regression F(1,8)= 0.1065, p = n.s., korr $r^2 = 0.01$), so all calculations on diaspore removal were made with the original data R_i. However, independence of ants' activity and removal activity was not found in the experiments with dummies and scent-standardized seeds: the number of removed pearls and dummies was closely connected (regression F(1,9) = 11.14, $p < 0.01$, korr $r^2 = 0.55$), as well as the number of removed pearls and scent-standardized seeds (regression F(1,8) = 12.89, $p < 0.01$, korr $r^2 = 0.62$). In these cases the different activity of ants at the trays had significantly influenced the removal of the items, so we calculated the standardized removal rates R_s (see methods) (Peters et al. 2003). After correction we found no influence of R_p on R_s for dummies (regression F(1,9) = 0.774, p = n.s., korr $r^2 = 0.07$) and scent-standardized seeds (regression F(1,8) = 0.1065, p = n.s., korr $r^2 = 0.01$). For both items we used R_s for further evaluation of the data.

Removal of diaspores, dummies and scent-standardized seeds

Removal of diaspores started immediately after presentation of the trays; within short time most diaspores of the three Viola odorata type species, *Asarum europaeum* (ASA), *Corydalis cava* (COCA) and *Helleborus foetitus* (HFOE), were removed by the ants, while removal of the other species occurred at a much lesser rate (Fig. 2). Forty-five minutes after the start of the experiment removal rates R_i of diaspores differed significantly between most species when tested by multiple Fisher's exact tests (with control of FDR, significance threshold corresponding to a p-level of 0.05 was 0.0111; see Fig. 3). Viola type species had the highest removal rates, however, did not differ among each other. *Mercurialis perennis* (MEP) and *Anemone nemorosa* (ANN) had medium removal rates and differed significantly from a larger group of species with low removal rates, while the non-myrmecochorous *Ranunculus acris* (RAC) had the lowest removal rate of only 0.2 diaspores per experiment (S.D. = 0.42, n=10) and differed from all other species (Fig. 3).

When we assessed removal of diaspore types, removal rates of Viola type diaspores were much higher (424 removed vs. 76 left) than those of the Hepatica type (106 vs. 294), the Puschkinia type (72 vs. 128) or the non-myrmecochorous seeds; all types differed among each other except Puschkinia and Hepatica type (multiple chi-square tests with control of FDR, significance threshold corresponding to a p-level of 0.05 was 0.01667, see Fig. 4).

Our dummy experiment excluded all possible non-chemical clues for myrmecochory and confirmed that ants removed diaspores due to their chemical signals. Standardized removal rates R_s of dummies were significantly correlated with removal rates R_i of diaspores (Pearson correlation $r = 0.829$, $t = 3.95$, $p < 0.01$). R_s patterns of dummies were similar to R_i patterns of the diaspores, however, dummies were separated into two groups: those dummies that were quickly removed by the ants (Viola type and ANN) and the dummies of all other species that did not differ in their removal rates from those of the controls (CON), that were perlites that were only treated with pentane (multiple U tests with control of FDR, significance threshold corresponding to a p-level of 0.05 was 0.02818, see Fig. 5). However, these differences were gradually, e.g. dummies of ANR and of MEP were not different from the Viola type dummy of ASA, as well as from CON. The low separation of dummies from CON was partly due to our conservative approach of standardization. This did not change when we pooled dummies according to diaspore types. The Viola type dummies were the only ones that differed from the controls and all other types, the dummies of the Hepatica type differed significantly from those of the non-myrmecochorous types (multiple U tests with control of FDR, significance threshold corresponding to a p-level of 0.05 was 0.03, see Fig. 6).

In the next step we wanted to access the sole influence of diaspore morphology on ant removal patterns and tested scent-standardized diaspores (SSD) at the trays. After Soxleth extraction diaspores had lost some of their volume and weight and all of their chemical substance of content. A standard administration of oleic acid to each SSD ensured that ants were attracted to the SSD. Standardized removal rates R_s of SSD did not correlate with that of the diaspores (Pearson correlation $r = 0.226$, $t = 1.0$, $p =$ n.s.), however, differed significantly among the species, reflecting the varying morphology of the SSD (Kruskal-Wallis-Test: $H (9, N = 100) = 44.32$, $p < 0.0001$). Interestingly, the non-myrmecochorous diaspores of the Ranunculaceae were those that had the lowest removal patterns and differed from all other types, especially also from the Hepatica type diaspores that comprised the morphologically very similar taxa of the same family (multiple U tests, with FDR control, significance threshold corresponding to a p-level of 0.05 was 0.025, see Fig.7 and compare morphology in Fig. 1). This result shows that different removal patterns among species were also influenced by the morphology of the diaspores.

Removal of fatty acid dummies

In a series of tests we explored ants' preferences for fatty acids and presented dummies prepared with five different fatty acids and controls in bioassays. Standardized removal rates R_s of these dummies showed a distinct pattern: the two saturated fatty acids, stearic and palmitic acid, and the unsaturated linoleic acid had low R_s rates (means: 0, -0.1, 1.2; n :10, 10, 21) and did not differ significantly from the control (mean -0.33, n :12). The unsaturated oleic and linolenic acid, however, had mean R_s of 2.1 and 1.8 (n: 23, 22) that differed from the control, but not from each other (see Fig. 8).

Fatty acid composition of the diaspores

Free fatty acid composition of the diaspores varied significantly for all the four fatty acids that were in focus of this investigation (see Tab. 2, ANOVAs, p for all < 0.0001; v1 = log (oleic acid) F (9, 60) = 33,7971; v1 = log (palmitic acid) F (9, 60) = 42,7599; v1 = log (linoleic acid) F (9, 60) = 95,8331; v1 = log (linolenic acid) F (9, 60) = 109,1141). Fatty acid concentrations differed also among types (e.g. in oleic acid, see Fig. 9, multiple U tests with FDR control; significance threshold corresponding to a p-level of 0.05 was 0.035). Besides from oleic acid, logarithmized fatty acid concentrations were significantly highly correlated with each other

(PA with LL r = 0.90, $p < 0.001$; PA with LN r = 0.81, $p < 0.05$; LL with LN r = 0.95, $p < 0.001$).

Statistical analyses of removal data and fatty acid patterns

A Spearman correlation of fatty acid contents with diaspore weight and removal rates of dummies and diaspores showed a positive interaction of R_i of the diaspores and the content of all focus fatty acids (see Tab. 3). However, R_s of dummies was only correlated with the content of oleic acid and palmitic acid. Diaspore weight was positively correlated with diaspore removal and the content of fatty acids, except for oleic acid.

In a multiple stepwise regression analysis of the content of focal fatty acids and diaspore weight on the removal patterns of the diaspores all fatty acids had a significant impact (korr. $R^2 = 0.958$, $F(4,5) = 52.669$, $p< 0.001$, see Tab. 4 upper part). Similarly, all of those fatty acids influenced the removal pattern of the dummies (korr. $R^2 = 0.864$, $F(4,5) = 15.272$, $p < 0.01$, see Tab. 4 lower part). In both regressions diaspore weight was excluded from the analyses because of its low F value. Interestingly, in both cases only oleic acid and linoleic acid were positively correlated with the removal of diaspores and dummies and had the highest partial correlations coefficients.

To evaluate the value of single fatty acids for myrmecochory further, we used stepwise discriminant analysis. We considered as group 1 those diaspore species that differed from the control in the removal analysis of the dummies (ASA, COCA, HFOE and ANN, see Fig. 5). Group 2 included those species with the lower removal values. The content of free oleic acid in the diaspores was found to discriminate significantly between both groups (Wilks' Lambda: 0.4324, approx. $F(1,8) = 10.504$ $p < 0.012$), while all other fatty acids were removed from the analysis (see Tab. 5), thus supporting our hypothesis that the free oleic acid is the trigger substance that induces diaspore removal by ants.

This was corroborated when we had a closer look to the removal patterns of the sister genera *Anemone* and *Ranunculus* that differed clearly: *Anemone* was significantly more often removed from the trays (U-test U = 223.5, Z = 3.43, n = 30, $p < 0.001$). When we looked for differences in the fatty acid patterns of those genera, both groups differed significantly only in the concentration of oleic acid (T-test, t (33) = -10.3, $p < 0.001$) and palmitic acid (U-test U = 37, Z = -3.70, $p < 0.001$). For linolenic acid (T-test, t (33) = -1.27, p = n.s.) and linoleic acid (T-test, t (33) = -1.73, p = n.s.) we found no significant differences. Because palmitic acid has proved to be inactive in regard of ants' seed removing behaviour in our experiments, the much more effective seed removal of *Anemone* seems to be a result of the higher concentration of free oleic acid in the diaspores of these genera.

Integration of all factors

We used a factor analysis to integrate all variables into one plot that reflects our current knowledge on the differences of the examined diaspores (Fig. 10). The eigenvalues of the two axes are 5.53 and 1.04, both axes together account for 82 % of the total variability. The factor loadings of the axes are given in Tab. 6. While factor 1 accounts mostly for the chemical characteristics of the diaspores, factor 2 correlates with their morphological characteristics.

Discussion

While former studies focused mainly on the influence of the elaiosome on the seed removal behaviour of ants (Boulay et al. 2006; Brew et al. 1989; Lanza et al. 1992), our study investigated the diaspore as the unit of dispersal. As we have hypothesized and shown in our results, a separate elaiosome is not necessary for triggering ants behaviour; diaspores without it were removed from the trays as well, e.g. ANN or MEP. In two of the three observed diaspore types removal of diaspores by ants took place without reward for the ants which is in contrast to former studies that stresses the impact of ant rewards for the removal of seeds (Edwards et al. 2006; Gorb and Gorb 2003; Mark and Olesen 1996). In the Puschkinia type it is hardly possible for the ants to scratch pieces from the hard seed coat that bears the oil containing cells. In the Hepatica type we have never observed ants feeding on the fruit flesh, although ants may gnaw on the swollen peduncle during transport of the diaspore. In any case, in relation to a Viola type elaiosome ants get hardly any compensation for their transport activity, thus it is questionable whether the interaction of these species with ants can be called "mutualism". However, removal rates of these diaspore types were reduced compared to the Viola type.

Fatty acid patterns are reported to influence seed carrying behaviour in ants (Boulay et al. 2006; Brew et al. 1989; Hughes et al. 1994; Marshall et al. 1979; Pizo and Oliveira 2001; Skidmore and Heithaus 1988). When we tested a set of pure fatty acids on perlite dummies, significant enhanced removal rates were found for those dummies that had been prepared with oleic acid and lionolenic acid. As both unsaturated fatty acids are essential for ants and seem to enhance growth of the larvae (Gammans et al. 2005), this may well explain ants' preferences. Saturated fatty acids elicited no response. These results influenced our selection of potential trigger substances for myrmecochory by seed extraction.

As in some diaspores the elaiosome can not be separated from the seeds, we extracted diaspores as a whole. Our extraction method focused on the free fatty acids, which have been reported to be especially important for diaspore removal (Boulay et al. 2006). We evaluated four free fatty acids, two of them, oleic acid and linoleic acid have been formerly found to influence seed removal behaviour (Brew et al. 1989; Lanza et al. 1992), a third one, lionolenic acid influenced ants' behaviour in our dummy experiments. All of the examined fatty acids, even palmitic acid that was inactive in our fatty acid dummy experiments, were shown to influence removal patterns of dummies and diaspores in a regression analysis. However, only contents of oleic acid and linoleic acid were found positively connected with higher removal rates. Except from oleic acid contents of all other fatty acid were highly correlated with each other, thus it was not possible to separate their influence on removal patterns clearly by further stepwise regression analysis. As a statistical alternative we used discriminant analysis and found that only the content of free oleic acid made the difference between those diaspores with high and low removal rates.

The free fatty acids serve –depending on diaspore type- also as a reserve for the embryo. Larger seeds that contain a larger embryo may need more reserves, this may -a least partly- explain, why the content of fatty acids was mostly correlated with diaspore weight. As this does not hold for oleic acid this may be an additional cue to the outstanding function of this fatty acid. As already Brew et al. (1989) have stated, a generally nutrient hypothesis alone is insufficient to explain the patterns of removal, myrmecochory is based on a trigger substance.

The relatively low content of oleic acid in the whole diaspores that we have detected is in sharp contrast to the 66 % content of free oleic acid in the elaiosome from Spanish plants that has been reported by Boulay and coworkers (2006). However, the relative content of fatty acids in whole diaspores of HFOE that we have found (OA:10%, PA12%,LL29%,LN49%) was quite similar to the results of Aitzetmueller et al. (1999)(OA:11%, PA8%, LL23%, LN46%), who also used whole diaspores for their analysis. While the elaiosomes in the Spanish study contained only traces of Linolenic acid, we found a high content (48.9 %) in the whole diaspore that will have been included in the seeds. As linolenic acid was also found to trigger removal of fatty acid dummies in our experiments, this substance may enhance diaspore removal, too, although its influence was not responsible for the differential dispersal of both groups in our dummy experiment with diaspore extracts.

While some former studies stressed the importance of the diglycerid 1-2-diolein (Marshall et al. 1979) that consists of two molecules of oleic acid, we focused in our study on the free fatty acids that can be detected by gas chromatography with polar columns. Our results corroborate a comparative study on *H. foetidus* from Spain (Boulay et al. 2006), where elaiosomes of seeds with higher dispersal rate had a relatively higher content of free oleic acid, but were less concentrated in free palmitic acid and free linoleic acid, while diglycerids did not contribute to their higher attractiveness. Oleic acid is known as a chemical releaser of necrophoric behaviour in ants and has been reported to induce transport of dead nestmates to the nest middens (Wilson et al. 1958).

As we have proven by the experiment with the scent-standardized seeds the morphology of the seeds plays an additional role in improving diaspores' removal rates by ants. Recently, Gomez et al. (2005) have demonstrated that the structure of the elaiosome can serve as a handle for the ants and may improve the handling qualities of the seeds. Thus some of the seeds, e.g. *Corydalis cava*, which has a completely smooth surface, are hardly to be moved by the ants when the elaiosome is missing (own observations). Interestingly, although all types of myrmecochorous diaspores did not differ in their removal patterns from each other after scent standardization, they were more readily removed from the tray than the non-myrmecochorous diaspores that had the same scent and this held even for the quite similar diaspores of the Ranunculaceae.

The scent-standardized seeds with the highest removal rate were those of *Allium ursinum*, however, this may have still chemical reasons, as even after soxleth extraction these seeds preserved their characteristic smell that may have influenced ants behaviour. In how far these and other additional, non-fatty acid chemicals may have influenced removal pattern we could not clear with our experiments.

When seeds of the Viola odorata type are those with the best removal rates, what are the advantages of the both other types for the plants? First of all they save the costs for rewarding ants, but if they have very low removal rates in return this may be not sufficient for an evolutionary success. However, both examined types of myrmecochores have certain advantages compared to the Viola odorata type: the Puschkinia type is almost round and thus especially useful for diplochores with ballistic dispersal. Here an additional handle may seriously impede the ballistic properties of the diaspore. The Hepatica type on the other hand, has a permanent handle that is fixed at the seed, while most seeds of the Viola odorata type will loose their handle, once the elaiosome has been removed. This is especially useful when seed fate should not end in ants' nests and plants of e.g. *Anemone nemorosa* are distributed over the whole forest floor, rather than to be restricted to "favourite sites" near ant nests. As Gomez and coworker (2005) have demonstrated a handle for ants is necessary for the seeds to leave ants' nest again. Additionally, such a structure is a tool against such ants that remove elaiosomes from the diaspores instead of transporting them. As most seeds are dropped by ants during dispersal (Gorb and Gorb 1999) and may be later relocated by other ants a permanent handle ensures multiple transport possibilities.

All detected differences between plant species have been summarized in Fig. 10 that supports the typology of Sernander (1906) with chemical, morphological and removal data. Now, as we realize that most types of myrmecochores have been ignored by ecologists so far, research on myrmecochory faces a wide range of new and interesting questions.

Acknowledgements

We thank Johannes Stökl for his valuable advice in the chemical analyses and Andrea Weiß for skilful technical assistance. We are grateful to Claus Markstädter, Bianka Pink and Jens

Rister, Biocenter of the University of Würzburg for discussion, technical assistance and help in the field during a former attempt to solve the riddle of myrmecochorous diaspore removal some years ago. That work allowed us to improve our experiments this time. Likewise we thank Kurt Aitzetmüller for interesting discussions and helpful comments during this study period. The artwork in figure 1 was provided by Verena Kutschera, University of Ulm, and we are grateful for this fine work.

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Figure captions

Fig. 1 Overview about the different diaspores that we used in our experiments. Viola odorata type: A *Asarum europaeum.* B *Helleborus foetitus.* C *Corydalis cava.* Hepatica type: D *Anemone nemorosa.* E *Anemone ranunculoides.* F *Ranunculus auricomus.* Puschkinia type: G *Allium ursinum.* H *Mercurialis perennis.* Non-myrmecochorous species: I *Ranunculus acris.* J *Ranunculus lanuginosus.*

Fig. 2 Mean removal rates R_i of different diaspores by ants (n = 10 for each species). Species were compared after 45 minutes, see Fig. 3.

Fig. 3 Mean removal rates R_i of different diaspores by ants after 45 minutes (n = 10 experiments for each species). Means marked by the same letter are not significantly different (Chi-square test, significance threshold corresponding to a p-level of 0.05 was 0.0111). Viola odorata type species are ASA, COCA, HFOE; Hepatica type species are ANN, ANR, RAU, Puschkinia type species are ALU and MEP, while RAC and RLA represent non-myrmecochorous plant species. See Table 1 for a list of the species names.

Fig. 4 Removal of diaspores sorted to Sernander's (1906) dispore types.

Fig. 5 Mean standardized removal rates R_s of dummies by ants after 45 minutes. Means marked by the same letter are not significantly different (multiple U-tests, significance threshold corresponding to a p-level of 0.05 was 0.028). Four myrmecochorous dummy types (ASA, COCA, HFOE, ANN) differed significantly from the control (CON, dummies that were only treated with solvent), as well as from the non-myrmecochorous dummies (RAC, RLA). See table 1 for the abbreviations of the species.

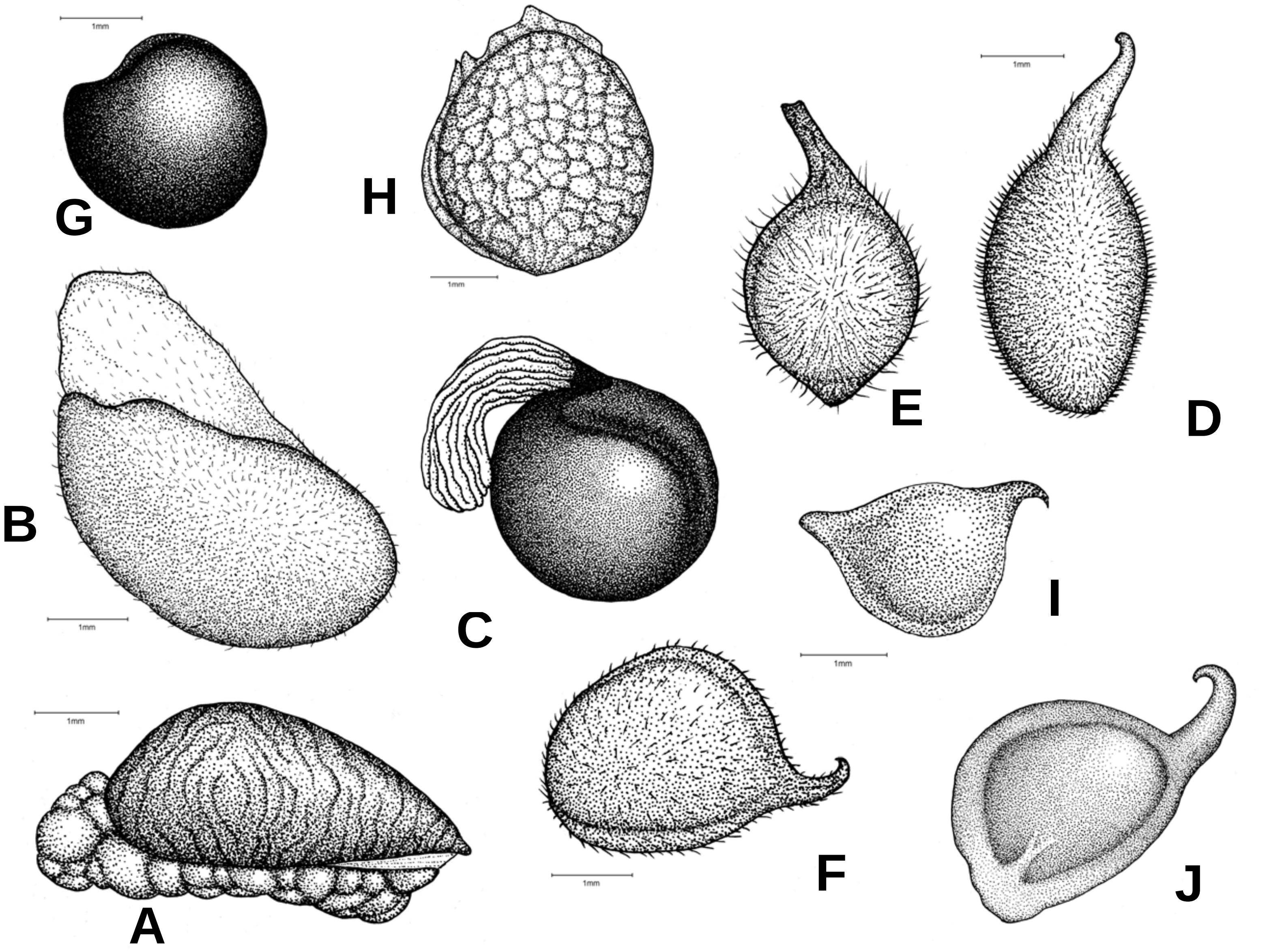
Fig. 6 Mean standardized removal rates R_s of dummies sorted by diaspore types.

Fig. 7 Removal of scent-standardized seeds regarding diaspore types. The non-myrmecochorous diaspores were those that had the lowest removal rates and differed from all other types.

Fig. 8 Removal of dummies that were soaked with fatty acids. Means marked by the same letter are not significantly different (multiple U-Tests, significance threshold corresponding to a p-level of 0.05 was p = 0.03).

Fig. 9 Content of oleic acid in diaspores of different types. The not significant differences in multiple U tests are marked with letters; significance threshold corresponding to a p-level of 0.05 was 0.035. Hepatica type and non-myrmecochorous diaspores had a tendency to differ significantly ($p_{uncorr.}$ = 0,048).

Fig. 10 PCA of the diaspore characteristics. Both axes accounted for 82% of the observed variability. All factors were negatively correlated with axis 1, while especially the removal of the scent-standardized seeds was negatively correlated with axis 2. See table 5 for factor loadings.


1mm
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I
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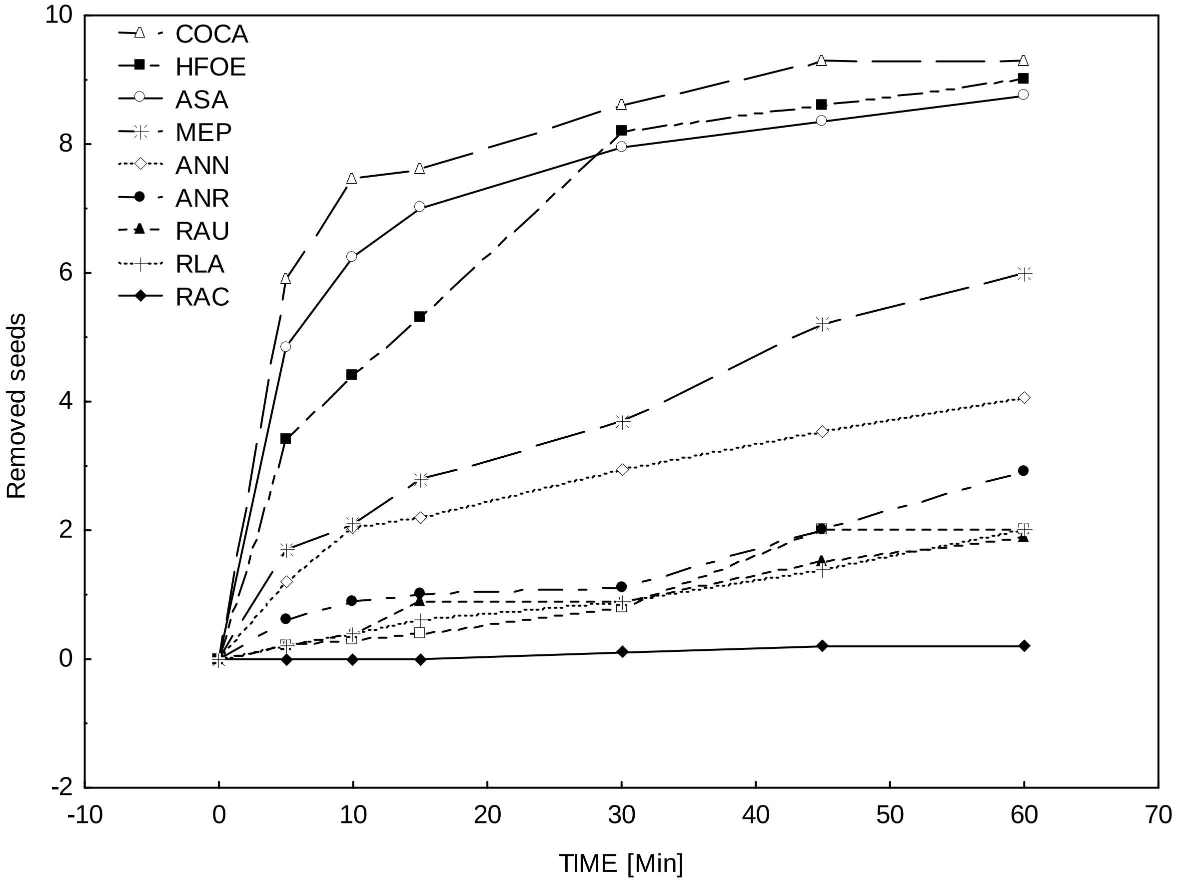
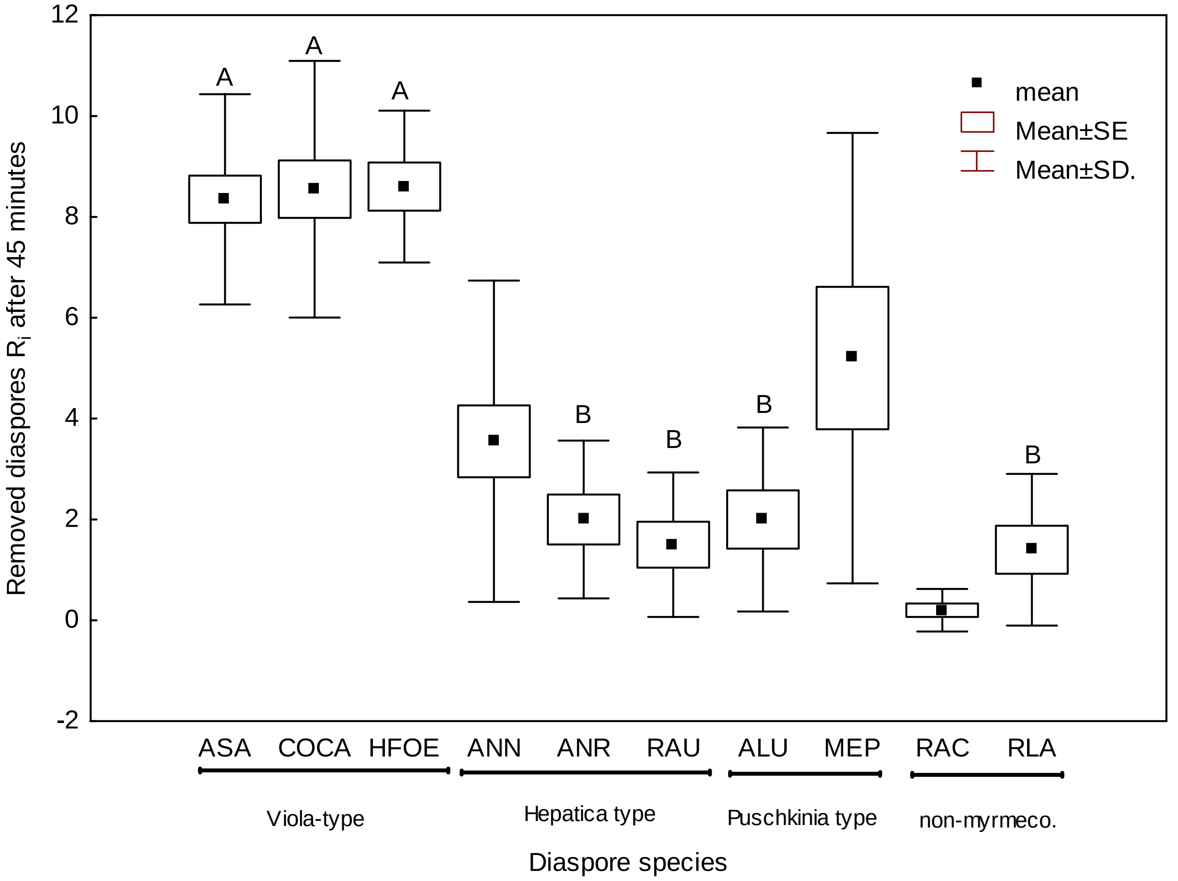
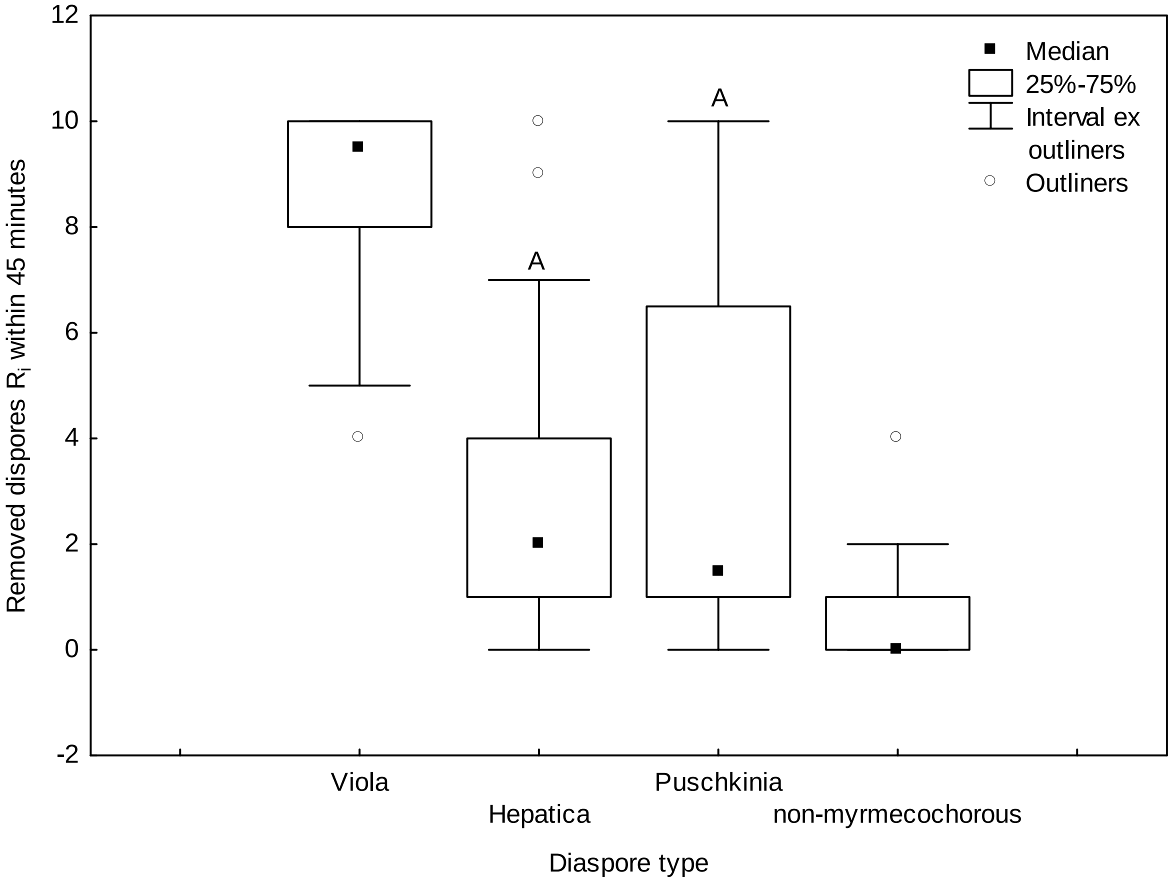
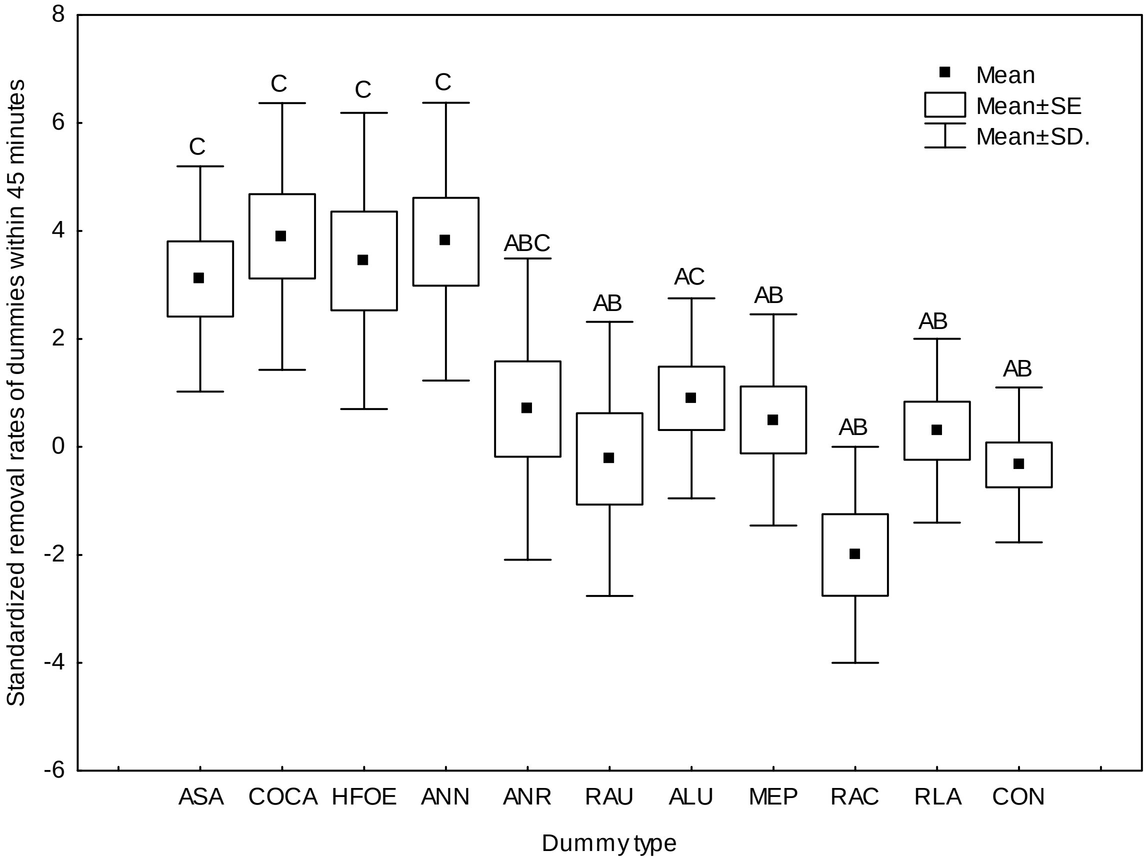
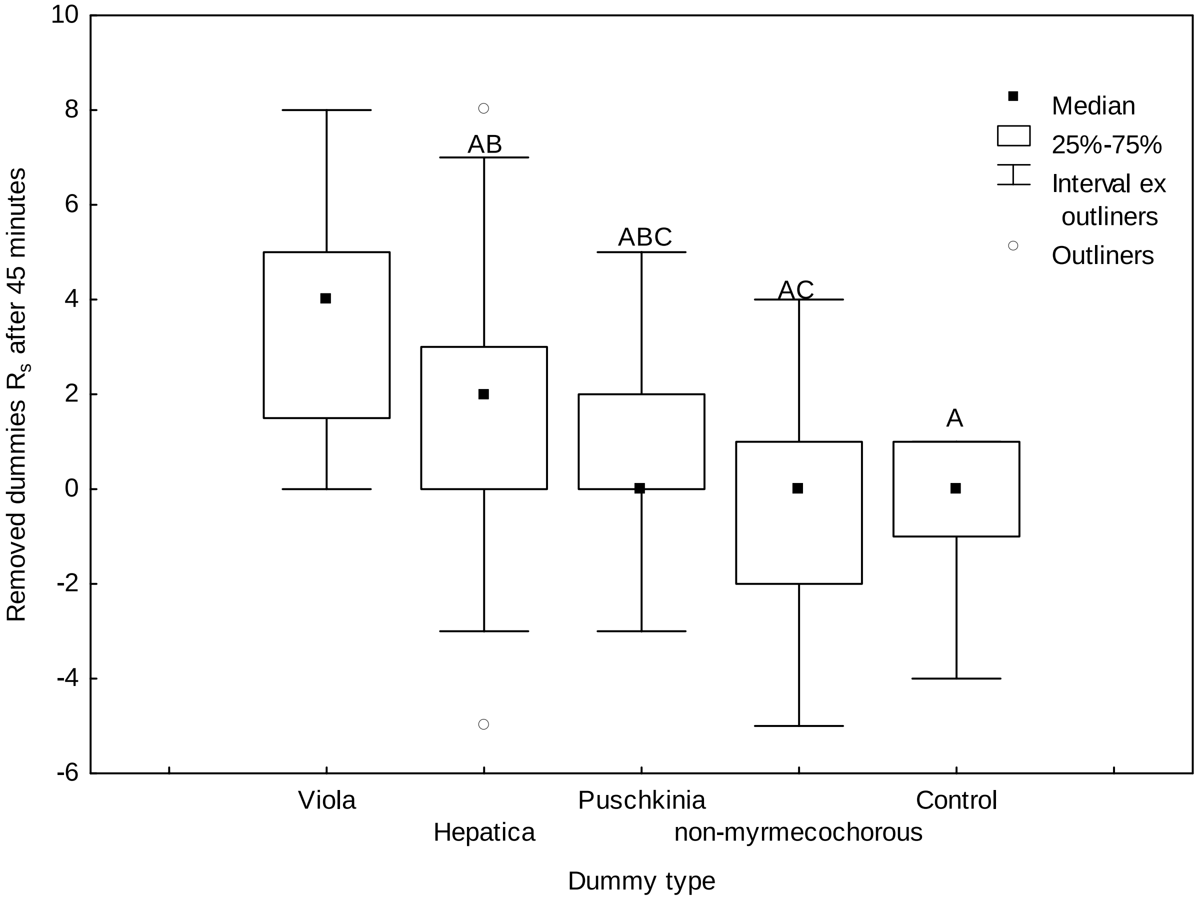
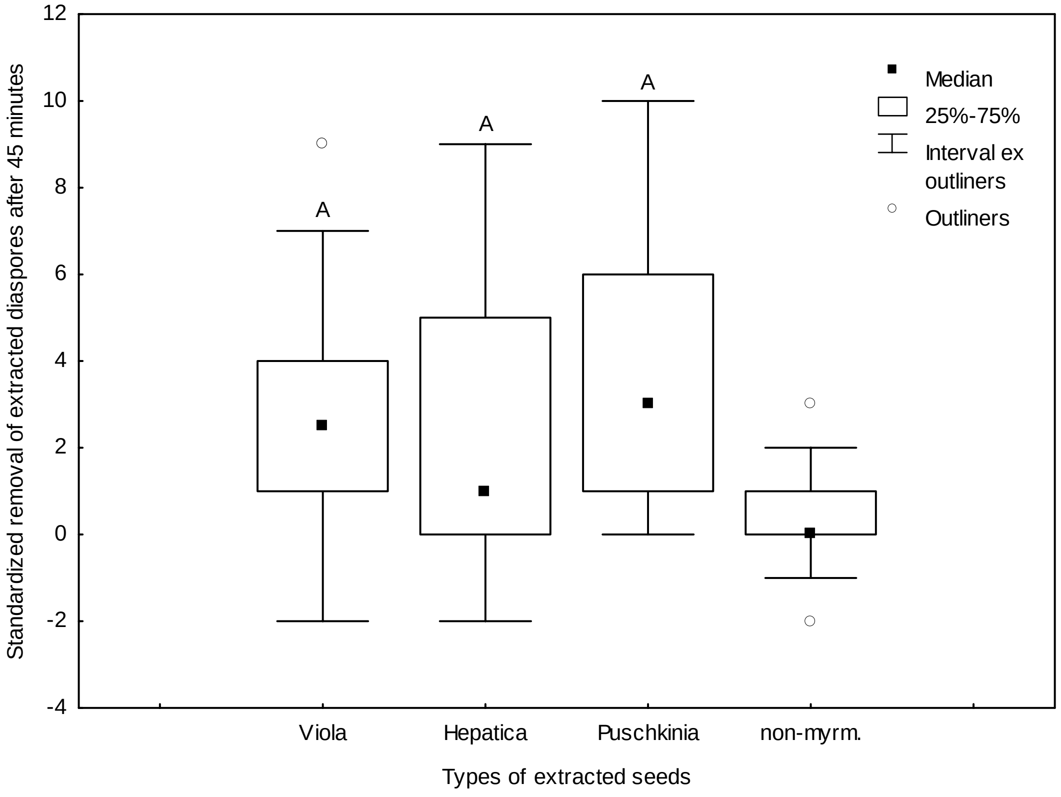

COCA
HFOE
ASA
MEP
ANN
ANR
RAU
RLA
RAC
Removed seeds
TIME [Min]
10
8
6
4
2
0
-2
-10
0
10
20
30
40
50
60
70

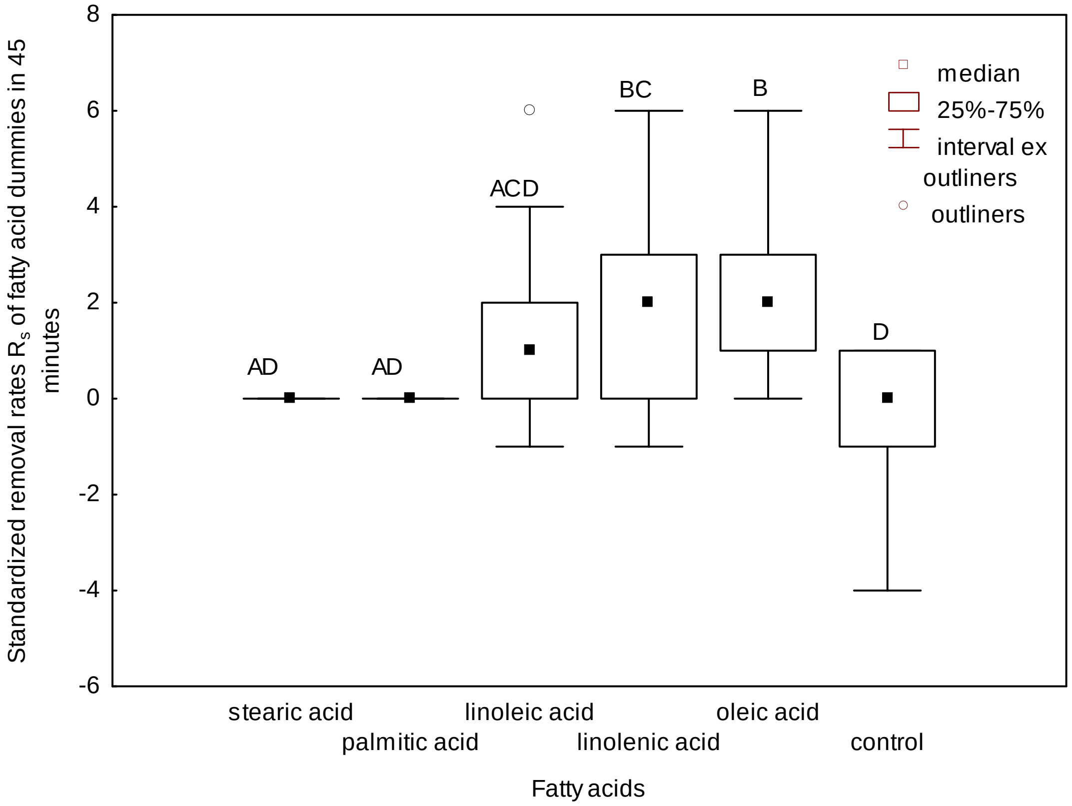

mean
Mean±SE
Mean±SD.
Removed diaspores R_i after 45 minutes
Diaspore species
12
10
8
6
4
2
0
-2
A
A
A
B
B
B
B
ASA
COCA
HFOE
ANN
ANR
RAU
ALU
MEP
RAC
RLA
Viola-type
Hepatica type
Puschkinia type
non-myrmeco.

