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Diversity and ecology of arboreal ant communities in a tropical lowland forest

Ph.D. Thesis

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Annotation:

The thesis focuses on the study of arboreal ant communities in a highly diverse tropical rainforest in Papua New Guinea. In the first study of its kind, whole patches of forest were sampled extensively for ants foraging and nesting in tree trunks and canopies. An extraordinary amount of material collected from 684 felled trees and 260 bait stations in plots of primary and secondary forest was used to study the mechanisms structuring the diversity and species coexistence of this ecologically important insect group at the local scale. *The first chapter* addresses the question 'Why are ant communities more species rich in primary than in secondary forests?' and explores the main environmental traits that influence their diversity in tropical trees. *The second chapter* compares the community diversity and composition and nesting preferences of ant species between both forest types. The final *third chapter* introduces a novel method, involving large-scale manipulation of ant communities that could serve as a template for future studies focused on complex tropical food-webs of canopy arthropods and plants. In summary, the results of the thesis highlight the importance of primary vegetation in conserving the diversity of native ant communities and the relevance of nesting microhabitats and their turnover between trees, rather than tree taxonomic diversity, for sustaining the diverse arboreal fauna in tropical forests.

Key words: ants, Formicidae, foraging activity, nesting preferences, rainforest ecosystem, species richness, tree canopy, tropics.

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Declaration:

I declare that I worked out my Ph.D. thesis on my own, and in collaboration with the co-authors, specified below, using only cited literature.

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Petr Klimeš

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Petr Klimeš

List of original papers and author contribution:

I. **Klimeš P.**, Novotný V., Idigel C., Rimandai M., Janda M., Weiblen G. D. (2011): Whole-forest diversity of arboreal ants: Why are there more species in primary than secondary tropical forests?
(manuscript to be submitted to *Diversity and Distributions*)

P. K. supervised the work and insect data collection in the field, sorted and determined the ant material, made the analyses and led the writing. V. N. significantly contributed to ideas and text. C. I. and M. R. led the field work and data entering, M. J. contributed to study design and identification of the ant taxa, G. D. W. led collection of the plant data.

II. **Klimeš P.,** Idigel C., Rimandai M., Janda M. (2011): Diversity, composition and nesting preferences of arboreal ant communities in a primary and secondary tropical forest.
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P. K. supervised the work and data collection in the field, sorted and determined the ant material, conceived and made the analyses and led writing. C. I. and M. R. led the field work and data entering. M. J. contributed to the ideas, text and identification of the ant taxa.

III. **Klimeš P.**, Janda M., Ibalim S., Kua J. and Novotný V. (2011): Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities. *Ecological Entomology* 36: 94-103. (IF = 1.85)

P. K. contributed substantially to the design and methods of the study, supervised the work and data collection in the field, sorted and determined the material, made the analyses and led the writing. M. J. and V. N. conceived the study and contributed to the text. S. I. and J. K. led the field work and data entering.

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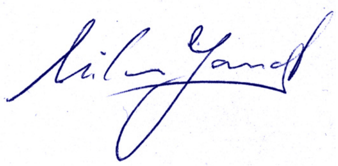
Coauthors listed below fully acknowledge the contribution of Petr Klimeš as the first author of all presented papers. They hereby agree with publication of the papers in this thesis and support this statement with their signatures.

Prof. RNDr. Vojtěch Novotný, CSc.



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INTRODUCTION

General perspective

Tropical forests belong to the most diverse and threatened ecosystems in the world. Rainforest trees and especially their upper stratum - the canopy - play a crucial role in the maintenance of global biodiversity and ecosystem processes (Ozanne *et al.*, 2003; Primack & Corlett, 2005). Forest trees are estimated to support 40% of extant animal species of which 10% are thought to be canopy specialists mainly consisting of various invertebrate animals such as arthropods (Hammond, 1992; Basset *et al.*, 2003; Ozanne *et al.*, 2003). Despite the considerable growth of scientific interest in canopy research during the last three decades, we still know relatively little about the arboreal arthropod fauna and the processes maintaining its diversity and distribution (Basset *et al.*, 2003; Ozanne *et al.*, 2003; Ellwood *et al.*, 2009). There are still disputes about the proportion of undescribed species of arthropods living in rainforest trees and even the elementary information about the ecology of most known species is lacking (Basset *et al.*, 2003; Novotny *et al.*, 2006; Hamilton *et al.*, 2010). However, such knowledge is crucial as primary forests are being converted to disturbed habitats and are increasingly under threat from logging, large scale agriculture and the spread of invasive species (Primack & Corlett, 2005).