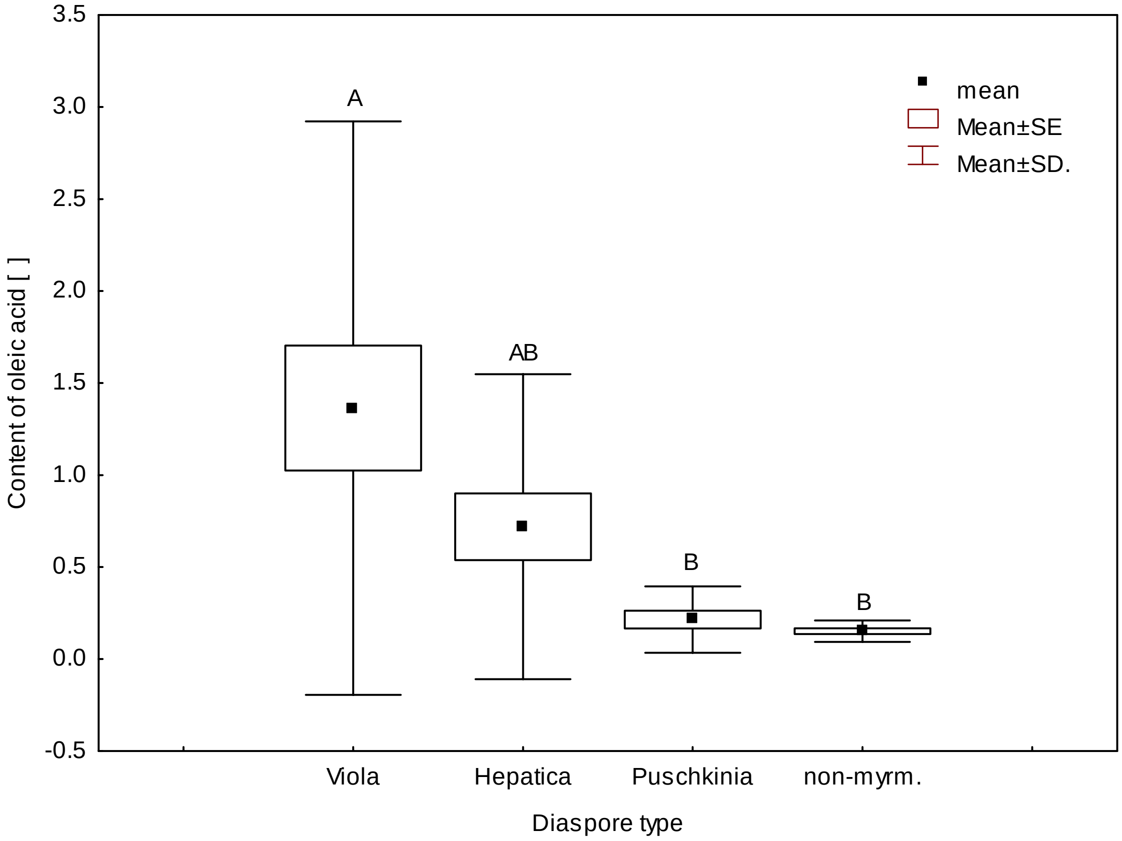

12
10
8
6
4
2
0
-2
Removed dispores R$_i$ within 45 minutes
■ Median
25%-75%
Interval ex outliners
○ Outliners
A
A
Viola
Hepatica
Puschkinia
non-myrmecochorous
Diaspore type

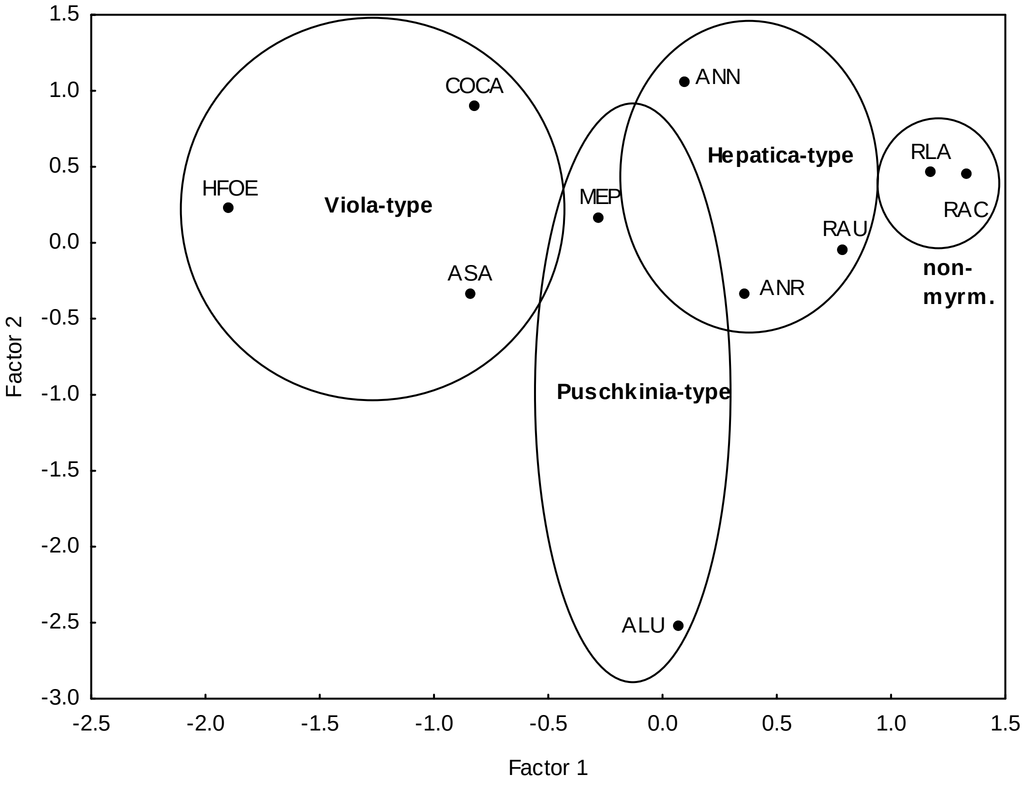

8
6
4
2
0
-2
-4
-6
Standardized removal rates of dummies within 45 minutes
■ Mean
Mean±SE
Mean±SD.
C
C
C
C
ABC
AB
AC
AB
AB
AB
AB
ASA
COCA
HFOE
ANN
ANR
RAU
ALU
MEP
RAC
RLA
CON
Dummy type


10
8
6
4
2
0
-2
-4
-6
Removed dummies R_s after 45 minutes
AB
ABC
AC
A
Median
25%-75%
Interval ex outliners
Outliners
Viola
Hepatica
Puschkinia
non-myrmecochorous
Control
Dummy type


12
10
8
6
4
2
0
-2
-4
Standardized removal of extracted diaspores after 45 minutes
A
A
A
Median
25%-75%
Interval ex outliners
Outliners
Viola
Hepatica
Puschkinia
non-myrm.
Types of extracted seeds


Standardized removal rates R_s of fatty acid dummies in 45 minutes
8
6
4
2
0
-2
-4
-6
AD
AD
ACD
BC
B
D
median
25%-75%
interval ex outliners
outliners
stearic acid
palmitic acid
linoleic acid
linolenic acid
oleic acid
control
Fatty acids


Content of oleic acid [ ]
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
A
AB
B
B
mean
Mean±SE
Mean±SD.
Viola
Hepatica
Puschkinia
non-myrm.
Diaspore type



Tab. 1: Plant species that have been used in this study, their abbreviations used in this article and their elaiosome type according to Sernander (1906) and Bresinsky A (1963).

Species	Family	Abbreviation	Elaiosome type
Asarum europaeum	Aristolochiaceae	ASA	Viola odorata type
Corydalis cava	Papaveraceae	COCA	Viola odorata type
Helleborus foetitus	Ranunculaceae	HFOE	Viola odorata type
Allium ursinum	Liliaceae	ALU	Puschkinia type
Mercurialis perennis	Euphorbiaceae	MEP	Puschkinia type
Anemone nemorosa	Ranunculaceae	ANN	Hepatica type
Anemone ranunculoides	Ranunculaceae	ANR	Hepatica type
Ranunculus auricomus	Ranunculaceae	RAU	Hepatica type
Ranunculus acris	Ranunculaceae	RAC	not myrmecochorous
Ranunculus lanuginosus	Ranunculaceae	RLA	not myrmecochorous

Tab. 2 Free fatty acid composition of the examined diaspores as revealed by gas chromatography of pentane extracts with a polar column. Given are the mean values and standard deviations for 5 diaspores per sample (n =7).

	Palmitic acid		Oleic acid		Linoleic acid		Linolenic acid	
Species	Mean [µg]	S.D.	Mean [µg]	S.D.	Mean [µg]	S.D.	Mean [µg]	S.D.
ASA	0.38	0.49	0.54	0.29	0.98	0.76	1.05	1.25
COCA	0.51	0.16	0.58	0.29	1.41	0.47	0.72	0.26
HFOE	3.64	2.38	2.97	1.84	8.87	5.54	14.80	8.97
ANN	0.27	0.14	1.55	0.97	0.04	0.03	0.01	0.00
ANR	0.15	0.07	0.52	0.20	0.07	0.04	0.04	0.02
RAU	0.18	0.13	0.08	0.02	0.09	0.02	0.02	0.01
ALU	0.29	0.21	0.06	0.04	0.33	0.16	0.06	0.02
MEP	0.23	0.07	0.37	0.12	0.49	0.14	0.58	0.30
RAC	0.03	0.01	0.17	0.04	0.02	0.01	0.02	0.01
RLA	0.02	0.02	0.14	0.07	0.02	0.01	0.02	0.02

Tab. 3 Spearman rang correlations coefficients for the correlation of diaspore weight and content of fatty acids with absolute removal rates R_i of diaspores and standardized removal rates R_s of the dummies. Correlation coefficients in bolt are statistically significant after controlling FDR, significance threshold corresponding to a p-level of 0.05 was 0.0179.

	Diaspore weight	Oleic acid	Palmitic acid	Linoleic acid	Linolenic acid
R_i seeds	**0.78**	**0.75**	**0.91**	**0.89**	**0.84**
R_s dummies	0.45	**0.73**	**0.82**	0.60	0.50
Diaspore weight	-	0.27	**0.75**	**0.87**	**0.87**

Tab. 4 Results of multiple regression of the removal rates of the diaspores (korr. $R^2 = 0.958$, $F(4,5) = 52.669$, $p< 0.001$, upper part) and the dummies (korr. $R^2 = 0.864$, $F(4,5) = 15.272$, $p < 0.01$, lower part) on the mean logarithmed concentrations of four examined fatty acids. Given are the constants, the Beta and Bs with their standard errors, the semi partial correlation coefficents, the R-square, t-values and significance value p.

Diaspores	BETA	S.E.	B	S.E.	Semipart.	Part. R^2	t(5)	p
Constant			5.196	0.501	-	-	10.366	> 0.001
log(oleic acid)	1.060	0.175	2.810	0.463	0.413	0.848	6.068	> 0.01
log(palmitic acid)	-1.633	0.323	-3.700	0.732	-0.344	0.956	-5.057	> 0.01
log(linoleic acid)	3.508	0.627	5.529	0.988	0.381	0.988	5.597	> 0.01
log(linolenic acid)	-1.721	0.455	-2.389	0.632	-0.258	0.978	-3.782	> 0.05
Dummies								
Constant			1.532	0.550	-	-	2.784	> 0.05
log(oleic acid)	1.638	0.316	2.636	0.508	0.638	0.848	5.188	> 0.01
log(palmitic acid)	-1.849	0.583	-2.545	0.803	-0.390	0.956	-3.169	> 0.05
log(linoleic acid)	5.047	1.132	4.832	1.084	0.548	0.988	4.458	> 0.01
log(linolenic acid)	-3.663	0.822	-3.088	0.693	0.548	0.978	-4.456	> 0.01

Tab. 5 Results of the stepwise discriminant analysis. The logarithm of the oleic acid concentration was the factor that discriminated between those diaspores that were readily removed from the trays and those that had lower removal rates. All other factors were not significant. Given are Wilk's Lambdas, patial Lambda, F-values for inclusion in (FG 1,8) or removal from (FG 1,7) from the final solution, p-values and tolerance-values for each of the considered variables.

Factor	Wilks' Lambda	Part. Lambda	F-values	P-values	Tolerance
log(oleic acid)	1.00	0.43	10.50	0.012	1.000
log(palmitic acid)	0.37	0.87	1.08	n.s.	0.940
log(linoleic acid)	0.40	0.93	0.56	n.s.	0.942
log(linolenic acid)	0.36	0.84	1.36	n.s.	0.999

Tab. 6 actor loadings for the PCA of all observed diaspore variables. The accounted variance was 0.691 for factor 1 and 0,130 for factor 2, the respective eigenvalues were 5.531 and 1.044.

	Factor 1	Factor 2
Removal of diaspores	-0.927	0.210
Removal of dummies	-0.794	0.223
Removal of scent-standardized seeds	-0.431	-0.723
Weight [g]	-0.881	-0.283
log(oleic acid)	-0.674	0.567
log(palmitic acid)	-0.926	-0.064
log(linoleic acid)	-0.949	-0.147
log(linolenic acid)	-0.932	0.007

Journal of Tropical Ecology (2004) **20**:705–708. Copyright © 2004 Cambridge University Press
DOI: 10.1017/S0266467404001695 Printed in the United Kingdom

SHORT COMMUNICATION

Myrmecochory in the Zingiberaceae: seed removal of *Globba franciscii* and *G. propinqua* by ants (Hymenoptera – Formicidae) in rain forests on Borneo

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(*Accepted 3 February 2004*)

Key Words: ant-dispersal, aril, diaspores, dispersal distances, elaiosome, morphology, mutualism, Malaysia, rain-forest herb, seed dispersal

The Old-World tropics encompass one of the floristically richest zones of the world and some of the hot spots of ant diversity. This results in a large variety of ecological interactions between both groups. One of them is the phenomenon of myrmecochory, seed dispersal by ants, which is also well known from temperate forests (Gorb & Gorb 2003, Ulbrich 1919), and which is most prominent in sclerophyll shrublands of Australia and southern Africa (Andersen 1988). Beattie (1983), who reviewed the distribution of ant-dispersed plants (at least 80 plant families worldwide) proposed that species richness and abundance of myrmecochores and diaspore-dispersing ants increases with decreasing latitude and thus predicted a greater variety of ant-dispersal systems in the tropics. However, up to now, few tropical myrmecochores have been described (Horvitz 1981, Horvitz & Schemske 1986), especially in the palaeotropics (Kaufmann *et al.* 2001). Here we report myrmecochory in two species of rain-forest herb of the Zingiberaceae, give the first evidence for seed dispersal by ants in this plant family and present a list of seed-dispersing ant species. An important benefit of myrmecochory is the dispersal distance of the ant-transported seeds (Andersen 1988), that has been found to be positively correlated with ant size (Gomez & Espadaler 1998a, Pudlo *et al.* 1980). In this study, we checked whether this correlation is also true for the conditions of the tropical rain forest, where *Globba* plants occur.

Bornean *Globba* (Zingiberaceae) species are plants of the primary rain forest usually found in moist, shady places along streams and waterfalls. The slender herbs are 0.5–1 m high, with delicate small, yellow, white or violet inflorescences and flowers on the top of the leafy shoots. *Globba* species produce fruits infrequently but often reproduce vegetatively by bulbils or vegetative miniature plantlets (Larsen *et al.* 1999, Smith 1996). Their inflorescences often point downwards or are pendulous (Weber 1995), which may hint towards myrmecochory, as many ant-dispersed plant species have limp fruit stalks that facilitate the collection of seeds by ants (Ulbrich 1919).

We studied two species: *Globba franciscii* Ridl. and *G. propinqua* Ridl. Seeds of both species are embedded in a fruit capsule including a mean of 13 diaspores in *G. propinqua* (SD = 5.83, n = 20) and 33 diaspores in *G. franciscii* (SD = 7.33, n = 6) (photographs of plants ants and seeds can be obtained at: http://www.antbase.de/myrmecochory.htm). Fruiting occurs over a long period as several capsules may form on one shoot while the plant is still flowering. When fruits are ripe, the capsule bursts open to present the seeds. As commonly occurs in the Zingiberaceae, the seeds of *Globba* have an aril, a fleshy appendage that partially encloses the seed and attaches to the seed coat at the micropylar region (Liao & Wu 2000). Aril cells are usually rich in lipids and also contain proteins, starch grains and other polysaccharides (Liao & Wu 2000).

Field work was conducted from January to March 2000 and from February to March 2001 in the Kinabalu National Park (N 6°2′, E 116°42′) and in the Tawau Hills Park (N 4°23′, E 117°53′), both in Sabah, Malaysia (see also Smith 1996). We observed seed handling by ants under natural conditions and experimentally studied removal of seeds. In each of the experiments (n = 46) we presented 10 seeds of one of the examined *Globba* species

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Table 1. Ant species that removed seeds of *Globba franciscii* and *G. propinqua* during our experiments and all other observations (pooled). The mean tibia length of ant species, number of removed seeds, mean transport distances, standard deviations of transport distances (SD), and number of measured seed transports (N) are provided. Species in bold contribute to the regression analysis (Figure 1). Direct observations of feeding on the seed arils are marked with X. Subfamilies are coded as follows: Dol = Dolichoderinae, For = Formicinae, Myr = Myrmicinae and Pon = Ponerinae.

Species	Subfamily	Tibia length of minors (mm)	No. of removed seeds	Mean distance of seed transport (± SD) (cm)	N	Feeding on aril (direct obs.)
***Dolichoderus* sp. 1**	Dol	2.0	10	10 ± 0	9	X
Dolichoderus sp. 2	Dol	1.0	9	–	0	X
***Camponotus (Colobopsis)* sp. 1**	For	2.1	14	48.8 ± 2.5	10	X
Camponotus (Colobopsis) sp. 2	For	–	4	6 ± 0	4	X
***Camponotus gigas* Latreille**	For	7.3	5	> 437 ± 346	5	–
***Camponotus* sp. 3**	For	3.2	9	170 ± 0	3	–
***Oecophylla smaragdina* Fabricius**	For	3.6	27	> 500	5	–
***Paratrechina* sp.**	For	0.9	15	72 ± 5.35	15	–
***Polyrhachis* sp. 1**	For	3.8	44	184 ± 174	27	X
Polyrhachis sp. 2	For	–	10	7 ± 4.2	4	X
***Crematogaster inflata* Smith**	Myr	1.1	10	6.8 ± 2.3	6	X
***Lophomyrmex bedoti* Emery**	Myr	0.3	18	11 ± 1.7	9	X
Pheidole aristotelis Forel	Myr	0.4	2	–	0	–
***Pheidole quadrensis* Forel**	Myr	0.8	13	40 ± 0	7	X
***Pheidole cariniceps* Eguchi**	Myr	0.6	9	20 ± 10	4	–
Pheidole sp. 1	Myr	–	10	10 ± 0	4	X
***Pheidologeton* affinis Jerdon**	Myr	0.6	5	35 ± 21	4	–
Pheidologeton pygmaeus Emery	Myr	–	2	–	–	–
***Pheidologeton* sp. 1**	Myr	0.8	16	99 ± 65	16	X
***Diacamma* cf. *rugosum* Le Guillou**	Pon	3.5	18	193 ± 144	6	–
***Leptogenys* sp. 1**	Pon	2.1	1	150 ± 0	1	–
***Leptogenys* sp. 2**	Pon	2.1	10	150 ± 70.7	2	–
***Odontoponera* cf. *transversa* Smith**	Pon	2.3	66	105 ± 15.1	11	–

on a small wooden tray (10 × 10 cm) on the forest floor to attract terrestrial ant species. Seed depots were randomly placed along walking trails with a minimum distance of 15 m between them, so that each seed pile constituted an independent sample. The behaviour of the ants towards the seeds was observed and we recorded the number of seeds they removed within 1 h. Seed transport distances of different ant species were noted as beeline over ground. In only two of the observed 152 cases were seeds dropped to the ground before ants reached their nests, however, in some cases we lost the foragers after several metres. Ants were collected with forceps and stored in vials with 85% alcohol. Determination to subfamilies took place according to the key of Bolton (1994), then specimens were assigned to morphospecies that could partly be identified at species level. Many ant species show positive allometry for leg size with body mass and longer leg sizes (or tibia lengths) are an indicator for better mobility of the species (Kaspari & Weiser 1999). To obtain mean tibia lengths ten worker ants of most of the observed ant species were measured using a Wild M5A binocular scope (Wild Ltd., Switzerland). Statistical analyses were performed using the STATISTICA 6.1 package (Statsoft, Inc. 2003. Tulsa, USA, http://www.statsoft.com).

In both *Globba* species examined the fleshy aril formed a large elaiosome (ant fruit) that served as food for ants and allowed them to handle the seed easily. Generally, ants removed seeds from trays rapidly after their encounter and transported them directly back to their nests. However, one species (*Camponotus* (*Colobopsis*) sp. 2) fed on the seed arils and also transported separate aril pieces into the nest, but mostly without taking away seeds from trays. In total, in 11 experiments with *Globba propinqua*, 77 seeds were removed by seven ant species (removal rate = 7 seeds h^{-1}, n = 11, SD = 4), while in 35 samples with *Globba franciscii* 228 seeds were removed by 17 species of ants (mean removal rate = 6.51 seeds h^{-1}; n = 35, SD = 3.7). The removal rates for the two species of *Globba* did not differ statistically (Mann–Whitney U-test, U = 174, Z = 0.49, $P > 0.05$).

Altogether, we observed 23 species of ant from 12 genera and 4 subfamilies that transported the seeds (or fed on the seed arils) of these two *Globba* species (see Table 1). We noted Formicinae, Dolichoderinae and Myrmicinae and also mainly carnivorous species such as Ponerinae. Ant species that removed seeds in our experiments comprised ground-living as well as predominantly arboreal species that were recorded near the base of tree trunks where they descended to the ground. Only one species, *Polyrhachis* sp. 2, a widely distributed arboreal ant, was observed to remove seeds directly from the dehisced fruit capsules. Dispersal distances achieved by this ant were notably long and reached more than 800 cm. However, we lost most individuals of arboreal species before they reached their destination.

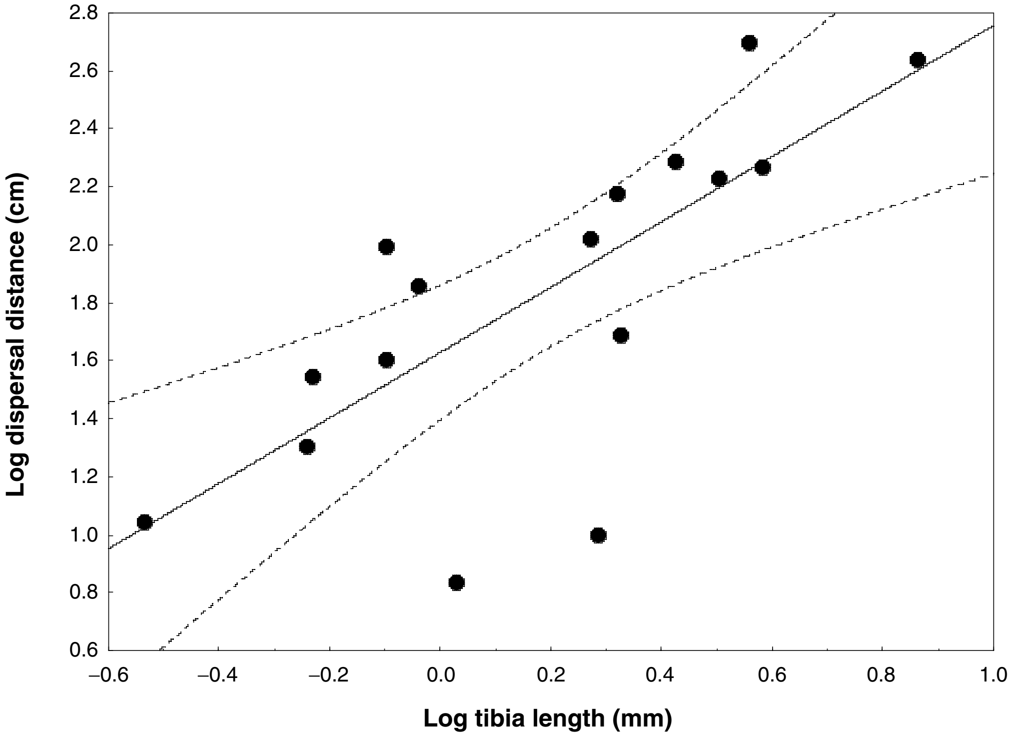

Figure 1. Relationship between logarithm of tibia lengths of ant species that transported seeds and logarithm of their dispersal distances. A linear regression line is shown, together with its 95% confidence interval (linear regression equation: $Y = 1.63 + 1.13\ X$, $F(1,15) = 17.1$; adjusted $r^2 = 0.50$, $P < 0.001$).

Our measurements of mean tibia lengths of the transporting ant species ranged from 0.3 to 7.3 mm ($n = 19$, median = 2.1). Logarithms of dispersal distances were significantly correlated with logarithms of tibia lengths of the transporting ant species ($n = 17$, $r = 0.73$, $P < 0.001$, Figure 1). The median dispersal distance of all seeds was 55 cm ($n = 132$, range 4–800 cm, mean = 112 cm, SD = 143). Though in most species (including tiny *Pheidole*) single workers removed seeds, in some ant species, e.g. *Paratrechina*, cooperative seed transport was performed by several workers.

Among the forest herbs that occur in tropical Asia, the Zingiberaceae are an especially rich group with about 1000 species (Larsen *et al.* 1999). As they flower near to or directly at the ground and do not possess specialized dispersal mechanisms except arillate seeds, animals may play an important role as their potential seed dispersal vectors. Here we show for the first time that the seed aril in *Globba* indeed functions as an elaiosome and that myrmecochory can serve as a mechanism of seed dispersal in the Zingiberaceae. Seed collecting behaviour of ants in the Palaeotropics has already been observed in ant-gardens on the giant bamboo, *Gigantochloa scortechinii*, in West Malaysia (Kaufmann *et al.* 2001). However, diaspores of the vascular epiphytes that had been tested in that study had no elaiosomes and the ants' carrying behaviour was only released by chemical cues, not by food rewards (Kaufmann *et al.* 2001). Our experimental results in *G. propinqua* and *G. franciscii* are consistent with occasional observations of arillate seed dispersal by ants in *G. pendula* Roxb. and in other species of ginger (e.g. *Zingiber pseudopungens* R. M. Smith) (M. Pfeiffer, unpublished data) and demonstrate that ant-dispersal due to elaiosomes is a potential mechanism of seed distribution in the Old World tropics.

Mean observed seed dispersal distance of *Globba* spp. was 112 cm, about the global mean distance of myrmecochorous dispersal of 96 cm ($n = 2524$; range 0.01–77 m) (Gomez & Espadaler 1998b). As we have shown, dispersal distances were significantly correlated with tibia lengths of the transporting ant species: as larger ant species have larger foraging ranges, they are able to transport seeds over longer distances. Our results agree with those of Gomez & Espadaler (1998a), however, these authors showed that seed dispersal distances of ant species are also significantly influenced by their nest distances and nest densities; and as larger ants have lower nest densities than smaller ant species, their seed dispersal distances are longer (see also Andersen 1988).

In our study many of the larger ant species were partly arboreal and used trunk roads in the lower canopy to reach their foraging areas on the forest floor or in the lower vegetation. But most of those species have nests in or near the ground (Pfeiffer & Linsenmair 2000, M. Pfeiffer *pers. obs.*), so discarded seeds will end up in the soil.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit (EPU, Malaysia) for research permission and Sabah Parks for providing logistic help. We are grateful to Alim Biun, Sabah Parks, for the determination of the plants, to Katsuyuki Eguchi, Kagoshima University, for the identification of the *Pheidole* specimens and to Konstans Wells and Njikoha Ebigbo, both University of Ulm, for commenting an earlier draft of this paper.

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RESEARCH ARTICLES BELONGING TO CHAPTER 7

Wells K, Pfeiffer M, Lakim MB, Linsenmair KE (2004) Use of arboreal and terrestrial space by a small mammal community in a tropical rainforest in Borneo, Malaysia. *Journal of Biogeography* 31:641-652

Wells K, Pfeiffer M, bin Lakim M, Linsenmair KE (2004) Arboreal spacing patterns of the large pencil-tailed tree mouse, *Chiropodomys major* (Muridae), in a rainforest in Sabah, Malaysia. *Ecotropica* 10:15-22

Wells K, Lakim MB, Pfeiffer M (2006) Nest sites of rodents and treeshrews in Borneo. *Ecotropica* 12:141-149

Journal of Biogeography (*J. Biogeogr.*) (2004) **31**, 641–652

ORIGINAL ARTICLE

Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia

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ABSTRACT

Aim Small mammals were live-trapped in a primary rain forest to evaluate the relative distribution of species to each other and to microhabitat properties on the ground and in the canopy.

Location Kinabalu National Park in Borneo, Sabah, Malaysia.

Methods Seven trapping sessions were conducted along two grids with 31 trap points at distances of 20 m on the ground and in the lower canopy at an average height of 13.5 m.

Results Species diversity and abundance of small mammals proved to be high: 20 species of the families Muridae, Sciuridae, Tupaiidae, Hystricidae, Viverridae and Lorisidae were trapped, with murids being dominant in both habitat layers. The terrestrial community was significantly more diverse with 16 captured species (Shannon–Wiener's diversity index $H'_{\mathrm{terr}} = 2.47$), while 11 species were trapped in the canopy ($H'_{\mathrm{arb}} = 1.59$). The Whitehead's rat, *Maxomys whiteheadi*, and the red spiny rat, *Maxomys surifer*, dominated the terrestrial community whereas the large pencil-tailed tree mouse, *Chiropodomys major*, was by far the most abundant species in the canopy. Other abundant species of the canopy community, the dark-tailed tree rat, *Niviventer cremoriventer*, and the lesser treeshrew, *Tupaia minor*, were also abundant on the ground, and there was no clear boundary between arboreal and terrestrial species occurrences.

Main conclusions As most species were not confined to specific microhabitats or habitat layers, species seemed to rely on resources not necessarily restricted to certain microhabitats or habitat layers, and separation of species probably resulted mainly from a species' concentrated activity in a preferred microhabitat rather than from principal adaptations to certain habitats. Ecological segregation was stronger in the more diverse terrestrial community, though microhabitat selection was generally not sufficient to explain the co-occurrences of species and the variability between local species assemblages. Constraints on small mammal foraging efficiency in the three-dimensional more complex canopy may be responsible for the similarity of microhabitat use of all common arboreal species. Community composition was characterized by mobile species with low persistence rates, resulting in a high degree of variability in local species assemblages with similar turnover rates in both habitats.

Keywords

Canopy, community dynamics, ecological separation, habitat segregation, microhabitat use, niche overlap, species turnover, tropical biodiversity, Muridae, Tupaia.

INTRODUCTION

Today's knowledge about the impact of small mammals on rain forest ecosystems is sparse, but small mammal communities in various tropical forests were implicated as considerable ecological forces due to their seed and seedling consumption (e.g. Asquith *et al.*, 1997; Struhsaker, 1997; Adler & Kestell, 1998; Guariguata *et al.*, 2000). Especially because of species impoverishment and community alteration resulting from habitat loss and fragmentation of tropical rain forests (Soulé *et al.*, 1992; Laidlaw, 2000), it is becoming crucial to understand the coexistence patterns and roles of native species in their ecosystems and their ability to cope with recent habitat changes. In particular, many small mammal species are suited for the exploitation of heterogeneous and patchy environments and are able to deal with changing habitat conditions. Basically characterized by their high mobility and homoiothermic physiology, enhancing their wide geographic distribution, their relative small size favours habitat segregation on various spatial and temporal scales, thus providing one of the bases for species differentiation and coexistence. This coexistence in species-rich communities has led to an increased effort to link ecosystem and community ecology to understand the effects of interacting small mammal species on ecosystem functioning and stability (see Jones & Lawton, 1995; Naeem & Li, 1997; Schwartz *et al.*, 2000), considering their diversity as well as the population dynamics of interacting species (e.g. Brown *et al.*, 2000; Ernest & Brown, 2001).

However, little is known about habitat utilization and segregation of small mammals in tropical forest communities, although their exceptional high species richness and unique taxonomic composition compared to temperate communities is emphasized (Bourliere, 1989). This sluggish progress in our knowledge may be mainly a consequence of the difficulties connected with conducting studies in the rain forest environment, especially as most species are highly cryptic in their appearance and behaviour. Another difficulty is vertical forest stratification, with an easy observable increase in habitat complexity towards the canopy. In both Neotropical and Paleotropical rain forest sites, arboreal small mammal communities are estimated to comprise nearly as many or even more species than terrestrial communities (Harrison, 1962; Emmons *et al.*, 1983; Kays & Allison, 2001). This rich arboreal fauna has been attributed to affluent food resources, particularly the abundant fruit crop, and to a structurally more complex habitat (Fleming, 1979; August, 1983). However, systematic and intensive trapping in the true canopy (above 10 m height) has been attempted only during the last decade, revealing distinct small mammal communities in terrestrial and arboreal habitats in various rain forest sites (Malcolm, 1995; Zubaid & Ariffin, 1997; Maklarin, 1998; Malcolm & Ray, 2000). Recently, food intake of species in different habitat layers has been specifically investigated in a Neotropical rain forest by analysing stable isotopes (Mauffrey & Catzeflis, 2003).

The canopy is the most productive rain forest layer and the more demanding habitat both in terms of the wider variability and larger fluctuations of climate conditions and structure, which requires adaptations for climbing or jumping in this complex three-dimensional space. However, the occurrence and abundance patterns of arboreal and terrestrial species may be linked by factors such as fruit resources, as terrestrial species also profit from canopy fruits once they have fallen to the ground. For example, Fleming (1973) and August (1983) both found that small mammal richness on the ground increased more than arboreal richness as forests increased in vertical complexity, and therewith also in productivity. Changing environmental factors may alter habitat use and abundance patterns of terrestrial small mammal communities: their populations were observed to vary seasonally in tropical forests with distinct climate seasons and fruiting patterns (e.g. Langham, 1983; Rabinowitz & Nottingham, 1989). However, little is known to what extend arboreal and terrestrial small mammal communities differ in terms of habitat segregation and demographic patterns. The great diversity of tropical trees creates abundant variation in canopy structure and resources for foraging, predator avoidance and nesting, and theory suggests that these features should enhance community diversity and specialization in this environment (MacArthur *et al.*, 1966; August, 1983), while the apparently scarce and unpredictable occurrence of some of these rain forest resources should relieve habitat segregations in all habitat layers. Nevertheless, up to date there is a lack of knowledge on how these conditions may influence species assemblages in different terrestrial and arboreal habitats.

To examine whether diversity, microhabitat use and population demography differ between arboreal and terrestrial small mammal assemblages, we compared assemblages of small mammals in a primary rain forest habitat on the ground and in the lower canopy.

MATERIALS AND METHODS

Study area

The 754 km^2 Kinabalu National Park is located in Sabah (Malaysia), in the North of Borneo (Fig. 1). The Kinabalu area is mostly covered with tropical montane rain forest (37%) and lowland rain forest (35%) and contains more than 4000 vascular plant species (Beaman & Beaman, 1990). Lim & Muul (1978) estimated the number of mammal species as about 100, nearly half of all mammalian species recorded for Borneo. The dipterocarp forest – structurally distinct from forests elsewhere in the tropics – is characterized by large numbers of emergent trees, usually growing with tree crowns separated from each other. The interconnected and light-screening canopy occurs much lower at heights between 10 and 40 m.

Our study area was located in a lowland rain forest between 800 and 900 m above sea level near the village of Poring Hot Spring. The forest site comprised a primary forest, although the area was affected by anthropogenic disturbances. The

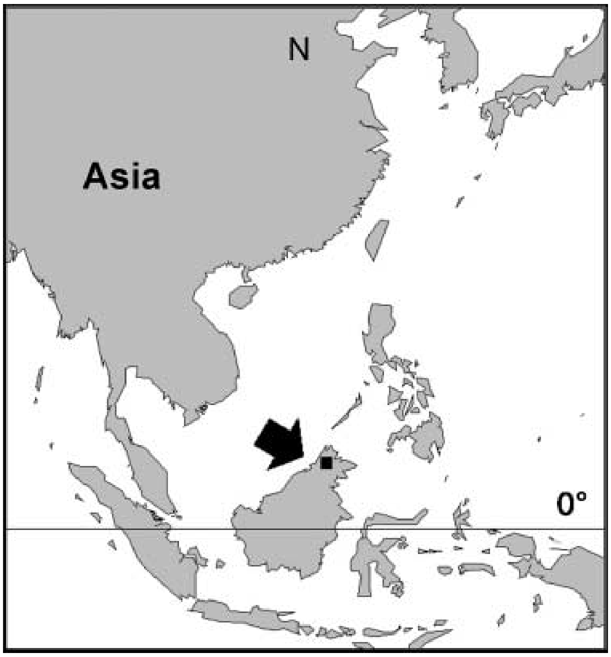

Figure 1 Map of South East Asia. The Kinabalu National Park (arrow) is located in Sabah, northern Borneo and surrounds Kinabalu (4.101 m, 6°5′ N, 116°33′ E), the highest mountain of this area.

increasing attraction of a nearby established canopy walkway system as well as illegal hunting activity led to some degree of wildlife disturbance in the park. However, these influences were assumed to affect mainly larger mammals with no obvious impact on the studied species, given the fact that there were no hidden secondary effects via altered predator–prey interactions.

Trapping design

We set up two sampling grids separated by *c.* 200 m (grids were on either side of a steep ditch). Each grid had 31 trap points that were separated by 20 m, but the distribution of points differed in the two areas due to topographic constraints. Grid 1 comprised six rows with 4, 4, 5, 6, 6 and 6 trap stations each, and covered an area of *c.* 0.8 ha. Grid 2 comprised eight rows with 5, 4, 5, 4, 4, 3, 3 and 3 trap stations each, covering *c.* 0.78 ha (note that these estimates do not include a boundary area). At each grid point we placed one terrestrial and one arboreal trap, at heights between 6 and 25 m (averaged 13.5 m). Trees were climbed initially using slings as 'foot belts', and subsequently by conventional single rope climbing equipment.

We used locally produced wire mesh live traps (280 mm × 140 mm × 140 mm and some bigger traps measuring 350 mm × 140 mm × 140 mm), covered with plastic sheet for rain protection. Arboreal traps were fixed with wire on horizontal branches near trunks. Traps were baited with ripe bananas, checked every morning and rebaited immediately after captures or after 4 days. Each sampling period lasted for 16 consecutive days. Grids were sampled seven times from March to September 2001. The traps were baited and left open for 4 days prior to trapping activity. The entire time of our study was characterized by a relatively constant climate with little rainfall (Wells, 2002).

Handling of animals and data gathering

Species identification was based on Payne *et al.* (1985) and comparisons with specimens of the museum collection of Sabah Parks' Headquarters, Kundasang, Malaysia, where voucher specimens were deposited. The captured animals were anaesthetized with diethyl ether prior to marking and measuring and released on the ground near the station of capture immediately following data collection. We marked animals with a subcutaneously placed transponder (AEG), which allowed a permanent identification with no obvious restriction of animals' locomotion and behaviour.

Habitat characterization

The vegetation structure of every trap station ('microhabitat') was assessed using 11 habitat variables. We assessed the understorey foliage density (1) using a 'profile board' technique (see Malcolm & Ray, 2000). The visibility of a 2-m plastic pole with alternating red and yellow 10-cm segments placed near the ground traps was scored from 2 and 5 m distances in six different directions (starting at the northern direction) determined with a compass. The sum of the number of segments covered by foliage was used as a score for understorey density. The diameter at breast height (DBH) of the tree (2) with the arboreal trap and the distances to the five nearest trees (DBH $\geq$ 10 cm) (3) were measured. To evaluate tree sizes and their distribution we used a simple 'thumb relascope' method: a 2-cm-broad plastic block was held in a constant distance from the left eye by the stretched right arm. The number of visible trees (DBH $>$ 10 cm) (4) around the grid point with a DBH extending beyond the focused plastic piece was used as a score. Further, we scored the proximity and sizes of logs (5) near the ground traps on a scale from 0 to 3 (0: no log in a distance of $d < 5$ m; 1: small logs ($<$ 20 m long) in 0.5 m $< d <$ 5 m; 2: one log $>$20 m long and/or numerous small logs in 0.5 m $< d <$ 5 m away from the trap; 3: one log $>$ 20 m and/or numerous small logs less than 0.5 m away from the trap). The extent of branch connections from an arboreal trap tree to its neighbouring trees (6) was counted with a score range from 0 (no branch contact) to 3 (more than or equal to five branches interconnected). The crown density in the vicinity of about 10 m around the arboreal trap (7, 8) was visually evaluated and scored on a scale from 0 to 3 (0: $<$ 30% of the surrounding area covered by foliage; 1: 30–60%; 2: 60–80%; 3: 80% covered) separately for the foliage above and below the trap. The roughness of the bark of the trap tree (9) was evaluated on a scale from 0 (nearly smooth) to 3 (rough). We also recorded the presence/absence of the extended gaps

(10) (gap of at least 10 m diameter with the crown of the tree with a trap station exposed to the open space) and the presence of lianas in trap trees (11).

Data analysis

Single traps and trapping periods were characterized by microhabitat variables (assessed in the vicinity of a trap station) and local small mammal assemblages, for which spatial and/or temporal variability were analysed in respect to the presence and abundances of different species. Data matrices of species assemblages were based on the number of captured individuals (captures), recorded separately for terrestrial and arboreal captures.

For α-diversity estimates, we used the parametric Fisher's α, the nonparametric Shannon–Wiener H', and Simpson's D indices (for discussion see, e.g. Colwell & Coddington, 1994). The diversity of the arboreal and terrestrial habitats was compared with a randomization test (10,000 runs). All diversity calculations were done with the software packages BIODIVERSITY PRO (McAleece, 1997), SPECIES DIVERSITY AND RICHNESS 2.3 (Henderson & Seaby, 1998) and PROGRAM FOR ECOLOGICAL METHODOLOGY, 2nd edition (Kenney & Krebs, 1998). In order to reduce the set of microhabitat variables to two descriptors describing as much variability as possible, we applied a factor analysis (FA), using STATISTICA 6.0 (StatSoft, 2001). The probability of capture of a species at certain trap points was related to microhabitat features derived from FA using multiple logistic regression. Microhabitat use for the most common species within the arboreal and terrestrial communities was also analysed for preferences of trap points described by single, not yet FA-lumped microhabitat variables. For this purpose, habitat profiles of all common species (trapped at least at five different traps, considering any individual only once per trap station) were developed using the means of microhabitat variables of the respective trap points. These habitat profiles were compared to the means of microhabitat variables from all trap stations separately for arboreal and terrestrial traps. Though these profiles included replicates of individuals if trapped at different stations, we assumed that an individual's activity in different microhabitats reflects also the microhabitat range used by this species and thus these profiles are representative of species specific microhabitat utilization. Univariate analysis of variability (ANOVA) of microhabitat use and the averaged microhabitat variables was done for the parametric habitat variables 'tree size distribution', 'understorey density', 'tree distances', and 'tree diameters'. We applied a Kruskal–Wallis test to the nonparametric habitat variables 'log abundance', 'bark', 'tree connection', 'liana', 'canopy density', and 'gap'. To analyse how far not only single species but also entire species assemblages differed in their preference for certain microhabitats, we described the variability in species composition at different trap points by detrended correspondence analysis (DCA), using the software PC-ORD 4.0 (McCune & Mefford, 1999), and tested for any correlation of DCA axes with the corresponding microhabitat parameters (single variables and factors extracted from FA).