Ants (Hymenoptera: Formicidae) are one of the most diverse, abundant and ecologically important animal groups in most terrestrial ecosystems (Hölldobler & Wilson, 1990; Folgarait, 1998; Lach *et al.*, 2010). Some of species are very important in their roles as ecosystem engineers, predators, decomposers and seed-dispersion agents. There are currently nearly 12,000 species described (Bolton *et al.*, 2011) and perhaps a similar number remains to be discovered. It has been estimated that ants constitute about 15% of the total animal biomass in tropical forests (Fittkau & Klinge, 1973). This success seems to be connected to their highly organized eusocial lives in colonies and to their great ability to adapt to different environments. As a result, ants play crucial role in the structuring of plant and animal interactions at both evolutionary and ecological scales (Hölldobler & Wilson, 1990; Heil & McKey, 2003; Moreau *et al.*, 2006). These attributes, coupled with a fairly good taxonomic knowledge base and their sensitivity to environmental changes, make them an ideal model group for biodiversity and ecological studies (Agosti *et al.*, 2000).

The extraordinary abundance of ants is known from tropical forest canopies, where they can represent 20 - 60% of the whole arthropod biomass and up to 90% of individuals (Floren & Linsenmair, 1997; Davidson *et al.*, 2003; Dejean *et al.*, 2007). Diversity of canopy fauna has also been estimated to be high as dozens of ant species were found to occur on a single tropical tree (e.g. Wilson, 1987; Floren & Linsenmair, 2000; Tanaka *et al.*, 2010). However, those communities are typically dominated by just one to three species despite their moderate to high overall diversity (Dejean *et al.*, 2007). Hence, one of the most intriguing questions for naturalists has been 'how do so many ant species coexist in a single tree?' This question has not yet been answered satisfactorily and we still know relatively little about which factors contribute to the high diversity and structure of dominance in their communities.

As a consequence of high abundance and organized social behavior, ants are considered a keystone group of predators in tropical trees exerting a high predation pressure on insect herbivores (Novotny *et al.*, 1999; Floren *et al.*, 2002; Dejean *et al.*, 2007). However, recent studies have stressed that many species can act as mutualists of plants and/or of insect herbivores (Davidson *et al.*, 2003; Blüthgen *et al.*, 2004). It has been suggested that these mutualistic interactions are a major contributor to maintaining the exceptionally high biomass of ants in the canopies via their "cryptic herbivory" on exudates produced by insect symbionts and plant extrafloral nectaries (Davidson *et al.*, 2003; Hunt, 2003). The role of ants in rainforests is thus very complex in that they are capable of having both beneficial (i.e. as predators protecting plants against herbivores) and harmful effects on plants (e.g. via deterrence of other predators, support of mutualistic herbivores).

The diversity of the terrestrial fauna (i.e. ground-dwelling species) and their ecology has been historically studied in much more detail than their arboreal counterparts (Agosti *et al.*, 2000). As a result, the most current knowledge about the diversity and distribution of canopy ant species in diverse rainforests is thus still based on extrapolation from samples collected by canopy-fogging with insecticides. Direct sampling has been used just in a handful of studies that were usually limited to a few trees (e.g. Blüthgen *et al.*, 2003; Tanaka *et al.*, 2010) or focused on only common species (Davidson *et al.*, 2007; Dejean *et al.*, 2010). **Complex studies of arboreal ant communities, including explicit data on their diversity, nesting preferences and distribution are needed if we are to understand the general mechanisms of their coexistence and dominance structure in tropical forest trees.**

This thesis focuses on detailed analysis of communities living in a highly diverse rainforest of Papua New Guinea. It represents the first complex study of tropical arboreal ants on a "whole-forest" scale. The following parts summarize the status of the current knowledge of the subject and provide the background and aims of individual thesis chapters.