We estimated whether pairs of species avoided using the same trap or overlapped in trap use with a simple approximation (see Shanker, 2001): the probability of captures of two common species at particular traps was used to calculate the expected number of traps that would capture both species during the entire trapping effort (except for *Lenothrix canus* and *Tupaia gracilis*, which were only trapped in area 1):

$$\exp = a \times b/n$$

where exp is the expected number of traps that capture both species, a the total number of traps capturing species 1, b the total number of traps capturing species 2, and n the total number of traps ($n_1 = 31$ or $n_{1+2} = 62$).

Calculations were done for 14 pairs of species where the calculated number exceeded the critical value of the chi-square distribution for $P < 0.05$ [χ^2 (d.f. $= 1) = 3.84$], with species occurring at a minimum of nine different traps. Microhabitat utilizations were only analysed for frequently trapped species of murids and tupaiids. Comparisons within and across these two phylogenetic groups seemed to be justified due to overlaps in resource utilizations and trap responses of some of these species (Wells, pers. obs.).

RESULTS

Small mammal survey

A total trapping effort of 6.745 trap nights during the trapping periods yielded 644 captures of 118 individuals, thus comprising a total trap success of about 9.5%. Twenty different species were trapped from the six families Muridae, Sciuridae, Hystricidae, Tupaiidae, Viverridae and Lorisidae (Table 1). Trap success differed significantly between the arboreal and terrestrial habitats: 384 (59%) captures were recorded for the canopy and 260 (41%) captures for the ground ($\chi^2 = 23.88$, $P < 0.01$). Murids were most abundant with a total of 533 captures (82%) and seven out of 20 species.

Eleven species were trapped in the canopy and 16 species on the ground. *Chiropodomys major* was by far the most abundant species in the canopy, comprising 54% of all arboreal captures. *Niviventer cremoriventer* and *Tupaia minor* were common not only in the canopy (ranks two and three in rank abundance distribution) but also on the ground. *Maxomys whiteheadi* (24% of all terrestrial captures), *Maxomys surifer* (13%), *N. cremoriventer* (9%), *T. gracilis* (9%) and *Leopoldamys sabanus* (7%) were the most common species on the ground. Out of the common ($n \geq 6$ captures) species *C. major*, *L. canus* and *T. minor* were recorded significantly more often in the arboreal habitat [χ^2 (d.f. $= 1) > 7$, $P < 0.05$ for all species], while the trap success for *M. surifer*, *M. whiteheadi* and *T. gracilis* was significantly higher in the terrestrial habitat [χ^2 (d.f. $= 1) > 4$, $P < 0.05$ for all species). *Niviventer cremoriventer*, although relatively common (12 captures in total), showed no significant preference for either the arboreal or

Table 1 Twenty species of small mammals from six different families were trapped, for which the number of captured individuals (total number of captures in parenthesis) in the arboreal and terrestrial habitats are given below

	Species name		Captures		
	English	Scientific	Arboreal	Terrestrial	Total
Rodentia					
Muridae	Large pencil-tailed tree mouse	*Chiropodomys major*	34	2	34 (285)
	Whitehead's rat	*Maxomys whiteheadi*	–	16	16 (72)
	Red spiny rat	*Maxomys surifer*	–	9	9 (34)
	Dark-tailed tree rat	*Niviventer cremoriventer*	6	6	8 (80)
	Grey tree rat	*Lenothrix canus*	6	–	6 (15)
	Long-tailed giant rat	*Leopoldamys sabanus*	1	5	5 (39)
	Small spiny rat	*Maxomys baeodon*	–	2	2 (8)
Sciuridae	Low's squirrel	*Sundasciurus lowii*	–	4	4 (8)
	Horse-tailed squirrel	*Sundasciurus hippurus*	2	3	3 (11)
	Brooke's squirrel	*Sundasciurus brookei*	2	1	3 (3)
	Plantain squirrel	*Callosciurus notatus*	1	–	1 (1)
	Red-cheeked flying squirrel	*Hylopetes spadiceus*	1	–	1 (1)
Hystricidae	Long-tailed porcupine	*Trichys fasciculate*	–	1	1 (1)
Scandentia					
Tupaidae	Lesser treeshrew	*Tupaia minor*	8	4	9 (40)
	Slender treeshrew	*Tupaia gracilis*	–	6	6 (24)
	Plain treeshrew	*Tupaia longipes*	–	4	4 (6)
	Large treeshrew	*Tupaia tana*	–	3	3 (11)
	Pentail treeshrew	*Ptilocercus lowii*	1	–	1 (1)
Carnivora					
Viverridae	Short-tailed mongoose	*Herpestes brachyurus*	–	1	1 (1)
Primates					
Lorisidae	Slow lori	*Nycticebus coucang*	1	1	1 (3)
		Total	63	68	118 (644)

terrestrial habitat. Simpson's measure of evenness showed a less strict pattern of dominance for the arboreal sample ($E1/D_{\mathrm{arb}} = 0.28$) than for the terrestrial community ($E1/D_{\mathrm{terr}} = 0.59$). Terrestrial diversity for the entire sample was significantly higher than arboreal diversity ($P < 0.05$ by randomization test for all diversity measures) with a Shannon–Wiener index of $H'_{\mathrm{terr}} = 2.47$ for the terrestrial community and $H'_{\mathrm{arb}} = 1.59$ for the arboreal sample.

Use of microhabitat by species

The distribution of microhabitat features at trap stations resulting from FA (eigenvalues: $\lambda_1 = 1.99$, $\lambda_2 = 1.84$) revealed that the means of factor 1, mainly negatively described by 'tree distances'/'tree size distribution', significantly differed between the trapping sites (t-test, $P < 0.01$) with bigger averaged tree sizes in area 2. There was no significant difference in the means of factor 2, which was positively associated with 'tree connection'/'liana'. Nevertheless, the two areas were generally featuring similar microhabitats. To portray patterns of habitat occupancy by different species, the presence of the most frequently trapped species were plotted in the multivariate space derived from the FA of microhabitat variables, and the outer points were connected to obtain a 'minimum multivariate habitat space' occupied by the species of interest (Fig. 2). Although these plots did not directly assess the microhabitat characteristics related to capture frequency, it can be seen on the first sight that the microhabitat where species seemed to forage overlapped considerably for most species. For example, the microhabitat used by *C. major* comprised nearly the entire sampled arboreal microhabitat. Utilization of the overall available microhabitat space was less intense by other species, but there was still a high overlap for other common arboreal species as well as for terrestrial murids and tupaids. However, the probability of captures along the microhabitat gradient described by the FA factors differed significantly for some species as revealed by multiple logistic regression analysis (Table 2). Univariate analysis of habitat profiles revealed further specific microhabitat use as shown in Table 3. There was no evident distinction between any specific arboreal microhabitat use and the overall sampled habitat analysed by discriminant analysis of the FA factors [Wilks' $\lambda = 0.95$, F (8, 566) = 1.7, $P > 0.05$]. In contrast, microhabitat use of various terrestrial species and the overall sampled habitat described by the two FA factors were significantly distinct [discriminant analysis, Wilks' $\lambda = 0.75$, F (22, 444) = 3.1, $P < 0.01$].

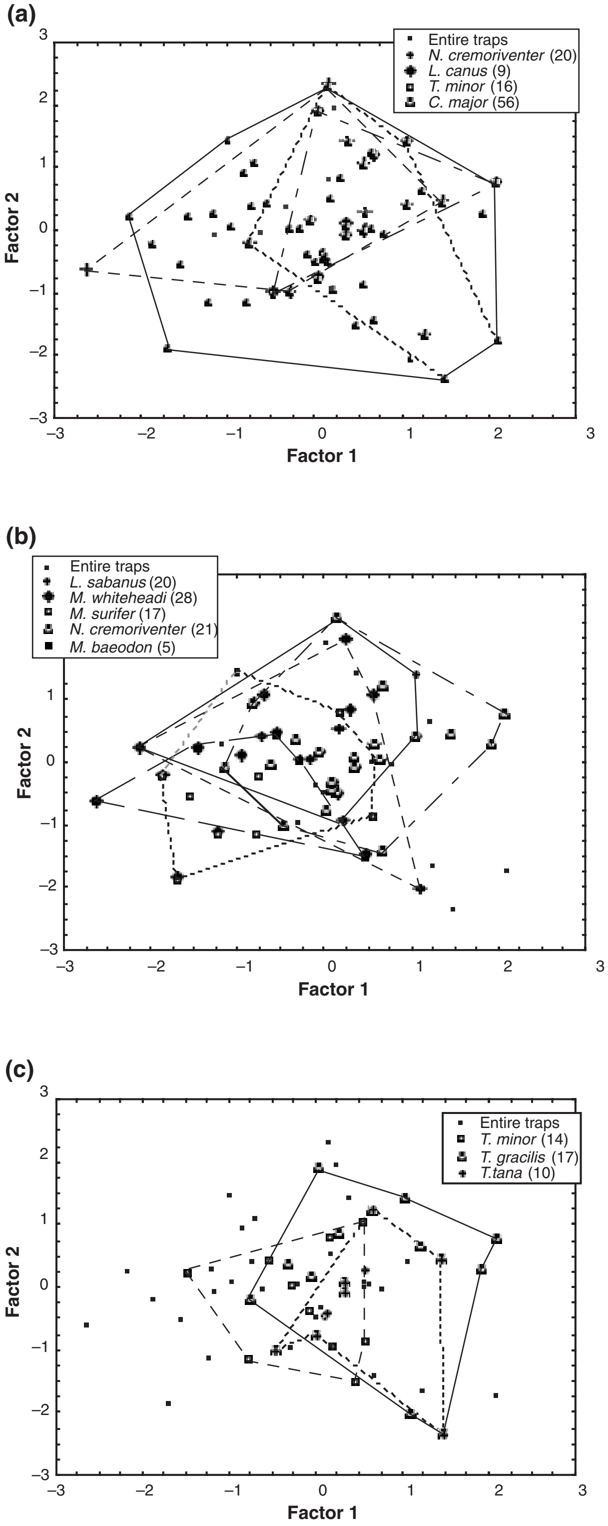

Figure 2 Distribution of all traps and traps used by (a) common arboreal species, (b) terrestrial murids and (c) terrestrial tupaids in the multivariate space derived from FA. Outermost points are connected to obtain a 'minimum multivariate habitat space', and numbers of specifically used traps are indicated in parentheses (for interpretation of factors see text).

Table 2 Species-specific microhabitat preferences evaluated by multiple logistic regression analysis [for all χ^2 (d.f. = 2) > 6, $P < 0.05$], based on a correlation between capture probability and FA factors (microhabitat). A positive correlation with factor 1 is interpreted as more surrounding trees with smaller tree distances near points of captures, while a positive association with factor 2 stands for an increase in tree connectivity by branches and lianas

Species	Factor 1: 'Tree distances/ tree size distribution'	Factor 2: 'Tree connection/liana'
Arboreal		
Niviventer cremoriventer	−	+
Lenothrix canus	−	+
Terrestrial		
Maxomys whiteheadi	+	None
Maxomys surifer	−	−
Tupaia gracilis	+	None

Table 3 Univariate analysis of habitat profiles (ANOVA for 'tree size distribution' and Kruskal–Wallis for 'gap' and 'liana') revealed significant microhabitat preferences compared to the overall sampled microhabitat as shown below (for all tests $P < 0.05$; a positive correlation stands either for an increase in surrounding trees and/or bigger trees, or an increase in the presence of gaps or liana, respectively, at point of capture).

Variable	Species	Correlation
Arboreal		
Tree size distribution	*T. minor*	−
Gap	*C. major*, *N. cremoriventer*, *L. canus*	−
Liana	*C. major*, *N. cremoriventer*, *L. canus*	−
Terrestrial		
Tree size distribution	*L. sabanus*, *M. whiteheadi*, *M. baeodon*	+
Gap	*L. sabanus*, *N. cremoriventer*, *S. lowii*, *T. longipes*	−
	M. whiteheadi, *T. tana*	+
Liana	*L. sabanus*, *M. whiteheadi*, *T. minor*	−
	T. gracilis	+

Use of microhabitat by species assemblages

The comparison of species composition by DCA [terrestrial: eigenvalues $\lambda_1 = 0.64$, $\lambda_2 = 0.50$, total variance ('inertia') $\upsilon_{\mathrm{terr}} = 5.01$; arboreal: $\lambda_1 = 0.50$, $\lambda_2 = 0.28$, $\upsilon_{\mathrm{arb}} = 2.45$] and microhabitat characteristics at different trap points revealed that microhabitat properties were more influential on terrestrial than on arboreal species assemblages (Fig. 3). The variability of arboreal species assemblages at different trap points was significantly correlated with the parameters 'tree connection' and 'bark' (Spearman's *R*, $P < 0.05$ for both variables). The influence of microhabitat variability on local species assemblages was more obvious for terrestrial assemblages: the variability in species assemblages on the ground was

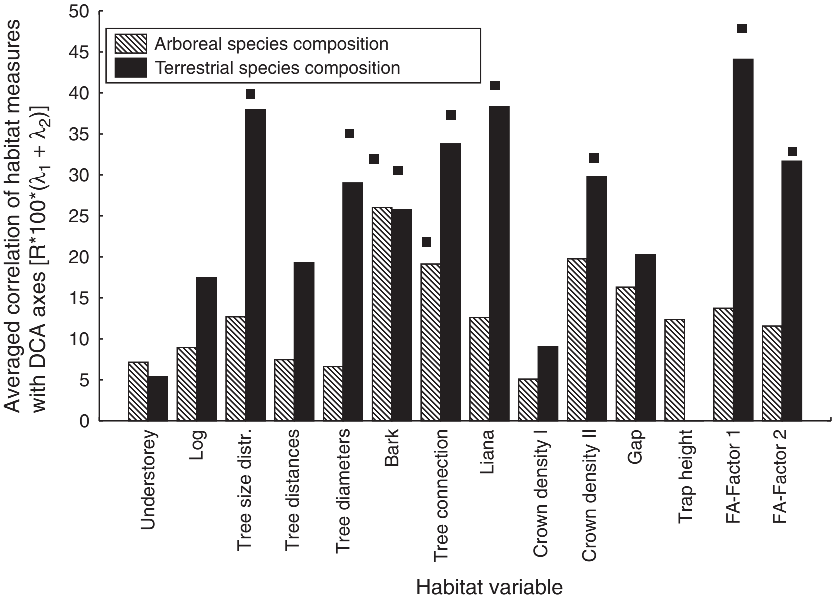

Figure 3 The impact of microhabitat variables and FA factors on arboreal and terrestrial species assemblages. The size of bars represents the averaged Spearman correlation ($R \times 100$) with the sum of all three axes derived from DCA of species assemblages. Microhabitat parameters showing a significant correlation with any axis are marked with ■.

Table 4 Persistence of marked individuals of common species expressed as the number of trapping sessions between first and last capture

Species	Number of individuals	Number of trapping sessions							
		Single	1	2	3	4	5	6	Mean
Chiropodomys major	34	18	–	7	–	7	–	2	1.59
Lenothrix canus	6	5	–	1	–	–	–	–	0.33
Niviventer cremoriventer	8	4	–	2	1	–	–	1	0.88
Maxomys whiteheadi	16	10	–	6	–	–	–	–	0.75
Maxomys surifer	8	5	–	1	–	2	–	–	1.25
Leopoldamys sabanus	5	2	–	2	–	1	–	–	1.60
Tupaia minor	9	5	–	1	–	2	–	1	1.78
Tupaia gracilis	6	5	–	1	–	–	–	–	0.33
Total	92								1.21

significantly correlated with the variables 'tree size distribution', 'tree diameter', 'bark', 'tree connection', 'liana' and 'tree crown density below' (Spearman's R, $P < 0.05$ for all variables). There was also a significant correlation between the terrestrial species assemblages and the variability in the overall sampled microhabitat described by the two factors derived from FA ($P < 0.05$).

Occurrence of species at particular traps

There was a significant higher overlap in trap use by *N. cremoriventer* and *L. canus* in arboreal traps in area 1 ($\chi^2 = 4.08$, d.f. = 1, $P < 0.05$) than expected by chance. In the terrestrial community, there was a significant overlap in trap use by *N. cremoriventer* and *Tupaia tana* ($\chi^2 = 3.85$, d.f. = 1, $P < 0.05$). For all other comparisons, there was no difference in the observed and expected number of traps with captures of a pair of species, suggesting that there was neither a strong overlap nor any separation in the pattern of space use by most species.

Persistence rates and resemblance of local species assemblages

The persistence of marked individuals was low (Table 4). The recapture rate in consecutive trapping sessions of individuals recorded within the first five trapping sessions was 51 ± 12% with no evident difference for arboreal and terrestrial species. Even in the last three trapping sessions, at least 43% of all captured individuals were trapped the first time. Overall persistence rates (Pr) were significantly biased by sex and age [Kruskal–Wallis H (2, $N = 90$) = 14.95, $P < 0.05$]: the average persistence of males (Pr = 1.41 trapping sessions, $n = 41$) was lower than for females (Pr = 2.73, $n = 19$), and immature individuals revealed the lowest averaged persistence rate (Pr = 0.67, $n = 39$).

The averaged species turnover estimated with the Sørensen index was the same in both habitats with $S_{\mathrm{terr}} = 0.55 \pm 0.14$ and $S_{\mathrm{arb}} = 0.55 \pm 0.15$.

DISCUSSION

Species survey and diversity

The sampled study site contained a rich small mammal fauna with 16 species sampled on the ground and 11 species recorded in the canopy. Concerning the number of trapped species, it should be considered that apart from the low and short-dated sampling effort, sampling was quite selective by using a single type of trap and bait, and by trapping during a dry season. Differences in the ability to trap between dry and wet seasons have been recorded for several tropical forest sites, and higher trap success in wet seasons has been mainly contributed to changes in resource abundance and shifts in habitat use (Rudd, 1979; Woodman *et al.*, 1995; Adler & Lambert, 1997). However, the number of 16 terrestrial species exceeds the number of approximately 10 ground-living species reported for tropical forest sites elsewhere in tropical Asia (Langham, 1983; Kemper & Bell, 1985). In a primary rain forest on peninsular Malaysia, Zubaid & Ariffin (1997) trapped 17 species in both layers, while Maklarin (1998) trapped altogether 13 species in a plot near our study area. As reported for most other rain forest sites (e.g. Emmons, 1995), murids were most dominant in terms of species number (seven) and abundances both in the arboreal and terrestrial habitat. Sciuridae and Tupaiidae were represented both with five species, but sciurids were trapped in low numbers, so that all common species were either rats or tree shrews. Interestingly, both groups contain morphologically juxtaposed species that are not necessarily closely related (probably due to repeated sea level changes in glacial periods that allowed species immigration from time to time; see Ruedas & Kirsch, 1997; Han *et al.*, 2000). Further, similar patterns of habitat utilizations and correlations in trap response can be observed for species of both taxa (Wells, pers. obs.), although they are ecologically well separated by their circadian activity periods.

Most species were not strictly confined to a single habitat layer: *N. cremoriventer* and *T. minor* used both habitats intensively, and most of the species recorded in the canopy were also trapped on the ground or are known to occur there from literature (e.g. *L. canus*, Maklarin, 1998) or personal observations (e.g. *C. major*, Wells, pers. obs.). On the other hand, some species that we caught at the ground had also been observed to climb (e.g. *L. sabanus*, Lim, 1970; *T. tana*, Emmons & Biun, 1991). However, not all species able to climb can be found in the true/upper canopy, and whereas murids can be found in all habitat layers, tupaiids seemed to have diversified mostly in the terrestrial and scansorial habitats. This poses the questions where to place the boundary between different foraging zones, and why more species were recorded on the ground – a result that is not *per se* self-evident if considering the structurally more complex arboreal habitat and the resources provided in the canopy. Previous distinction between a ground community separated from a scansorial/arboreal community (see August, 1983; Woodman *et al.*, 1995; Adler *et al.*, 1999) might be biased by a lack of sampling in the true canopy. However, Malcolm (1995) and Malcolm & Ray (2000) recorded distinct arboreal and terrestrial species compositions in an Amazonian and a Central African forest. The aspect of community zonation becomes even more complex if the dipterocarp canopy structure of SE Asian rain forests is considered.

Our study was designed to sample arboreal mammals in the lower canopy, below 30 m, a stratum that allows horizontal travelling for non-volant mammals due to its frequent interconnection of tree crowns by branches and lianas, whereas the upper layer is non-continuous and horizontal movements are thus confined to gliding or volant species. Larger mammals like monkeys and civets have been observed to travel in the lower canopy and climb up into food trees from there (Emmons, 1995), but it is not clear whether this strategy is also applicable for small species for which the environmental perception and the ability to cross gaps is confined to a more narrow scale. The changing stratificational constraints in vegetation structure might lead to additional shifts in community composition along the vertical axis. Squirrels, such as the giant squirrel, *Ratufa affinis*, and Prevost's squirrel, *Callosciurus prevostii*, can be frequently observed in the upper canopy strata, and might be more effective in exploiting these layers. Further, the fauna in Borneo includes a considerable number of gliding species that are well adapted to cross gaps in the upper canopy: the flying lemur, *Cynocephalus variegatus*, and 12 species of flying squirrels (Petauristinae), of which we trapped only one (the number of species in Kinabalu NP is unknown). Although the community compositions in the upper strata are not yet sufficiently examined, it is obvious that the zonation exceeds a simple dichotomy of arboreal and terrestrial distinct communities. The species mentioned above indicate that particularly the more variable conditions in the upper canopy strata require some adaptations. However, as most of the trapped species were not necessarily confined to either the ground or canopy, it seems that trade-offs in foraging efficiency or locomotion rather than principal adaptations determine which strata are used by these species at a given time.

Most small mammal species seem to rely on a wide variety of food items (e.g. Langham, 1983; Emmons, 2000) and, intuitively, it can be assumed that food resources for non-volant small mammals, although not necessarily more abundant, are easily accessible on the ground. Terrestrial foraging species (and also species descending only shortly to the ground for easier progression) might thus profit from a variety of primary resources growing on the forest floor, fallen fruits and other items from the canopy, and easier catchable animal prey. Particularly foraging on animal prey appears to be more constraining in the canopy, where the proportionally most frugivorous species occur. Even mammalian groups with a carnivorous origin such as the Viverridae contain canopy living species that feed mainly on fruits (Emmons *et al.*, 1983; Payne *et al.*, 1985). However, easier accessible food resources on the ground may be also indicated by abundance patterns rather than the number of species. In both habitats we found some common and many rare species, a pattern that is known from other studies (e.g. Walker & Rabinowitz, 1992; Chandrasekar & Sunquist, 1996; Wu *et al.*, 1996). But the proportion of rarely captured species (≤2 captures during the entire sampling) was 63% in the canopy and 31% on the ground. Only four species were frequently trapped in the canopy, of which *N. cremoriventer* and *T. minor* were also abundant on the ground. In contrast, seven species of murids and tupaids can be considered as common on the forest floor, and the diversity indices confirmed a significant higher terrestrial diversity of small mammals. Interestingly, the most abundant species on the ground were all rats with a similar appearance: *M. whiteheadi* (head–body length, HB = 119 mm; weight, $m = 52$ g), *M. surifer* (HB = 167 mm, $m = 161$ g) and *L. sabanus* (HB = 228 mm, $m = 364$ g) differed in body size, but all three species were found to feed on plant material and arthropods (Wells, 2002), thus showing no obvious specializations on certain food items. Further, *L. sabanus* and *M. surifer* showed the same coloration and were observed to use similar ground nests (pers. obs.). In contrast, the majority of rare species such as *Ptilocercus lowii*, *Nycticebus coucang* and *Trichys fasciculata* were on the first sight in both the arboreal and terrestrial habitat taxonomically and morphologically the most distinct species. Although not much is known about any particular diet composition and abundance of food items, especially the tropical richness of arthropods may indicate that food resources of insectivorous (or omnivorous) species in the tropics seem to be large enough to support syntopic species with similar food requirements – while niche overlap in co-occurring small insectivorous mammals in temperate regions appears to be much lower (e.g. Cotgrave & Stockley, 1994).

Microhabitat and space use

The overlap in habitat use was high in all common species with widely overlapping ranges of microhabitats. Furthermore, the species occurrences in traps showed no deviation from a stochastic distribution for most of the common species, supporting the hypothesis that habitat segregation did not occur by the restriction of species to distinct microhabitats. However, these first assessments do not sufficiently reflect the activity of species inside the used space, which are the specific preferences of particular subsites of the overall utilized habitat. Even if the same habitat space is used by similar species, there might be some segregation due to preferences of particular sites. The habitat profiles revealed that some environmental variables were significantly related with the specific frequencies of captures (though these microhabitat preferences might not necessarily result from a direct response to these parameters *per se*). Remarkably, 'tree size distribution' was most influential on arboreal as well as terrestrial habitat use as revealed by logistic regression analysis and by ANOVA. An influence of the canopy structure and an impact of large trees were also found by Kemper & Bell (1985) and by Emmons & Gentry (1983). However, Adler (2000) rather found that the composition of tree species, partly representing resource availability, was more influential than canopy structure on the demography of a neotropical spiny rat (*Proechimys*).

Although the investigated species showed some specific microhabitat use, a segregation of co-existing species on this scale was not the feasible. In the canopy, *N. cremoriventer* and *L. canus* both revealed the same affinities for traps with sufficient tree connections and a high score for the parameter 'tree size distribution'. Further, all common arboreal rats showed some relations to gaps and lianas. On the ground, *L. sabanus*, *M. whiteheadi* and *M. baeodon* all displayed a significant preference for traps with a relatively high score on the tree size distribution. Thus, it seems that a considerable number of mainly generalistic species favour similar microhabitats, which can be regarded as particularly suitable for locomotion, foraging or avoiding predators, thus indicating an increased probability of using similar or even the same food resources.

There is a noteworthy difference concerning the relationship of habitat variability and community compositions for arboreal and terrestrial species assemblages. While multivariate tests failed to strongly discriminate arboreal species assemblages along a microhabitat gradient, the more variable species compositions on the ground displayed significant correlations to several microhabitat variables as well as to the multivariate factors derived from FA, although the ground was conspicuously less heterogeneous than the sampled canopy layer.

This increase in microhabitat segregation towards the more homogenous ground necessitates to ask whether beside habitat structure, the presence of other small mammal species is influential in determining specific habitat use and local population abundances. Indeed, the observation of differential occupancy of habitat types by a single species and the apparent interaction with co-existing species has led to the suggestion that interspecific competition may serve to enhance habitat selection (e.g. Dueser & Brown, 1980; Kelt *et al.*, 1995; Valone & Brown, 1995). However, it also has been argued that interspecific effects on patterns of habitat choice are weak (e.g. Connell, 1983; Shanker, 2001), and in several small mammal communities segregation on the microhabitat dimension between common species was found to be slight (e.g. Chandrasekar & Sunquist, 1996; Shanker, 2001). Particularly in rain forests, fluctuations in limited and unreliable food resources are probably influential on species occurrences, and each species can be assumed to respond uniquely to any combination of environmental changes that may alter the relative competitive status of each species in the community (e.g. Frost *et al.*, 1995; Morris *et al.*, 2000).

In this context, it is of interest to consider the high turnover rates in our study: high fluctuations in the presence of species and individual activity led to considerable variability in local species assemblages. However, we cannot generally rule out that trap shyness may have led to a misinterpretation of our capture data as high turn over rates. Trap shyness has been reported from other rodent studies: individuals that had been trapped once, avoided traps in further life (e.g. Perrin *et al.*, 1992). But there are two reasons against this argumentation: (1) persistence rates were significantly biased by sex and age and (2) the high percentage (43%) of individuals that were trapped for the first time in the last three trapping sessions; both these reasons indicate population fluctuations, rather than trap shyness, because otherwise rodents would have had extremely high abundances for which we found no further indications. So we exclude trap shyness as a major factor for the high fluctuations of individuals.

The relatively low persistence rates are in accordance with results from other studies in the tropics, where individuals of small mammals appeared to persist only for a few months (Mares & Ernest, 1995; Woodman *et al.*, 1995). However, the causes are not clear and can be multi-sided. First, predation is likely to have some impact on the high turnover rates, and a high predation pressure may also influence the activity and mobility of species as a trade-off between anti-predator behaviour versus foraging and mating behaviour (see Hanski *et al.*, 2001). But low persistence due to predator-induced mortality cannot hold for all of the reported dynamics, as turnover rates were much higher than reproductive replacement during this relatively short course of sampling. Disappearance of individuals could be a result of movement and migration, necessary, e.g. to forage for scattered food resources or to leave the natal area in search of a mate. Presumably, the highest dispersal rates can be expected for immatures, as confirmed by our results. Remarkably, persistence and species turnover rates were the same on the ground and in the canopy, suggesting that species mobility and fluctuations in both strata may be driven by similar mechanisms. So, even within this single type of rain forest and the relatively short observation period patterns of species occurrences did not display any static level. A stronger microhabitat segregation on the ground appeared to be related to a more diverse community of mainly opportunistic small mammals, but fluctuations appeared to be the same in both habitats.

ACKNOWLEDGMENTS

We are grateful to the Economic Planning Unit of Malaysia for a research permit and to Dr Jamili Nais, Assistant Director of Sabah Parks, for permission to conduct this study in Kinabalu National Park. For various kinds of support and hospitality in the field we are thankful to the staff of Sabah Parks and the people in Poring, particularly Fred Tu and Alim Biun. We thank several anonymous reviewers for helpful comments on drafts of the manuscript. Financial support was kindly provided by the Arthur-von-Gwinner Stiftung. We also thank the 'Deutsche Forschungsgemeinschaft' (DFG) for granting the infrastructure for our activities within the framework of the 'DFG Schwerpunktprogramm Mechanismen der Aufrechterhaltung tropischer Diversität'.

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BIOSKETCHES

Konstans Wells is currently working on his PhD at the University of Ulm, Germany, about the effects of habitat degradation on demography and genetic variability of rats and tree shrews in Sabah, Malaysia. This work was conducted as part of his MSc thesis at the University of Würzburg, Germany, supervised by K.E. Linsenmair and M. Pfeiffer.

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ECOTROPICA 10: 15–22, 2004

ARBOREAL SPACING PATTERNS OF THE LARGE PENCIL-TAILED TREE MOUSE, *CHIROPODOMYS MAJOR* (MURIDAE), IN A RAINFOREST IN SABAH, MALAYSIA

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Abstract. Spacing patterns and demography of the arboreal large pencil-tailed tree mouse, *Chiropodomys major* Thomas, 1893, was examined by live trapping in the subcanopy of a primary rainforest in Sabah, Malaysia over five months. Traps were placed on the ground and in the canopy at an average height of 13.5 m, where tree crowns are well interconnected. *C. major*, which was mainly active in the canopy, was by far the most frequently trapped species in this habitat layer. Home range areas were calculated as 90 % core convex polygons for 18 individuals, for which ≥ 5 recaptures (mean of 13) were obtained. Home range size varied between sexes, with males generally having larger home ranges (2971 ± 1104 m^2) than females (1580 ± 780 m^2). Home range areas of both sexes overlapped with those of consexuals and with individuals of the opposite sex, suggesting that individuals do not maintain exclusive ranges. *C. major* used nearly the entire examined arboreal habitat space, but analysis of microhabitat preferences revealed that the activity of this arboreal rodent was positively associated with an increase in tree connections and the presence of lianas and gaps. *Accepted 16 June 2003.*

Key words: *home range estimate, microhabitat use, persistence, rodents, tropical rainforest canopy.*

INTRODUCTION

Many rodent species have proved valuable as models for studies of spacing patterns. Basically, observed space-use and the resulting mating systems have been examined by evaluating resource availability and spacing of the opposite sex (e.g., Ims 1988, Ostfeld 1990). While some species appear to maintain territories exclusive of consexuals (e.g., Ims 1988, Lambin & Krebs 1991), other species show considerable intrasexual overlap in the utilised space (e.g., Ims 1988, Adler *et al.* 1997). However, most studies were conducted on terrestrial species in relatively species-poor communities in temperate regions, whereas only a few studies dealt with home ranges of tropical rat species in species-rich communities (e.g., Sanderson & Sanderson 1964, Adler *et al.* 1997, Sommer 1997, Lindsey *et al.* 1999). Even less is known about arboreal species (Kays & Allison 2001), for which studies on spacing patterns and mating systems are confined to a few larger species such as primates (e.g., Sterck *et al.* 1997, Di Bitetti 2001, Eberle & Kappeler 2002), squirrels (Wauters & Dhondt 1990, Saiful *et al.* 2001), kinkajous (Procyonidae) (Julien-Laferriere 1993, Kays & Gittleman 2001), or marsupials (e.g., Soderquist 1995, Lindenmayer 1997, McCarthy & Lindenmayer 1998). However, trapping in the true canopy of tropical forests has shown that small mammals, particularly murids, are abundant dwellers of the canopy, living in diverse communities (Malcolm 1995, Zubaid & Ariffin 1997, Malcolm & Ray 2000).

Species foraging in the canopy clearly have to face differing environmental conditions compared with those confined to the ground, as the canopy is a more variable habitat both in terms of its three-dimensional complexity and structural heterogeneity as well as its more pronounced climatic fluctuations (e.g., Emmons 1995). Particularly the outstanding diversity of many of the evergreen, perhumid lowland rainforests, where several hundred tree species per hectare occur, with a considerable variety in growth forms and fruiting patterns (Newberry *et al.* 1992), should lead to a highly variable resource distribution both in space and time.

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The high floristic heterogeneity, and the resulting resource dispersion was found to influence the distribution and population demography of terrestrial spiny rats, *Proechimys*, in the Neotropics (Adler 1994, 2000). Resource abundance and its distribution was also reported as a major determinant of spacing patterns of some larger arboreal mammals (e.g., Lurz *et al.* 2000, Di Bitetti 2001, Kays & Gittleman 2001). Furthermore, locomotion in the canopy for non-volant and non-gliding species is necessarily confined to suitable pathways, which are prone to considerable changes due to the growth and breaking of branches. Thus the characteristics of tropical forest canopies, with their unique patterns of food abundance and variability in food availability, should be of major importance for the spacing of arboreal mammals, especially those relying on plant resources. Present knowledge of resource use and spacing patterns of arboreal mammals, particularly for small mammals, is very limited. As only a few species have been studied thoroughly, there is still a fundamental need for more data on arboreal spacing patterns in order to gain a less fragmented picture and to evaluate the impact of canopy features on foraging activity and social organization of these species.

In this paper, we describe observations on spacing patterns of the large pencil-tailed tree mouse, *Chiropodomys major* Thomas, 1893, an arboreal nocturnal species endemic to Borneo. These investigations were part of a study comparing the diversity and space use of arboreal and terrestrial small mammals (Wells *et al.*, accepted), in which *C. major* was the most frequently trapped species. There is little information on this genus of tree mouse, which consists of six known species (Musser 1979, Jenkins & Hill 1982, Wu & Deng 1984). All these mice occur in South-East Asian forest sites and are assumed to be mainly arboreal. Their feet are relatively short and broad, characterized by a semi-opposable hallux with a flat nail, an adaptation typical for a canopy dweller. Most information has been gathered on *C. gliroides* Blyth, 1856, a species found in various forest types throughout Indochina and the Sunda Shelf region (possessing the most extensive geographic range within the genus), which is mostly associated with bamboo stands. Females of this species are polyestrous. They have estrous periods of one day at intervals of only seven days and breed throughout the year, at least in Peninsular Malaysia (see Nowak 1991). However, very little is known of the biology of *C. major*, which is recorded only from a few localities in the northern part of Borneo (Musser 1979, Payne *et al.* 1985).

The aim of the present study was to assess the use of space by *C. major* in the subcanopy layer of a primary rainforest, investigating home ranges and microhabitat utilization of this species. Although the data represent a period of only half a year, our paper gives a first insight into the spacing of a little-known arboreal species.

STUDY AREA

Fieldwork was conducted in the primary lowland rainforest of Kinabalu National Park (754 km^2) in Sabah (Malaysia) in the north of Borneo. The majority of vegetation in Kinabalu National Park consists either of tropical montane rainforest (37 %) or lowland rainforest (35 %) (Kitayama 1992). The number of mammal species was estimated as about 100 (Lim & Muul 1978), nearly half of all species recorded for Borneo. Three species of tree mouse are known to occur on Borneo (*Chiropodomys major*, *C. gliroides*, *C. muroides*; Payne *et al.* 1985), as well as two species of the similar and probably closely related mice *Haeromys* sp. (see Musser & Newcomb 1983). The dipterocarp forest is characterized by its emergent trees (mainly Dipterocarpaceae and the legume *Koompassia*), rising up to heights of 50–70 m, well above the actual interconnected, multi-layered, and light-screening canopy that occurs at heights of between 10 and 40 m. The heterogeneous canopy structure is a result of the vast floral diversity of the Bornean rainforest: up to three hundred tree species can be found on a single hectare (Kitayama 1992, Newberry *et al.* 1992).

The study area was located in the lowland rainforest at an elevation of between 800 and 900 m near the village of Poring Hot Spring. This site comprised a basically undisturbed primary forest, though the area at large is not completely unaffected by anthropogenic disturbances. Poaching as well as touristic activities on a public canopy walkway system have affected the diversity of wildlife adversely. Probably these influences do not affect small species such as *C. major*, though unknown secondary effects such as predator-prey interactions cannot be excluded.

MATERIALS AND METHODS

Trapping design. Trapping was conducted within two sampling grids separated by a distance of approximately 200 m (and by a ravine). As our fieldwork also intended to compare small mammal assemblages on the ground and in the canopy, capture activity included both arboreal and ground traps. In each area 31 grid points were established. Grid points were separated by 20 m, but the distribution of points differed in the two areas due to topographic constraints. Grid 1 sampled approximately 0.80 ha, comprising 6 rows with 4, 4, 5, 6, 6, and 6 trap stations, respectively. Grid 2 comprised 8 rows with 5, 4, 5, 4, 4, 3, 3, and 3 trap stations, covering roughly 0.78 ha. At each grid point we placed one arboreal trap at a height between 6 m and 25 m (mean 13.5 m) and one ground trap. Trees were climbed initially using slings as 'foot belts', and after establishing a hoist line, conventional single rope climbing equipment was used. This method benefits from the little equipment required, a flexible choice of trees for trapping, and little damage or alteration to the canopy structure or tree bark.

We used locally produced wire mesh live-traps (28 cm × 14 cm × 14 cm, and some larger traps measuring 35 cm × 14 cm × 14 cm), equipped with a roof made from plastic sheet for protection from rain. Arboreal traps were fixed with wire on horizontal branches near trunks. Traps were baited with ripe bananas, checked every morning, and rebaited immediately after captures or after four days. Total trapping effort was 6445 trap-nights during 7 trapping sessions, each lasting for 16 consecutive days. Trapping sessions were conducted alternately in the two areas, with a break of approximately 20 days between trapping sessions in a single area.

Fieldwork was conducted from April to August 2001 during a dry period at this rainforest site. Though rainfall usually increases in Kinabalu Park from May to July (Kitayama 1992), the entire trapping period was characterized by a similar pattern of low rainfall (Wells 2002).

For each trap station, we estimated ten vegetation parameters. Tree sizes and their distribution were evaluated by a simple 'thumb relascope' method: a 2-cm-broad plastic block was held at a constant distance from the left eye by the stretched right arm. The number of trees visible (with a diameter at breast height, DBH, > 10 cm) when extending the plastic piece while focusing it was used as a score. Further, the DBH of the tree with the arboreal trap and the distances to the five nearest trees (DBH ≥ 10 cm) were measured. We assessed the understory foliage density using a 'profile board' technique (see Malcolm and Ray 2000): the visibility of a 2-m plastic pole with alternating red and yellow 10-cm segments placed near ground traps was scored from 2 and 5 m distances in six different directions determined with a compass (60° angles, starting from North). The number of segments covered by foliage was used as a score for understory density and summed for both distances. We also scored the proximity and sizes of logs near the ground traps on a scale from 3 to 0 (3: one log > 20 m long and/or numerous small logs (< 20 m) less than 0.5 m away from the trap; 2: logs of that size at a distance d of $0.5 < d < 5$ m away from the trap; 1: small logs at $d = 0.5 < d < 5$ m; 0: no log at $d < 5$ m). Close to the arboreal trap, the extent of branch connections of the tree to its neighbors was censused, with a score range from 3 (≥ 5 branches interconnected) to 0 (no branch contact to neighboring trees). Crown density in the vicinity of about 10 m around the arboreal trap was visually evaluated and scored on a scale from 3 to 0 (3: ≥ 80 % of the surrounding area covered by foliage; 2: 60–80 %; 1: 30–60 %; 0: < 30 % covered) both for the foliage above and below the trap. The bark of the trap tree was scored to evaluate the roughness on a scale from 3 (rough) to 0 (nearly smooth). We also recorded the presence/absence of extended gaps (gap of at least 10 m diameter with the crown of the trap station tree partially exposed to the open space) and the presence/absence of lianas in trap trees.

Handling of animals and data collection. Captured animals were anesthetized with diethyl ether before marking and measuring, and released near the station of capture immediately following data collection. We marked individuals with a subcutaneously placed transponder (Trovan, AEG), which allowed permanent and reliable identification and was relatively painless for the animal, leading to no obvious restriction of locomotion and behavior after release. All individuals were weighed and lengths of total body (front of nose to base of tail), tail, hind foot (excluding the nail), and anal-genital distance measured. Animals with scrotal testes or visible mammae were classified as adults, whereas all other individuals with no visible sex organs but non-juvenile pelage were classified as immatures.

A spool-and-line device was tested on four individuals of *Chiropodomys major* for locating nests, using quilting spools ('cocoon bobbins'; Danfield Ltd., Moss Industrial Estate, U.K.), which weighed approximately 1.7 g and contained 180 m of nylon thread. Spools were placed in a piece of shrinking tube (normally used in electric engineering) with the thread able to trail easily from inside the spool. Spools were applied to the back of anesthetized animals with glue (cyanoacrylate), and the end of the thread was tied to vegetation. Threads were followed the next day.

Data analysis. Home range analysis was performed by calculating the 90 % core convex polygon centered on the arithmetic mean based on individuals with five or more captures, with the computer package *TRACKER 1.1* (Camponotus AB & Radio Location Systems AB 1994). Individual home ranges were calculated for captures over the entire study, which was justified because of the relatively sedentary behavior of individuals for which sufficient captures were obtained (see results). Persistence rates were calculated as the number of trapping sessions between first and last capture of an individual. Further, we developed a habitat profile by comparing the cumulative means of habitat variables for traps where individuals were captured with the means of all trap locations, which represented the overall sampled habitat. To reduce any bias arising from philopatric behavior or trap affinity, individuals were considered only once for a single trap station. All statistical analyses were performed using STATISTICA 6.0 (Statsoft 2001).