Distribution and coexistence of arboreal ants in trees

Considerable attention has been given to understanding species coexistence and distribution in ant assemblages. At large geographical scales they respond to temperature, rainfall, eco-regional and other environmental factors (Dunn *et al.*, 2009; Delsinne *et al.*, 2010; Lach *et al.*, 2010). These responses seem to be similar for both terrestrial and arboreal fauna (Weiser *et al.*, 2010). At the local scale, competition and other interspecific interactions are usually considered important for structuring the assemblages (Andersen, 1992; Arnan *et al.*, 2011). However, contradictory patterns have been observed as well (e.g. Soares & Schoereder, 2001; Narendra *et al.*, 2011). To what extent the environment and species traits play active role in these interactions is still not well understood (Lach *et al.*, 2010). This is especially true for ants living on tropical trees (Powell *et al.*, 2011). Because tree canopies are hard to access, most of our knowledge of species living there comes out indirect methods, such as fogging and use of various canopy traps, rather than direct observations (Floren & Linsenmair, 1997; Dejean *et al.*, 2007; Powell *et al.*, 2011; Yusah *et al.*, 2011). Moreover, studies of ant distribution in tropical trees have been made at larger scale only in highly disturbed habitats as plantations and agro-forests (e.g. Philpott & Foster, 2005; Pfeiffer *et al.*, 2008). The few existing studies on undisturbed forests are usually limited to low strata and/or a low number of trees (e.g. Floren & Linsenmair, 2000; Basset *et al.*, 2003; Tanaka *et al.*, 2010).

One of the essential theories explaining spatial distribution of ants is the *'ant mosaic theory'*, originally described by Leston (1973) from coconut plantations. It has been built on the assumption that negative and positive associations exist between ant species. The theory predicts that the spatial structure of ant assemblages is determined by the distribution of colonies belonging to dominant (behaviorally and/or numerically) ant species, which maintain exclusively non-overlapping territories. Consequently, communities with the same dominant species are more similar to each other in species composition than communities dominated by different species (Dejean *et al.*, 2007). Ant mosaics have been described from a number of tropical agricultural habitats and disturbed secondary forests (e.g. Room, 1975; Majer, 1993; review in Dejean & Corbara, 2003). Some researchers have also applied the theory to primary forest (e.g. Majer, 1991; Dejean *et al.*, 2000; Dejean & Corbara, 2003; Davidson *et al.*, 2007), whereas others have used modern statistical approaches as null models to argue that the structure of native rainforest communities is produced by stochastic events and therefore they are rather unpredictable in space and time (e.g. Floren & Linsenmair, 2000; Ribas & Schoereder, 2002; Sanders *et al.*, 2007). Hence, general validity of the mosaic theory in forests remains still disputable. It should be also stressed that the majority of the studies that tested the pattern were usually limited to data from fogged trees and hence did not include environmental traits which may cause the non-random patterns of ant communities as well, e.g. distribution of nesting resources and complexity of microhabitats.

Relatively recently, it has been suggested that important structuring forces of the distribution of arboreal ants might be the food resources such as homopteran symbionts and extrafloral nectaries and that their spatial availability might result in a pattern that resembles the mosaic at the local scale (Blüthgen *et al.*, 2004; Blüthgen & Stork, 2007). It has also been shown that many other factors such as habitat disturbance (Schulz & Wagner, 2002; Dunn, 2004), the presence of an invasive ants (Dejean *et al.*, 2010), microenvironmental conditions (Ellwood *et al.*, 2009; Tanaka *et al.*, 2010) and plant diversity (Ribas *et al.*, 2003) can play an important role for the diversity and distribution of ants in trees. Some studies of less diverse ecosystems went yet further and demonstrated the importance of nest site availability and heterogeneity for arboreal species coexistence using a manipulative experiment (Philpott & Foster, 2005; Powell *et al.*, 2011). However, reliable data on highly diverse rainforests are still very scarce and findings often differ, perhaps due to different methods and the scale of the studies.