RESULTS

Demography and home ranges. With 275 captures of 40 individuals, *Chiropodomys major* was by far the most frequently trapped species in the canopy. The same trapping effort on the ground resulted in captures of only two individuals of *C. major*. Other small mammal species trapped in the canopy (numbers of captures in parenthesis, total: 101) were the murids *Niviventer cremoriventer* (52), *Lenothrix canus* (15), *Leopoldamys sabanus* (1); the sciurids *Sundasciurus hippurus* (2), *S. brookei* (2), *Callosciurus notatus* (1), *Hylopetes spadiceus* (1); the tupaiids *Tupaia minor* (24), *Ptilocercus lowii* (1); and the lorisid *Nycticebus coucang* (2). In area 1, we trapped 22 individuals of *C. major* (9 males, 7 females, 3 immatures, 3 unidentified) 174 times, and there were 101 captures of 18 individuals (7 males, 7 females, 3 immatures, 1 unidentified) in area 2. Adult males weighed on average 41.4 ± 5.4 g (n = 16), while females weighed 38.4 ± 4.4 g (n = 14) with no significant differences between the sexes. However, males appeared to be slightly larger in head-body measurement (males: HB = 106.7 ± 3.6 mm (n = 12), females: HB = 99.6 ± 2.4 mm (n = 7); Mann-Whitney U-test, U = 16.5, $p < 0.05$).

No individual was trapped at both trapping sites, and maximum observed distance traveled was 113 m by a male. On two occasions, we trapped two individuals (an adult female with an immature, and the same female with an adult male) in a single trap.

The persistence rates of individuals were significantly biased by age (Mann-Whitney U-test, U = 42, $p < 0.05$): the average persistence rate P_r of adults (P_r = 2.88 trapping sessions, n = 16) was higher than that of immatures (P_r = 1.33, n = 6).

Single individuals were caught up to 11 times within a trapping session (mean 4.3 ± 2.8). All individuals with more than five captures in total persisted for an average of P_r = 4.22 ± 1.83 trapping sessions, significantly longer than the mean in the study area (Mann-Whitney U-test, U = 40.5, $p < 0.01$). We thus assumed that these individuals were resident and temporally coinciding in their presence, and calculated their home range areas from data of the entire study. Home range analysis included 18 individuals (7 males, 10 females, 1 immature. Fig. 1) with a total of 234 captures (mean 13 ± 6.2). The mean home range size for males varied from 1600 m^2 to 4600 m^2 (mean 2971 ± 1104 m^2) and was significantly larger than that for females (t-test, t = –3.06, $p < 0.01$), which varied from 200 m^2 to 2600 m^2 (mean 1580 ± 780 m^2). There was no correlation between home range size and the number of captures (Spearman, r = 0.23, p = n.s., 5–27 captures per individual). On average, home range overlap of consexuals was significantly larger in males than in females (male: 2.3 ± 0.5 individuals, female: 1.0 ± 0.7, Mann-Whitney U-test, U = 5.0, Z = –2.93, $p < 0.01$). Comparing intersexual overlap, we found that a male's home range overlapped on average those of 3.4 ± 1.3 females, while a female's home range overlapped those of 2.5 ± 1.0 males.

Trap and microhabitat use. Chiropodomys major was trapped in 56 out of 62 arboreal traps, thus was distributed throughout the sampled habitat space. However, comparing the habitat profile of *C. major* with the entire sampled habitat space revealed a significant impact of the presence of gaps and lianas on the trap success of trap stations. *C. major* was most frequently trapped at stations in the proximity of gaps (Mann-Whitney U-test, U = 522.5, Z = - 4.77, $p < 0.01$) and in traps on trees with lianas present (Mann-Whitney U-test, U = 170.0, Z = –4.22, $p < 0.01$). None of the parametric habitat parameters showed any significant differences between the estimated habitat profile of

C. major and the overall available habitat (t-test, $p > 0.6$, n.s. for all variables). There was no correlation between trap height and number of captured individuals or captures. The spool-and-line device was not the right size for normal behavior of *C. major*, as most individuals recognized the presence of the spool after recovering from anesthesia and tried to remove it. However, individuals with an attached spool were still able to climb, and four (of eight) threads were followed successfully. One individual nested in a tree hollow approximately four meters above the ground. Another individual had to move over the ground to reach its den inside the stump of a dead tree (approximately five meters above the ground), as there was no connection between the stump and the canopy. Two others descended into holes in the ground near tree roots and a log respectively.

DISCUSSION

Chiropodomys major was an abundant species in the subcanopy layer of the studied primary rainforest sites,

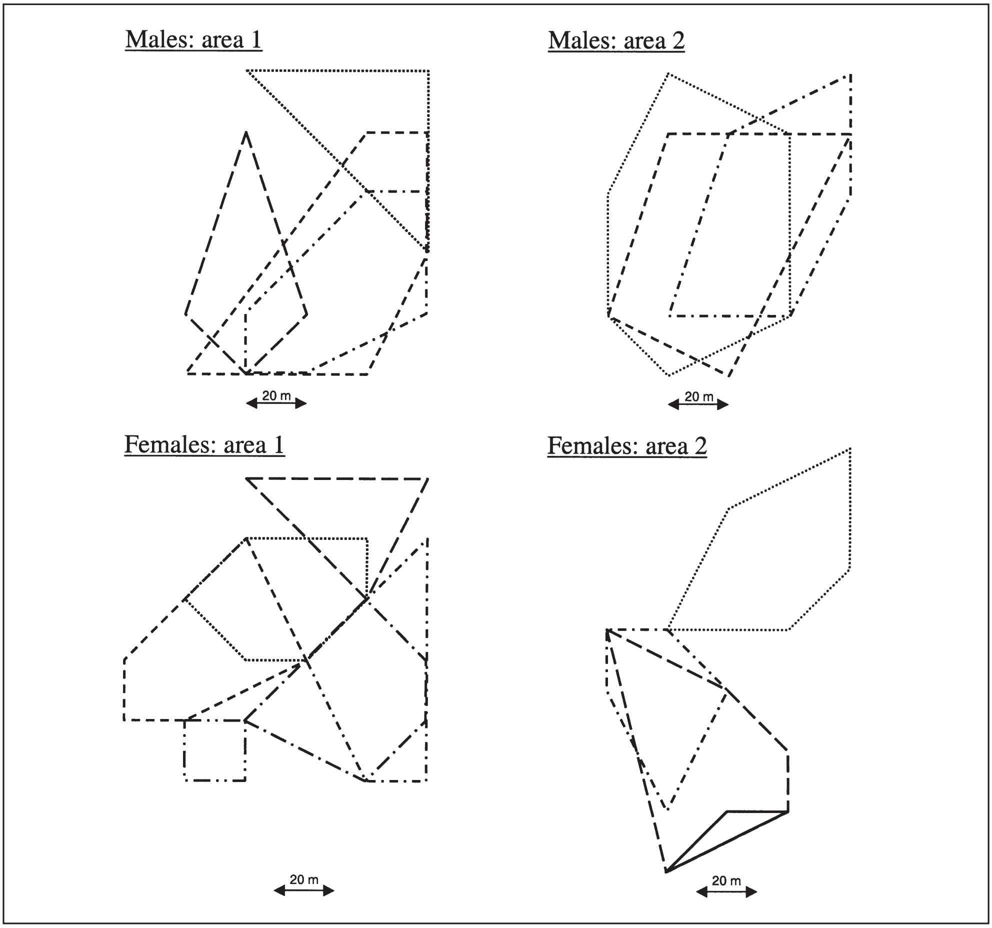

FIG. 1. 90 % core convex polygons representing home range areas utilized over the entire sampling period for all adult males and females. In area 1 we mapped four home ranges of males and six of females, in area 2 three home ranges of males and four of females.

using nearly the entire sampled habitat space. The relatively frequent captures and recaptures gave some insight into the spacing patterns and range use of this species, although it has to be considered that observations were limited to a single layer of the subcanopy in a rather complex three-dimensional habitat (see Risch & Brady 1996), and also by the spatial and temporal limitations of observations intrinsic to the live-trapping design. Of course, these point estimates of the presence of different individuals have to be evaluated carefully, and a more accurate concept of an individual's activity and its home range would necessitate the use of radio telemetry or other advanced techniques (Jones & Sherman 1983). However, a number of studies using both telemetry and trapping data on terrestrial species revealed similar patterns of space use when a sufficient number of captures was obtained over a short time (Jones & Sherman 1983, Lambin & Krebs 1991, Quin *et al.* 1992). Some authors suggest that live trapping is even a conservative approach, as movements of individuals appear to be more restricted when the spatial data are collected through trapping (Price *et al.* 1994, Szacki 1999). The home ranges presented here might be underestimates of the total sizes, as the sampling areas were not large enough to encompass complete home ranges of all individuals, and several ranges were along the edges of the grid area. Yet our data clearly show that ranges are overlapping and territories are not maintained. As our study is based on a mean of 13 observations per individual, and because we found no correlation between capture frequency and calculated territory size, we assume that our trapping data give an initial insight into the spatial activity patterns of individuals within the studied population of *C. major* during the sampled season. Home range estimates from the present data were mostly obtained for adult individuals (17 out of 18), while immature individuals seemed to remain for much shorter periods in the study area. Both sexes revealed considerable overlap with other individuals of both sexes, arguing against the defense of exclusive ranges. However, our data are based on a half-year study period during a dry period, and changing resource availability during the course of a year might lead to some shifts in home range use between seasons. For example, an arboreal trapping survey of 234 trap nights in the same area in December 2002 (beginning of the rainy season, more than one year after this study) included no captures of *C. major*, most probably due to differences in resource availability (K. Wells, unpublished). A lack of exclusive ranges was also reported for the Neotropical spiny rat *Proechimys*, for which Adler *et al.* (1997) suggested that food resources in the rainforest environment might be too scattered and unpredictable for efficient establishment of exclusive territories. This might also be the case for *C. major*, as this species also relied on plant resources, with most of its foraging activity in the heterogeneous canopy. There is a lack of knowledge of the vertical spacing of individuals, but the application of the spool-and-line device revealed that at least some nesting or hiding places are located near the ground, indicating that individuals frequently travel in the vertical dimension and even down to the ground. A presumably agile movement behavior of *C. major* in the canopy is also confirmed by the microhabitat utilization, as nearly the entire sampled habitat space was used. Though *C. major* preferred trapping points with an increased number of tree connections by branches and lianas, it was observed to drop down to lower foliage layers when there were no suitable branches to walk on (this drop-and-go strategy was also used for escape), a behavior that was not observed for larger rats such as *N. cremoriventer* or *L. canus* (pers. obs. K. Wells). Apparently, tree mice are the smallest non-volant mammalian species in the canopy (see Payne *et al.* 1985), a feature that should promote an agile movement on branches and vertical trunks.

The observed spacing patterns suggest that each adult can be expected to encounter several other individuals of both sexes in its foraging area. The locations of polygons showed no association between certain pairs of males and females, and the overlap patterns, with each individual overlapping with several others of the opposite sex, make a promiscuous mating system possible. Females revealed less overlap with individuals of the same sex than males. Assuming that female spacing is driven by the relatively high energy expenditure of reproduction and need for a sufficient resource supply (e.g., Emlen & Ohring 1977, Ostfeld 1985), competition for primary food resources might be reduced by avoiding too much female intrasexual overlap. However, it is not clear whether this concept – basically derived from temperate species – is accurate for a species residing in a tropical rainforest canopy. Too little is known about resource distribution and also about the expenses of locomotion in this habitat, and the ultimate reasons for any consexual overlap may range from tolerance due to a scattered and unpredictable resource dispersion up to an inefficiency of habitat defense due to the complex canopy structure. Furthermore, we need much more species-specific data on taxonomic, morphological, and physiological adaptations or constraints to properly evaluate spacing patterns and social organization of arboreal species. Since sympatric species in diverse small mammal communities in rainforests show a differing extent of arboreal activity and resource utilization along the vertical axis of the canopy habitat (e.g., Mauffrey & Catzeflis 2003), and also differ in their abundance patterns (Malcolm 1995), intensive comparisons of different species and sites would be of much value for a better understanding of arboreal adaptations and species distributions.

ACKNOWLEDGMENTS

We thank the Economic Planning Unit of Malaysia for a research permit and Dr. Jamili Nais, Assistant Director of Sabah Parks, for permission to conduct this study in Kinabalu National Park. The staff of Sabah Parks, particularly Fred Tu and Alim Biun, and the inhabitants of Poring provided various kinds of support and friendly hospitality in Malaysia. Prof. Elisabeth Kalko, Department of Experimental Ecology, University of Ulm, Prof. Jörg Ganzhorn, Institute of Zoology, University of Hamburg, and Dr. Pierre Charles-Dominique, Laboratoire d'Ecologie Générale MNHN, Centre National de la Recherche Scientifique, Brunoy gave constructive and helpful comments on the manuscript. Financial support was kindly provided by the Arthur-von-Gwinner Stiftung. We are also grateful to the 'Deutsche Forschungsgemeinschaft' (DFG) for granting the infrastructure for research activities in Malaysia.

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ECOTROPICA 12: 141–149, 2006

NEST SITES OF RODENTS AND TREESHREWS IN BORNEO

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Abstract. We used spool-and-line and radio-tracking to discover 83 nests of seven non-volant small mammal species in the tropical rainforest of Borneo. Terrestrial rats of the genus *Maxomys* (*M. rajah* and *M. surifer*), and the occasionally arboreal rat *Leopoldamys sabanus*, used mostly subterranean burrows, whereas the arboreal rat *Niviventer cremoriventer* utilized above-ground nests of plant fiber or leaves fixed on various branches. The scansorial squirrel *Sundasciurus lowii* nested both in tree cavities and in nests made of plant fiber. Treeshrews (*Tupaia tana* and *T. longipes*) used both subterranean and above-ground nesting sites. Nesting patterns were thus distinct among species, but revealed no apparent association between any nest type and features of the surrounding habitat such as vegetation density. Above-ground nests made of plant fibers were of similar size and construction for *S. lowii* and *T. tana*, and an individual of *M. rajah* was seen entering a burrow that had been previously occupied by *L. sabanus*, indicating that there is likely some interspecific overlap in nest sites. *Accepted 29 June 2006.*

Key words: *Muridae*, *nesting behavior*, *tree cavities*, *tropical rainforest*, *Tupaiidae*.

INTRODUCTION

As one makes one's bed, so must one lie in it, and nearly all species of small mammals require nests as denning sites, shelter, sleeping sites, or places to raise offspring (we use the term 'nest' for all types of nests/shelters/refuges because we were not able to distinguish between these uses). The architectural characteristics and location of nests are of key importance in many aspects of a small mammal's life. Nests must provide protection from predators and adverse climate (Kolbe & Janzen 2002). When resting or raising offspring, mammals may have altered metabolism and be less alert to counteract ambient influences. The available space inside a nest determines the number of individuals that can aggregate, and nest size might be chosen based on the inhabitants' social organization. Further, nest conditions can influence parasite prevalence and transmission, which in turn might determine host distribution patterns and frequency of nest switching (e.g., Roper *et al*. 2002, Krasnov *et al.* 2003). For species that depend on pre-existing structures such as tree cavities, distribution and population density may be limited by the availability of such cavities or woody debris. Human-caused forest changes, such as logging of tropical rainforests, may further reduce the availability of tree cavities and woody debris (e.g., Laurance 1990, Ganzhorn & Schmid 1998, DeWalt *et al*. 2003). Features of nest sites, including nest concealment, architecture, and accessibility to various predators, may affect the inhabitant differently under different habitat conditions. (e.g., Cooper & Francis 1998). Therefore, type and location of nest sites are likely to affect survival and reproductive success and may also play a role in structuring small mammal communities.

It can prove difficult to locate the nest sites of cryptic and little-known small mammals in rainforests, and, for most species, habitat types used for nesting and architecture of nests are unknown. However, spool-and-line tracking has improved our ability to locate nests (e.g., Miles *et al*. 1981, Boonstra & Craine 1986, Briani *et al*. 2001).

Furthermore, in Borneo, nests of treeshrews have been located and described by radio-tracking of various species (Emmons 2000), revealing distinctive nesting patterns among species. Conversely, the burrows of rodents, which are the most common species in terrestrial and arboreal small mammal assemblages on Borneo and elsewhere in the tropics (Bernard 2004; Wells *et al*. 2004a), have not yet been described.

Here we report on nest sites of seven common small mammal species from the families Muridae, Sciuridae, and Tupaiidae in a Bornean rainforest, for

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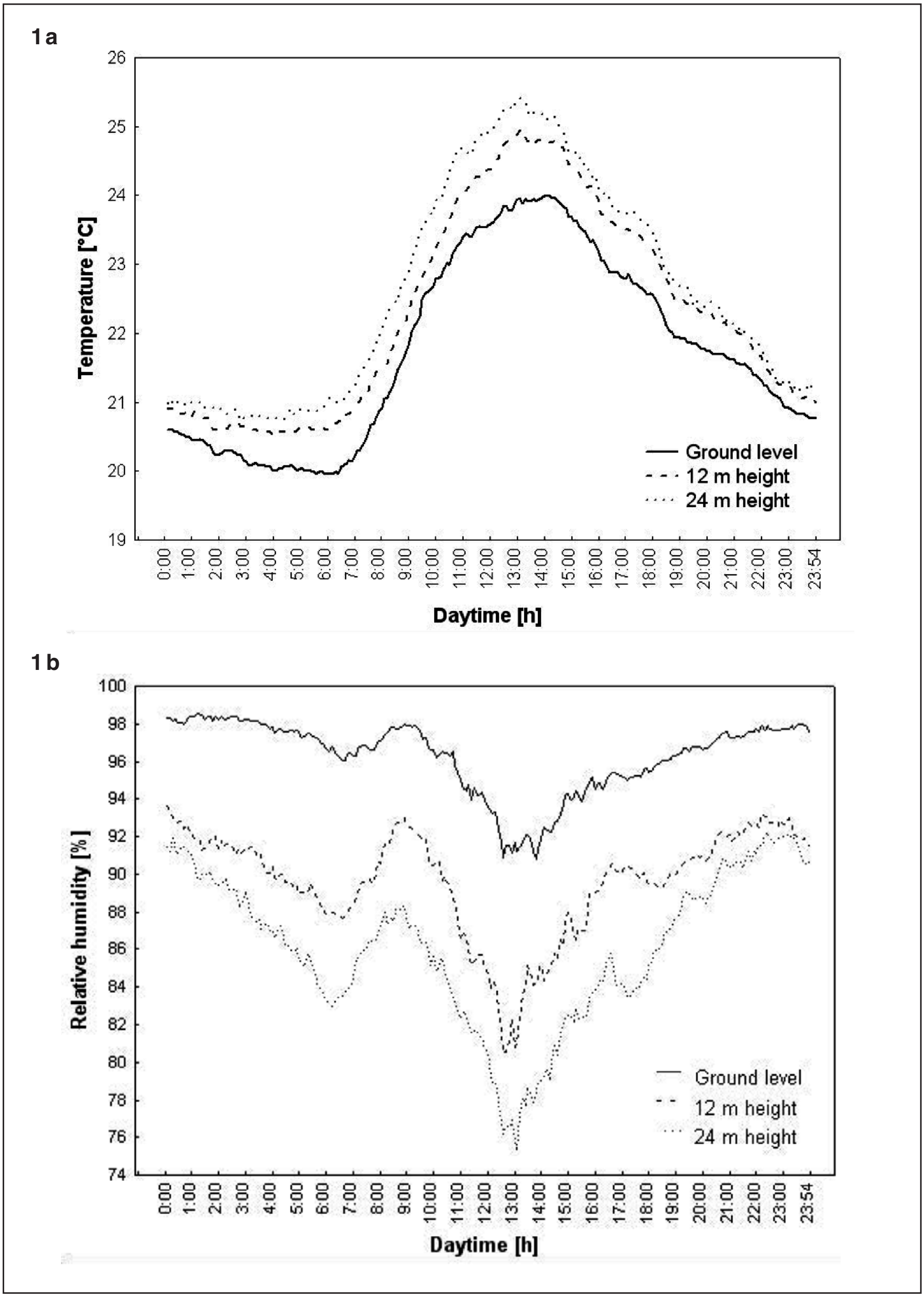

FIG. 1 a, b. Daily temperature (a) and humidity (b) curves at three different heights, averaged over 15 days between March and September 2001 in the unlogged forest of Kinabalu Park.

which we tracked individuals while pursuing aspects of small mammal movement and habitat utilization in logged and unlogged rainforests (Wells *et al.* 2006).

METHODS AND MATERIALS

The tropical lowland forests on the island of Borneo harbor more vascular plant species than any other ecoregion on earth (Kier *et al.* 2005), including 3000 species of trees (MacKinnon *et al.* 1996). In this structurally complex habitat, temperature and humidity differ along the vertical axis from the ground to the canopy, as revealed by digital thermohygrometers (HOBO H8 Pro, Onset) placed at three different heights (Wells 2002) (Fig. 1 a, b). The lowland rainforest is home to approximately 130 species of non-volant mammals (Payne *et al.* 1998). Despite the extensive and ongoing clearing of forests, remaining forest areas are estimated to cover 50 % of the land, although large proportions of this forest have been subject to high-grade commercial logging (WWF 2005).

We selected a total of six study sites: three in unlogged lowland rainforest and three in logged rainforest, which had been selectively logged *ca.* 15–25 year previous to our study. All sites were situated in northern Borneo (Sabah, Malaysia) at altitudes of 200–900 m above sea level (unlogged forests: Kinabalu National Park at 06°02'N, 116°42'E; Tawau Hills National Park at 04°23'N, 117°53'E; Danum Valley Conservation Area at 04°57'N, 117°48'E; logged forests: Kg. Monggis at 06°13'N, 116°45'E; Kg. Tumbalang at 06°08'N, 116°53'E; Luasong Field Centre at 04°36'N, 117°23'E). The unlogged forest stands were characterized by relatively undisturbed vegetation with emergent trees up to 60 m tall. Conversely, canopy heights at the logged forest sites reached only *ca.* 25–30 m, with only a few remaining larger trees of no commercial value (e.g., *Ficus* spp.). Compared to unlogged forests, logged forests had pronounced gaps dominated by fast-growing plants, such as climbing bamboo (*Dinochloa* spp.), sago palms (*Metroxylon* spp.), and rattan (*Calamus* spp.).

Between September 2002 and November 2004 small mammals were live-trapped with wire-mesh cage traps baited with banana. We conducted 18 trapping sessions and alternated between the six study sites, leading to a total of three sampling units, each lasting for 16 days, per site. Captured animals were sedated and marked with transponders. Selected individuals were equipped with a spool-and-line device consisting of a quilting cocoon (Danfield Ltd., U.K.) of approximately 120 m of nylon thread encased by a heat-shrunk plastic (total weight approximately 1.7 g), which was glued with cyanoacrylate (Pattex, Henkel, Germany) to the fur between the shoulders. Tracks were followed the next day to investigate habitat use and movement trajectories, until the end of the thread or a nest was found (Wells *et al.* 2006). Additional burrow records for the giant rat *Leopoldamys sabanus* were obtained from radio-tracking data.

For all nests, we recorded the nest type, utilised construction material, and characters of the surrounding environment, if applicable.

TABLE 1. Number of subterranean and above-ground nests found for seven species of non-volant small mammals in Borneo. Body mass of all adults captured throughout the study are given with the number of individuals (n) in parenthesis.

Species Scientific name	Common name	Family	Body mass (g)	Subterranean nests	Above-ground nests
Leopoldamys sabanus	Long-tailed giant rat	Muridae	368 ± 64 (n = 101)	20	4
Maxomys rajah	Brown spiny rat	Muridae	160 ± 35 (n = 28)	21	2
Maxomys surifer	Red spiny rat	Muridae	157 ± 47 (n = 38)	12	1
Niviventer cremoriventer	Long-tailed tree rat	Muridae	69 ± 13 (n = 142)	2	4
Sundasciurus lowii	Low's squirrel	Sciuridae	96 ± 22 (n = 24)	1	4
Tupaia longipes	Common treeshrew	Tupaiidae	196 ± 25 (n = 59)	–	2
Tupaia tana	Large treeshrew	Tupaiidae	218 ± 27 (n =126)	1	6
Total				56	24

RESULTS

We recorded 83 nest sites of seven species of small mammals (Table 1). Sample sizes for the different species did not permit the use of statistics to determine the influence of forest types on nesting patterns. However, all nests made of plant fibers and leaves, as described below, were found in logged forest near vegetation typically abundant in logged forests, such as *Metroxylon* palms and *Dinochloa* bamboo. Locations of all nests appeared to be independent of vegetation cover for all species, since we observed nests concealed within dense undergrowth and others where there was little understory cover.

Maxomys rajah/surifer. Nests of spiny rats of the genus *Maxomys* were mostly subterranean (33 out of 36), with no observed differences in nest characteristics between the similar species *M. rajah* and *M. surifer*. Thus we describe nest characteristics/attributes together for both species.

Only three nests were above ground: two were in hollow logs of 10–25 cm diameter, and the third was inside a hollow root of an emergent tree. From inside the subterranean burrows, we retrieved uncoiled sections of threads of up to 2.2 m before finding a ball of thread, indicating a distance of about 2 m to the chamber of the burrow.

Most burrows (65 %, 15 out of 23 for *M. rajah* and 7 out of 11 for *M. surifer*) were most probably self-made with round entrance holes 4–6 cm in diameter. In eight records, we found spiny rats entering two different entrances/burrows. Both species covered entrance holes with leaves from inside their burrows (Fig. 2).

Leopoldamys sabanus. We located 24 nests of *L. sabanus* by spool-and-line and radio-tracking. Twenty nests were subterranean, of which four were located close to a stream, with partly wet ground inside (Fig. 3). The smallest entrance hole was 40 mm in diameter,

FIG. 2. Subterranean burrow of *Maxomys rajah*. The nylon thread leads inside the burrow and the entrance is covered by leaves.

FIG. 3. Subterranean burrow of *Leopoldamys sabanus*. The entrance is located near a stream, and the inside of the burrow is wet after several days of rain.

whereas most (13 out of 20) entrances were between 50 and 80 mm in diameter. One burrow had two separate entrances. Three burrows were located in cavities of trees or logs with entrances 1–1.6 m above ground level. We further detected a resting site made of plant fibers formed into a pad in a cavity below a dense stand of climbing bamboo *Dinochloa* spp. in a logged forest. In two instances, we observed an adult male sharing a burrow with an adult female. In one case, a female was recorded sharing a burrow with a juvenile, and in another case two juveniles were observed sharing a burrow. Up to four juveniles were recorded in the proximity of the same burrow. A spiny rat (*M. rajah/surifer*) entered a burrow that had been previously occupied by an immature giant rat (*L. sabanus*) 12 days before.

Niviventer cremoriventer. We recorded six nests of the arboreal rat *N. cremoriventer*. Only two nests were subterranean, another two were under dense clusters of logs and branches, and two were 1–1.5 m above the ground. One above-ground nest measured 10 x 10 x 15 cm and was woven from leafs of *Dinochloa* sp. with an entrance funnel made of around 10 leaves. The other above-ground nest was made of rotten plant fibers (probably from *Metroxylon* sp.), hanging from a branch of a sapling (Fig. 4). We observed two litters of four newborns.

Sundasciurus lowii. We discovered five nests of the scansorial squirrel *S. lowii*. Of these, one was subterranean, with an entrance hole of 6 cm in diameter, near an emergent tree.

Two nests were in tree cavities: one in an emergent tree at a height of 2 m with nest material of leaves and plant fibers inside, the other at a height of 0.5 m in a stump. Two nests consisted of 10–15 cm-diameter balls of woven plant fibers and leaves, at heights of 2 and 3.5 m between branches of *Metroxylon* palms.

Tupaia longipes. We observed only two nests for the treeshrew *T. longipes*. One was located under a dense cluster of dead branches covered additionally with loose leaves. Another was in a tree cavity 10 cm in diameter, at a height of 1.1 m.

Tupaia tana. Of seven nests observed for *T. tana*, five were underground cavities at the base of large tree

FIG. 4. Above-ground nest of *Niviventer cremoriventer* made of woody fiber.

roots. A sixth nest was a cavity in the ground below a rotten log. The seventh nest, inhabited by a male, was woven of plant fibers, and was very similar to the nests described for *S. lowii* (see above). It was fixed between *Metroxylon* branches at a height of *ca*. 1.5 m (Fig. 5).

DISCUSSION

Our study documents distinctive patterns of nest location and construction for the seven species studied. In general, we were able to distinguish among five overall types of nest: 1) self-made subterranean burrows, 2) ground cavities with natural entrances between the soil and roots or rocky crevices, 3) nests below dense accumulations of woody debris, 4) tree cavities, and 5) above-ground nests made of woody fiber or leaves. Although our small sample size only provides limited insight into nest location and construction, the observed patterns suggest that nesting behavior largely reflects species' space use. For example, species that forage on the ground nested mostly below ground, whereas the number of nests above ground increased with the tendency of a species to forage in trees (Emmons 2000, Wells *et al*. 2006). The terrestrial spiny rats *M. rajah* and *M. surifer* were found to nest exclusively in subterranean burrows or in natural cavities with entrances on the ground. The terrestrial rat *L. sabanus*, which undertakes occasional forays into the canopy, used mostly subterranean burrows but some above ground. Conversely, the arboreal rat *N. cremoriventer* was the only rat species that repeatedly used nests above ground. Similarly, the above-ground location of nests of *S. lowii* and the treeshrews *T. longipes* and *T. tana* reflect their scansorial activity. Consistent with these observations, Emmons (2000) recorded nesting sites of the arboreal treeshrews *T. minor* and *Ptilocercus lowii* well above ground, whereas the arboreal mouse *Chiropodomys major* seems to inhabit cavities at ground level and also higher in trees (Wells *et al.* 2004a,b).

These nesting patterns are not only of interest with respect to the spacing patterns of these species within this speciose community, but also because of the different structural and floristic requirements necessary to ensure nest establishment, which in turn may influence small mammal density. The distinctive nesting patterns among species indicate that they differ in their requirements of structural and compositional aspects of the rainforest environment for the establishment of suitable nesting sites. Self-made subterranean burrows would depend more on the animals' digging capabilities rather than the available material. Conversely, nests of leaves or woody fibers above ground level require particular materials for construction, suitable branch texture for nest suspension, and runways for efficient access and escape. Furthermore, the availability of tree cavities depends largely on the type of forest stand (e.g., DeWalt *et al.* 2003). This might be particularly important for treeshrews as they frequently change their daily refuges (Emmons 2000). They are known to utilize a large range of material for nesting, and are also likely to use abandoned refuges from squirrels or birds (Martin 1968, Emmons 2000). This idea is supported by our results, as refuges made of woody debris occupied by *T. tana* and *S. lowii*, which were located at the same logged forest site, were similar in the type of architecture and size. Conversely, rats of the genera *Maxomys* and *Leopoldamys* were frequently observed returning to the same subterranean burrows (K. Wells,

FIG. 5. Nest of *Tupaia tana* anchored between a tree trunk and branches of a *Metroxylon* palm.

pers. obs.). Presumably, these rats use a long-term housing strategy despite environmental variation (e.g., the presence of fruit resources) in the vicinity of nest sites. This is also supported by observations that spiny rats consume and/or store seeds (e.g., hard-shelled *Lithocarpus*) inside their burrows (Wells & Bagchi 2005), presumably for later consumption. Although construction of subterranean burrows requires considerable energy expenditure, it may reduce predation risk and provide the small mammal with increased independence from external conditions (Nevo 1979). The vertical distance from the ground to the nest, and its exposure to sun and rain, might also influence small mammal energetic aspects, because average temperature increases with height, while relative humidity decreases along the vertical axis (Fig. 1 a, b). Such considerations are of particular concern with respect to the ongoing human-caused forest degradation, which affects habitat conditions for many animals (DeWalt *et al.* 2003). Negative effects of logging on nesting, because of differences in structure and available material, have been reported, for instance, for tropical marsupials (Laurance 1990), mouse lemurs (Ganzhorn & Schmid 1998), and orangutans (Ancrenaz *et al.* 2004), despite their flexibility in nesting requirements. We were not able to record any differences between logged and unlogged forest sites, possibly because of the small samples sizes of above-ground nesting species that would have been expected to be most strongly affected. However, all nests made of woody fiber were found in logged forests and were likely to include material from the sago palm *Metroxylon*, which was usually abundant close to these nests but much less common in unlogged forests (K. Wells, pers. obs.). Logged forests are also depauperate in downed woody debris such as large hollow logs and stumps (DeWalt *et al.* 2003), which may serve as denning sites for many species (McCay 2000). The effects of logging on nests reach beyond the initial impacts on population density of a particular small mammal species, as nesting conditions might affect interspecific interactions with predators and parasites. Differences in predation rates for different nest types and habitats, for example, have been recorded for birds (e.g., Remeš & Martin 2002, Martin & Joron 2003). Moreover, nesting patterns should receive more attention in studies investigating host-parasite interactions in the context of unravelling the infestation patterns of particular small mammal species and how these relationships are altered in modified forest environments. Fleas (Siphonaptera) collected from *T. tana* and *S. lowii*, for instance, were congeneric *Medwayella* species (Beaucournu & Wells 2004), congruent with the likely overlap in nest utilization of the two host species. Further, gastrointestinal parasite assemblages (specifically Nemathelminthes), in which direct transmission of species depends on frequent host interactions, were found to be influenced by habitat modifications (K. Wells, unpublished data; see also Gillespie *et al.* 2005). The role of nest characteristics and the plasticity in nesting behavior of different species remain largely unknown for the tropics. Our comprehension of the interplay of small mammals with their environment should be improved by future research on small mammal nesting behavior, which may clarify the role of nesting patterns in shaping small mammal populations subject to different local conditions.

ACKNOWLEDGMENTS

We thank Sabah Parks, Yayasan Sabah and Universiti Malaysia Sabah for forest access and support in the field, and the Economic Planning Unit, Malaysia, for a research permit. Fieldwork was made possible and most effective by the warm hospitality and assistance of the people and staff at all forest sites. We are particularly indebted to Alim Biun, Lajimi Mail, Awang Matamin, Jickson Sankin, Suati Selimon, Jadda Suhaimi, and Fred Tuh. Early drafts of the manuscript were improved by comments by Kristina Cockle, Christoph F.J. Meyer, and two anonymous reviewers. This study was partially funded by a scholarship from the German Academic Exchange Service (DAAD) to KW.

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RESEARCH ARTICLES BELONGING TO CHAPTER 8

Wells K, Kalko EKV, Lakim MB, Pfeiffer M (2007) Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography* 34:1087-1099

Wells K, Pfeiffer M, Lakim MB, Kalko EKV (2006) Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo. *Journal of Animal Ecology* 75:1212-1223

Wells K, Kalko EKV, Lakim BM, Pfeiffer M (accepted) Movement and ranging patterns of a tropical rat in logged and unlogged rainforests *Journal of Mammalogy*

Wells K, Smales LR, Kalko EKV, Pfeiffer M (2007) Impact of rain-forest logging on helminth assemblages in small mammals (Muridae, Tupaiidae) from Borneo. *Journal of Tropical Ecology* 23:35-43

Journal of Biogeography (*J. Biogeogr.*) (2007) **34**, 1087–1099

ORIGINAL ARTICLE

Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia

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ABSTRACT

Aim The effects of logging and habitat degradation on the richness and abundance of small mammals in Asian rain forests are largely unknown. This work compares the species richness, dominance and evenness of small non-volant mammals between logged and unlogged forests, and assesses whether assemblage variability (β-diversity) is similar between forest types.

Location Southeast Asia, northern Borneo (Sabah, Malaysia), Sunda-shelf.

Methods We surveyed species-rich assemblages of small non-volant mammals in three unlogged and three logged forests for 2 years. At each forest site, we sampled a permanently marked transect and two additional sites in three trapping sessions. All analyses were performed at both levels to include the effects of local abundances and point estimates, separately from the relative abundances of species on a more regional scale.

Results We trapped a total of 1218 individuals of 28 species. Eleven common species accounted for 95% of all captures. Species richness and diversity were significantly higher in unlogged forest (27 species) than in logged forest (17 species). This was mainly attributable to the smaller number of rarely recorded species in logged forest (five compared with 16 in unlogged forest, with a total of fewer than 10 captures). However, all common species were present in both logged and unlogged forests, and our analyses revealed similar patterns of dominance, evenness and fluctuations in abundance. Hence overall assemblage composition in multivariate space did not differ greatly between forest types. Assemblages of Muridae and Tupaiidae showed similar population fluctuations in space and time, indicating that the ecology of these taxa may be partially driven by the same environmental factors.

Main conclusions Although species were distributed patchily within sites, analyses at local and regional scales revealed similar patterns in diversity and assemblage variability, suggesting that effects of forest modification did not differ extensively locally and regionally, but had a profound effect on rare species. Our results emphasize the importance and conservation value of logged forest stands that are able to hold a large proportion of the small mammals also found in unlogged forests. Rare and more specialized species are more vulnerable to forest degradation than commonly caught species, resulting in the complete loss, or a decrease in numbers, of certain groups, such as arboreal small mammals and Viverridae.

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Keywords

Community structure, forest structure, logging impacts, Sabah, small mammals, spatial scale, Sunda region, Tupaia.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2006.01677.x

INTRODUCTION

The species diversity and structure of local assemblages of rain-forest animals are influenced by many factors, including habitat complexity and patch heterogeneity, leading to differences in the spatio-temporal availability of resources. Tropical rain forests, in which tree diversity provides the essential resources of food and structural heterogeneity, consist of dynamic patches that are frequently affected by local disturbances such as tree-fall (Denslow, 1995; Condit *et al.*, 2000; Schnitzer & Carson, 2001). The impact of naturally occurring, low-to-intermediate disturbance levels is not necessarily negative; it can also enhance diversity through an increase in heterogeneity and patchiness of the environment (intermediate disturbance hypothesis: Connell, 1978; Molino & Sabatier, 2001). However, large-scale and high-intensity disturbances, which are prominent in many commercially logged forests, often have negative overall effects on species assemblages, even though logging can resemble naturally occurring large tree-fall gaps if reduced-impact logging is applied (Sist *et al.*, 2003).

Given the ever-increasing anthropogenic pressure on natural environments, and in view of the continuing degradation of rain forests, ecologists and conservationists face a growing challenge in trying to understand more fully the effects of human land-use on species, assemblages and ecosystem functioning. Borneo contributes considerably to the high biodiversity of Southeast Asia (Myers *et al.*, 2000), although many functional groups of flora and fauna have only rarely been subjected to detailed studies (Sodhi & Liow, 2000). Deforestation in this area is progressing more rapidly than in any other rain-forest biome worldwide (Curran *et al.*, 2004; Sodhi *et al.*, 2004). Most forests in Borneo will probably be logged in the foreseeable future, leaving the largest proportion of land area either deforested, or covered with logged forest of reduced economic and ecological value. The recovery and succession of the remaining forest stands depend on the availability of plant resources such as seeds, and on the presence of herbivores and their predators (Howlett & Davidson, 2003; Brearley *et al.*, 2004). Following the loss or alteration in numbers of resources, species or functional groups, the interactions of the remaining species will probably be negatively affected.

Because of their seed and seedling consumption, small mammals are assumed to play a central role in changes occurring within logged rain forest in terms of the composition and succession of plant species (Asquith *et al.*, 1997; Blate *et al.*, 1998; Lambert *et al.*, 2005; Wells & Bagchi, 2005). Increases in the abundance of some small mammals can lead to an increase in seed predation, which may suppress forest regeneration (Struhsaker, 1997). Moreover, the consumption of plant material and herbivorous arthropods by small mammals will have a further impact on plant regeneration. As small mammals are versatile and exploit tropical rain forests in three-dimensional space, including a wide variety of habitat patches that are inaccessible to larger vertebrates (Bourliere, 1989), they may even influence forest structure in areas that are at an early stage of succession.

Although the effects of forest fragmentation on small non-volant mammal assemblages (Laurance, 1994; Lynam & Billick, 1999; Goodman & Rakotondravony, 2000) and the surrounding matrices (Gascon *et al.*, 1999; Pardini, 2004) have been intensively studied, less work has been done that addresses the effects of logging on small-mammal communities in Asian tropical forests (Wu *et al.*, 1996; Laidlaw, 2000; Yasuda *et al.*, 2003; Bernard, 2004) or elsewhere in the tropics (Laurance & Laurance, 1996; Malcolm & Ray, 2000; Lambert *et al.*, 2005). As a result, our current knowledge of the impact of habitat degradation on small-mammal assemblages is still poor for many areas, particularly for dipterocarp rain forests. Most studies in the dipterocarp rain forests of Southeast Asia have included only two sites (logged vs. unlogged) and no replication, although it is becoming increasingly evident that the effects of habitat degradation on species diversity and animal dynamics are strongly dependent on the spatial scale of sampling and landscape heterogeneity (Condit *et al.*, 2002; Hill & Hamer, 2004). These aspects thus require multi-site approaches and a larger sampling effort.

Within unlogged dipterocarp rain forests, a large proportion of small mammals are generalists (e.g. some abundant murids and tupaiids) with overlapping dietary composition and microhabitat use (Langham, 1983; Emmons, 2000; Wells *et al.*, 2004, 2006). This large overlap and flexibility in habitat use might blur possible scale-dependent effects on the occurrence of species within a heterogeneous forest matrix, although patchiness in the distribution of key resources might influence demography, even in generalist species (Adler, 2000). The demography of small mammals is also expected to differ along habitat gradients according to the degrees of specialization and colonization ability of the species (Seamon & Adler, 1996), including preferences for small-scale perturbations such as tree-fall gaps (Beck *et al.*, 2004).

The floral composition of logged forests differs from that of unlogged forests. These differences affect not only overall structure and resource availability, but also the scale of habitat heterogeneity (Cannon *et al.*, 1998). On one hand, logging may lead to simultaneous changes in species composition and a strong increase in species that are tolerant to logging-induced habitat changes (Cottingham *et al.*, 2001); on the other hand, species composition might change but compensatory changes in species populations might maintain certain community properties, such as overall abundance, at a relatively constant level (Ernest & Brown, 2001). Whether the effects of habitat alterations are largely compensated for at the local or regional level, or whether they are chiefly influenced by habitat conditions, depends on the extent of environmental perturbation and tolerance of key species (Brown *et al.*, 2001). The assessment of what species persist in logged forests, and an examination of whether and under what conditions certain properties of small-mammal assemblages are maintained (and at what level) are therefore particularly important. The collection of these data may prove crucial in unravelling whether, and in what manner, functional groups or taxa respond to logging, eventually allowing generalizations about particular sets of species and the creation of conservation strategies that preserve as many species as possible.

To fill these gaps in our knowledge of the species richness and assemblage dynamics of small mammals in Southeast Asia, we compared species richness, dominance and evenness of small non-volant mammals between logged and unlogged forests, and assessed whether assemblage variability (β-diversity) is similar between forest types. Furthermore, we investigated factors that lead to changes in assemblage composition and analysed the ways that specific taxonomic groups (Tupaiidae and Muridae) react to forest degradation.

METHODS

Study area

Borneo is the second largest tropical island after New Guinea. It harbours a diverse flora and fauna of approximately 3000 tree species (MacKinnon *et al.*, 1996) and around 130 non-volant mammal species (Payne *et al.*, 1998), comprising both Sundaic elements and a high degree of endemism. The moist tropical climate, with annual average rainfall of 2670 mm and annual mean temperature of 26.7°C (Danum Valley Conservation Area), is characterized by two periods of pronounced rainfall in May–June and October–January (Walsh & Newbery, 1999). Droughts induced by El Niño events affect fruit production by triggering synchronous fruiting of dipterocarp trees, a key resource for many vertebrates (Curran & Webb, 2000). Despite extensive and ongoing clearance, the remaining forest areas at present are estimated to cover half (48%) of the land surface; this includes large forest patches (Sabah Forest Department, personal communication). However, extensive areas of forest have previously been logged at least once and are thus altered to some extent.

We selected a total of six study sites: three in unlogged lowland rain forest and three in logged lowland rain forest, all situated in northern Borneo (Sabah, Malaysia) at altitudes of 200–900 m (Fig. 1). All forest stands were at least 1000 ha and between 17 and 236 km (mean 130 ± 80) apart. Unlogged forests: Danum Valley Conservation Area at 04°57′ N, 117°48′ E, 'Uf1'; Poring, Kinabalu NP at 06°02′ N, 116°42′ E, 'Uf2'; Tawau Hills NP at 04°23′ N, 117°53′ E, 'Uf3'; logged forests: Luasong Field Centre at 4°36′ N, 117°23′ E, 'Lf1'; Kg. Monggis at 06°13′ N, 116°45′ E, 'Lf2'; Kg. Tumbalang at 06°08′ N, 116°53′ E, 'Lf3'. Whereas the unlogged forest stands were characterized by relatively undisturbed vegetation, with emergent trees rising up to 60 m, canopy heights at the logged forest sites, which had been selectively logged *c.* 15–25 years prior to our study, reached only *c.* 25–30 m, and the few remaining larger trees (e.g. *Ficus* spp.) were of no commercial value. Harvesting practice in the highly productive Bornean forests may exceed 10 trees ha^{-1}, damaging more than 50% of the original stand (Sist *et al.*, 2003).