New Guinea and the knowledge of its arboreal ant fauna

New Guinea (NG) is one of the three major tropical wilderness areas remaining on Earth and ranks ninth among the most forested tropical countries of the world (Mittermeier *et al.*, 2003). This largest tropical island supports approximately 5% of global biodiversity and its forest flora is among the most diverse in the world with over 20,000 species of vascular plants (Johns, 1993). In contrast to other tropical regions, the majority of people in NG still practice subsistence agriculture and customary ownership of land is protected under the nation's Constitution (Novotny, 2010). These conditions provide an excellent opportunity for studying biodiversity patterns in super-diverse and relatively intact forests.

However, the global trends of deforestation in the tropics do not exclude NG. Although the NG is still one of the largest native forested regions in the tropics, the island is also experiencing high rates of deforestation, particularly in the more accessible lowland areas where loss already exceeds 30% (Shearman & Bryan, 2011). Between 1972 and 2002, about 15% of the NG forests were cleared and 8% degraded through logging in Papua New Guinea (Shearman *et al.*, 2009). Approximately half of the remaining unlogged lowland forest has already been allocated to logging concessions, whereas less than 2% have any form of protection (Shearman *et al.*, 2009). Despite these worrying figures, we still do know very little about the effects of rainforest disturbance on the arboreal fauna and the ants are no exception. At the time of writing, there is no study quantitatively comparing the NG ant communities of primary and secondary (disturbed) forests.

Ant diversity in NG is among the highest worldwide. There are up to 120 ant species in a single patch of 400 m^2 of forest (Janda *et al.*, 2007) and almost 900 species have been recorded in NG so far (Janda *et al.*, 2011). As a result of the enormous diversity and relatively short research history, a large proportion of NG ant fauna (20-30%) are estimated as undescribed (Snelling, 1998), and this figure is perhaps yet higher for arboreal species. Since the time of pioneer descriptive study of Wilson (1959), there have been only a few ecological studies on arboreal ants in NG, mostly limited to plantations (Room, 1975; Leponce *et al.*, 1999) or focused on myrmecological plants (Huxley, 1978; Letourneau *et al.*, 1993). Until the recent study of Janda & Konecna (2011), virtually no data on NG primary rainforests were available. In this study, rather low diversity of canopy assemblages was found with an average of 3.6 ant species per tree. Furthermore, tree species and site had no effect on the species composition suggesting random processes in structuring NG communities. However, the authors searched for ants in only 19 trees of two species and the sampling was limited to baits and hand-collections in trees. Hence, studies at a larger scale and in more habitats are still required.

Background and aims of the thesis

This thesis brings together the first insights and results from the processing and analysing of unique data about the ant fauna occurring in tropical trees and their nesting ecology. It builds on an extensive ant and plant material that has been collected as part of international project led by the New Guinea Binatang Research Centre and the team of prof. V. Novotný from 2006–2008 (NGBRC, 2011). The study site, where all sampling and experiments took place, was located in a tropical lowland forest area near Wanang village, Madang province, Papua New Guinea. All trees with diameter at the breast height (DBH) ≥ 5 cm were sampled for several arthropods guilds in two plots of size of one hectare. Both plots were established in an area marked for traditional subsistence agriculture. The main aim of this project was to generate complete plant-insect food webs from one ha of primary and one ha of secondary lowland rainforest for the first time. The plots were gradually felled with the cooperation of the indigenous landowners. Each felled tree within the plots was measured and its entire foliage was weighed. This offered an ideal opportunity to study the arboreal ant communities as each sampled tree could be easily and extensively searched for ant nests and foragers. The project results regarding the plant data and densities of herbivores are currently being published elsewhere and are not part of this thesis (Whitfeld *et al.*, 2011).

The author personally participated on the above project in 2007, gaining an opportunity to study the canopy ants and their ecology. The unique ant data obtained during that period are the subject of this thesis and include two comparable datasets from two plots of 0.32 ha size (40 x 80 m) that were sampled in the primary and secondary rainforest. Furthermore, in a separate experiment, whole ant communities at the site were monitored and experimentally manipulated with treated bait stations to test the feasibility of a large-scale experiment to suppress arboreal ants. In total, samples from 684 felled trees (*Chapters 1 and 2*) and 260 bait stations (*Chapter 3*) in continuous plots of primary and secondary forest were processed by author during last few years. This material represents the most comprehensive ant dataset ever collected in rainforest trees. The novel approach of sampling whole patches of a highly diverse rainforest ecosystem enabled assessment of ant community composition and distribution across trees in primary and in secondary forest and to test for the various ecological mechanisms structuring their diversity.

The aim of *the first chapter* is to assess the main environmental traits affecting the diversity of arboreal nesting ants at the whole-forest level and analyse why their communities are more species-rich in primary than secondary forest. We hypothesize that the richness of communities in primary forest is considerably higher than those in secondary forest due to disparities in vegetation between the forest types. In particular, we test for the effects of tree size, density and species richness, which has been suggested to influence ant diversity (Schulz & Wagner, 2002; Ribas *et al.*, 2003). Our unique sampling across all trees allows for very first time to test separately for such effects. Firstly, we assess specifically how the species richness correlates with tree size in the both forest types and explore the effect of plant taxonomic diversity on the communities. Secondly, proportions of the difference in ant species richness between both forests are explained due to different (a) tree density, (b) tree size and (c) tree diversity using a random selection of trees and the additive partitioning of their ant species richness to its alpha and beta components (i.e. diversity per tree and species turnover between trees respectively).

The focus of *the second chapter* is to explore the complete diversity, taxonomic composition and nesting preferences of the above communities, and to assess the relative differences between the primary and secondary forest ecosystem. It has been noted that figures about the ant diversity in individual trees might be largely overestimated as foragers from nearby trees and the ground are usually considered as part of the arboreal fauna (Hammond, 1992; Schulz & Wagner, 2002; Floren & Linsenmair, 2005). However, the precise figures are still missing. Here, we study the diversity and composition separately for foraging and arboreal nesting ants. To our knowledge, only one such study of ant communities exists (Tanaka *et al.*, 2010) but no one has attempted to study whole patches of forest and compare different forest types so far. For the first time, our study attempts to reveal the proportion of species actually nesting in individual trees and how foraging individuals contribute to the overall diversity estimates. Furthermore, the unique direct sampling of nests allows us to test for the effect of nesting preferences on the species composition. We hypothesize that higher diversity and availability of nesting microhabitats in the native forest might significantly contribute to higher ant richness when compared to disturbed forests. In particular, ant nesting preferences within each forest type to (a) forest stratum (trunks and crowns), (b) nest sites and (c) tree species are assessed. The suitability of ants as bio-indicators of forest disturbance and the differences in their community composition are demonstrated, including the presence of invasive species.

The last third chapter introduces a novel method involving large-scale manipulation of ant communities. Plant-insect food webs of tropical forests are so complex that manipulative experiments are one of the few feasible approaches to their study (Morris *et al.*, 2004). This is particularly true for ants that often play multiple and conflicting roles in the same ecosystem (Lach *et al.*, 2010). Here, we test a new 'whole-forest' method of their exclusion, using canopy bait stations treated by insecticides and placed in isolated rainforest plots (25 x 25 m) in primary and secondary forest. The experiment represents the largest manipulative treatment of ants in tropical forest to date. The presented methods could be useful for future tropical food-web studies of canopy arthropods and plants. Apart from the methodological aspect, the last chapter reveals further insights into patterns of foraging activity and community structure of tropical ants, including the two main forest strata, understorey and canopy.