Details of the logging histories at the various sites were not available, although all logged sites were structurally similar. Half the original stands were damaged to a certain degree, as is usual in conventional logging practice where trees are cut and then transported through the unlogged areas to nearby roads. Compared with unlogged forest, disrupted canopies and pronounced gaps in logged forest lead to differences in plant composition and understorey, in which fast-growing plants such as climbing bamboo (*Dinochloa* spp.), sago palms (*Metroxylon* spp.) or rattan (*Calamus* spp.) dominate. The hunting of most vertebrates is common in nearly all forest areas. Small, non-volant mammals in particular are hunted in logged forests because of the large number of rural villages nearby and easy access via logging roads (K.W., personal observation). However, these influences were assumed to have little effect on our sampling, as the hunting of small mammals did not take place near our study locations.

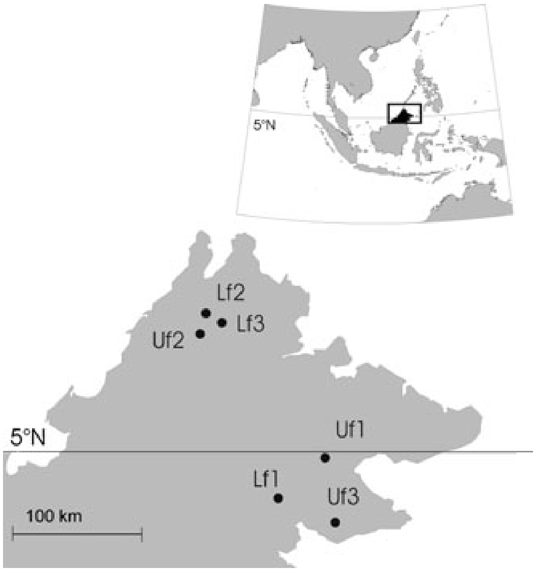

Figure 1 Map of Borneo with the six study sites. Unlogged forests: Danum Valley Conservation Area 'Uf1'; Kinabalu NP 'Uf2'; Tawau Hills NP 'Uf3'; logged forests: Luasong Field Centre 'Lf1'; Kg. Monggis 'Lf2'; Kg. Tumbalang 'Lf3'.

Animal capture and handling

Animals were captured with locally made wire-mesh live traps equipped with a plastic roof for rain protection (280 × 140 × 140 mm) between September 2002 and November 2004. We conducted 18 trapping sessions, alternating between six study sites with a mean interval of 103 ± 50 days between consecutive trapping sessions at the same forest site, giving a total of three sampling units per site. Trapping was carried out at equal intervals throughout the seasons and year for both forest types (Uf1: Mar 03, Dec 03, Sep 04; Uf2: Dec 02, Jun 03, Feb 04; Uf3: Oct 02, Aug 03, Apr 04; Lf1: Apr 03, Sep 03, May 04; Lf2: Nov 02, May 03; Jan 04; Lf3: Jul 03, Mar 04, Nov 04). At each forest site, we established a randomly located and permanently marked transect of 40 traps set 20 m apart in two parallel lines on the forest floor. Additionally, 60–116 traps were placed arbitrarily at two additional locations about 0.5–1.1 km away from the transects, except in Poring where the distance was only 300 m because of the topography. Additional traps were set at various places to enhance data on species diversity. The traps were baited with banana and checked every morning for 16 consecutive days during each trapping session.

The mean trapping effort was 2148 ± 408 trap-nights (traps active for 24 h) per session. Captured animals were briefly anaesthetized (we used diethylether, which had no apparent long-term impact on animal sedation), marked with a pit tag (ARE 162 transponders, AEG, Germany), measured, then released at the point of capture. Although some rats at arbitrarily sampled sites were marked only by ear punching, they could be identified reliably as recaptures during the entire study period. Species identification was based on Payne *et al.* (1998) and on comparison with specimens from the Sabah Parks Museum (Kundasang, Sabah, Malaysia). Specimens of accidentally killed animals, or individuals collected during the last trapping sessions, were deposited either at the Sabah Parks Museum or at the Senckenberg Museum, Frankfurt, Germany.

Data analysis

We examined species richness in logged and unlogged forests by using sample-based rarefaction curves based on the total trapping effort throughout the study period. This approach incorporated spatial heterogeneity, which is inherent to almost all samples (Colwell *et al.*, 2004). We then estimated the expected number of species for logged and unlogged forest with Chao2 and Jack1 species-richness estimators (Colwell *et al.*, 2004).

We established data matrices that included the number of individuals of each species trapped in transects during the 16-day periods (483 individuals in 18 transects, 'trans') and the first 54 individuals from a trapping session pooled from captures in transects and additional locations ('sess'). Two trapping sessions were excluded from analysis because of small sample size, leaving 864 individuals in 16 sessions for analysis. We analysed our data at the assemblage level and with respect to two taxonomic groups, murids and tupaiids, which dominated in all of our samples. All analyses were performed at both levels to include the effects of local abundances and point estimates (trans), separately from the relative abundances of species on a more regional scale (sess). As some immature spiny rats (*Maxomys rajah* and *M. surifer*) were not distinguishable in the field, we added the unidentified individuals proportionally to the number of identified individuals of both species for analyses (45 out of a total of 171 individuals, Table 1).

For each matrix, we used the coefficient of variation (CV = SD/average number of individuals) to describe variations in species abundances within sites, and the non-parametric Shannon–Wiener index H' to analyse species diversity (Magurran, 2004). Bray–Curtis (quantitative Sørensen) similarity matrices were used for comparisons across species assemblages from local and regional estimates. Based on these matrices, we conducted a two-dimensional non-linear ordination with multidimensional scaling (NMDS), which is a particularly robust ordination technique (Clarke, 1993). Axes scores for axis 1 of the NMDS were correlated to features of assemblages and taxonomic groups, respectively, using Spearman's correlation. We tested similarity matrices of species assemblages for possible relationships of temporal (chronological time differences in days), seasonal (shortest time differences between months of respective sessions), and geographical (kilometres between sites) distances between all trapping sessions by using Mantel statistics with 1000 permutations. We approximated species-specific relative persistence rates of individuals in consecutive sessions as $\mathrm{PR} = \mathrm{re} \times \Delta t / (N_t \times N_{t-1})$, where re is the number of recaptured individuals, Δt is the time lag [days] between sessions, N_t is the number of individuals in the session, and N_{t-1} is the number of individuals in the previous session. Diversity estimates were calculated with the software EstimateS (ver. 7.5, R. K. Colwell, http://purl.oclc.org/estimates), Mantel tests were conducted with PC-ORD 4.0 (B. McCune & M.J. Mefford, 1999), and further non-parametric statistics [Mann–Whitney (MW) U, Kruskal–Wallis (KW) ANOVA, Spearman's correlation, χ^2 test] were performed with STATISTICA 6.0 (StatSoft, 2001). Values are given as means ± 1 SD.

RESULTS

α-Diversity in logged and unlogged forests

During the entire study, we trapped a total of 1218 individuals (trapped at 3809 different times in total) from 28 species, representing 17 genera from eight families, with a sampling effort of 40,552 trap-nights (Table 1). In the unlogged forests, we found more species but fewer individuals (27 species, 547 individuals) than in the logged forests (17 species, 671 individuals). The only species that was not recorded in unlogged forests was the shrew *Chimarrogale himalayica*, but this was captured only once in logged forest. Being an insectivore, it was probably not attracted to our bait.

Accumulation curves indicated that the unlogged forests contained a richer small non-volant mammal assemblage, with a steeper accumulation curve, than the logged forests (Fig. 2). Estimates of predicted species richness were higher for unlogged forests, with 29 ± 3 (Chao2) to 32 ± 2 (Jack1) estimated species, than for logged forests, with 22 ± 6 to 21 ± 2 estimated species. These estimates confirmed that species richness was lower in logged forests (Fig. 2). Estimates of species richness for data sets from the transects (Chao2: 17 ± 3 for Uf, 14 ± 1 for Lf; Jack1: 19 ± 1 for Uf, 16 ± 1 for Lf) or standardized sessions (Chao2: 27 ± 4 for Uf, 14 ± 0.2 for Lf, Jack1: 28 ± 3 for Uf, 15 ± 1 for Lf) were in part lower than the total number of documented species; this was probably the consequence of rare and therefore slowly accumulating species that were under-represented in single trapping sessions.

Table 1 Number of individuals of all species trapped in the various study areas. Total trap effort for each area in parentheses. Additional trapping efforts in Uf2 and Uf3 during the period of field work that was not part of the analyses are included to provide a more complete species record.

Species	Latin name authority	Total number of individuals	Unlogged forest (Uf)			Logged forest (Lf)		
			Uf1 (7092)	Uf2 (7545)	Uf3 (8115)	Lf1 (6469)	Lf2 (6040)	Lf3 (5291)
Rodentia								
Muridae								
Chiropodomys major	Thomas 1893	1	1	–	–	–	–	–
Lenothrix canus	Miller 1903	2	–	2	–	–	–	–
Leopoldamys sabanus	Thomas 1887	175	9	76	18	12	39	21
Maxomys baeodon	Thomas 1994	5	1	–	–	1	1	2
Maxomys ochraceiventer	Thomas 1894	2	–	2	–	–	–	–
Maxomys rajah	Thomas 1894	76	25	1	3	37	9	1
Maxomys surifer	Miller 1900	50	7	4	10	14	9	6
Maxomys cf. *surifer/rajah*		45	25	4	4	3	8	1
Maxomys whiteheadi	Thomas 1894	73	12	10	26	18	3	4
Niviventer cremoriventer	Miller 1900	265	28	26	9	19	55	128
Rattus rattus	Linnaeus 1758	4	2	–	2	–	–	–
Sundamys muelleri	Jentink 1879	41	3	1	1	–	–	36
Sciuridae								
Lariscus hosei	Thomas 1892	1	–	–	1	–	–	–
Callosciurus notatus	Boddaert 1785	11	–	5	–	1	4	1
Callosciurus prevostii	Desmarest 1822	4	–	3	1	–	–	–
Sundasciurus brookei	Thomas 1892	1	–	1	–	–	–	–
Sundasciurus hippurus	Geoffroy 1831	7	1	1	4	–	–	1
Sundasciurus lowii	Thomas 1892	45	8	2	21	5	5	4
Hystricidae								
Trichys fasciculata	Shaw 1801	2	–	–	2	–	–	–
Insectivora								
Chimarrogale himalayica	Gray 1842	1	–	–	–	–	–	1
Erinacaeidae								
Echinosorex gymnura	Raffles 1822	4	–	–	2	2	–	–
Scandentia								
Tupaiidae								
Ptilocercus lowii	Gray 1848	1	–	1	–	–	–	1
Tupaia gracilis	Thomas 1893	24	1	9	4	4	2	4
Tupaia longipes	Thomas 1893	117	28	10	42	23	4	10
Tupaia minor	Günther 1876	76	1	25	2	–	4	44
Tupaia tana	Raffles 1821	173	22	15	12	15	54	55
Carnivora								
Viverridae								
Arctogalidia trivirgata	Gray 1832	2	–	1	1	–	–	–
Paradoxurus hermaphroditus	Pallas 1777	6	4	–	2	–	–	–
Viverra tangalunga	Gray 1832	3	3	–	–	–	–	–
Total		1218	181	199	167	154	197	320
Number of species		28	17	19	19	12	12	16

Eleven species, each represented by more than 20 captures, were classified as commonly caught. These species accounted for 95% of all captures and were recorded at all forest sites, except for *Sundamys muelleri*. Murids were most abundant in both forest types, accounting for 57% and 63% of all captures in unlogged and logged forests, respectively. Tupaiids were recorded with lower capture rates (31% and 33% of all captures) in unlogged and logged forest.

Shannon–Wiener diversity estimates showed no clear differences between single site estimates from logged vs. unlogged forest sites (MW U test, trans: $U = 4.0$, $P = 0.83$; sess: $U = 3.0$, $P = 0.51$) but the overall diversity between both forest types was significantly lower in logged forest (trans: $H'_{\mathrm{Uf}} = 2.35 \pm 0.02$, $H'_{\mathrm{Lf}} = 2.08 \pm 0.05$; sess: $H'_{\mathrm{Uf}} = 2.43 \pm 0.03$, $H'_{\mathrm{Lf}} = 2.12 \pm 0.04$).

Dominance and abundance of common species

The most abundantly trapped species recorded in the sessions were *Niviventer cremoriventer* (most abundant in $n = 5$

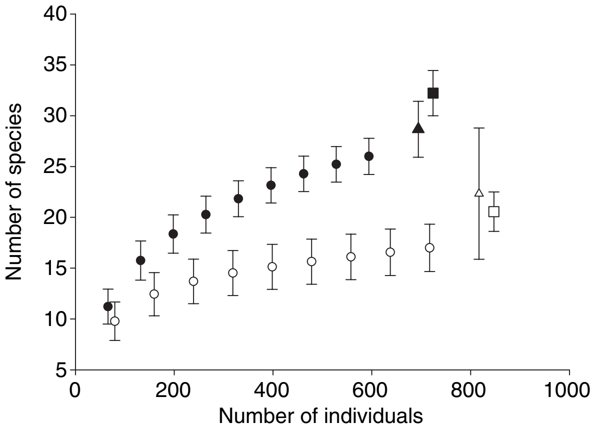

Figure 2 Rarefied species-accumulation curves representing the average number of species for a given number of captured individuals for the entire regional trapping effort (sessions) in unlogged forest (●) and logged forest (○). Triangles and squares refer to the estimated number of species based on Chao2 and Jack1 estimators, respectively. Bars are 95% CI.

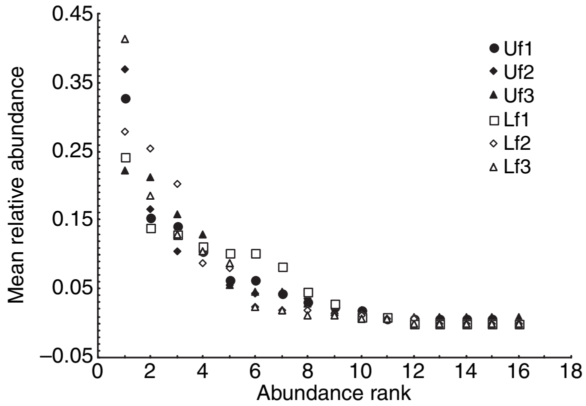

Figure 3 Mean relative abundances of species pooled over trapping sessions at various study sites. No significant differences in the shape of the rank abundance curves were detectable (all Kolmogorov–Smirnov two-sample tests, $P > 0.10$). Note that the numbers of species are lower than actually recorded in some sessions because of data standardization.

sessions), *M. rajah* ($n = 4$), *Leopoldamys sabanus* ($n = 3$), *Tupaia longipes* ($n = 3$), *Tupaia tana* ($n = 2$) and *Maxomys whiteheadi* ($n = 1$). The three most abundantly trapped species varied within and between study sites. Whereas they were mostly the same within a study site (Sørensen index, S_{mean} (site) $= 0.70 \pm 0.19$), the abundant species differed more often between sites of the same forest type (S_{mean} (Uf) $= 0.39 \pm 0.26$, S_{mean} (Lf) $= 0.50 \pm 0.29$) with no obvious differences in dominance patterns between Uf and Lf (S_{mean} (Uf × Lf) $= 0.42 \pm 0.27$).

Fluctuations in the abundance of the 11 most commonly caught species, as determined by the CV from each site, did not differ across sites (MW U test, trans: $U \leq 3.0$, $P > 0.08$; sess: $U \leq 3.0$, $P > 0.08$). Mean CVs ranged from 0.65 at Uf3 to 1.14 at Uf1 for transect data, and from 0.33 at Lf1 to 1.07 at Lf3 for sessions, with no recognizable difference in abundance fluctuations between species (KW ANOVA$_{\mathrm{trans}}$, $H_{10,53} = 12.00$, $P = 0.28$; KW ANOVA$_{\mathrm{sess}}$, $H_{10,60} = 10.73$, $P = 0.38$). Overall, the mean abundance fluctuations pooled for the different forest types did not differ between logged and unlogged forests (MW $U = 397.0$, $P = 0.43$). Likewise, the relative abundance of the 11 most dominant species did not differ between sessions in logged and unlogged forests (MW $U = 36$, $P = 0.79$), while the overall abundance distributions as indicated by rank abundance curves were not distinct between logged and unlogged forests (all Kolmogorov–Smirnov two-sample tests ($n = 15$) $P > 0.10$) (Fig. 3). However, mean capture frequencies were significantly larger for *N. cremoriventer* and *T. tana* in logged than in unlogged forest (both MW $U > 15$, $P < 0.05$).

Spatio-temporal variation in assemblage structure

NMDS ordinations of species assemblages and seasonal/temporal similarities between trapping sessions extracted two-dimensional solutions in which all raw stress factors, ϕ, were ≤ 0.15, indicating that the original relationships in matrices were represented sufficiently by the resulting NMDS axes (Clarke, 1993). Changes in assemblage structure at the local level based on transect data (trans, Fig. 4) were significantly correlated with changes at the regional level based on data from complete sessions (Mantel test, $r = 0.79$, $P < 0.01$).

Although the number of tupaiid species was correlated with the composition of assemblages (NMDS axis 1) at the local level based on transect data (trans: Spearman $R_{n=18} = -0.60$, $P < 0.009$), the number of murid species was correlated with species composition at the regional level, based on data from complete sessions (sess: Spearman $R_{n=18} = 0.68$, $P < 0.004$; Fig. 5a). Changes in the regional assemblage composition of murids and tupaiids were significantly correlated (Mantel test, $r = 0.27$, $P < 0.05$), suggesting that part of this pattern was

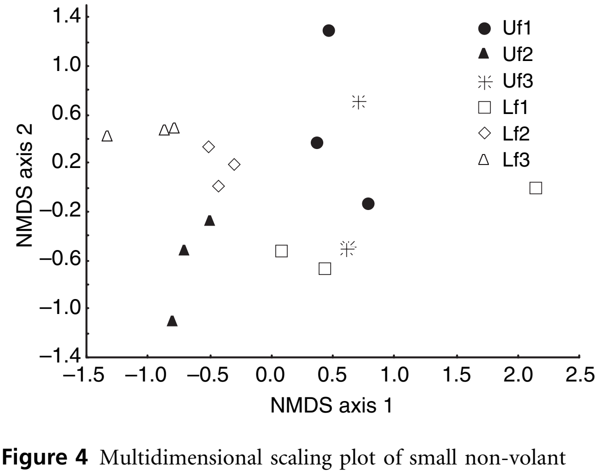

Figure 4 Multidimensional scaling plot of small non-volant mammal assemblages based on local censuses (trans) during the 18 trapping sessions.

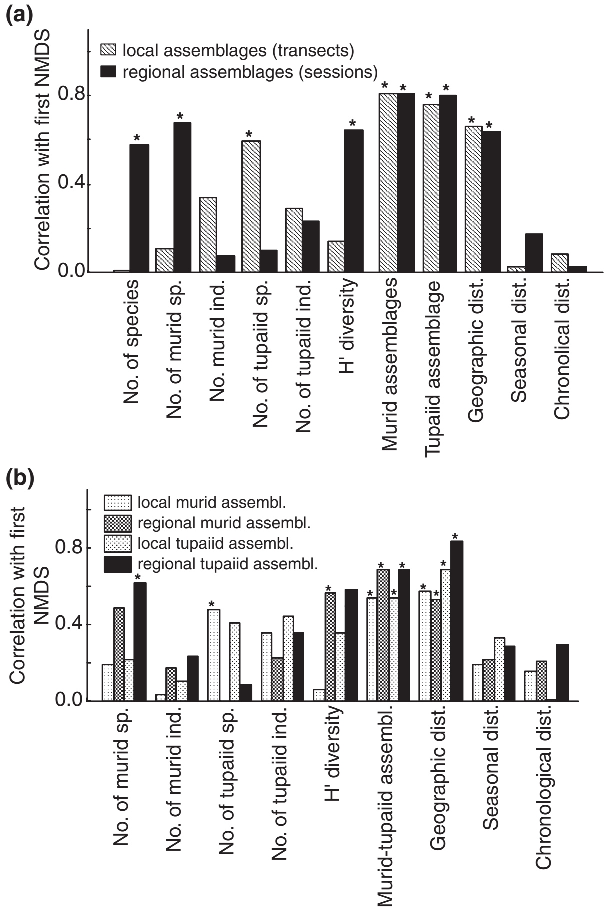

Figure 5 Impact of selected variables on changes in community composition in (a) assemblages of all species and (b) murid and tupaiid assemblages, on both local and regional scales. Bars represent *R* values from Spearman's correlations for numbers of species and individuals and for *H*′ diversity, and *r* values from Mantel statistics for murid/tupaiid assemblages and geographical/temporal distances. Note that we considered only the first non-linear ordination with multidimensional scaling (NMDS) axes in these figures. *Significant correlations ($P < 0.05$).

driven by similar environmental fluctuations (Fig. 5b). We traced this relationship down to the species level and found that murid assemblages described by NMDS axis 1 scores were correlated with the relative abundances of *T. minor* and *T. longipes* (sess: both Spearman $R_{n=16} > \pm\ 0.75$, $P < 0.0006$). Tupaiid assemblage scores (NMDS axis 1) were correlated with the relative abundances of *N. cremoriventer*, *M. rajah* and *M. whiteheadi* (sess: all $R_{n=16} > \pm\ 0.50$, $P < 0.05$). Species assemblages were also correlated with respective *H*′ diversity estimates, but not with number of captured individuals (Fig. 5a,b).

An impact of geographical distance between sites on assemblage similarity (quantitative Sørensen distances) was detectable for both local and regional species assemblages and for murid and tupaiid assemblages (Mantel tests, all $r > 0.29$, $P < 0.01$).

Capture success was lowest during fruiting seasons in September and October (Fig. 6), although we found no significant general impact of seasonal or temporal differences on assemblage compositions (Mantel tests, all $r < 0.18$, $P > 0.05$). Composition of species assemblages as described by NMDS axis 1 scores was most similar within sites and less similar across sites (site as fixed factor: KW anova axis 1, trans: $H_{5,18} = 14.45$, $P < 0.02$; sess: $H_{5,16} = 14.01$, $P < 0.02$). NMDS axis 1 scores of assemblages in unlogged and logged forest were indistinguishable from each other at the local level (trans: both MW $U > 25$, $P > 0.17$). However, NMDS scores of assemblage composition at the regional level differed between unlogged and logged forest on the first ordination axis (sess: MW $U = 11$, $P < 0.03$).

Distribution of species

The spatial distribution of species was heterogeneous among localities (transects and additional locations) within a study site. A comparison of observed and expected distributions of commonly caught species, based on the total number of captures at different locations, revealed significant deviations from a random distribution among locations within each site in 20 out of 146 cases ($\chi^2 > 6.1$, $P < 0.05$). These patterns of spatial heterogeneity regarding species distribution were similar for unlogged and logged forest, and were most pronounced for *L. sabanus*, *Sundasciurus lowii* and *Tupaia gracilis*.

Persistence of individuals

We recaptured 15% ($n = 120$ individuals) of 784 marked individuals. Persistence rates of individuals in consecutive

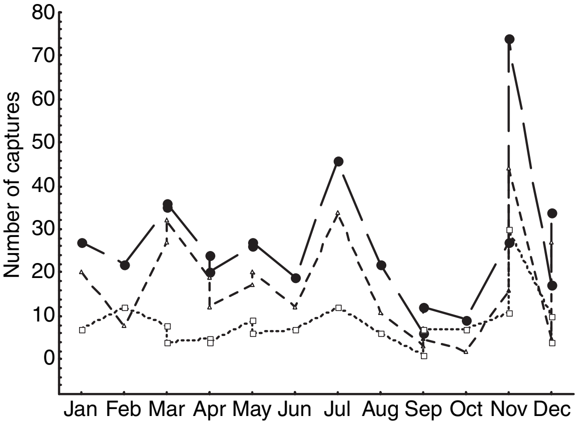

Figure 6 Number of captures in transects throughout the year. Total numbers of captured individuals (●), murids (△) and tupaiids (□) are given. Although the trap success for murids and tupaiids was not correlated (Spearman $R_{(n=18)} = 0.16$, $P = 0.54$), and the verification of general seasonal patterns was weak, the trapping success for both taxa was lowest during the fruiting season in September/October. Note that some months contain more than one sample.

trapping sessions differed between forest sites (KW ANOVA $H_{5,110} = 18.15$, $P < 0.003$), as persistence rates were relatively high in Uf3 but low in Lf1. They were marginally lower in logged than in unlogged forest (MW $U = 1203$, $P = 0.07$). The mean persistence rate was highest for *M. surifer*, *M. rajah* and *T. gracilis*. However, the means differed only slightly between species because of the large variability of persistence rates between sites (KW ANOVA $H_{5,110} = 18.15$, $P = 0.08$) (Table 2). The longest persistence was recorded for a *T. minor* individual, which had been marked in a previous study in 2001 (Wells *et al.*, 2004) and was recaptured after 636 days.

DISCUSSION

Small mammal diversity in logged and unlogged forests

In tropical forests, a high structural diversity and great variability in resources are considered key elements in the maintenance of diverse small-mammal assemblages (August, 1983). Furthermore, occurrence and assemblage patterns of small mammals are determined by the degree of specialization, flexibility and general demography of the constituent species (Adler, 2000). Species flexibility should not only ensure persistence and abundance in spatially and temporally heterogeneous forest matrices, but also tolerance of logging and habitat disturbance. Although rain-forest logging resulted in a significant loss of rare small mammal species in our study, the ubiquitous presence of commonly caught species at all forest sites, both logged and unlogged, suggests that assemblage dynamics are mainly determined by these species. Multiple comparisons of replicates within and between sites have revealed that fluctuations in abundance and assemblage variability appear to be little affected by logging, raising the question of how far synchronous responses to environmental fluctuations account for variation in local species assemblages, and whether this can be traced to the same dominant species.

Table 2 Maximum recorded persistence times for commonly caught species.

Species	Max. persistence (days)	Site of record	Total number of recaptured individuals	Mean persistence rate PR ± SD
L. sabanus	534	Uf3	14	3.8 ± 5.8
N. cremoriventer	494	Lf3	20	0.5 ± 0.9
M. rajah	573	Uf1	23	20.8 ± 41.0
M. surifer	537	Uf3	5	20.1 ± 37.8
M. whiteheadi	273	Uf1	5	7.4 ± 14.6
S. muelleri	250	Lf3	1	0.2 ± 0.7
S. lowii	262	Uf3	3	0.6 ± 1.8
T. gracilis	287	Uf3	4	19.3 ± 33.1
T. minor	636	Uf2	6	0.4 ± 1.0
T. longipes	590	Uf3	9	2.2 ± 2.8
T. tana	547	Uf3	19	6.9 ± 13.7

The pronounced decline in species richness and diversity in logged forests was mainly attributable to the reduction in rare species, whereas commonly caught species of omnivorous murids or tupaiids were recorded almost equally often at all sites. This pattern is consistent with other studies on small non-volant mammals in Australia (Laurance & Laurance, 1996), Malaysia (Zubaid & Ariffin, 1997; Yasuda *et al.*, 2003) and Venezuela (Ochoa, 2000).

Common vs. rare species

In our study, species affected by logging could be arranged in various functional groups, but no evidence was found for a single factor explaining the lack of certain species in logged forests. Four of the rare species we recorded only in unlogged forests are endemic to Borneo (*Chiropodomys major*, *Maxomys ochraceiventer*, *Lariscus hosei*, *Sundasciurus brookei*), and their restricted geographical distribution might be associated with less tolerance to environmental variability compared with species that inhabit a larger geographical area. Species decline in logged forest was most evident in civets, which are known to be sensitive to habitat degradation (Heydon & Bulloh, 1996; Colon, 2002). The mainly arboreal rats (*C. major*, *Lenothrix canus*) and squirrels (*Callosciurus prevostii*, *S. brookei*) are less prevalent in logged forests, which might be because of reduced canopy space and altered tree composition and texture (Saiful *et al.*, 2001; Yasuda *et al.*, 2003; Wells *et al.*, 2004) compared with unlogged forest. The question remains as to whether resource availability, or structure and habitat space, is the main determinant of reduced species richness in logged forest, and whether these proximate parameters affect particular species groups more than others. Some studies have suggested that the consequences of habitat disturbance differ with the type and spatial extent of disturbance. Favourable circumstances, such as an increase in herbaceous vegetation, a decrease in canopy and sapling density, and more abundant arthropods and fruits (Malcolm, 1997; Struhsaker, 1997; Lambert *et al.*, 2003) may lead to increases in small non-volant mammal densities in disturbed habitats (Malcolm & Ray, 2000; Lambert *et al.*, 2005). We found an increased abundance of *N. cremoriventer* and *T. tana* in logged forests. Although it has been suggested that *T. tana* prefers dense undergrowth and gap structures (Emmons, 2000; Wells *et al.*, 2004), whether structural features or particular resources are important *per se* remains unclear. Furthermore, whether conclusions from gap vs. understorey dynamics are applicable to logged forest conditions is also uncertain.

Species richness and resource aggregation

If the decline in species in logged forests is mainly attributable to resource specialization, a consideration of whether the occurrence and abundance patterns of species are driven by the presence of particular resources and/or by certain patterns of resource allocation would be of interest. For instance, tree species that play a significant role in overall forest architecture and resource availability are often not randomly distributed within tropical forests (Condit *et al.*, 2000). Rather than overall forest structure, such patchy distribution patterns of key resources have been shown to influence the demography of the Neotropical *Proechimys* rat, which concentrates its activity mainly around fig (*Ficus*) trees, one of its main food resources (Adler, 2000). Therefore small mammals with specialized feeding habits and a dependence on spatially clumped resources seem to be mostly aggregated. Conversely, common species with omnivorous diets cope well with a wide range of resources and exhibit greater tolerance towards spatio-temporal resource availability. If the area covered by the spatial variability of plant and other resources exceeds the foraging areas of generalist feeders, then more specialized species should be able to cope more efficiently with a subset of the resources in some localities. This, in turn, might lead to a balanced overall dynamic of the assemblage, as the number and abundance of specialist and generalist species might compensate each other. High resource diversity and its specific distribution in heterogeneous forests therefore should promote the presence and abundance of both specialist and generalist species. With respect to capture probabilities, the chances of capturing a specialized species should be lower because of its reduced abundance, and higher for more generalist species.

Plant composition and distribution differ in logged forests (Cannon *et al.*, 1998). The proportion of animal-dispersed and mammal-pollinated trees, as well as arthropod assemblages that may serve as food sources for small mammals, may be affected by logging (Davis *et al.*, 2001; Chazdon *et al.*, 2003; Cleary, 2003). For instance, the reduced availability of particular fruit resources in logged forests has been reported as negatively influencing densities of the fruit-eating mouse deer *Tragulus* spp. (Heydon & Bulloh, 1997). As outlined above, such resource alteration should mostly influence the occurrence and density of more specialized small non-volant mammals. This is in agreement with our results, as analysis of commonly caught species reveals some aggregation at the level of individuals, but they are also widely dispersed in different locations and forest sites. Reduced species richness in logged forests probably occurs mostly as a consequence of reduced overall species densities and/or lower abundance of rare species, as most of the rare species that we trapped only in unlogged forests are known also to be present in logged forests (*L. canus*, *C. prevostii*, *Trichys fasciculata*, all civets; personal observation).

Tolerance of logging by common species, and the pronounced prevalence of rare species in unlogged forests, have also been found for birds in the same geographical region (Sodhi, 2002; Lammertink, 2004). However, other studies conducted at different spatial scales with birds and butterflies led to contrasting results, with both decreased and increased diversity (Hill & Hamer, 2004).

The amount of intraspecific aggregation of a species within a set of assemblages should concomitantly decrease α-diversity and increase β-diversity (Veech, 2005). Therefore the spatially clumped distribution of species should also be considered in the interpretation of variability in assemblages both within and among forest types. Surprisingly, the variability in assemblages from unlogged vs. logged forest, as determined by multivariate analysis, differed at neither the local nor the regional level. Furthermore, we found no differences in abundances of commonly caught murids and tupaiids within a forest type, and no evidence for differential impacts of logging on these functional groups. However, some fluctuations in the assemblage of both taxa are evident: while the number of tupaiid species were associated with assemblage fluctuations at the local level, murid species had more influence on assemblage fluctuations on a regional scale (Fig. 5a).

Logging effects on small-mammal assemblages

Based on the observation that different plant or invertebrate taxa respond inconsistently to anthropogenic habitat alteration (Lawton *et al.*, 1998; Ricketts *et al.*, 2002), we conclude that habitat disturbance in the form of logging may not necessarily lead to the synchronous alteration of food availability for different groups of small mammals. Unfortunately, the diet of murids and tupaiids is not well known, although they are thought to include a large range of arthropods and plant material (Langham, 1983; Emmons, 2000). However, interesting differences exist in their morpho-physiological traits related to food processing. Tupaiids have weak jaws in combination with short intestinal transition times and simplified colons (Emmons, 1991) that do not allow the processing of the hard dipterocarp and lithocarp fruits that are favoured by murids during the fruiting season in unlogged forests (Curran & Webb, 2000; Wells & Bagchi, 2005). Surprisingly, although these fruits comprise a key resource in unlogged forests, differences in local abundance related to habitat disturbance resulted neither in detectable differences in murid fluctuations between unlogged and logged forest, nor in any asynchronous changes in murid and tupaiid assemblages. Nevertheless, some impact of season in relation to fruiting can be inferred from the reduced trapping success during the main fruiting peak; this time interval also coincides with the main reproductive period of murids in unlogged forests (personal observation).

Another factor contributing to the observed assemblage structure patterns in our study could be the geographical locality and the distance between study sites. Geographically distinct areas differ in climate, altitude and edaphic factors that influence plant and resource composition on a regional scale (Ashton & Hall, 1992; Newbery *et al.*, 1996). Three of the sites, one unlogged and two logged (minimum distance between sites 17–24 km; Uf2, Lf2, Lf3), were close to Mount Kinabalu, a mountain that strongly influences the topography, soil mineral content and climate of this region (Kitayama, 1992). Such geographically related factors might be of greater importance than factors sensitive to logging in influencing abundance fluctuations and assemblage dynamics. Overall, the similarities in assemblage features between forest types suggest that fundamental ecological or abiotic features of the biome, rather than profound differences between unlogged and logged forest, are major driving forces in shaping assemblage structure and abundance patterns.

Although logged forests are generally characterized by distinctly altered plant composition and physical structure compared with unlogged forest, many kinds of logging damage might in some ways be equivalent to the naturally occurring perturbations and alterations to which a large proportion of common non-volant small mammal species are well adapted. Most of the commonly caught species from our study, such as *L. sabanus*, *M. surifer* or *M. whitheadi*, have inhabited a wide geographical range in the Sunda region of Southeast Asia throughout their evolutionary history (Gorog *et al.*, 2004). This supports the idea of the long-term adaptation to, and tolerance of changes in, habitat conditions by these species.

CONCLUSIONS

Logging does not appear consistently to cause strong changes in species assemblages with respect to ubiquitously present generalist species. We know little about the multiple interactions of small non-volant mammals with other components of the ecosystem. Further work is required to determine whether fundamental ecosystem processes in logged forests are altered by changes in resource availability, competitors or carnivorous predators, even if the same small mammal species are present (Terborgh *et al.*, 2001). The role of rare species remains even more elusive, although the reduced species richness in our study clearly suggests that some species are vulnerable to severe population reductions or extinction by logging-induced changes. The inconsistency in logging responses among species, and the large habitat variability that is intrinsic to rain forests and that is further generated by various anthropogenic impacts, present a challenge when selecting areas for conservation. Hitherto, general statements on logging effects can be made for different species groups. Although logged rain forests might house large proportions of the small-mammal assemblages found in undisturbed forests, some rare species will remain unprotected if unlogged forests are not conserved, as these forests remain the major source of the region's immense species richness.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit, Malaysia, for a research permit, and Sabah Parks, Yayasan Sabah and Universiti Malaysia Sabah for forest access and various kinds of support in the field. Field work was made possible and supported in the most effective way by warm hospitality and assistance from the people and staff at all forest sites. We are particularly indebted to Alim Biun, Aloysius Mail, Jadda Suhaimi, Jickson Sankin, Suati Selimon and Awang Matamin, among many others. Thanks are also due to K. Eduard Linsenmair and Brigitte Fiala for logistic support. We are grateful to Thomas D. Lambert, Jon Sadler and several anonymous reviewers for reading and commenting on drafts of the manuscript. Financial support was kindly provided by the German Academic Exchange Service (DAAD) to K.W.

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Editor: Jon Sadler

Journal of Animal Ecology 2006
75, 1212–1223

Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo

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Summary

1. Non-volant animals in tropical rain forests differ in their ability to exploit the habitat above the forest floor and also in their response to habitat variability. It is predicted that specific movement trajectories are determined both by intrinsic factors such as ecological specialization, morphology and body size and by structural features of the surrounding habitat such as undergrowth and availability of supportive structures.

2. We applied spool-and-line tracking in order to describe movement trajectories and habitat segregation of eight species of small mammals from an assemblage of Muridae, Tupaiidae and Sciuridae in the rain forest of Borneo where we followed a total of 13 525 m path. We also analysed specific changes in the movement patterns of the small mammals in relation to habitat stratification between logged and unlogged forests. Variables related to climbing activity of the tracked species as well as the supportive structures of the vegetation and undergrowth density were measured along their tracks.

3. Movement patterns of the small mammals differed significantly between species. Most similarities were found in congeneric species that converged strongly in body size and morphology. All species were affected in their movement patterns by the altered forest structure in logged forests with most differences found in *Leopoldamys sabanus*. However, the large proportions of short step lengths found in all species for both forest types and similar path tortuosity suggest that the main movement strategies of the small mammals were not influenced by logging but comprised generally a response to the heterogeneous habitat as opposed to random movement strategies predicted for homogeneous environments.

4. Overall shifts in microhabitat use showed no coherent trend among species. Multivariate (principal component) analysis revealed contrasting trends for convergent species, in particular for *Maxomys rajah* and *M. surifer* as well as for *Tupaia longipes* and *T. tana*, suggesting that each species was uniquely affected in its movement trajectories by a multiple set of environmental and intrinsic features.

Key-words: community structure, forest degradation, small mammal stratification, vertical habitat segregation.

Journal of Animal Ecology (2006) **75**, 1212–1223
doi: 10.1111/j.1365-2656.2006.01144.x

Introduction

The exploitation of a heterogeneous and patchy environment by an animal is likely limited by its adaptations to a preferred habitat, where habitat structure and resource distribution determine effective detection and movement towards essential resources. The potential of a species to cope with environmental variability is therefore crucial for species distribution on local to regional scales. This aspect is particularly important for animal communities in tropical rain forests. The diversity and distribution of trees that form the basis for high resource availability and structurally rich habitats, which in turn

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affect the occurrence of animals using these resources, varies already within single habitats up to regional and ultimately global scales (e.g. Hubbell 1979; Newberry *et al.* 1992; Potts *et al.* 2002). Consequently, the role of environmental variability in structuring populations and communities has gained much interest among ecologists (August 1983; Eisenberg 1990; Emmons 1995). Recently, environmental variability has become even more important because of the rapid fragmentation and conversion of rain forests (Sodhi *et al.* 2004).

Many generalist species, such as small mammals, that exploit the entire three-dimensional space of a forest and that are characterized by various degrees of niche specificity and climbing activity (e.g. Bourliere 1989; Wells *et al.* 2004), often vary in their responses to anthropogenic driven habitat fragmentation and alteration (Laurance & Laurance 1996; Laidlaw 2000; Malcolm & Ray 2000; Lambert, Malcolm & Zimmermann 2005). Small mammals moving through degraded forests encounter differences in structure (e.g. more dense undergrowth in combination with a reduced canopy stratum) and resources availability (e.g. different floral composition). This results in differences in habitat heterogeneity and patch properties (Cannon, Peart & Leighton 1998; DeWalt, Maliakal & Denslow 2003).

To gain a better understanding how species persist and move through such variable environments is therefore of fundamental importance for the assessment of responses by wildlife to habitat changes and the potential of species to cope with altered forest habitats on a long-term basis. Currently, niche utilization of sympatric small mammals in tropical rain forests has been mainly derived from the relationship of their local abundance and associated habitat features, thus attributing partitioning mostly to structural features (Tomblin & Adler 1998; Shanker 2001; Williams, Marsh & Winter 2002) or floral diversity and resource availability (Adler 2000; Kanowski, Irvine & Winter 2003; Beck *et al.* 2004). The differential use of forest strata by small mammals has been repeatedly reported for both neotropical (Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1995; Cunha & Vieira 2002) and palaeotropical (Malcolm & Ray 2000; Saiful *et al.* 2001; Wells *et al.* 2004) forest sites. However, differential substrate use by syntopic species has been suggested to require a finer scale of segregation than a simple arboreal–terrestrial dichotomy (Charles-Dominique *et al.* 1981).

As most studies of non-volant small mammals are limited to trapping data, they frequently comprise only small-scale sampling of a limited number of (micro)habitats along transects and give an incomplete view of habitat patches and vertical layers used by small mammals. It is very unlikely that the patterns derived from those studies are fully representative of the habitat use of small mammals. This misconception has led to the widespread concept of a rather fixed microhabitat segregation derived mostly from data on local scales. However, recent studies stress the importance of data on larger spatial scales to explain why species might use a certain type of microhabitat in one location and a different microhabitat in another one (Bowers & Dooley 1993; Jorgensen 2004; Kneitel & Chase 2004). Furthermore, habitat types often from a continuous gradient instead of strictly limited 'patches'. So far, niche segregation in small mammals has been largely regarded as trade-offs within assemblages caused by environmental constraints on the level of individuals, including local habitat characteristics, resource distribution, and presence of predators (Price & Kramer 1984; Kotler & Brown 1988). Recent advances, however, take the analysis of vertebrate movement patterns in heterogeneous and patchy environments into account with a focus on geographical and/or individual variation (e.g. Morales *et al.* 2004; Austin, Bowen & McMillan 2004).

It is reasonable to assume that movement patterns of animals closely follow the structure of the environment, exhibiting, for example, an increased path tortuosity (divergence from a straight line movement) in dense patches with many obstacles and/or discontinuous structural supports. Furthermore, movement patterns with a broad distribution of long movements alternating with a concentration of shorter moves in favoured patches might be most suitable for movement in heterogeneous rain forests (Viswanathan *et al.* 1999; Ramos-Fernández *et al.* 2004). Such patterns may change with the scale of environmental heterogeneity and its perception by the moving animal (e.g. Johnson *et al.* 2002; Nams & Bourgeois 2004). Furthermore, differences in habitat organization and variability suggest that efficient habitat exploitation requires an adjustment of movement strategies along the vertical axis (Solé, Bartumeus & Gamarra 2005). Consequently, logged rain forest might equally require modified movement behaviours compared with unlogged in response to compositional and physical habitat differences.

Structural path properties (e.g. step lengths and path tortuosity) as well as habitat features along the path may improve our understanding of habitat selection and how individuals exploit their environment. Particularly with respect to generalist and wide-ranging small mammal species, an analysis of movement trajectories in both logged and unlogged rain forest should reveal a separation of species by their substrate use and path properties and should further permit investigating the proximate mechanisms leading to such patterns. This might ultimately contribute to a better understanding of interspecific variation in adaptability to a variable forest environment and explain part of the reasons of the decline or persistence of small mammals in altered rain forest habitats.

Moving efficiently through structurally altered forest types will depend on the potential of a species to adapt to variable environmental parameters with regard to the differences in its utilized habitat range. Overall, the responses of small mammals should differ depending upon the magnitude of the physical constraint faced by the species within or between foraging strata. We therefore hypothesized that the different physical structure in logged forest should lead to different path trajectories. Because species with a similar habitat use are likely to encounter similar features along their path, we expected further that movement trajectories of ecologically and morphologically similar species should be similarly affected by disturbance in relation to habitat partitioning.

Methods

STUDY AREA

The lowland rain forest in Sabah (Malaysia) in northern Borneo has been extensively logged for timber harvesting and for land conversion to implement agricultural plantations, especially oil palms. Currently, only *c.* 5% of the land surface is protected to some extent. About half (*c.* 48%) of the land area is covered with undisturbed or disturbed forest (Sabah Forest Department, pers. comm.). Our study was conducted in three protected and largely undisturbed, unlogged rain forests (Kinabalu National Park 6°2′ N, 116°42′ E, Tawau Hills National Park 4°23′ N, 117°53′ E, Danum Valley Conservation Area 4°57′ N, 117°48′ E) and three logged forests (Kg. Monggis 6°13′ N, 116°45′ E, Kg. Tumbalang 6°8′ N, 116°53′ E, Luasong Field Centre 4°36′ N, 117°23′ E) (Fig. 1). All of the forest stands comprised at least 1000 hectares; they were 17–236 km apart and situated at altitudes of 200–900 m. The sites in unlogged rain forest are characterized by large numbers of dipterocarp trees rising up to 60 m. Whereas the emergents usually grow with their tree crowns separated from each other, trees at medium heights (10 and 40 m) form an interconnected and thus light-shielding canopy. The forest floor is mainly covered by saplings. Dense ground vegetation is limited to patchily distributed treefall gaps and other perturbations. In contrast, the sites in logged forest are characterized by smaller trees with heights of less than 25 m as a result of uncontrolled selective logging about 20–30 years prior to our study. Because of the relatively open canopy, the understorey is typically covered by dense vegetation of abundant plant species, such as ginger (Zingiberaceae), climbing bamboo *Dinochloa* spp. and other vines, sago palms *Metroxylon* spp. and rattan *Calamus* spp. This leads to a structurally highly complex habitat within the first few metres above-ground.

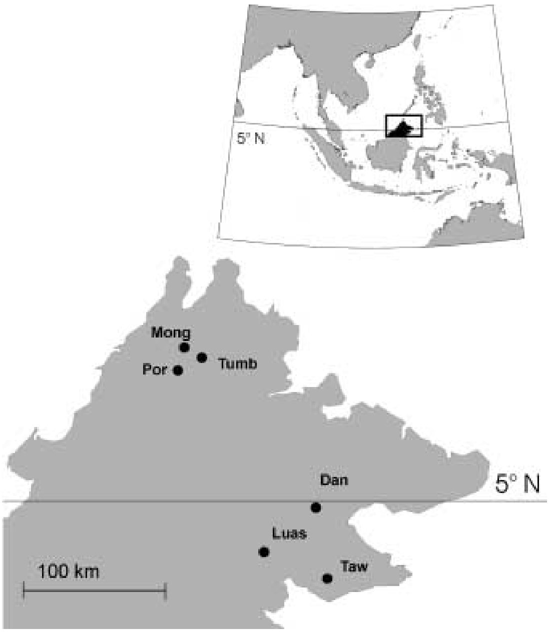

Fig. 1. Map of Borneo with the six study sites. Unlogged forest: Kinabalu NP 'Por'; Tawau Hills NP 'Taw'; Danum Valley Conservation Area 'Dan'; logged forest: Kg. Monggis 'Mong'; Kg. Tumbalang 'Tumb'; Luasong Field Centre 'Luas'.

ANIMAL HANDLING AND SPOOL APPLICATION

Our study focused on eight small mammal species from the families Muridae, Tupaiidae and Sciuridae (Table 1). All are common and occur in unlogged as well as in logged forests.

We classified all species as terrestrial or scansorial (semiterrestrial, active in the first few metres above-ground) except *Niviventer cremoriventer*, which is active both on the ground and in the canopy, and *Leopoldamys sabanus*, which has been occasionally recorded in the canopy (see Lim 1970; Wells *et al.* 2004).

Animals were captured between September 2002 and November 2004 as part of a mark–recapture study on effects of habitat degradation on small mammals at the six study sites. We conducted 18 trapping sessions of 16 days each, alternating between the different forest sites. Locally made wire-mesh live traps (280 mm × 140 mm × 140 mm) baited with banana were placed on the ground in one transect area of 40 trap stations and in two additional areas well separated from each other (usually 0·5–1·1 km, and somewhat less in Kinabalu Park because of topographic conditions). Captured animals were anaesthetized, measured (HF = hind feet, T = tail, and HB = head–body length) (Table 1) and marked with subcutaneous transponders (AEG Trovan, Identification systems, Germany).

For movement analysis, a spool-and-line device consisting of quilting cocoons of approximately 120 m nylon thread (Danfield Ltd, UK) encased by a heat-shrinking tube (total weight *c.* 1·7 g) was glued with cyanoacrylate (Pattex, Henkel, Germany) on to the fur on the back of selected individuals. Fur loss and minor skin irritations caused by the spool had disappeared in all animals that were recaptured about 2 weeks later. Cocoons with threads of different colours were used to facilitate distinction of individual tracks. The free end of the thread was tied to nearby vegetation and labelled. The threads were usually tracked on the day following the animal's release. As initial movements upon release were sometimes influenced by handling, the first 5–10 m of track were discarded and recordings started after the first subsequent change in direction.

Table 1. Studied species, their biometric measurements, and the numbers/lengths of spools recovered in unlogged (UF) and logged (LF) forest. Biometric measurements are given as the mean proportions of hind feet (HF) and tail (T) to head–body length (HB) with one SD

	Biometric measurements of adults			Spools recovered	
Species	Weight (g)	HF/HB (mm)	T/HB (mm)	No. in UF/LF	Total length (m)
Long-tailed giant rat	368 ± 64	0·22 ± 0·01	1·64 ± 0·11	25/24	2 704
Leopoldamys sabanus	(*n* = 101)	(*n* = 84)	(*n* = 74)		
Brown spiny rat	160 ± 35	0·22 ± 0·02	1·12 ± 0·09	10/13	1 341
Maxomys rajah	(*n* = 28)	(*n* = 25)	(*n* = 13)		
Red spiny rat	157 ± 47	0·24 ± 0·02	1·16 ± 0·13	12/4	1 018
Maxomys surifer	(*n* = 38)	(*n* = 35)	(*n* = 23)		
Long-tailed tree rat	69 ± 13	0·21 ± 0·01	1·49 ± 0·09	9/6	720
Niviventer cremoriventer	(*n* = 142)	(*n* = 144)	(*n* = 108)		
Low's squirrel	96 ± 22	0·27 ± 0·02	0·74 ± 0·09	4/4	448
Sundasciurus lowii	(*n* = 24)	(*n* = 22)	(*n* = 22)		
Large treeshrew	218 ± 27	0·25 ± 0·01	0·93 ± 0·06	28/31	3 990
Tupaia tana	(*n* = 126)	(*n* = 110)	(*n* = 106)		
Common treeshrew	196 ± 25	0·27 ± 0·03	1·03 ± 0·07	26/12	3 069
Tupaia longipes	(*n* = 59)	(*n* = 51)	(*n* = 50)		
Slender treeshrew	81 ± 19	0·30 ± 0·01	1·31 ± 0·08	1/3	235
Tupaia gracilis	(*n* = 14)	(*n* = 13)	(*n* = 13)		
Total				212	13 525

Tracks of animals were marked with plastic poles to determine steps lengths (STEPL) of straight-line sections with similar habitat characteristics and no change in direction. The lengths of these sections were measured with a measuring tape to the nearest 10 cm. Changes in direction between steps were assessed with a sighting-compass (Recta DP 65) to the nearest 2°. Threads were followed until they either ran out, had snapped or had been shed off with the spool. Occasionally, the habitat was too difficult for further tracking including movements in nonclimbable trees and in a few cases movement through very dense undergrowth below treefalls.

During tracking, we classified undergrowth density from 0 to 1 m height for an area of approximately 1 m to the left and the right of the track into four groups: (1) light (ground barely covered; plant cover < 20%); (2) intermediate (ground covered mainly by saplings/small trees with litter still visible; plant cover > 20–70%); (3) dense (litter hardly visible because of high density of saplings and gap vegetation; plant cover > 70–90%); and (4) very dense (surroundings completely covered by dense vegetation, litter not visible, mainly forest gaps; plant cover > 90%). For movements of the animals above-ground, we additionally recorded type, diameter and maximal height of supportive structures above-ground.

DATA ANALYSIS

Vertical habitat utilization was categorized into five classes (GR: ground; C1: 1–50 cm above-ground; C2: 50–100 cm above-ground; C3: 1–5 m above-ground; C4: > 5 m above-ground). Nine habitat variables were used to characterize the movement of species within the habitats (see Table 2). We analysed habitat variables for species comparison by pooling data from unlogged forest only. Differences in habitat use were further analysed between sites in logged and unlogged forest for all species.

As the scale of our measurements allowed us only to assess proportions rather than absolute values, we used nonparametric Kruskal–Wallis ANOVA and Mann–Whitney *U* statistics for all variables, using Bonferroni correction for *post-hoc* pair-wise comparisons of variables. To evaluate the overall differences of specific

Table 2. Explanations for variables used to distinguish habitat utilization along movement tracks. Analysis of variables was either individual-based (I) or pooled (P). Some variables were analysed with respect to different above-ground classes C1–C4

Variable	Description	Analysis
NCLIMB	Number of climbing up movements/thread recovered (m)	I, C1–C4
ABVGR	Total length of movements above-ground (m)/thread recovered (m)	I, C1–C4
HTMOV	$\sum$ (Step length (m) * height above-ground (m))/thread recovered (m)	I
MAXHT	Maximum height (m) reached	I
LOGMOV	Movement on logs (m)/thread recovered (m)	I
DIAM	Diameter of supportive structures used (mm)	P, C1–C4
UNDENS	Proportion of movement in the various undergrowth classes ((1)–(4))	I
STEPL	Step length (m) (straight-line sections with no directional or habitat-related change)	I
TANGL	Turning angle between consecutive steps	I

Table 3. Mean of variables given as values relative to 100 m of track length averaged for all individuals except for the variables DIAM, STEPL and TANGL, which were calculated as medians for the pooled data

Habitat variable	*Leopoldamys sabanus*	*Maxomys rajah*	*Maxomys surifer*	*Niviventer cremoriventer*	*Sundasciurus lowii*	*Tupaia longipes*	*Tupaia tana*	*Tupaia gracilis*
NCLIMB C1–C4 (m/100)	4·4	3·3	3·5	8·4	9·6	5·2	4·9	7·2
NCLIMB C2–C4 (m/100)	2·4	0·4	0·9	6·1	4·2	1·6	1·9	3·1
NCLIMB C3–C4 (m/100)	1·4	0·0	0·4	3·6	2·3	0·6	0·6	0·9
ABVGR C1 (m/100)	9·1	6·3	5·1	8·7	16·7	12·5	9·8	13·2
ABVGR C2 (m/100)	3·8	0·6	1·1	6·8	8·8	3·7	5·9	11·4
ABVGR C3 (m/100)	8·0	0·0	2·3	27·8	11·4	2·7	3·0	6·3
HTMOV (m/100)	31·4	1·8	7·2	96·7	29·7	10·9	12·3	26·9
MAXHT (m)	1·7	0·3	0·6	4·1	1·7	1·0	1·1	1·6
LOGMOV (m/100)	6·5	4·4	2·3	4·6	15·4	9·0	9·0	3·8
DIAM (mm)	10·2	11·6	12·2	5·6	14·8	13·2	13·0	11·1
UNDENS (1) (m/100)	14·5	17·2	15·6	13·9	2·0	11·3	4·4	4·2
UNDENS (2) (m/100)	75·9	69·8	67·5	70·7	79·7	61·6	73·9	52·0
UNDENS (3) (m/100)	9·1	12·5	15·9	14·8	17·9	24·5	20·9	42·7
UNDENS (4) (m/100)	0·5	0·4	1·0	0·6	0·4	2·6	0·9	1·1
STEPL (m)	1·9	1·7	1·8	1·6	1·7	2·1	1·9	1·7
TANGL (°)	47	45	47	60	37	45	47	54

paths used by the species, we applied principal components analysis (PCA) to ordinate means of habitat variables for all tracked species in unlogged forest and separately for the five most intensively tracked species in logged and unlogged forest. These ordinations allowed estimation of differences between species or populations by reducing the entire set of parameters to two descriptors encompassing as much variability as possible. Hence, we were able to evaluate movement trajectories of species and populations in different forest types in relation to each other.

The frequency distributions of step lengths were tested in relation to different movement models by using a log-log regression (see Turchin 1998). For this, we pooled data among forest types and applied a Student's *t*-test assessing differences in regression slopes among species in unlogged forests and among populations in logged vs. unlogged forests. As most individuals moved with persistence in one particular direction and as tracks were assumed to comprise orientated paths, we estimated path tortuosity (D/L) as the ratio between the distance from the starting to the final point and the path travelled to reach this distance (see Benhamou 2004).

Results

We obtained a total of 212 movement tracks comprising a total length of 13 525 m from at least 188 individuals (some tracked several times) of the eight focal species. The lengths of individual records varied from 30·1 to 119·1 m (mean 63·8 ± 26·7 m). Additional spooling threads were recovered for a ninth species, the lesser treeshrew *Tupaia minor*. However, this species was not included in our analysis as it spent a large proportion of its activity high in the canopy (> 10 m). Most individuals climbed up vertical trunks or on vines and other supportive structures straight into the canopy after moving a few metres on the ground. This did not permit proper tracking. Similarly, *N. cremoriventer* also frequently approached the upper canopy. Half of all trial threads (50%) could not be fully recovered.

INTERSPECIFIC VARIATIONS IN MOVEMENT TRAJECTORIES

Movement patterns differed significantly between species with regard to most variables (all Kruskal–Wallis ANOVA $H > 15·8$, $P < 0·05$) (Table 3, Fig. 2), except for the proportion of movement in medium and very dense undergrowth (UNDENS (2), (4)), the movement on logs (LOGMOV) and the number of climbing up movements (NCLIMB C1–C4) (all Kruskal–Wallis ANOVA $H < 13·5$, $P > 0·05$). *Post-hoc* pair-wise species comparisons for all dependent variables revealed 135 variables of 518 (26%) that were significantly describing the movement tracks of the eight species. *Niviventer cremoriventer* ($n = 51$), *Maxomys rajah* ($n = 45$) and *T. longipes* ($n = 36$) accounted for most of these differences. For the closely related species *T. longipes* and *T. tana*, we found only a difference in the diameter of supports used 1–5 m above ground (DIAM C3, Mann–Whitney *U*-tests $U = 432$, $P < 0·018$). We found no differences for *M. rajah* and *M. surifer*.

Similar patterns of species segregation were also obtained from PCA (eigenvalues: $\lambda_1 = 10·83$, $\lambda_2 = 4·38$). The first PCA axis represented a gradient of above-ground activity and explained 54% of variability in the movement patterns, whereas the second axis explained 22% of variability mostly attributable to movements on logs, diameter of supports, and undergrowth density (Fig. 3).

The diameter of supportive structures used by small mammals generally declined with movement heights (DIAM, Kruskal–Wallis ANOVA $H_{n=974} = 100·12$, $P <$ 0·01). Vice versa, species that climbed more often than others moved significantly less in light undergrowth

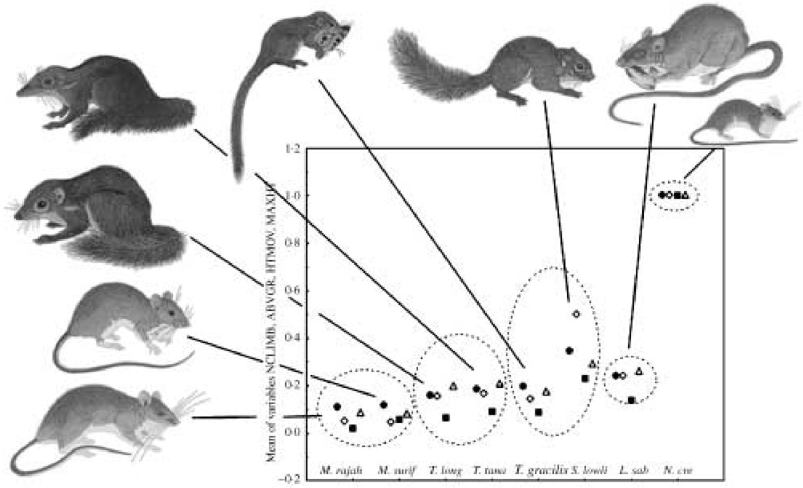

Fig. 2. Mean of variables describing vertical habitat use in eight small mammal species. The three categories (C1–C4) for the variables NCLIMB and ABVGR were pooled so that the mean of all classes were multiplied by class number and an overall mean was calculated. The variables NCLIMB (●), ABVGR (◇), HTMOV (■), and MAXHT (△) are given for all study species. Species with similar habitat use are encircled. The illustrations of the small mammals are reproduced from Payne, Francis & Phillipps (1998) with kind permission from the Sabah Society (Kota Kinabalu, Malaysia).

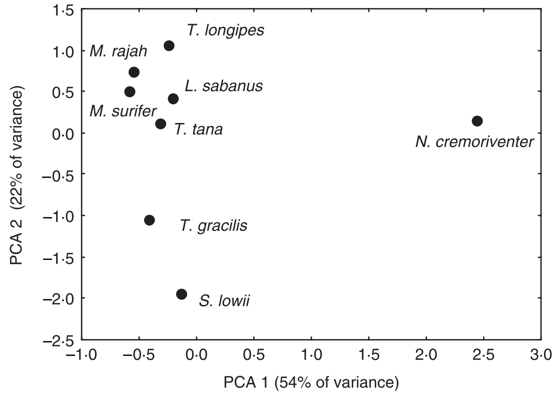

Fig. 3. Principal components analysis (PCA) plot of movement patterns of eight small mammal species based on the means of habitat variables. The first PCA axis represents a gradient in above-ground activity (MAXHT, HTMOV, NCLIMB C2, ABVGR C4), whereas the second axis is mostly explained by LOGMOV, DIAM C2, C3 and UNDENS C2, C1. Eigenvalues: $\lambda_1 = 10{\cdot}83$, $\lambda_2 = 4{\cdot}38$.

(NCLIMB C1, Spearman's $R_{n=8} = -0{\cdot}83$, $P < 0{\cdot}05$) than in denser undergrowth.

The average body mass of species was positively correlated to step length (STEPL, Spearman's $R_{n=8} = 0{\cdot}76$, $P < 0{\cdot}05$). However, we did not find a correlation between body mass and diameter of supports (DIAM, Spearman's $R_{n=8} = 0{\cdot}17$, $P = 0{\cdot}69$) or any other variable. The biometric proportion of hind feet to head–body length (HF/HB, see Table 1) was positively correlated with the movements of the species above-ground and the proportion of movement in dense undergrowth (ABVGR C1, UNDENS 4, both Spearman's $R_{n=8} > 0{\cdot}77$, $P < 0{\cdot}05$) and negatively to the movement in light undergrowth [UNDENS 1, Spearman's $R(n = 8) = -0{\cdot}73$, $P < 0{\cdot}05$]. The biometric proportion of tail length to head–body length (T/HF) was negatively related to the diameter of supports (DIAM, Spearman's $R_{n=8} = -0{\cdot}93$, $P < 0{\cdot}01$).

For the five most intensely tracked species, step-length distributions in unlogged forest did not correspond to a probability distribution that could be normalized (regression slopes $-1{\cdot}15 < \mu < -0{\cdot}74$ (all $r^2 > 0{\cdot}37$) (Fig. 4a,b), indicating that random walk models were not applicable to these movements. The frequency distributions of steps lengths (all Student's *t*-test $t_{v \geq 82} < 1{\cdot}24$, $P > 0{\cdot}20$) and path tortuosity (D/L, Kruskal–Wallis ANOVA $H_{n=101} = 11{\cdot}82$, $P = 0{\cdot}11$) did not differ among these species, indicating that principal structural path organization was similar among species.

MOVEMENT PATTERNS IN LOGGED VS. UNLOGGED FOREST

All species differed in their movement patterns between logged and unlogged forest, with most changes recorded for *L. sabanus* (Table 4). *Maxomys rajah* and *L. sabanus* travelled significantly longer distances at heights of 1–50 cm in unlogged than in logged forest (ABVGR C1, both Mann–Whitney *U* test $U > 30$, $P < 0{\cdot}05$). However, whereas these differences in the above-ground movements at this height indicated more above-ground activity for *M. rajah* in unlogged forest, the opposite was true for *L. sabanus*, which moved on average longer distances (although not significantly) at heights between 1 and 5 m in logged forest and was recorded three times to climb up in the canopy > 5 m in logged forest, but never in unlogged forest. *Niviventer cremoriventer* climbed more often above heights of 50 cm in unlogged forest (NCLIMB C2–C4, Mann–Whitney *U* test, $U = 8$, $P < 0{\cdot}05$) and travelled longer distances at heights between 1 and 50 cm in unlogged than in logged forest (ABVGR C1, Mann–Whitney *U* test, $U = 10$, $P < 0{\cdot}05$). Whereas *M. rajah* used the above-ground habitat more intensely

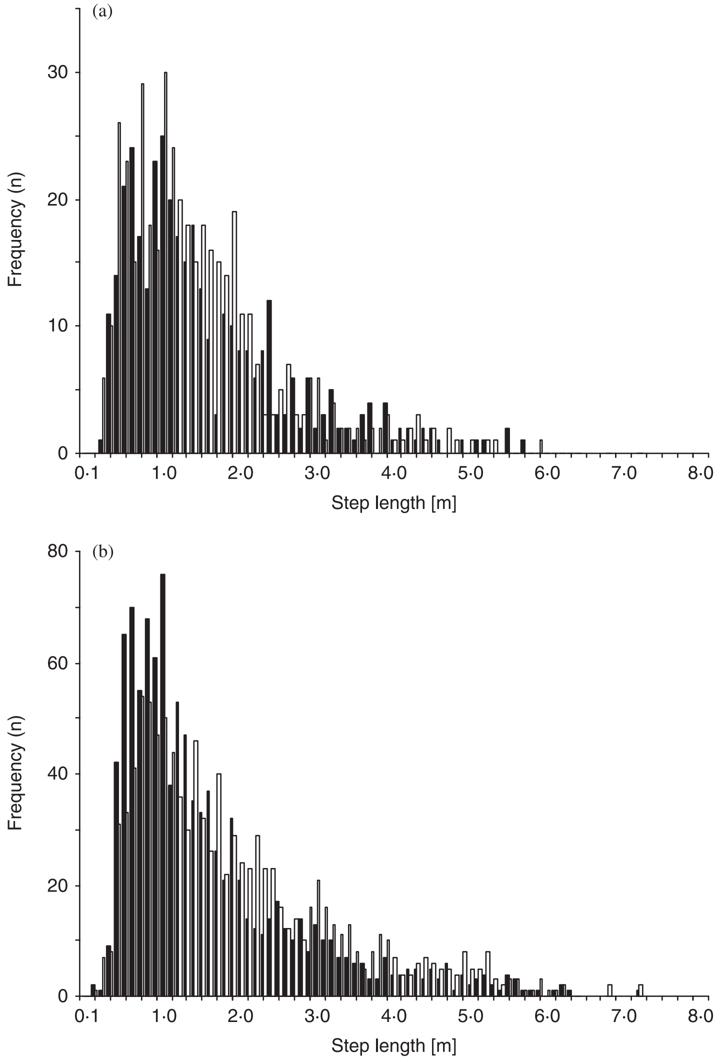

Fig. 4. Frequency distribution of step lengths (STEPL) for *Maxomys rajah* (a), and *Tupaia tana* (b). Distributions are given for movements in unlogged (black bars) and logged (white) forest. Data comprise a total of 804 steps for *M. rajah* and 1090 steps for *T. tana*.

in unlogged forest (HTMOV, Mann–Whitney *U* test, $U = 33{\cdot}0$, $P < 0{\cdot}05$) and climbed on average higher up in unlogged than in logged forest (MAXHT, Mann–Whitney *U* test, $U = 27{\cdot}5$ $P < 0{\cdot}05$), *T. longipes* used the above-ground habitat more intensely in logged forest (HTMOV, Mann–Whitney *U* test, $U = 82{\cdot}5$, $P < 0{\cdot}05$). Thus, *T. longipes* and *L. sabanus* revealed an increase in above-ground movement in logged forest, whereas *M. rajah* decreased in its above-ground activity in logged forest.

Table 4. Intraspecific differences in movement trajectories between unlogged and logged forest. The two means refer to relative values from 100 m of track length in unlogged–logged forest. *Z*-values indicating significant differences for means of variables with $P < 0{\cdot}05$ (Mann–Whitney *U* tests) are given in parenthesis. Positive values refer to higher averaged values for unlogged forest, whereas blank cells represent nonsignificant comparisons

	Leopoldamys sabanus	*Maxomys rajah*	*Maxomys surifer*	*Niviventer cremoriventer*	*Sundasciurus lowii*	*Tupaia longipes*	*Tupaia tana*	*Tupaia gracilis*
NCLIMB C2–C4	–	–	–	10–3 (2·24)	–	–	–	–
ABVGR C1	13–5 (2·11)	10–3 (2·14)	–	16–5 (2·00)	–	–	–	–
HTMOV	–	3–1 (1·98)	–	–	–	8–14 (–2·31)	–	–
MAXHT	–	0·44–0·13 (2·33)	–	–	–	–	–	–
LOGMOV	11–2 (3·35)	–	–	–	44–6 (2·00)	–	–	–
DIAM	15–6 (5·88)	–	–	–	27–10 (3·62)	15–11 (2·04)	–	27–4 (2·76)
UNDENS (1)	24–5 (2·44)	–	–	–	–	–	–	–
UNDENS (2)	68–84 (–2·56)	–	–	–	–	–	79–69 (2·24)	–
UNDENS (3)	–	–	–	–	–	–	16–25 (–2·09)	–
STEPL	2·2–1·7 (6·90)	–	1·5–1·9 (–3·51)	–	–	2·3–1·9 (4·33)	1·7–2·1 (–6·57)	–
TANGL	49–44 (–3·46)	–	–	–	–	–	–	–

Both *L. sabanus* and *S. lowii* moved longer distances on logs in unlogged than in logged forest (LOGMOV, both Mann–Whitney *U* test $P < 0·05$). The diameter of supportive structures used by *L. sabanus*, *T. longipes*, *T. gracilis* and *S. lowii* were larger in unlogged forest (DIAM, for all Mann–Whitney *U* test $U > 24·0$, $P < 0·05$) and marginally larger for all other species in logged than in logged forest. *L. sabanus* moved greater distances in regions with light undergrowth and shorter distances in intermediate undergrowth areas in unlogged forest (UNDENS, both Mann–Whitney *U* tests $U > 170$, $P < 0·05$). *T. tana* moved longer distances in areas with intermediate undergrowth but shorter distances in dense undergrowth in unlogged than in logged forest (UNDENS, both Mann–Whitney *U* tests $U > 286$, $P < 0·05$). Step lengths were shorter for *L. sabanus* and *T. longipes* in logged forests, whereas step lengths were longer for *M. surifer* and *T. tana* in logged forest (STEPL, all Mann–Whitney *U* tests $U > 196{,}291$, $P < 0·01$). Absolute turning angles between steps were smaller for *L. sabanus* in logged forest (TANGL, Mann–Whitney *U* test, $U = 206{,}593$, $P < 0·01$). However, despite these differences in path properties, we found no differences in the frequency distributions of step lengths (all Student's *t*-test $-0·55 < t_{\nu \geq 88} < 0·80$, $P > 0·20$) or path tortuosity (D/L, all Kruskal–Wallis ANOVA $P > 0·12$) among forest types for any of the five most intensively tracked species.

Analysis of differences of variable means between species and population of the five most intensively studied species in unlogged and logged forest by PCA (eigenvalues: $\lambda_1 = 8·68$, $\lambda_2 = 4·52$, Fig. 5) confirmed that all species changed their movement patterns, whereby the changes were most obvious for *L. sabanus*. Notably, the directions of changes in the resulting multivariate space were opposite for the species pairs *T. longipes* and *T. tana* as well as for *M. rajah* and *M. surifer* (Fig. 5).

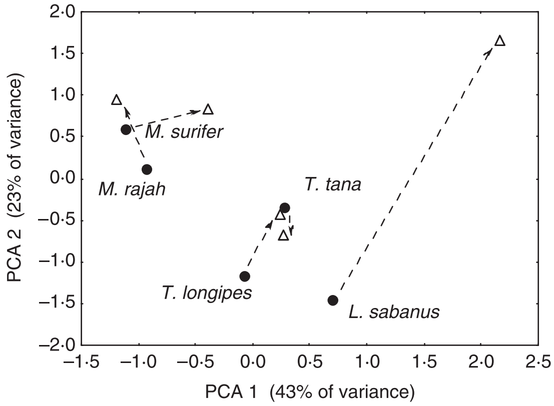

Fig. 5. Principal components analysis plot of movement trajectories of the five most intensively tracked species in unlogged (closed circles) and logged (open triangles) forest based on the means of variables. Arrows indicate the direction of changes in movement patterns in multivariate space between unlogged and logged forest. The first axis is mainly explained by MAXHT, ABVGR C2, C3 and HTMOV, whereas axis 2 is mainly described by LOGMOV, NCLIMB C1, and TANGL. Eigenvalues: $\lambda_1 = 8·68$, $\lambda_2 = 4·52$.

Discussion

INTERSPECIFIC VARIATIONS IN MOVEMENT TRAJECTORIES

The segregation of small mammals in tropical assemblages along vertical strata and/or by body size is considered to favour coexistence in species-rich communities (e.g. Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1995; Voss & Emmons 1996; Bakker & Kelt 2000; Cunha & Vieira 2002). Although most studies have been conducted up to now in the neotropics and less is known about small mammal assemblages in the forests of South-east Asia, similar patterns in substrate use have been suggested for the neo- and the palaeotropics because of general constraints in climbing ability and adaptations to the arboreal/scansorial habitat (Emmons 1995).

Our results demonstrate that small Bornean mammals, which are mostly characterized as terrestrial/scansorial, differ in their movement trajectories with regard to several structural habitat features. Conversely, we found no differences in structural path properties that might indicate differences in movement patterns of species that differ in habitat use or morphometric features, despite the increase in step lengths with body size. Our results contrast with a study on small-scale movement strategies of American martens that were associated with structural features (Nams & Burgeois 2004). The small-scale movement pattern should differ from movements on larger scales as a response to resource distribution, which might more likely represent large-scale effects of habitat variability (e.g. Johnson *et al.* 2002; Ramos-Fernández *et al.* 2004; Solé *et al.* 2005).

Overall, our results revealed for the local assemblages on Borneo five groups of small mammals in relation to habitat use: (1) terrestrial species (*M. rajah*, *M. surifer*); (2) species that were mostly active on the ground but occasionally reached the upper canopy (*L. sabanus*); (3) terrestrial species with frequent scansorial activity (*T. tana*, *T. longipes*); (4) scansorial species that were not active in the canopy (*T. gracilis*, *S. lowii*); and, finally (5) arboreal species that occasionally approached the ground (*N. cremoriventer*, *T. minor*). We confirmed occasional arboreal activity of *L. sabanus*, although this species spends proportionally much more time on the ground than the scansorial species *S. lowii* and *T. gracilis*.

The general activity patterns were similar to those noted for mammal assemblages in the neotropics (see Charles-Dominique *et al.* 1981; Voss & Emmons 1996; Cunha & Vieira 2002). However, in contrast to studies at neotropical sites, climbing activity of small mammals was not related to body size but rather to morphometric measures (HF/HB and T/HB), indicating that species of variable sizes are adapted to cursorial vs. arboreal activity. Although some convergences of small mammals have been reported for neo- and palaeotropic assemblages (see Emmons 1995), patterns in body-size distribution cannot necessarily expected to be equivalent. It has been suggested that arboreal vertebrates in the neotropics are in general smaller than palaeotropical vertebrates because canopy structure is reported to be more fragile in the neotropics (Cristoffer 1987). Differences in morphological modifications such as gliding that occurs predominantly in the palaeotropics or prehensile tails that are prevalent in the neotropics may in turn affect accessibility and use of vegetation structures (Emmons & Gentry 1983). On the other hand, studies on neotropical assemblages of small mammals that contained only few species usually included also some larger bodied, mostly terrestrial didelphids, such as *Didelphis* spp. or *Metachirus* spp. (body mass > 500 g and 1 kg, respectively; references above) that might have biased the conclusions on body size distribution drawn from these assemblages.

Interestingly, habitat segregation was weak between the two species pairs based on similarities in morphology: *Maxomys rajah* and *M. surifer* as well as *T. longipes* and *T. tana*. However, as both species pairs exhibit paraphyletic relationships (Ruedas & Kirsch 1997; Han, Sheldon & Stuebing 2000), similarities in morphological appearance and body size represent convergent adaptations to their similar life styles and ecological niches. In contrast, the two smaller treeshrews *T. gracilis* and *T. minor*, which also exhibited substantial convergence in body size and morphology (Han *et al.* 2000), used distinct habitats along the vertical axis. Whereas *T. gracilis* was confined to the scansorial layer, *T. minor* was active in the upper canopy with occasional descents to the ground.

The two larger treeshrews *T. longipes* and *T. tana*, which have been mainly described as terrestrial based on field observations (Emmons 2000) and morphological traits (Sargis 2001), revealed greater climbing activity than terrestrial spiny rats, with half of all of their tracks reaching heights of 1 m or higher. Although both species were similar with regard to their movement trajectories, the higher scansorial activity of *T. tana* was not expected because it had been reported to actively dig in the leaf litter and soil for foraging, whereas the prey of *T. longipes* is probably located more on the surface of the forest floor (Emmons 2000). Therefore, with regard to our findings, orientated movement and foraging of these species may take place in different microhabitats and utilization of resource patches and interpatch movement may be independent of each other.

If rain forest mammals partition resources along the vertical axis, the finding that closely related species share a similar habitat is of much interest. The described patterns demonstrate that many factors determine assemblage structure and resource partitioning, where morphological characteristics are as important as further unknown factors, such as possible energetic constraints along the vertical axis. Further, if habitat heterogeneity and scaling effects differ between different strata, we would expect more pronounced effects of vertical habitat partitioning on the overall movement strategy contrary to our results on this single investigated scale of orientated paths.

MOVEMENT PATTERNS IN LOGGED VS. UNLOGGED FOREST

One reason that species occur in particular sets of habitats is that they are adapted to specific ecological conditions. Therefore, the potential of a species to cope with environmental variability is an important determinant in species distribution from a local to regional scale and throughout its geographical range, particularly in the heterogeneous rain forest environment. We found little evidence that any of the investigated species was restricted to a single set of habitat type and structure. Our comparisons of movement trajectories of small mammals between logged and unlogged forests clearly showed that highly modified forest structures in logged forests affected the movement trajectories of all species. The observed shifts in movement trajectories might result from the altered structure *per se*, changes in vertical partitioning of resources (e.g. Cunha & Vieira 2002) or differences in spatial orientation and environmental perception by the respective species because of the altered habitat structure (e.g. Grobety & Schenk 1992; Jacobs & Shiflett 1999). Contrary to our expectations, we found no evidence that pathways were adjusted to possible shifts in habitat heterogeneity and variability, as overall movement strategies were found to be similar in logged and unlogged forests. This weak effect of physical habitat differentiation on pathway structures reinforces the conclusion of a rather fixed movement strategy for the examined scale, as we found no differences across species or populations in different forest types.

As the response of individual species to habitat alteration was very variable, the effects of changes in habitat structure on small mammal assemblages are difficult to interpret when only single species are examined. Our results show convincingly that one needs to address the entire set of focal species for a given habitat type to reach a valid conclusion. Some general shifts in habitat use become evident when we consider the most drastic habitat change with regard to disturbance, here the reduction of canopy space and structure caused by the extraction of emergent trees in logged forests. As a consequence, arboreal species and biomass may shift from the canopy to the ground in logged forests (Malcolm 1997; Struhsaker 1997). Furthermore, differences in branch dimension and structure may alter connectivity and thus movement tracks of animals (Malcolm 1995). The predicted shifts in vertical movement patterns in response to habitat differences between understorey and canopy of logged vs. unlogged forest were less evident as we encountered terrestrial and scansorial species in logged forest with denser undergrowth and a higher variety of supportive structures at almost equal proportions. Probably, species might quickly change between two neighbouring habitat layers (here ground vs. understorey supports) and habitat differences such as microclimate between these layers might affect the species less than expected, leading to a continuous gradient in habitat use rather than a strict terrestrial–arboreal dichotomy.

A general difference of movement trajectories between the two habitat types was only found for the diameter of supportive structures, which declined in logged forests. It needs to be noted that this general pattern refers to an overall difference in branch diameters rather than to particular preferences of small mammals for particular supportive structures. There were, for example, fewer large logs or thick arboreal branches in logged forests, whereas the abundance of thin supports increased in the understorey particularly because of the fast growing and highly abundant climbing bamboo with diameters between 1 and 3 cm that is frequently used for climbing by various species of small mammals (pers. obs.). Smaller climbing mammals might profit from thin supports because of less body mass (Lemelin 1999; Cunha & Vieira 2002), although Charles-Dominique *et al.* (1981) did not find a relationship between the diameter of supports and body sizes in an assemblage of mammals in the neotropics. However, the potential consequences of thinner supports in logged forests for individual species or the entire assemblage remain unclear. For example, *L. sabanus*, the largest focal species, frequently used thin supports (*c.* 20% of used supports = 2 cm) and showed increased climbing activity in logged forests, whereas the climbing activity of the much smaller *N. cremoriventer* was reduced in logged forests, although this species showed in general a clear preference for small diameters (Table 3). This observed variability might not be independent of other features, such as texture or the interconnectivity of supports. No general trend was found for the proportion of movements in dense undergrowth, although all species faced denser undergrowth in logged forests. Only *T. tana* and *L. sabanus* moved longer distances in dense undergrowth in logged forests. Diurnal treeshrews might profit from dense ground cover as a strategy for predator avoidance (Emmons 2000) as they generally move greater distances in dense undergrowth than nocturnal rats. Although this strategy has been suggested for several tropical small mammals (e.g. Emmons 2000; Lambert & Adler 2000; Vernes 2003) it needs to be tested with behavioural experiments and with further information with respect to associated structural, abiotic and biotic habitat features. Little is known about such differences between logged and unlogged forests. Studies comparing small mammals in undisturbed forests and tree-fall gaps therein indicate that various factors such as resource availability or protection from predators may differ in their impact on syntopic small mammals and the pay-off for them to move in densely covered gaps (Beck *et al.* 2004).

The arguments so far led us to the conclusion that any particular habitat change such as structural differences between logged and unlogged forests is closely linked to other habitat variables that might have either synergistic or reciprocal effects on small mammal movement, depending on the specific combination of intrinsic and environmental factors. Therefore, changes in movement trajectories between forest habitats must be analysed in a multivariate approach. Our analysis suggests that specific movement patterns differ between logged and unlogged forest whereby variables related to climbing activity play a dominant role (see Fig. 5). We did not detect any trends in shifts of movement patterns with regard to body size, taxonomic grouping or vertical stratification. Further, no parallel trends were seen in the shift of movement trajectories for congeneric species pairs such as *M. rajah* and *M. surifer* or *T. longipes* and *T. tana* despite their strong convergence in morphology and habitat use.

These results highlight the importance of qualitative habitat alterations and their impact on small forest-dwelling mammals. Fortunately, most of the common species such as those in our study were able to persist in logged forest habitats. However, preliminary data from our study as well as other studies suggest that more specialized species that are rare in logged forest react negatively to environmental variability (e.g. Henein, Wegner & Merriam 1998; Purvis *et al.* 2000; Wells, pers. obs.). The results presented here are preliminary in that neither the ultimate reasons for changes in movement trajectories nor the consequences for foraging success, individual survival and population establishment can be given because of the lack of knowledge regarding the ecology of the species, in particular the rarer ones. However, first data on how species react in their movement patterns to habitat disturbance provide a promising approach for a better understanding of interspecific variation in adaptability to altered ecological conditions, determining decline or persistence of tropical rain forest mammals in local assemblages. The observed inconsistency in the species' responses to logging cautions the approach to extrapolate results obtained from a few species to a whole assemblage, underlining the importance of species-based approaches in understanding the effects of habitat degradation on speciose assemblages.

Acknowledgements

We thank the Economic Planning Unit, Malaysia, for a research permit and Sabah Parks, Yayasan Sabah, the Royal Society SE-Asia Rainforest Research Programme (SEARR), and the University Malaysia Sabah for support during our fieldwork and for allowing us access to various forest sites. We are grateful to Doreen Fetting, Awang Kiddra, Tobias Lenz, Manuel Hitzler, Caroline Rosenberger and Jickson Sankin, among others for their help in the field and their patience following threads in habitats obviously not made for the movements of larger mammals. We thank Karl Vernes, Graeme Hays, and anonymous referees for improving earlier drafts of the manuscript. Danfield Ltd, UK, provided the tracking spools without charge. Financial support was kindly provided to K.W. by the German Academic Exchange Service (DAAD).

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Received 15 March 2006; accepted 14 June 2006

MOVEMENT AND RANGING PATTERNS OF A TROPICAL RAT (*LEOPOLDAMYS SABANUS*) IN LOGGED AND UNLOGGED RAINFORESTS

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ABSTRACT: Knowledge of how animals move through the environment is important for predicting effects of habitat change on faunal distributions. Logging of tropical rainforests produces habitat changes on multiple scales that may affect movement and habitat use by small mammals. To explore the effects of such habitat changes, we compared movement and ranging patterns of the long-tailed giant rat (*Leopoldamys sabanus*) in logged and unlogged rainforests on Borneo. On a small scale, movement was quantified using spool-and-line tracks; on a larger scale, movement was quantified via radio-tracking. At the small scale, paths (49 tracks of 55.2 ± 20.7 m each) were relatively straight, with similar step (straight-line section) length distributions in both forest types. At the larger scale, the rats (16 individuals tracked for 4 nights each, mean = 1,443 ± 991 m of movement per night) moved with similar speed through both forest types (mean distance covered per 10-min interval = 32 ± 45 m). Based on telemetry data, mean nightly activity periods for individual rats averaged 485 ± 109 min (areas covered = 2,083 - 9,829 m^2), with no statistically significant differences between logged and unlogged forests. The large variability in individual movement parameters was not predicted by sex or forest type, suggesting that the paths taken were most likely responses to the local distribution of resources in a heterogeneous rainforest environment. We conclude that the logged and unlogged forest did not differ with respect to features that are important to movement and ranging patterns of *L. sabanus*, suggesting that general differences associated with logging may not predict the effects of this type of disturbance on habitat use by individual species of small mammals.

KEY WORDS: Foraging, forest structure, home range, logging, movement trajectories, Muridae, radio-tracking

INTRODUCTION

The decision rules that determine animal movement patterns are likely influenced by environmental features. Animals perceive those features and respond to them by modifying their movement patterns to optimize resource use. The resources that animals search for (e.g., food, mates, shelter) are components of an interaction-dispersion matrix, in which a forager's movements are determined by environmental conditions and the distribution of resources in the habitat. For example, the tortuosity (divergence from a straight line movement) of movement paths is tightly linked to features of the landscape. Consequently, features such as logs, branches, and dense undergrowth that non-volant mammals use to move through habitats may influence their progression through the habitat. Since resources in heterogeneous landscapes are often patchily distributed (Solé and Manrubia 1995), the manner in which animals use movement to encounter those resources has generated considerable interest (Kotliar and Wiens 1990; Johnson et al. 2002; Fauchald and Tveraa 2003; Fritz et al. 2003; Boyer et al. 2006).

Understanding how animals interact with their environment requires selecting the proper scale for analysis and determining how to describe movement trajectories. In this context, the description of movement patterns using a diffusion equation modified from a Brownian motion model of independent straight-line movements (step lengths) has been successfully employed to predict dispersal over limited spatiotemporal scales (Kareiva and Shigesada 1983; Turchin 1998). However, such uncorrelated random walk models are based on the assumption of a landscape with even distribution of resources and do not take into account structural components such as the patchy distribution of resources in a heterogeneous rainforest matrix (Nolet and Mooij 2002; Morales et al. 2004). In tropical rainforests, the highly diverse tree assemblages that largely determine local habitat structure and resource distribution often vary in numbers and degrees of aggregation (Condit et al. 2000). This type of structure suggests that movement strategies consisting of long, straight-line movements of variable length interrupted by localized random motions (e.g., Lévy walk processes: Shlesinger et al. 1993; Bénichou et al. 2005; Boyer et al. 2006) are more efficient than are Brownian dispersal strategies (Viswanathan et al. 1996; Mårell et al. 2002; Ramos-Fernández et al. 2004; Solé et al. 2005; Boyer et al. 2006).

The rapid alteration and destruction of rainforests resulting from timber harvesting and agricultural land use adds a major component of habitat variability to tropical environments, with as yet unforeseeable consequences for wildlife species. Logged tropical rainforests differ from unlogged forests not only in terms of floral composition, but also in type and scale of habitat heterogeneity. The former contain fewer species of trees per area than unlogged forests, and are particularly depauperate in large emergent species (Cannon et al. 1998). Animals moving through logged rainforests encounter differences in structure (e.g., denser undergrowth in combination with a reduced canopy) and resource allocation (e.g., different floral composition leading to differences in plant resource variety and abundance) (DeWalt et al. 2003) that are likely to affect foraging strategies and constrain patterns of animal movements, for instance by changing movement speed, distance, and efficiency of resource encounter (Rettie and Messier 2000; Johnson et al. 2002; Fauchald and Tveraa 2003). Hence it is important to identify how forest degradation affects movement behavior and to understand the causes of differences in movement patterns between logged and unlogged habitats.

The long-tailed giant rat (*Leopoldamys sabanus*) is present throughout the Sunda region of SE Asia and is a common, generalist species in local assemblages of small mammals (Lim 1970). Giant rats are mostly active on the ground with occasional forays up into the canopy. In a recent analysis of habitat utilization by *L. sabanus* based on spool-and-line-tracks, we showed that in logged forests a larger proportion of movement occurs above ground and involves shorter step lengths compared to unlogged forests (Wells et al. 2006). Further, in logged forests, the diameters of supports (e.g., branches) used by the rats are smaller and logs are more frequently used as pathways (Wells et al. 2006). Based on these data, we predicted that the differences in physical structure between logged and unlogged forest should lead to differences in the geometry of path trajectories (e.g., distribution of step lengths, path tortuosity) at small spatial scales. We further predicted that the changes in forest structure due to anthropogenic disturbance should lead to larger scale differences in movement and ranging behavior (e.g., home range sizes) in logged versus unlogged habitats.

METHODS

Study sites. The study was conducted in 3 logged and 3 unlogged forest sites in northern Borneo (Sabah, Malaysia). The unlogged sites consisted of 3 of the few remaining remnants of unlogged lowland rainforest in Sabah that have been designated as national parks or conservation areas. The sites were located in the Danum Valley Conservation Area (UF1: 4°57'N, 117°48'E), Kinabalu National Park (UF2: 6°02'N, 116°42'E), and Tawau Hills National Park (UF3: 4°23'N, 117°53'E). The logged forest study sites were harvested 20-30 years before our study, resulting in the extraction of most dipterocarp and other large tree species. The logged sites were located at Luasong Field Centre (LF1: 4°36'N, 117°23'E), Kampung Monggis (LF2: 6°13'N, 116°45'E), and Kampung Tumbalang (LF3: 6°08'N, 116°53'E). Details on the logging histories of the study sites were not available, but all logged forest stands differed considerably from unlogged forests, with the former characterized by reduced canopy heights (approximately 15-25 m versus 60-70 m at unlogged sites), more frequent canopy gaps, and denser understory growth (see also Wells et al. 2007).

Animal capture and tracking techniques. Rats were captured with locally made wire-mesh cage traps (280 mm × 140 mm × 140 mm) baited with banana. Trapping was conducted daily during 18 consecutive trapping sessions at the study sites between December 2002 and November 2004. All rats captured were marked with transponders (ARE 162, AEG Identification Systems) implanted beneath the skin.

Small-scale movement patterns were quantified using spool-and-line tracking. A spool-and-line device consisting of a quilting cocoon containing approximately 120 m of nylon thread (Danfield Ltd) and encased in a heat-shrunk plastic tube (total weight: *ca*. 1.7 g) was glued onto the back of selected individuals with cyanoacrylate (Pattex, Henkel). One end of the thread was tied to nearby vegetation and labeled with the animal's identification number and the date of release. As the animal moved away from the point of capture, the thread was pulled from the cocoon, leaving a readily followed trace of the individual's movements. The path created by each thread was usually examined the day following the release of the animal. We used plastic poles to mark the sections of the track during which the animal had moved in a straight line, with no detectable changes in direction (i.e. no bends in the thread). The number of steps per thread was recorded and length of each straight section ('step length') was measured to the nearest 0.1 m. The angle of the change in direction between steps was recorded with a sighting-compass to the nearest two degrees.

Larger scale patterns of movement were examined using radiotelemetry. Individuals that had been followed with spool-and-line tracking were recaptured and fitted with radio collars (Biotrack). The radio transmitters used broadcast at ca 150 MHz and weighed less than 3% of an individual rat's body mass (Choate et al. 1998). Individual rats were tracked for at least 4 consecutive nights from dusk (17:00 h –18:30 h) until dawn (approximately 05:00 h). Radiotracking was halted if an animal returned to its den during the night and remained inactive for > 2 hours. Some tracking nights ended before dawn because of injury or fatigue of the investigator. Radio fixes were taken at 10-min intervals. Recordings were made using a hand-held Yaesu VR-500 receiver (Yaesu Musen Co Ltd) with a modified hand-held H-aerial antenna (Wagener Telemetrieanlagen). To estimate the locations of rats, compass bearings were recorded relative to selected reference points marked with plastic poles; for each fix, 2 compass bearings for the same animal were taken at 1-min intervals and the actual location of the rat was triangulated from these data. To facilitate movement of the investigators between reference points, dense undergrowth vegetation was removed to create easily traversable paths between reference points; the minimal vegetation cleared to create paths should not have affected movements or space use by the study subjects.

The hilly terrain and dense vegetation at all study sites made radio tracking difficult and resulted in an estimated error of 10-30 m (determined from collars put at known locations) for our triangulated radio fixes. For a moving animal, this error increased to 40-50 m because of the 1-min time lag between consecutive compass bearings for the same fix. Although rats were occasionally spotted near reference points, there was no noticeable impact of the investigator`s proximity on rat movement patterns (e.g., animals did not consistently move away from investigators). Despite the differences in undergrowth density and forest structure between logged and unlogged forests, to the best of our knowledge there was no consistent bias in the accuracy of tracking data from one habitat versus the other. At the end of the telemetry study, the rats were recaptured and their radio collars were removed. The animals were handled following the animal care guidelines of the American Society of Mammalogists (Choate et al. 1998). The study was approved by the Economic Planning Unit at the Prime Minister's Department in Kuala Lumpur.

Data analysis. Movements at both the small and large spatial scales were determined assuming that an animal walked in a straight line between consecutive bends in the thread or consecutive radio fixes (Figs. 1, 2). Analysis of paths was based on step lengths and turning angles and, for telemetry data, movement speeds. Measurements from spool-and-line tracking were made directly, as described above. For analyses of turning angles from spool-and-line tracks, we used Rayleigh's circular statistic to test the null hypothesis that the distribution of these angles was random (Batschelet 1981). Prior to analyzing the telemetry data, it was necessary to determine the specific locations of rats from our triangulated radio-tracking data; this was done using a maximum likelihood estimator contained in the LOAS software package (version 3.0.3, http://www.ecostats.com/software/). For these analyses, we excluded any points that fell more than 100 m from all other fix locations for the same animal and that had distances greater than 200 m to neighboring point estimates.

The frequency distributions of step lengths and movement speeds were tested for a power law distribution by a plotting method based on logarithmic binning (2k) with normalization prior to log transformation of both axes (see Sims et al. 2007). For this, we pooled data on forest type or sex and applied a Student's t-test for testing differences in regression slopes (Zar 1999). We analyzed the radio-tracking data by placing the distances moved per 10 min interval ('movement speed') into 10 m bins; despite the estimated error of 10-50 m between fixes, many of the distances moved were larger than this and thus we considered these analyses to be meaningful. We tested for possible relationships between the physical and temporal distances between changes in movement paths using Mantel (1967) statistics, with Mantel correlograms representing the extent of spatial autocorrelation in such paths (Cushman et al. 2005). Thus, generally straight-line movements should show a high degree of correlation in contrast to more tortuous (multi-directional) paths.

Home ranges were determined using the fixed kernel method (Worton 1989) at the 90% ('median range') and 50% ('core range') utilization levels. Telemetry data collected for the same animal on different nights were analyzed separately; subsequent analyses were conducted using mean or median nightly values. Estimations of home ranges were completed using the Animal Movement 2.04 extension (Hooge and Eichenlaub 1997) in ArcView 3.2a GIS (ESRI). Least squares cross validation (LSCV) was used to estimate the smoothing factor for these analyses; we applied a constant smoothing factor of h = 12.089. Because fixes were obtained at regular time intervals and over a standardized number of days, we assumed that the ranging behavior of individuals was most realistically described by the entire data set. Rather than estimating 'absolute' ranges, we focused on factors potentially determining the variance in nocturnal ranges within and between individuals.

We note that our radiotelemetry data may have been subject to problems of autocorrelation due to both the time interval between fixes and the potential error associated with our estimates of animal locations. While autocorrelation is typically expected to confound subsequent analyses of space use and movement (see Hurlbert 1984; Swihart and Slade 1985), an increasing number of studies emphasize the informative nature of non-independent measures for some questions (see De Solla et al. 1999; Cushman et al. 2005; Börger et al. 2006). To assess the potential effects of autocorrelation on our data set, we compared the distributions of movement speeds and home range sizes estimated from 10-min inter-fix intervals with those estimated using a 30-min inter-fix interval. Based on these analyses (see results), we retained the 10-min inter-fix interval and did not exclude the smallest distance measures from our analyses. Although our findings should perhaps be interpreted with caution, we believe that inclusion of these data is informative regarding the behavior of our study species.

To test for the effects of forest type and sex on home range size, movement speed, and total duration of nightly activity, we used linear mixed effects models with restricted likelihood estimation (Pinheiro and Bates 2000), as implemented in the 'nlme 3.1-81'-package (Pinheiro et al. 2007) for the open-source statistical software R, version 2.5.0 (R Development Core Team 2007). For these analyses, we fitted forest type and sex as fixed and random effects, respectively, while data were grouped according to study site and individuals were nested within the different sites. For estimates of the variation among consecutive measurements from individual paths, we used the coefficient of variation, which was calculated as $CV = (SD/\text{mean}) * 100$. Means are given as ± 1 *SD*.

RESULTS

We obtained a total of 49 spool-and-line tracks with total lengths > 30 m (mean length = 55.2 ± 20.7 m, $N = 25$ individuals in unlogged forest and 24 individuals in logged forest). Sixteen individuals (9 males and 7 females) were radio-tracked for at least 4 consecutive nights; 9 of these animals (3 males, 6 females) were from unlogged forest while 7 (6 males, 1 female) were from logged forests. From these animals, we obtained a total of 2,829 fixes (mean = 177 ± 44 fixes per individual), with individuals located and radio fixes obtained for approximately 80% of our radio tracking efforts.

Small-scale movement patterns. Distributions of step lengths followed a power-law distribution. Comparisons of slopes obtained from the regression of step length frequencies on binning classes revealed no significant differences between logged and unlogged forests (Student's t-test $t_{v=6} = 0.67$, $P > 0.05$, Fig. 3), despite the shorter step lengths in logged forests reported previously (Wells et al. 2006). Further, step length distributions did not differ between males and females in either habitat (both Student's t-test $t < 0.16$, $P > 0.05$). Although we found significant serial correlations between step length, the 2 prior, and the 2 subsequent steps for 3 of the 49 spool-and-line tracks examined (all Spearman rank $R > 0.31$, $P < 0.01$), no significant relationships between these variables were found for the remaining tracks considered. Step lengths were positively correlated with turning angles in 1 spool-and-line track ($R = 0.79$, $P < 0.01$), while a negative correlation between these variables was obtained for 6 other tracks (all $R < -0.35$, $P < 0.05$).

The mean turning angle recorded from spool-and-line tracks did not differ significantly between forest types (logged: 9 ± 11°, $N = 24$; unlogged: 9 ± 8°, $N = 25$; Mann-Whitney U-test *U*

= 274, $P = 0.60$). Persistence, defined as a non-random distribution of turning angles resulting in a relatively straight overall direction of movement, was observed in 33 out of 49 (67%) spool-and-line tracks (Rayleigh's $z > 0.322$, $P < 0.05$); the frequency of persistent tracks did not differ between logged and unlogged forest (Chi-squared test, $\chi^2 = 0.003$, $P = 0.95$). All spool-and-line tracks showed significant correlations between the number of steps moved and the respective straight-line distance covered (Mantel tests, all $P < 0.01$). Although most tracks tended to be relatively straight in overall structure (Fig. 1), individual tracks revealed considerable variation in step lengths and turning angles, as indicated by relatively large coefficients of variation for these variables (CV for step length = 153; CV for turning angle = 59).

Large-scale movement patterns. Giant rats emerged from their burrows between 17:40 and 20:40h (mean emergence time = 18:41 ± 0:33 h, $N = 16$) and were active for an average of 485 ± 109 min per night ($N = 16$). The shortest recorded period of nightly activity was for a male in logged forest that was only active for 138 min between 19:30 and 23:30 h. The longest period of nightly activity was for a female in unlogged forest that was active for more than 11 hours (at least 680 min) between 18:20 and 05:40 h. Although the duration of activity periods varied significantly among individuals (Kruskal-Wallis ANOVA, $H_{15,64} = 47.5$, $P < 0.01$; all $3 \leq CV \leq 43$), no significant differences in duration were detected between forest types or sexes (mixed effect model, forest type: $t = -1.02$, $P = 0.37$, sex: $t = -1.32$, $P = 0.22$, forest type:sex interaction: $t = 1.15$, $P = 0.28$). Ad libitum tracking during the daytime confirmed that giant rats were mainly inactive and remained inside their burrows during daylight hours, although 2 females were found to be active in the vicinity of their burrows during the daytime on a single day each.

The mean distance traveled during a single night was 1,443 ± 991 m ($N = 64$ animals). No significant differences in mean distance traveled were detected between forest types or sexes (mixed effect model, forest type: $t = 1.30$ $P = 0.26$, sex: $t = -1.02$, $P = 0.33$, fitted as fixed effects in separate models). The longest recorded average distance per night was 4,742 ± 1,085 m ($N = 4$) covered by a female, whereas the shortest nocturnal movement was 618 ± 231 m ($N = 4$) recorded for a male. A total of 2,432 movement speeds (distance covered in m per 10-min interval) were calculated. Movement speeds did not differ significantly between forest types or sexes (mixed effect model, forest type: $t = 1.14$, $P = 0.32$, sex: $t = 0.82$, $P = 0.43$, forest type:sex interaction: $t = -0.99$, $P = 0.35$). Mean movement speeds, however, differed significantly among individuals (Kruskal-Wallis ANOVA, $H_{15,64} = 45.5$, $P < 0.01$) and this variability may have masked effects of logging on movement patterns. The distributions of movement speeds resembled Lévy walk distributions (Fig. 4), with similar slopes for regressions of movement speed frequencies on binning classes for both forest types (Student's t-test $t_{\nu = 8} = -0.80$, $P > 0.05$). Regression slopes did not differ between data from 10-min-intervals and subset of data with 30-min-intervals in either forest types (unlogged forest: Student's t-test $t = -0.97$, $P > 0.05$, logged forest: Student's t-test $t = 0.10$, $P > 0.05$). Regression slopes did also not differ when excluding binning classes with distances small than estimated errors (Student's t-test $t_{\nu = 4} = -0.50$, $P > 0.05$).

Significant spatial autocorrelation among consecutive radio fixes for the same individual was detected for 26 of 64 (41%) nightly paths monitored (Mantel tests, all $P < 0.05$), suggesting that the remaining 38 paths were relatively tortuous. Comparatively long movements occurred more often than would be expected in a normal distribution (exponent $\mu \geq 3$). For all paths examined, movement speed for a given step was significantly correlated with speeds for the 1 preceding and 2 subsequent steps (all Spearman rank $R > 0.13$, $P < 0.01$), indicating that individuals may reduce movement speed by making several consecutive short moves (Fig. 2).

Moreover, movement speed was significantly correlated with absolute turning angles for 9 out of 16 individuals (all Spearman rank $R > 0.19$, $P < 0.01$). Collectively, these findings suggest that movement trajectories of radio-tracked giant rats were characterized by the accumulation of shorter, slower moves in some locations and occasional very long moves in other locations, indicating that these trajectories do not fit a Brownian random walk model (Turchin 1998).

Mean nocturnal home range sizes (90% kernels) varied from 2,083 to 9,829 m^2. Mean nocturnal core ranges (50% kernels) varied from 594 to 1,535 m^2. Median home range sizes did not differ between forest types or sexes (mixed effect model, forest type: $P = 0.83$, sex: $P = 0.98$). Median home range sizes varied significantly between individuals (Kruskal-Wallis ANOVA, $H_{15,64} = 25.8$, $P < 0.05$), despite the relatively large variation within individual samples over 4 nights (Fig. 5). We found no effect of forest types or sex on core range sizes (mixed effect model, forest type: $P = 0.39$, sex: $P = 0.50$). Across nights, individual variation in total and core home range sizes was high, with a mean CV of 26 ± 18 for median size and a mean CV of 27 ± 19 for core size. Mean nocturnal ranges and core ranges for the same individual calculated from 10-min-intervals (full data set) and 30-min-intervals (subset of data) were correlated (nocturnal ranges: Spearman rank $R = 0.85$, $P < 0.01$, core ranges: $R = 0.74$, $P < 0.01$, both $N = 64$). Analyses of range sizes using different data subsets revealed no effects of forest types and sex on range sizes (all mixed models $P > 0.05$). Thus, overall, while both analyses of movement parameters and home range sizes based on telemetry data revealed substantial inter-individual variation, no significant variation in these parameters was detected between forest types or sex (Table 1).

DISCUSSION

Given the pronounced diversity of trees and other environmental features that are heterogeneously distributed in the forest matrix, tropical rainforests represent a natural mosaic of habitat patches on multiple scales. Consequently, we expected that differences in forest structure and resource allocation between logged and unlogged forest should influence the movements of animals. However, contrary to our expectations, we did not find evidence that logging affected the movements or home ranges of *L. sabanus*. Given the limits of our data set - in particular the accuracy of radio fixes obtained in a complex environment – it is possible that impacts of logging on the movement and ranging patterns of *L. sabanus* remained undetected by our analyses. These limitations, however, should not have affected the results of our spool-and-line tracking studies, yet these data also failed to reveal differences between logged and unlogged forests, suggesting that the apparent changes in logged habitats may not have been important to patterns of movement by the study species.

At our smaller spatial scale (spool-and-line tracking data), animal movements were mostly directed toward the burrow, presumably with little foraging activity along the way. The path tortuosity that we observed at this scale was most likely governed by physical features of the environment such as the distribution of obstructions and supports that reduce straight-line movements. Path tortuosity can be interpreted as the result of the spacing of objects that serve as target or orientation points (e.g., bushes or trees). Travel may have been directed towards such objects on a small scale, but not at a larger scale when considering movement between multiple such points (Benhamou 1990). Alternatively, tortuous paths might simply represent the most efficient way through a heterogeneous medium, as has been suggested for albatrosses (*Diomedea* sp.), which use a tortuous path to continuously adjust their flight for optimal use of wind (Fritz et al. 2003). Similarly, the spatial distribution of structural supports or obstructions may explain path tortuosity in terrestrial rainforest environments. The likely impact of physical structures together with the large variability in step lengths of individuals suggest that the patchiness of local structures should have a strong influence on the movement patterns of *L. sabanus*. Marked variation in local habitat conditions may have obscured any difference between forest types, thus explaining why, despite habitat differences in step lengths (Wells et al. 2006), logging was not a strong predictor of changes in small-scale movement paths.

In contrast, larger scale patterns (radio tracking data) are more likely determined by foraging activity, since resource distribution is central in animal movement and spacing (Ostfeld 1990; Mitchell and Powell 2004). The large variety of patchily distributed food sources in dipterocarp rainforest that are consumed by many small omnivorous mammals (Lim 1970; Langham 1983; Emmons 2000) implies that giant rats face a heterogeneous habitat with considerable variability in resource distribution in space and time. Overall, we suggest that differences in search strategies, such as changes in movement speed and nightly paths, should reflect differences in resource clumping and abundance, which may lead to differences in range size and activity time. Many tropical fruits, such as dipterocarps or figs, are spatially clumped (e.g., Condit et al. 2002) and are exploited by frugivores until all ripe fruits have been consumed. Dipterocarp seeds in particular are a key seasonal resource for rats and other vertebrates in unlogged forests but are replaced by smaller fruits of pioneer trees in logged forests (Curran and Webb 2000; Wells and Bagchi 2005).

Regardless of the specific types of food ingested, the spatial distribution of these resources should be represented in movement paths, with an increased heterogeneity and patchiness in resource allocation leading to increased tortuosity in the large-scale paths of rats. Our observed movement patterns (e.g., serial correlations and high variability in movement speeds) resemble Lévy walks (Shlesinger et al. 1993; Viswanathan et al. 1996), which are characterized by an uneven coverage of the search area that results in exploitation of distant and independent patches. The occasional longer movements of the giant rats in our study may indicate a switch in patch use, which can be seen as an adaptation for the exploration of more profitable patches in a rainforest habitat with rather unpredictable and mostly sparsely distributed resources (see Ramos-Fernández et al. 2004). However, our findings regarding path trajectories do not fully correspond to Lévy walks because the rats regularly revisited sites and returned to the same burrows. Such discrepancies of movement traits in a single model are expected, because models only deal with select, simplified aspects of complex movements. As a generalist species, giant rats might change their search behavior (e.g., searching for fruits versus invertebrates) or exhibit distinct individual search strategies (attributable to local variations in resource availability or differences in individual energetic requirements), as has been suggested for other vertebrates (Mårell et al. 2002; Austin et al. 2004; Morales et al. 2004).

Although our study design did not permit us to compare directly movement trajectories across spatial scales, the impact of physical structure on small-scale trajectories may be associated with the effects of resource availability on large-scale trajectories. For example, undergrowth is usually more open near large and shady fruiting trees, whereas it is denser and faster-growing in tree-fall gaps or near streams (Newbery et al. 1999). Given more light and different vegetation, the arthropod prey of rats may be more common in tree-fall gaps (Davis et al. 2001; Hill et al. 2001), thereby influencing both small and large scale movement patterns with respect to habitat type. Specifically, rats may have to spend more energy in logged than in unlogged forest for the same net movement distance because of the increased density of undergrowth and obstructions. Alternatively, increased density of undergrowth in logged forests might facilitate locomotion of rainforest dwellers by providing more supports, as has been suggested for the arboreal tarsier *Tarsius* (Merker et al. 2005). Thus, although the specific effects of habitat structure on movement remain unknown for most small mammals, it seems logical that differences in forest structure and resource distribution would simultaneously affect movement on multiple spatial scales.

In summary, our data suggest that movement patterns are highly variable among individual giant rats and may reflect heterogeneity in habitat structure and resource availability. Our analyses do not provide strong evidence that logging affects movement by *L. sabanus*. While these findings may in part reflect the ability of our data collection techniques to detect changes in movement and activity, they may also indicate that logging does not alter forest structure in ways that are critical to movements by small mammals such as *L. sabanus*. Our results support the hypothesis that some common small mammals are able to persist in logged forests provided that a certain level of environmental diversity and resource availability are maintained after logging (Lambert et al. 2005; Wells et al. 2007). Plasticity in movement and searching behavior are essential prerequisites for adaptation to an anthropogenically altered landscapes and may obscure differences in movement trajectories between logged and unlogged forest. In logged rainforests, those species that are unable to cope with altered resource availability, or that fail to adapt their search and dispersal strategies, likely face reduced survival and dispersal. Understanding how individual species will respond to such changes is critical to preserving tropical forest faunas. The disappearance of intact rainforest is increasing rapidly, with the result that there is little time left to improve our understanding and, hence, ability to manage these habitats in a meaningful way.

ACKNOWLEDGMENTS

Our thanks are due to Sabah Parks, Yayasan Sabah, and the University of Malaysia Sabah for support during our fieldwork and for access to various forest sites, and to the Economic Planning Unit, Malaysia, for a research permit. We are grateful to D. Fetting, M. Hitzler, A. Kiddra, T. Lenz, C. Rosenberger, and J. Sankin among others for their help in the field. D. Haydon, E. Lacey and anonymous reviewers are thanked for constructive comments that improved earlier drafts of the manuscript. The German Academic Exchange Service (DAAD) kindly provided financial support.

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TABLE 1. Variation in movement and home range attributes for *L. sabanus* in logged and unlogged forests. Data were obtained by radio-tracking 16 animals over 4 consecutive nights each. For each variable, minimum and maximum values are shown, as are estimates of nightly and total *CV*'s. Significant correlations between variables are indicated in the second column and represent Spearman's R correlations for which $p < 0.05$. Nightly *CV*s were calculated from data from the same individual collected over 4 different nights and reflect individual variability in movement parameters. Total CVs were calculated from means for different individuals (data averaged across different nights of monitoring) and represent the variability in trajectories among animals. H-statistics from Kruskal-Wallis ANOVAs reflect differences among individuals for a given variable; significant values ($P < 0.05$) are marked with *.

Variable		Min. – Max. Means	Correlations	Nightly CV [%]	Total CV [%]	H from K.-W.-ANOVA
Nightly path length [m]	(PL)	278 – 6,328	ML, Cor, -Mr	28 ± 13	69	50.0*
Move length (10 min) [m]	(ML)	5 – 100	PL, -Med, Cor, -Mr	34 ± 20	56	45.5*
Activity time [min]	(T)	138 –	PL, Mr	14 ± 9	19	47.5*

	680				
Median range (90% kernel) [m^2] (Med)	2,083 – 9,829	-PL, ML, Cor, -Mr	26 ± 18	44	43.9*
Core range (50% kernel) [m^2] (Cor)	594 – 1,535	-PL, ML, Med, -MrRR	27 ± 19	26	29.3*
Mantel r (Mr)	-0.11 – 0.49	-PL, -ML, T, -Med, -Cor	92 ± 195	89	24.2

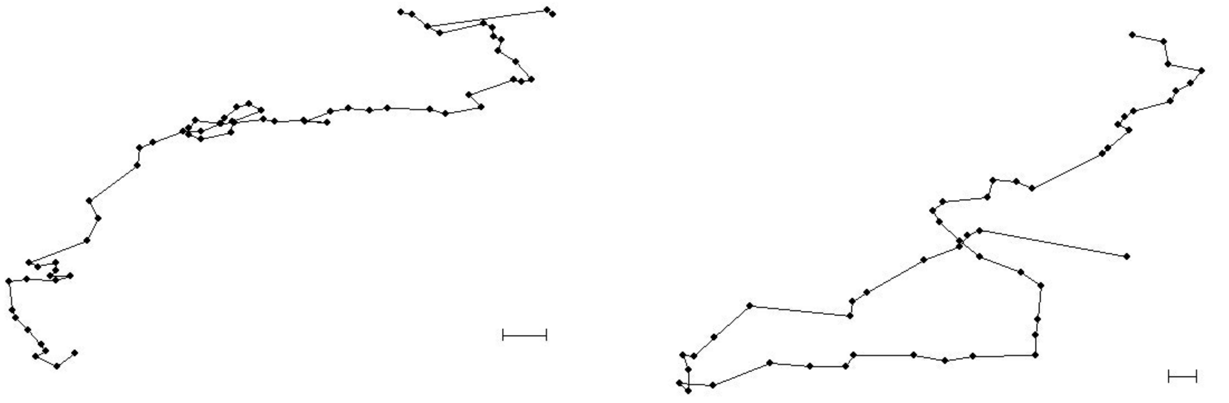

FIG. 1. Small-scale movement tracks of 2 *L. sabanus* obtained from spool-and-line tracking. The animal on the left was monitored in unlogged forest; the animal on the right was monitored in logged forest. Scale bars represent 1 meter.

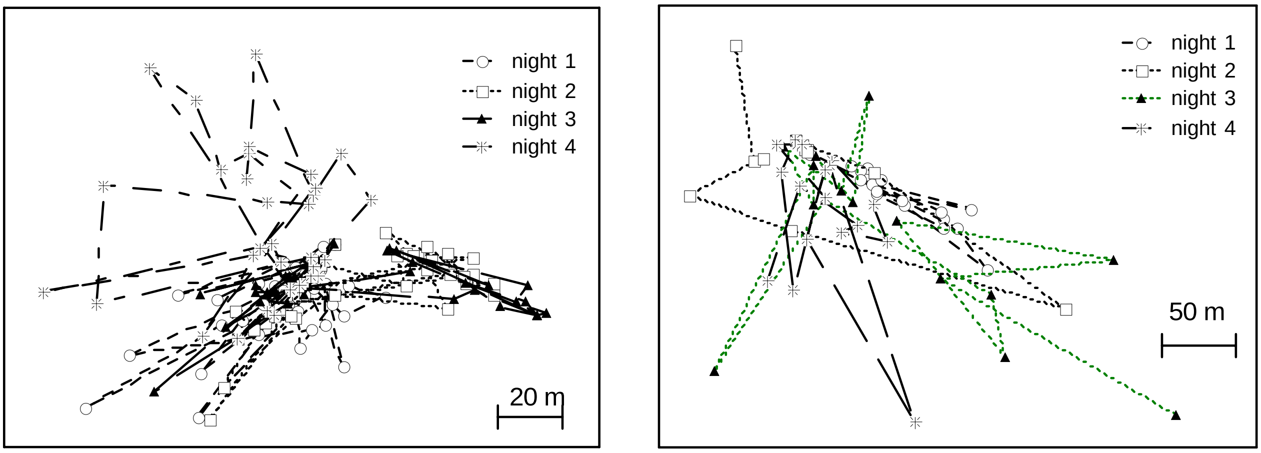

FIG.2. Large-scale movement paths of 2 *L. sabanus*. Radio-tracking of each individual was conducted on 4 consecutive nights, with radio fixes recorded at 10 min intervals. The animal on the left was monitored in unlogged forest; the animal on the right was monitored in logged forest.

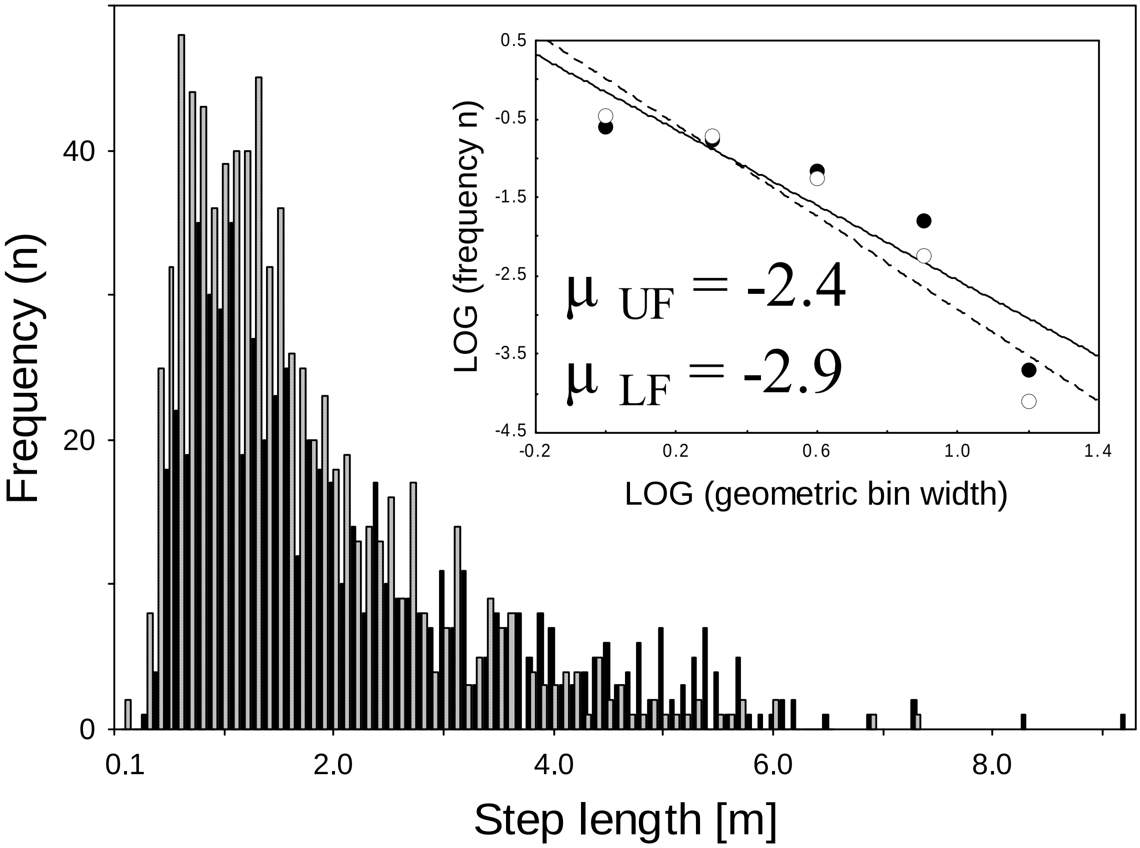

FIG. 3. Distributions of step lengths from spool-and-line tracking of *L. sabanus* in unlogged (black bars) and logged (hatched bars) forest. The inset shows a plot of the same data after logarithmic binning and transformation of the axes; estimates of μ for both forests types are consistent with a power-law distribution. Analyses are based on 629 steps recorded from 25 animals in unlogged forest and 795 steps recorded from 24 animals in logged forest.

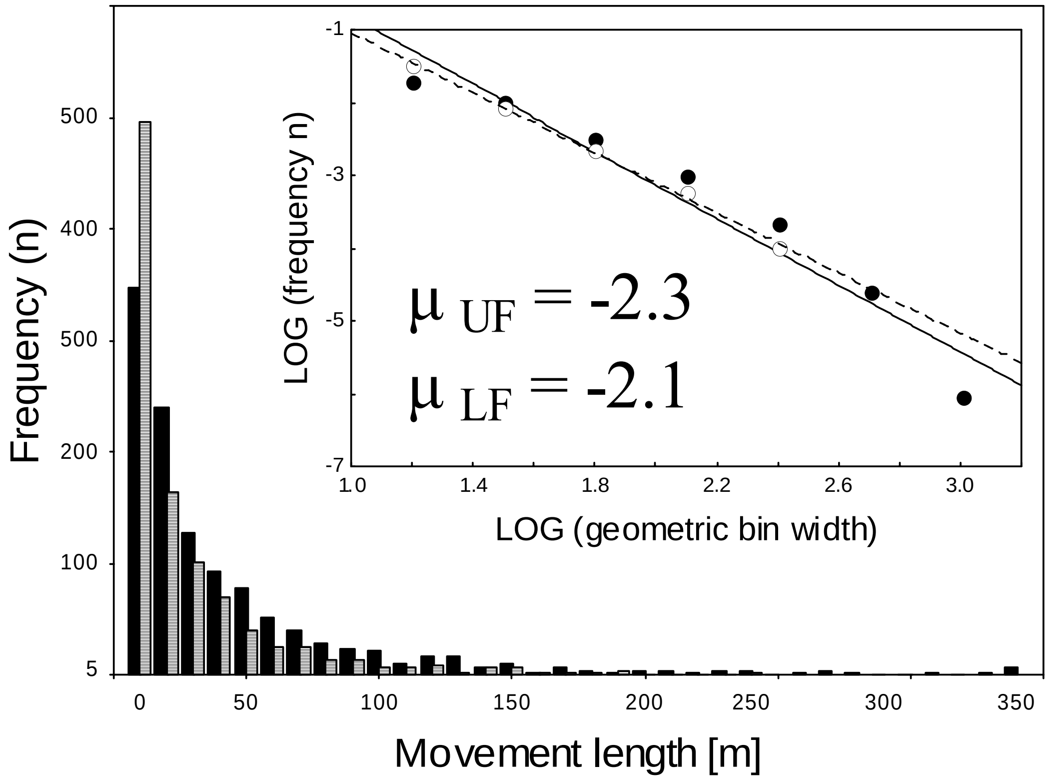

FIG. 4. Distributions of movement speeds from radio-tracking of *L. sabanus* in unlogged (black bars) and logged (hatched bars) forest. Individuals were tracked on 4 consecutive nights, with radio fixes recorded at 10-min intervals. The inset shows a plot of the same data after logarithmic binning and transformation of the axes; estimates of µ did not differ between forests types (Student's t-test $t_{v=8}$ = -0.80, $P > 0.05$). Analyses are based on 1,152 movements ($N = 9$ individuals) from unlogged forest and 989 movements ($N = 7$ individuals) from logged forest.

Journal of Tropical Ecology (2007) **23**:35–43. Copyright © 2007 Cambridge University Press
doi:10.1017/S0266467406003804 Printed in the United Kingdom

Impact of rain-forest logging on helminth assemblages in small mammals (Muridae, Tupaiidae) from Borneo

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(*Accepted 16 October 2006*)

Abstract: Parasites are ubiquitous in wild animals, with host-specific life histories considered as major determinants of prevalence and parasite assemblage patterns. It is predicted that habitat differences in logged rain forests influence population performances of small mammals and consequently may change the infection patterns of local animal populations with regard to endo- and ectoparasites. We investigated patterns of helminth species assemblages (Nematoda, Platyhelminthes) in two rat species (*Leopoldamys sabanus*, *Niviventer cremoriventer*) and two tree shrew species (*Tupaia tana*, *T. longipes*) in three logged and three unlogged rain forests in Borneo by examining 337 faecal samples with non-invasive faecal egg count (FEC). Nematode eggs prevailed in 95% of all samples with up to five (mean 1.9 ± 1.1) morphotypes. Whereas members of Strongylida were most prevalent in *L. sabanus*, *T. tana* and *T. longipes*, Spirurida dominated in *N. cremoriventer* that revealed at the same time the lowest average nematode prevalence and FEC. Cestode eggs were only found in *L. sabanus* and *T. tana*. Composition and abundance patterns of the parasitic helminth assemblages were influenced by logging. As hypothesized, species richness of nematode morphotypes and mean number of infections per host of *T. longipes* were larger in logged than in unlogged forest. In contrast, *L. sabanus* was more heavily infected with cestodes in unlogged than in logged forest and also revealed larger egg counts for strongylids and spirurids in unlogged forest. Our results suggest that forest degradation and altered environmental conditions influence helminth diversity and infection patterns of small mammals with contrasting trends among host species. The inconsistent logging-induced changes in helminth assemblages from different hosts indicate that specific sets of habitat-host-parasite interactions are uniquely influenced by the effects of logging. Consequently, predictions on changes of parasite diversity and prevalence with regard to habitat disturbance need to be based on the individual life histories of the hosts (and the parasites).

Key Words: Host-parasite interactions, infection risk, helminths, parasite diversity, logging, small mammals

INTRODUCTION

The bottom-up or top-down processes that regulate species occurrence and community composition are central themes in our understanding of mechanisms that maintain biodiversity in multifaceted trophic cascades (Brown *et al.* 2001, Terborgh *et al.* 2001). Such interactions can be very complex for organisms in highly diverse ecosystems such as the species-rich communities of small mammals in tropical rain forests and their associated ecto- and endo-parasites. Habitat disturbance profoundly affects and changes community diversity as well as species performances and interactions on various levels of trophic cascades (Terborgh *et al.* 2001), including host-parasite systems (Gillespie *et al.* 2005). Environmental stress may increase host susceptibility to diseases via reduced maintenance of the costly immune defence, whereas altered habitat conditions or host densities may reduce parasite transmission and establishment (Altizer *et al.* 2003, Lafferty & Holt 2003, Ostfeld & Holt 2004).

In tropical rain forests, non-volant small mammals comprise diverse assemblages, which exploit the entire three-dimensional space (Malcolm 1995, Wells *et al.* 2004). Their parasites encounter a diverse habitat with considerable variability in habitat traits (host-specific characters) and dynamics (host mobility and space

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utilization). Parasite speciation and establishment in particular hosts are explained both by parasite traits and by specific characteristics of the host ranging from invariable (e.g. host phylogeny, body size) to variable (e.g. diet, ranging behaviour) features. The high diversity, large number and patchy distribution of tree species and other plants in tropical forests provide complex and heterogeneous forest matrices in space and time (Condit *et al.* 2000). In this context, population-level responses of small mammals to variability in structure and resource availability are likely to differ among species that exhibit different degrees of specialization (Seamon & Adler 1996). The omnivorous feeding habits of generalist and common small-mammal species, for example, promote an overlap in diet and space use (Adler 2000, Emmons 2000, Wells *et al.* 2004). These potential overlaps between host species may be central for structuring parasite assemblages, as patterns of host sharing and host switching are subject to the segregation of hosts in habitat use and diet. Furthermore, generalist hosts that occupy a more variable and complex habitat are exposed to a wider array of parasites than specialist hosts with a more scattered distribution (Nunn *et al.* 2003).

The extent to which logging-induced disturbances affect parasites from small mammals remains largely unexplored. Many commercially logged rain forests differ drastically in structure and floristic composition from undisturbed forests (DeWalt *et al.* 2003). Small-mammal assemblages have been found to decline in species richness in logged forests (Lambert *et al.* 2005, Malcolm & Ray 2000, Wells, unpubl. data), although detailed information on causes and consequences for biotic interactions is largely lacking.

Due to rapidly progressing changes in land use in South-East Asia (Sodhi *et al.* 2004), small-mammal populations and associated parasites are exposed to various types of habitat disturbance that increase environmental stress for hosts (e.g. parasite resistance) or parasites (e.g. transmission) and consequently, alter risks and benefits of habitat disturbance from both perspectives.

Murids and tupaiids comprise important elements of small-mammal assemblages in South-East Asian rain forests. These assemblages differ in their biological history, such as geographical distribution, digestive system and social interaction. The aim of this study has been to determine whether human-caused alterations of the rain-forest environment play a role in generating patterns of parasitic helminth diversity in various small mammals. We thus hypothesized that differences in gastro-intestinal helminth assemblages between logged and unlogged forest are determined by taxonomic similarities among hosts and interspecific differences in host species performances in logged forest.

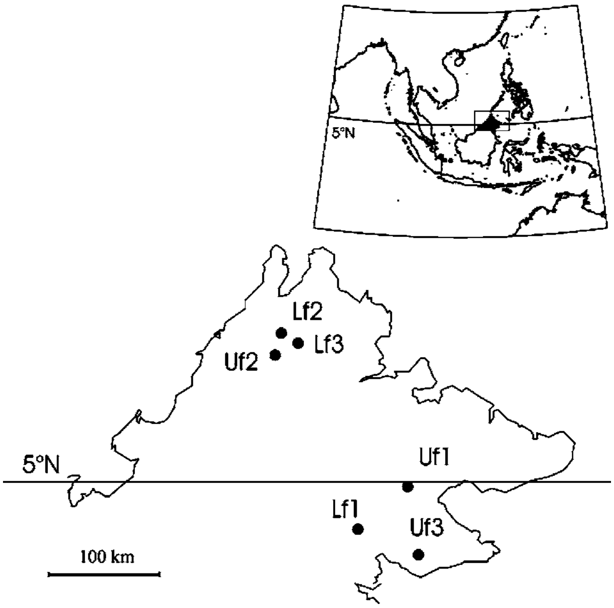

Figure 1. Map of northern Borneo with the six study sites. Unlogged forests: Danum Valley Conservation Area 'Uf1'; Kinabalu NP 'Uf2'; Tawau Hills NP 'Uf3'; logged forests: Luasong Field Centre 'Lf1'; Kg. Monggis 'Lf2'; Kg. Tumbalang 'Lf3'.

METHODS

Study site and sampling

Small mammals were captured on Borneo (Sabah, Malaysia) in three old-growth forest sites (Kinabalu National Park, 06°02′N, 116°42′E; Tawau Hills National Park, 04°23′N 117°53′E; Danum Valley Conservation Area, 04°57′N 117°48′E) and three logged forests (Kampong Monggis, 06°13′N, 116°45′E; Kampong Tumbalang, 06°08′N, 116°53′E; Luasong Field Centre, 04°36′N 117°23′E) (Figure 1). Study sites were located at distances between 17–236 km; all of the forest stands comprised at least 1000 ha. We placed 100–130 wire-mesh cage traps baited with banana in three localities within each study site and conducted a total of 16 sampling periods of 16 d each, continuously alternating between the different forest sites between September 2002 and June 2004. Faeces were collected in the morning after a trapping night. Animals were released once their sex, age (juvenile, subadults, adults; based on pelage and reproductive organs), weight and biometric measurements including head-body (HB), tail (T) and length of hind feet (HF) had been determined. First captures of individuals were permanently marked with transponders (ARE 162, AEG) and faeces were collected from the floor below the trapped animals and stored in 3% formalin. We analysed faeces from four common small-mammal species (Muridae, Tupaiidae; Table 1) that occurred in logged and in unlogged forests.

Table 1. Morphological and ecological characteristics of study species.

Species	Family	Weight (g)	Head–body length (mm)	Habitat
Leopoldamys sabanus	Muridae	368 ± 64 (n = 101)	292 ± 13 (n = 84)	Terrestrial, occasionally arboreal
Niviventer cremoriventer	Muridae	69 ± 13 (n = 142)	125 ± 8 (n = 144)	Terrestrial and arboreal
Tupaia tana	Tupaiidae	218 ± 27 (n = 126)	189 ± 7 (n = 110)	Terrestrial, scansorial
Tupaia longipes	Tupaiidae	196 ± 25 (n = 59)	191 ± 8 (n = 51)	Terrestrial, scansorial

Faecal egg count protocol

We counted all eggs from nematodes (Nematoda) as well as cestodes and trematodes (Platyhelminthes) from the faecal samples with a modified flotation and McMaster method (Meyer-Lucht & Sommer 2005). This non-invasive technique has been shown to be accurate for estimating the number of helminth eggs. However, egg counts do not fully correspond to adult worm burden (Moss *et al.* 1990, Seivwright *et al.* 2004, Skorping *et al.* 1991). We used potassium iodide solution (specific gravity 1.5 g ml^{-1}) for egg flotation. Samples of approximately 600 mg faeces (mean ± SD = 570 ± 92 g) were dissolved in 9 ml solution, sieved to remove large debris and screened for helminth eggs by counting the content of two chambers of a McMaster slide. All eggs were photographed and measured (Zeiss, AxioCam and AxioVision software; 10–40× amplification). Images were then assigned to operational taxonomical units (orders for nematodes, cestodes) based on features of eggshell and content and further distinguished by size classes and shell thickness for strongylids. We simultaneously counted the number of non-transparent arthropod fragments down to 10–200 μm on the McMaster slides to assess the proportion of arthropod consumption of the hosts. We noted the number of cuticles per gram (CPG) of faeces to obtain a faecal cuticle count (FCC).

Data analysis

We considered all egg morphotypes that could be identified as helminth eggs for analysis of overall infection patterns. However, we took only egg classes that could be identified to order for estimates of diversity and null model analysis of co-occurrence patterns. Infection status of individuals was indicated by the number of helminth morphotypes found in each individual and, for each morphotype, by the number of eggs per gram of faeces (EPG). Faecal samples from recaptures (14 out of 337) in consecutive sampling periods with more than 6 mo between captures were considered for analysis. The counts of eggs and number of cuticles per gram were log-transformed for analysis with $\text{FEC} = \log_{10}$ (EPG +1) and $\text{FCC} = \log_{10}$ (CPG +1). Samples were pooled for each host species among sites (n = 3) for analysis of differences in infection and parasite diversity between logged and unlogged forests. FEC were calculated separately for all eggs assigned to different orders and only nematode eggs, respectively.

Although we were only able to distinguish eggs by orders and size classes (194 out of 710 unclassified), we assume that the number of recorded morphotypes increases with the true species number in samples and therefore that diversity calculations based on presence-absence data of all classified eggs were accurate for comparative approaches. Diversity estimates were calculated with EstimateS 7.5 (http://purl.oclc.org/estimates).

As diversity estimates are strongly dependent on sample size and coverage, sample orders were randomized 50 times and all comparisons were made on standardized minimum sample sizes. Chao2 species richness estimator was chosen based on sample coverage (Brose *et al.* 2003). Nematode community diversity was determined using Simpson's (reciprocal) index D (Magurran 2004). We used non-parametric statistics for all comparisons among variables, as we merely intended to confirm that one variable was higher than another, rather than considering the extent of the divergence. Mean ± 1 SD is given and the significance of post hoc pair-wise comparisons was tested with Dunn's test.

RESULTS

Helminth diversity and interspecific host patterns

We screened a total of 337 faecal samples from four species of small mammal: 158 samples from *Leopoldamys sabanus* (with seven samples from individuals recaptured in a consecutive trapping session), 23 samples from *Niviventer cremoriventer* (23 individuals), 125 samples from *Tupaia tana* (118 individuals), and 31 samples from *T. longipes* (31 individuals). We found nematodes of the orders Strongylida, Spirurida, Enoplida and Oxyurida as well as cestodes. We found no acanthocephalan eggs and no trematode infection, although a single egg in a sample from *T. tana* might have been a trematode. As trematode eggs, unlike eggs from other helminths, are too heavy to reliably float up in potassium iodide solution, a few eggs may have been missed.

Combining samples from all species of small mammal, nematode eggs were prevalent in 319 out of 337

Table 2. Prevalence (per cent infected) of nematode orders and cestodes in the different host species. The numbers of faecal samples are given in parentheses.

	Prevalence (%)			
Helminth	*Leopoldamys sabanaus* (n = 158)	*Niviventer cremoriventer* (n = 23)	*Tupaia tana* (*n* = 125)	*Tupaia longipes* (*n* = 31)
Strongylida	74.1	30.4	75.2	90.3
Spirurida	34.8	56.5	35.2	19.4
Oxyurida	4.4	8.7	0	0
Enoplida	8.9	0	4.0	6.5
Cestoda	27.8	0	6.4	0
Total prevalence (%)	94.9	82.6	96.8	96.8
Mean number of nematode morphotypes	1.9 ± 1.1	2.1 ± 1.3	1.8 ± 1.0	1.2 ± 0.7

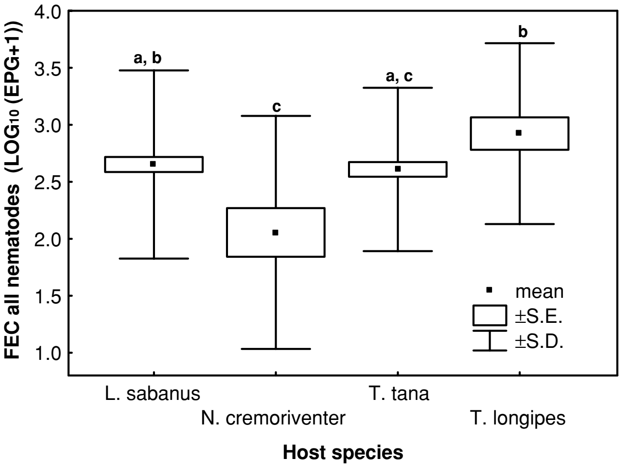

Figure 2. Mean faecal egg count (FEC) of all nematodes from the host species *Leopoldamys sabanus*, *Niviventer cremoriventer*, *Tupaia tana* and *T. longipes* (Kruskal–Wallis ANOVA $H_{3,337} = 12.9$, $P < 0.01$). Different letters above whiskers indicate significant differences (Dunn's test).

samples (95%) with zero to five (mean = 1.9 ± 1.1) morphotypes per host individual. Nematode eggs of the orders Strongylida (1–6 size classes per host species) and Spirurida (1–5 size classes) were prevalent in both rat and tree shrews, whereas Oxyurida were found only in rat samples (*L. sabanus*, *N. cremoriventer*). Enoplida (1–2 size classes) were not found in *N. cremoriventer* (Table 2). Strongylids were most prevalent in *L. sabanus*, *T. tana* and *T. longipes*, whereas spirurids dominated in *N. cremoriventer*. The number of nematode infections was significantly correlated with FEC of nematode eggs for all host species (all Spearman $R > 0.316$, $P < 0.01$). The mean number of nematode infections and egg counts differed significantly between host species (Kruskal–Wallis ANOVA $H_{3,337} = 12.9$, $P < 0.01$; Figure 2) with the lowest prevalence of nematodes in *N. cremoriventer* (Table 2). Cestodes occurred less frequently than nematodes and were only found in 44 out of 158 samples (28%) from *L. sabanus* and eight out of 125 samples (6%) from *T. tana* with zero to two (mean = 0. 2 ± 0.4) infections per individual.

Influence of host characteristics on infections

The number of nematode morphotypes was not related to host sex, age, weight or biometric measurements (HB, T, HF) for the four host species (sex: all Mann–Whitney U-tests $P > 0.44$, age: all Kruskal–Wallis ANOVA $P > 0.29$, biometric measures: all Spearman correlations $P > 0.19$). However, FEC measures differed significantly between age classes for *L. sabanus* and *N. cremoriventer* with an increased count for adults (both Kruskal–Wallis ANOVA $H > 9.2$, $P < 0.05$). Overall nematode egg count increased significantly with host weight, HB and T in *N. cremoriventer* (all Spearman $R_{n>21} = 0.45$, $P < 0.05$), while FEC was significantly correlated with HF size for *T. tana* (Spearman $R_{n=106} = 0.19$, $P < 0.05$). The abundance of cestode eggs increased among age classes of *L. sabanus* (Kruskal–Wallis ANOVA $H_{3,154} = 8.10$, $P < 0.05$).

Crude arthropod consumption and egg counts

The crude arthropod consumption as estimated by FCC was neither correlated to the number of nematode morphotypes nor to the entire nematode FEC for the four host species. However, strongylid egg counts were significantly correlated with the FCC for *L. sabanus* (Spearman $R_{n=117} = 0.26$, $P < 0.01$) where fewer cuticle fragments had been found in uninfected or only lightly infected (EPG 1–500) individuals compared with medium (EPG 501–1500) infected individuals (Figure 3). Further, FCC were higher for *L. sabanus* infected with cestodes than for non-infected individuals ($U_{85,32} = 1024$, $P < 0.05$). Egg counts of spirurids decreased with increasing FCC for *T. tana* (Spearman $R_{n=125} = -0.29$, $P < 0.01$), for which FCC were larger for non-infected individuals ($U_{81,44} = 1110$, $P < 0.01$).

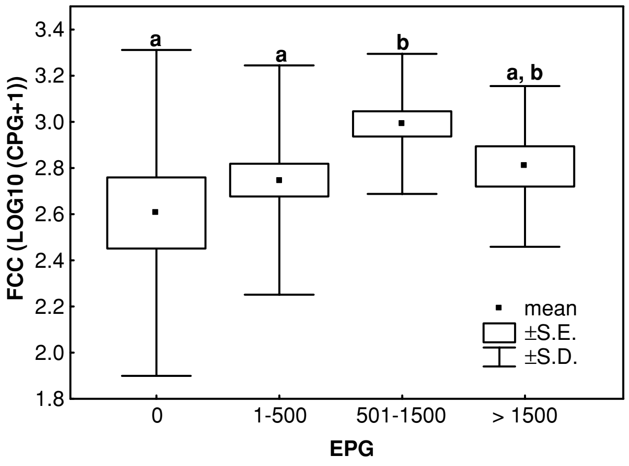

Figure 3. Mean cuticle counts (FCC) of samples from *Leopoldamys sabanus* in relation to relative abundance of strongylid eggs (EPG, Kruskal–Wallis ANOVA $H_{3,117} = 9.29$, $P < 0.05$). Different letters above whiskers indicate significant differences (Dunn's test).

Parasitic load of small mammals in logged versus unlogged forests

Randomized species accumulation curves revealed that species richness of parasites, based on morphotypes of nematodes did not differ between logged and unlogged forest for *L. sabanus* (Figure 4a). In contrast, nematode species richness estimated from accumulation curves was significantly higher in logged forest than in unlogged forest for *T. longipes* (Figure 4b). This was also confirmed by the Chao2 estimates, which were 8.3 ± 2.3 for logged forest and 4 ± 0.3 for unlogged forest for nematode eggs recovered from *T. longipes*. Different morphotypes accumulated faster in samples from unlogged forest than for logged forest for *T. tana* (Figure 4c). However, samples size was not sufficient for a reliable estimate of species richness in this host species.

Diversity patterns differed in all small-mammal species studied between logged and unlogged forest (Table 3) when combining species richness and heterogeneity with the Simpson's index. The mean number of nematode infections per host individual was significantly larger for

Table 3. Chao2 species richness estimate and Simpson's D diversity indices based on nematode morphotypes found in hosts captured in unlogged (UF) and logged (LF) forest. Calculations are based on a randomized order of the minimum standardized number of samples per forest type (given in parentheses). *Niviventer cremoriventer* is excluded from this analysis because of small sample size

	Chao2		Simpson's D	
Species	UF	LF	UF	LF
Leopoldamys sabanus (n = 60)	16.5 ± 5.8	20.8 ± 10.0	3.51 ± 0.51	2.7 ± 0.3
Tupaia tana (n = 30)	11.5 ± 2.1	9.1 ± 2.6	3.58 ± 0	2.7 ± 0.42
Tupaia longipes (n = 12)	4.0 ± 0.3	8.4 ± 2.3	2.7 ± 0.59	4.03 ± 0.15

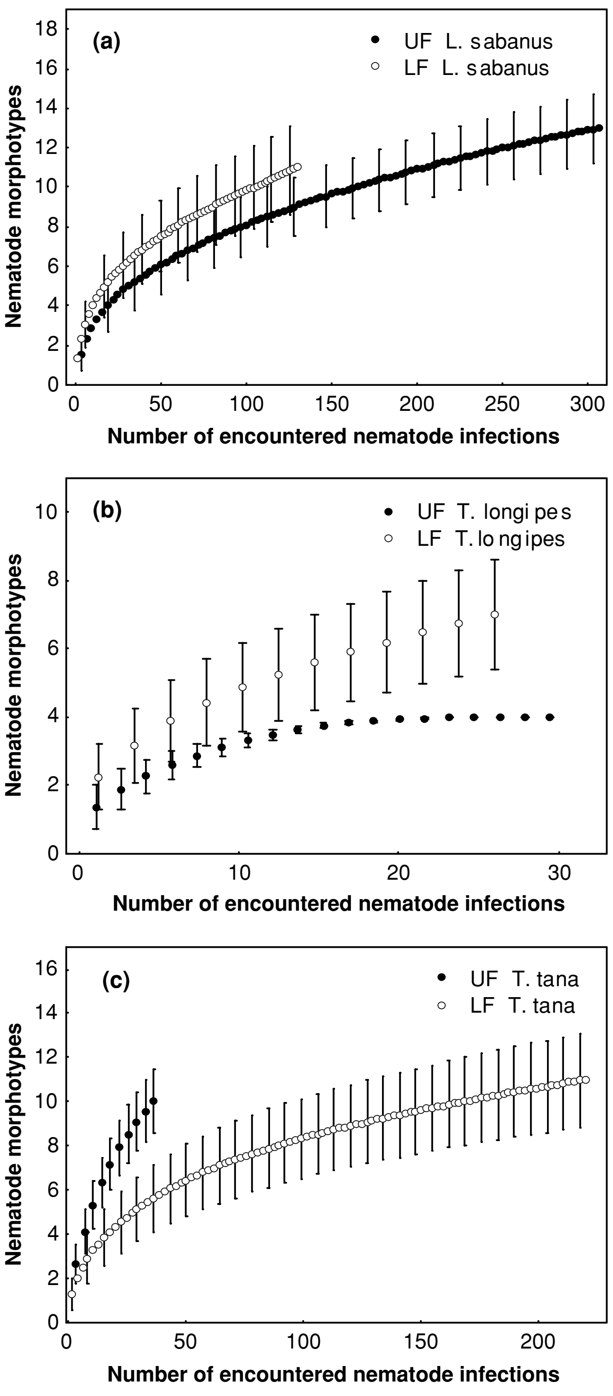

Figure 4. Rarefied species accumulation curves representing the average number of nematode morphotypes for a given number of nematode infections in unlogged (●) and logged forest (○) for *Leopoldamys sabanus* (a), *Tupaia longipes* (b) and *T. tana* (c). Curves are sample-based with host individuals as samples and plotted based on individuals (number of encountered nematode infections) for direct comparisons. Bars are 95% confidence intervals.

T. longipes in logged than in unlogged forest ($U_{19,12} = 39.5$, $P < 0.01$). Egg counts for strongylids and spirurids were significantly larger in unlogged than in logged forest for *L. sabanus* (both $U_{98,60} > 2066$, $P < 0.05$).

Cestodes were significantly more prevalent in *L. sabanus* in unlogged than in logged forest ($U_{98,60} = 2005$, $P < 0.01$); 19% of all individuals were infected in unlogged forest compared with 7% in logged forest. Counts of cestode eggs were also higher in unlogged forest ($U_{98,60} = 1875$, $P < 0.01$).

Overall, helminth assemblages did not show any apparent differences within or between logged versus unlogged forests in *L. sabanus* or *T. tana* in terms of overlap in helminth morphotypes (Sørensen similarity index; both $U_{6,9} > 25.5$, $P > 0.19$). We found two strongylid morphotypes in the faeces of *T. tana* in logged forests and none in unlogged forest.

DISCUSSION

Mammalian species comprise well-defined habitats for parasites with respect to a range of important characters such as body size, diet, mobility and spacing pattern. An important factor that is likely to add a high degree of variability into the system is the heterogeneity of rain-forest matrices that is likely to be associated with variable conditions for parasites via inconsistent patch and resource exploitation of host species. The present study assessed first data on distinct helminth assemblages in tropical small mammals, in particular murids and tupaiids, which were affected by rain-forest logging.

Interspecific differences in helminth assemblages among hosts were most apparent in the arboreal rat *Niviventer cremoriventer*, in which the nematode fauna was dominated by spirurids rather than strongylids as in the other three host species and where we recorded the lowest numbers and intensities (FEC) of infections. Conversely, the composition of helminth assemblages was most similar in *Leopoldamys sabanus* and *Tupaia tana*: both revealed similar prevalences of strongylids, spirurids and cestodes. Among host clades, the distribution of oxyurids was the only difference. They were recorded in rats but not in tree shrews. However, the absence of certain parasite groups must be treated with some caution, especially for *N. cremoriventer* and *T. longipes*, as helminth species are difficult to detect. Further, prevalences might be overestimated when sample size is relatively small (Poulin 1998).

Observed similarities in helminth assemblages need to be seen in the context of habitat overlap of host species, which might increase interspecific transmission of helminths via interspecific contact, use of contaminated substrate, or feeding on the same intermediate hosts. For instance, directly transmitted nematodes are likely to be more widespread if other host individuals forage within a contaminated habitat patch in which defecation has taken place (Ezenwa 2003, Vander Wal *et al.* 2000). Generally, ubiquitous small mammals overlap in habitat use with a number of other mammal species, increasing the probability for associated parasites by host sharing (generalist parasites) or shifting (specialist parasites). In particular, use of similar habitats has been found for the terrestrial/scansorial tree shrews *T. tana* and *T. longipes* (Wells *et al.* 2006). Further, habitat overlap is also likely between *T. tana* and *L. sabanus* (terrestrial and occasionally arboreal), as both species are affiliated to wet habitats and streams (Emmons 2000, K. Wells pers. obs.). In contrast, *N. cremoriventer* is the only species in this study that frequently forages in the canopy.

Presumably, variation in host habitat use, i.e. terrestrial and arboreal, provides divergent conditions for transmission and development across parasites (see Anderson 2000) because of the differences in abiotic and biotic factors encountered in the respective habitats (Emmons 1995). The arboreal activity of *N. cremoriventer* and other species might preclude the establishment of directly transmitted strongylids, as faeces is dropped during activity in the trees, thus reducing contamination of the occupied habitat. Further, arboreal activity reduces exposure of the hosts to the soil stages of some nematodes. This may explain the lower prevalence of strongylids compared with arthropod-transmitted spirurids in *N. cremoriventer*. Furthermore, the rapid relocation of faeces by dung beetles (Scarabaeidae) and ants (Formicinae) may also influence the spread of faecally transmitted eggs (e.g. directly transmitted strongylids), as has been discussed for seed removal from piles (McConkey 2005, Vander Wall *et al.* 2005).

While such complex dynamics may, on the one hand, reduce transmission, they may, on the other, promote vertical transfer among hosts by translocating eggs among different microhabitats. This may help to explain why directly transmitted helminths did not necessarily dominate. We are also aware that the result of relatively low parasite density recorded in the arboreal *N. cremoriventer* is solely based on one example. Moreover, some nematodes, such as trichostrongylids or the trichurid *Capillaria*, appear to share hosts that include both terrestrial and arboreal murids (Hasegawa & Syafruddin 1997, Lim *et al.* 1977).

Diet and nutritional status influence host interaction with parasites as well. The spectrum of invertebrates eaten by a host determines the exposure to intermediate hosts and the encounter probability of parasites with indirect life cycles. In particular, the high variability in food use of the examined small mammals suggests that feeding on invertebrates strongly varies with environmental conditions and resource availability. The observed relationships between crude arthropod intake and FEC did not reveal consistent patterns among host and parasite species. FEC of strongylids and the number of cestode infections in *L. sabanus* were positively correlated with crude arthropod intake, whereas spirurid egg counts and the number of infections were negatively related to arthropod debris in *T. tana*. Theoretically, a correlation between spirurid or cestodes eggs and arthropod debris should be more likely as ingested arthropods may serve as intermediate hosts, whereas this relationship does not account for strongylids and arthropod debris as found in *L. sabanus*. Probably, a higher abundance of arthropods fosters such a relationship in places where the area is contaminated by parasite eggs. In addition, low protein level of an animal may enhance feeding motivation and, consequently, parasite encounter by feeding preferably on arthropods (indirectly transmitted helminths) or extending foraging in space or time (monoxenous helminths).

Resource and nutrient availability in logged rain forests differ from undisturbed rain forests because of changes in plant (DeWalt *et al.* 2003) and invertebrate communities (Cleary *et al.* 2005, Davis *et al.* 2001, Floren & Linsenmair 2001). For instance, changes in nutritional conditions in logged forests have been suggested to increase gastro-intestinal parasite prevalence and richness in an African frugivorous primate in contrast to folivorous primates that were not affected (Gillespie *et al.* 2005). Although our data do not reveal any consistent relationship between arthropod debris and worm burdens, nor do we have detailed information on nutritional status of host species, our finding that nutrition and helminth infection are related in this host–parasite system adds another important point to the question how changes in helminth assemblages are influenced by rain-forest logging.

Interestingly, some of the observed differences in helminth infections between logged and unlogged forest cannot be interpreted consistently with known host traits. While helminth assemblages in *L. sabanus* and *T. tana* were less diverse in logged forest, diversity, species richness and the prevalence of helminths were higher in *T. longipes* in logged forest. This contrasts with the impact of logging on species demography which has been found to be rather weak for these generalist species (Wells, unpubl. data). Hence, the pattern of helminth parasitism in logged forests cannot solely be explained by changes in host densities, spacing patterns or taxonomy.

Overall, fluctuations in host abundance and inter-specific contact are predicted to have most impact on directly transmitted parasites. Conversely, variation in the abundance of vectors associated with the various definitive hosts may lead to variation in parasite species richness that is independent of the characteristics of host species (Arneberg 2002, Morand & Poulin 1998). Hence, the effects of forest degradation may differ among directly and indirectly transmitted parasites. Unfortunately, we do not have detailed information on the invertebrates ingested by the hosts nor on the effects of logging on potential intermediate hosts. Assuming that some intermediate host species do not tolerate logging because of alterations in arthropod communities, parasites with indirect life cycles should have a lower chance of encountering optimal conditions in an altered habitat and of following the colonization of disturbed habitat patches by their hosts. On the other hand, logging leads to greater canopy openness and respective changes in abiotic factors. Typically, rain-forest understoreys are moist and cool in contrast to the canopy. Extensive modifications caused by logging lead to changes in microclimate at the logged sites. Drier and hotter conditions may influence the conditions for free-living stages of directly transmitted parasites, for instance, by fostering hypobiosis (arrested development) (Anderson 2000).

Parasite establishment in any particular host is controlled by a set of factors that vary at the environmental, host and parasite level. Because of the multitude of factors, it is difficult to predict the outcome of particular changes in the system as each component may be affected differently. Our study confirms this notion as it demonstrated multidirectional outcomes of logging on parasite assemblages in small mammals. On one hand, parasite assemblages of small mammals were altered in composition and relative abundance of selected taxa in response to logging. On the other hand, however, our study also revealed contrasting patterns of parasitism which means that factors act differently on the individual components of the system.

Further research is needed to investigate whether more general patterns in altered parasite assemblages emerge if a larger quantity of host species is examined. Investigating changes in parasite assemblages provides a promising perspective to understand the various outcomes of different types of anthropogenic habitat disturbances on mammals and whether environmental stress in altered habitat is increasing host infection via reduced host immune defence or diminishes parasitism via adverse conditions for parasite transmission.

ACKNOWLEDGEMENTS

Many thanks are due to Maklarin B. Lakim, Sabah Parks, Malaysia, for his support and amicable collaboration during fieldwork. Sabah Parks, Yayasan Sabah, the Royal Society SE-Asia Rainforest Research Programme (SEARR), and the University Malaysia Sabah granted access to forest sites and are thanked for all kinds of support. The Economic Planning Unit Malaysia kindly issued a research permit. We are further indebted to Jörg Ganzhorn and Simone Sommer for providing laboratory facilities and hospitality at Hamburg University. Yvonne

Meyer-Lucht kindly shared her experience on faecal egg analysis. Many people in Sabah, among them Alim Biun, Awang Matamin, Jikson Sankin, Lajimi Mail and Suati Selimon, provided valuable help in the field. Thanks are due to anonymous referees for constructive comments on earlier drafts. The German Academic Exchange Service (DAAD) kindly provided financial support.

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WELLS, K., PFEIFFER, M., LAKIM, M. B. & KALKO, E. K. V. 2006. Movement trajectories and habitat partitioning of small mammals in logged and unlogged rainforests in Borneo. *Journal of Animal Ecology* 75:1212–1223.

CURRICULUM VITAE AND LIST OF PUBLICATIONS

DR MARTIN PFEIFFER

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Home: 49-(0)-731-502-2679 * *Office:* 49-(0)-731-502-2679
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Born 13 May 1961 in Nördlingen, Germany
married with Irmi Pfeiffer, née Wolf, since June 1992

Education

Doctor of Natural Science, 1997
University of Würzburg, Prof. Dr K E Linsenmair
"Social structure and behavioural ecology of giant ants *Camponotus gigas* Latreille 1802 in the rain forest of Malaysia on Borneo"

Study of Ethnology, Philosophy and Comparative Study of Religions
1989-1991, University of Bayreuth, Germany

Diploma of Biology, 1989
University of Bayreuth, Prof. Dr Th Bauer
"Hunting behaviour and eye structure in *Stenus comma* and *Dianous coerulescens* (Staphylinidae)"

Pre-diploma of Biology, 1985
University of Bayreuth

University Entry Exam, 1980
Markgraf Georg Friedrich Gymnasium, Kulmbach

Academic Experience

Research Associate, Oct. 2001 – Sept. 2007
University of Ulm, Institute for Experimental Ecology

Scientific Employee, 1992 – 1996
University of Würzburg, Department for Animal Ecology and Tropical Biology

Honours

Landeslehrpreis 2006 des Landes Baden-Württemberg

"Teaching Award of the State of Baden-Württemberg" received together with
Prof. Dr Elisabeth Kalko, Prof. Dr Manfred Ayasse, Dr Marco Taschapka, Dr Stefan Jarau,
University of Ulm, Institute for Experimental Ecology

Grants

German Research Council (DFG) LIS 1-55495 (2), currently
German Research Council (DFG) PF 441/ 3-1, currently
Arthur von Gwinner Foundation, 1999
German Academic Exchange Service (DAAD), 1992 to 1994

Teaching

Tropical Ecology, Plant-Animal Interaction, Chemical Ecology, Zoology, Invertebrate Morphology, Arthropod Functional Morphology, Evolution, Biogeography, Statistics for Scientists, Zoological Excursions

Research Interests

Ants, Community Ecology, Ecosystem Functioning, Evolution of Animal Communities, Spatial Patterns of Animals, Food webs, Myrmecochory and other Ant-Seed Interactions,Rain Forest, Arid Ecosystems, Small Mammals in Borneo, Behavioural Ecology of the Giant Ant *Camponotus gigas*, Tropical Soils

Field Research

May 2007	Field trip to Iran (PhD project O. Paknia).
2006/7	Project: “Community structure of ground living Formicinae and their role within the food web of the soil fauna in rain forests of Sarawak, Malaysia” (PhD project D. Mezger).
2005/6	Project: “Pattern and processes structuring ant communities (Formicidae) in plantations of oil palm *Elaeis guineensis* and other habitats of Malaysia”.
2002/4	Project: “Influence of habitat degeneration on the use of space and genetically variability of small mammal species (Muridae, Tupaiidae) in rain forests of Borneos“ (PhD project K. Wells).
2001/2	Project: “Ant-plant interactions in Malaysian rain forest on Borneo: seed predation and dispersion by ants (Formicidae)”.
1997, 99, 01	Expeditions to Mongolia.
1991-1995	Project: “Behavioural ecology of Giant Ants *Camponotus gigas*” (PhD project M. Pfeiffer).
1990	Field research in Ivory Coast.
Before:	Scientific expeditions and field trips to Sahara, Central Asia, Indonesia

Committee work

Alumni member of the audit committee of the German Exchange Service DAAD 1997
Board of Student Council, elected member, University of Bayreuth 1985 - 1986

Reviewer for Professional Journals

Biotropica, Ecography, Ecotropica, Insectes Sociaux, Myrmecological News, Oecologia, Physiological Entomology, Raffles Bulletin of Zoology, Zoology in the Middle East

PUBLICATIONS

Manuscripts

Pfeiffer M, Huttenlocher H and Ayasse M (manuscript). Myrmecochory in spring ephemerals with different types of elaiosomes: how chemical composition of seeds influences ant removal patterns.

Paknia O, Radchenko A, Alipanah H, **Pfeiffer M** (submitted). A review of the ant fauna (Hymenoptera: Formicidae) of Iran. Myrmecological News.

Editorial work

Pfeiffer M, John R. Fellowes (in press) **ASIAN MYRMECOLOGY.** A journal that is published by the Institute for Tropical Biology & Conservation, Universiti Malysia Sabah on behalf of ANeT — the International Network for the Study of Asian Ants. Vol I. pp 119.

Peer reviewed journals

Pfeiffer M, Ho CT, & Teh CL (in press). Exploring arboreal ant mosaics and the impact of exotic "tramp" species (Formicidae) in plantations of oil palm (*Elaeis guineensis*) in Borneo and Peninsular Malaysia. *Ecography*

Wells K, Kalko EKV, Lakim MB & **Pfeiffer M** (accepted) Movement and ranging patterns of a tropical rat in logged and unlogged rainforests*. Journal of Mammology*

Dunn RR, Sanders N J, Fitzpatrick M C, Laurent E, Lessard J-P, Agosti D, Andersen A, Brühl C, Cerda X, Ellison A, Fisher B, Gibb H, Gotelli N, Gove A, Guenard B, Janda M, Kaspari M, Longino JT, Majer J, McGlynn T G, Menke S, Parr C, Philpott S, **Pfeiffer M**, Retana J, Suarez A, and Vasconcelos H (accepted). Global Ant Biodiversity and Biogeography--A New Database and its Possibilities. *Myrmecological News*

Pfeiffer M & Linsenmair KE (in press). Trophobiosis in a tropical rainforest on Borneo: Giant ants *Camponotus gigas* (Hymenoptera: Formicidae) herd wax cicadas *Bythopsyrna circulata* (Auchenorrhyncha: Flatidae). *Asian Myrmecology* 1: 105 – 119

Pfeiffer M, Schultz R, Radchenko AG, Yamane S, Woyciechowski M, Ulykpan A and Seifert B 2007(2006). A critical checklist of the ants of Mongolia (Hymenoptera /Formicidae). *Bonner Zoologische Beiträge* 55 (1): 1-8

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Pfeiffer M, Nais J, Linsenmair KE (2006). Worker size and seed size selection in 'seed'-collecting ant ensembles (Hymenoptera: Formicidae) in primary rain forests on Borneo. *Journal of Tropical Ecology* 22 (6): 685-693

Wells K, Lakim MB & **Pfeiffer M** (2006). Nest sites of rodents and treeshrews in Borneo. *Ecotropica* 12, 141-149.

Wells K, Kock D, Lakim MB & **Pfeiffer M** (2006). Is *Rattus rattus* invading the primary rainforest on Borneo? *Malayan Nature Journal* 59(1) 73-79.

Wells K, **Pfeiffer M**, Lakim MB & Kalko EKV (2006). Movement trajectories and habitat partitioning of small mammals in logged and unlogged rainforests on Borneo. *Journal of Animal Ecology* 75, 1212-1223.

Stich HB, **Pfeiffer M**, Maier G (2005). Zooplankton communities in a large prealpine lake, Lake Constance: comparison between the Upper and the Lower Lake. *Journal of Limnology* 64(2): 129-138

Pfeiffer M, Nais J, Linsenmair K (2004). Myrmecochory in the Zingiberaceae: Seed removal of *Globba franciscii* and *G. propinqua* by ants (Hymenoptera Formicidae in rain forests on Borneo. *Journal of Tropical Ecology* 20: 705-708

Pfeiffer M, Chimedregzen, L and Ulykpan K (2004). Biodiversität und Struktur mongolischer Ameisengemeinschaften entlang eines Transektes von der Steppe bis in die Wüste Gobi. *Mitteilungen der DGaaE* 14: 149-152

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Pfeiffer, **M**, Chimedregzen, L and Ulykpan K. (2003). Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. *Journal of Biogeography* 30 1921-1935

Pfeiffer M, Linsenmair KE (2001). Territoriality of the Malaysian giant ant *Camponotus gigas* (Hym./ Form.). *Journal of Ethology* 19:75-85

Pfeiffer M, Linsenmair KE (2000). Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera Formicidae). *Insectes Sociaux* 47:123-132

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Pfeiffer M (2006- today). Antbase.NeT, approx. 3400 pages; http://www.antbase.net

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Pfeiffer M (2006). The transformation of a website on ants into a myrmecological networking platform: www.antbase.de changes into www.antbase.net. *ANeT newsletter* 9: 11-14

Pfeiffer M, Fellowes J, (2006). A call for contributions to Asian Myrmecology, the new scientific journal published by ANeT. *ANeT newsletter* 9: 2-3

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Pfeiffer M (1989). Hunting behaviour and the structure of eyes in *Stenus comma* and *Dianous coerulescens* (Staphylinidae)" Diplomarbeit Universität Bayreuth.

Conference contributions

Pfeiffer M, 2007. A potential link between Europe and Asia: www.antbase.net a myrmecological networking platform.Second report. International Conference on Ants and other Social Hymenoptera. 10th to 13th of October, 2007. Punjabi University Patiala.

Pfeiffer M, Fellowes JR and Jimbau P, 2007. ASIAN MYRMECOLOGY – ANeT's new journal. A report on the first issue and a discussion on the future of the journal *International Conference on Ants and other Social Hymenoptera*. 10th to 13th of October, 2007. Punjabi University Patiala.

Mezger DD, Jens and **Pfeiffer M**, 2007. Examining the role of ants in the food webs of leaf-litter ecosystems in two types of rainforests by use of stable isotope analysis – preliminary results *International Conference on Ants and other Social Hymenoptera*. 10th to 13th of October, 2007. Punjabi University Patiala.

Paknia O and **Pfeiffer M**, 2007. Myrmecological studies along ecological gradients in Iran, questions and methods *International Conference on Ants and other Social Hymenoptera*. 10th to 13th of October, 2007. Punjabi University Patiala.

Fellowes JR, Brühl CA and **Pfeiffer M**, 2007. Ants in biodiversity conservation: a proposed IUCN ant specialist group and its possible functions *International Conference on Ants and other Social Hymenoptera*. 10th to 13th of October, 2007. Punjabi University Patiala.

Mezger D, Dyckmans J and **Pfeiffer M**, 2007. Studying the impact of ants on leaf-litter food webs in Malaysian rainforests by stable isotope analysis – first results. In: 37th Annual Conference of the Ecological Society of Germany, Austria and Switzerland in Marburg, Germany: Verlag Die Werkstatt, p. 130.

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Pfeiffer M (2007). The importance of ecological research and the role of the ants in ecosystems. Talk at the University of Gorgan, Iran 5.05.2007

Pfeiffer M (2007). EDIT WP7 ATBI+M pilot sites: Proposal of Gunung Mulu National Park, Sarawak, Malaysia. In: *EDIT WP7 Workshop 14-16.03.2007*, Stuttgart, Museum Rosenstein (invited speaker)

Pfeiffer M (2007). www.antbase.net: a myrmecological networking platform. *20th annual meeting of the German Society for Tropical Ecology (gtö)*, 21-25 Feb 2007, Bonn

Wells K, **Pfeiffer M** & Kalko EKV (2007). Seed consumption by tropical small mammals from Borneo. *20th annual meeting of the German Society for Tropical Ecology (gtö)*, 21-25 Feb 2007, Bonn

Pfeiffer M, Ho CT, Teh CL (2006). Species richness of ants and the impact of invasive "tramp" ant species in plantations of oil palm *Elaeis guineensis* in Borneo and the Peninsula Malaysia. *19th annual meeting of the German Society for Tropical Ecology* (*gtö)*, Kaiserslautern

Wells K, **Pfeiffer M**, Kalko EKV (2006). Each to their own: inconsistent responses of small mammals to rainforest logging in their movement trajectories and gastrointestinal parasites. *19th annual meeting of the German Society for Tropical Ecology* (*gtö)*, Kaiserslautern

Pfeiffer M (2005). Internet-based research tools and the future of biodiversity research. *5th ANeT International Workshop and Seminar*, Kuala Lumpur

Pfeiffer M, Lay TC, Tuck Hc (2005). Ants (Formicidae) in oil palm plantations *Elaeis guineensis* - biodiversity assessment and study of ant community structure. *5th ANeT International Workshop and Seminar*, Kuala Lumpur

Pfeiffer M Ants in Golden Hope Estates (2005). Talk held at the plenary of the Golden Hope Research Centre, Baning, Malaysia.

Pfeiffer M, Mezger D (2005) Community structure of leaf litter ants and their role in the soil food web of different forest types in Gunung Mulu N P. Gunung Mulu National Park.

Pfeiffer M, Lay TC, Tuck Hc (2005). Changes in land use patterns in Malaysia: Ant communities (Formicidae) in oil palm (*Elaeis guineensis*) plantations - a biodiversity assessment. 18th annual meeting of the German Society for Tropical Ecology (*gtö)*, Berlin

Wells K, **Pfeiffer M**, Lakim MB, Kalko EKV (2005). Vanishing wildlife and the dilemma of conservation: The continuous dependence of rural villagers on bush meat in Sabah (Malaysia) on Borneo. 18th annual meeting of the German Society for Tropical Ecology (*gtö)*, Berlin

Pfeiffer M, Chimedregzen L, Ulykpan K (2004) Artvielfalt und Struktur mongolischer Ameisengemeinschaften entlang eines ökologischen Gradienten von der Steppe bis in die Wüste Gobi. Talk held at University of Kiel. 10.5.2004

Pfeiffer M (2004). www.antbase.de - A new website on Asian ants. 17th Ann. Conf. of the Society for Tropical Ecology (gtö), 18-20 February 2004, Bayreuth

Pfeiffer M, Nais J, Sinun W, Linsenmair KE (2004). Granivorous ant ensembles in three primary rain forests on Borneo: diversity patterns and community organisation. 17th Ann. Conf. of the Society for Tropical Ecology (gtö), 18-20 February 2004, Bayreuth

Wells K, **Pfeiffer** M, Lakim MB, Kalko EKV (2004). Small mammal diversity declines in secondary rainforests on Borneo: an effect of rare species? 17th Ann. Conf. of the Society for Tropical Ecology (gtö), 18-20 February 2004, Bayreuth

Wells K, Lakim MB, **Pfeiffer** M & Kalko EKV (2004). Small mammal diversity in rainforests on Borneo: Do secondary forest communities differ? BBEC Int. Conf. 2004, Feb. 2004, Kota Kinabalu, Sabah, Malaysia

Pfeiffer M, Chimedregzen L and Ulykpan K (2003). Community organization and biodiversity of ants along an ecological gradient in Mongolia. Proceedings of the GFOE, Vol 33 "Biodiversity - from patterns to processes" 8 – 129 2003, Halle

Pfeiffer M & Linsenmair KE (2003). Trophobiotic interactions of giant ants *Camponotus gigas* (Hymenoptera: Formicidae) and wax cicada *Bythopsyrna circulata* (Homoptera: Flatidae) on a Syzygium-tree (Myrtaceae) in the understorey of a tropical rainforest on Borneo. Proceedings of the British Ecological Society (BES). Special Symposium & Annual Meeting of the Association for Tropical Biology and Conservation, "Biotic interactions in the tropics", 7-10 July 2003, Aberdeen

Pfeiffer M, Nais J and Linsenmair KE (2003). Myrmecochory in Malaysian rain forest herbs Proceedings of the British Ecological Society (BES). Special Symposium & Annual Meeting of the Association for Tropical Biology and Conservation, "Biotic interactions in the tropics", 7-10 July 2003, Aberdeen

Wells K, **Pfeiffer M**, Lakim MB and Linsenmair KE (2003). Demography of *Chiropodomys major* in the canopy of Malaysian rainforests. Proceedings of the British Ecological Society (BES). Special

Symposium & Annual Meeting of the Association for Tropical Biology and Conservation, "Biotic interactions in the tropics", 7-10 July 2003, Aberdeen

Wells K, **Pfeiffer M**, Lakim MB, Linsenmair KE (2003). Spacing patterns of the large pencil-tailed tree mouse, *Chiropodomys major*, in the canopy of a Bornean rainforest. 16th Ann. Conf. of the Society for Tropical Ecology (gtö), 19-22 February 2003, Rostock

Pfeiffer M (2003) Naturgeschichte und Verhaltensökologie von Riesenameisen (*Camponotus gigas*) im Regenwald von Borneo. Talk held at University of Kiel. 13.1.2003

Wells K, **Pfeiffer M**, Lakim MB, Linsenmair KE (2002). Diversity, dynamics and spacing patterns of a small mammal community in a primary rainforest on Borneo, comparing an arboreal and terrestrial habitat. 15th Ann. Conf. of the Society for Tropical Ecology (gtö), 20-23 February 2002, Göttingen

Pfeiffer M, Nais J, Linsenmair KE (2001). Three myrmecochorous rain forest herbs (*Globba*, Zingiberaceae). In: Menzel R, Rademacher R (eds). Proceedings of the 2001 Berlin Meeting of the European Sections of IUSSI, Berlin, p. 44

Pfeiffer, **M** (1997). Verhaltensökologie und Sozialstruktur von Riesenameisen *Camponotus gigas.* Proceedings of the 10 Annual Conference of the German Society for Tropical Ecology, 13.2 – 16.2. 1997. Leipzig

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