REFERENCES

Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (2000) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, D.C.

Andersen, A.N. (1992) Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *American Naturalist*, **140**, 401-420.

Arnan, X., Gaucherel, C. & Andersen, A.N. (2011) Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. *Oecologia*, 1-12.

Basset, Y., Kitching, R.L., Miller, S.E. & Novotny, V. (2003) *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. University Press, Cambridge.

Blüthgen, N. & Stork, N.E. (2007) Ant mosaics in a tropical rainforest in Australia and elsewhere: a critical review. *Austral Ecology*, **32**, 93-104.

Blüthgen, N., Gebauer, G. & Fiedler, K. (2003) Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia*, **137**, 426-435.

Blüthgen, N., Stork, N.E. & Fiedler, K. (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos*, **106**, 344-358.

Bolton, B., Alpert, G., Ward, P.S. & Naskrecki, P. (2011) *Bolton's catalogue of ants of the world: 1758-2005*. Harvard University Press, Cambridge, MA. Updated online version at: http://gap.entclub.org/contact.html (accessed 22. July 2011).

Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua, T.H. (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, **300**, 969-972.

Davidson, D.W., Lessard, J.P., Bernau, C.R. & Cook, S.C. (2007) The tropical ant mosaic in a primary Bornean rain forest. *Biotropica*, **39**, 468-475.

Dejean, A. & Corbara, B. (2003) A review of mosaics of dominant ants in rainforests and plantations. *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (ed. by Y. Basset, V. Novotny, S.E. Miller and R.L. Kitching), pp. 341-347. Cambridge University Press, Cambridge.

Dejean, A., McKey, D., Gibernau, M. & Belin, M. (2000) The arboreal ant mosaic in a Cameroonian rainforest (Hymenoptera : Formicidae). *Sociobiology*, **35**, 403-423.

Dejean, A., Corbara, B., Orivel, J. & Leponce, M. (2007) Rainforest canopy ants: the implications of territoriality and predatory behavior. *Functional Ecosystems and Communities*, **1**, 105-120.

Dejean, A., Fisher, B.L., Corbara, B., Rarevohitra, R., Randrianaivo, R., Rajemison, B. & Leponce, M. (2010) Spatial Distribution of Dominant Arboreal Ants in a Malagasy Coastal Rainforest: Gaps and Presence of an Invasive Species. *PloS one*, **5**, e9319.

Delsinne, T., Roisin, Y., Herbauts, J. & Leponce, M. (2010) Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco. *Journal of Arid Environments*, **74**, 1149-1155.

Dunn, R.R. (2004) Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, **18**, 302-309.

Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerda, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gibb, H., Gotelli, N.J., Gove, A.D., Guenard, B., Janda, M., Kaspari, M., Laurent, E.J., Lessard, J.P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Pfeiffer, M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Weiser, M.D. & Sanders, N.J. (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, **12**, 324-333.

Ellwood, F.M.D., Manica, A. & Foster, W.A. (2009) Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters*, **12**, 277-284.

Fittkau, E.J. & Klinge, H. (1973) On Biomass and Trophic Structure of the Central Amazonian Rain Forest Ecosystem. *Biotropica*, **5**, 2-14.

Floren, A. & Linsenmair, K.E. (1997) Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, with special reference to Formicidae. *Canopy arthropods* (ed. by N.E. Stork, J. Adis and R.K. Didham), pp. 344-381. Chapman & Hall, London.

Floren, A. & Linsenmair, K.E. (2000) Do ant mosaics exist in pristine lowland rain forests? *Oecologia*, **123**, 129-137.

Floren, A. & Linsenmair, K. (2005) How reliable are data on arboreal ant (Hymenoptera: Formicidae) communities collected by insecticidal fogging? *Myrmecologische Nachrichten*, **7**, 91-94.

Floren, A., Biun, A. & Linsenmair, K.E. (2002) Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia*, **131**, 137-144.

Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221-1244.

Hamilton, A.J., Basset, Y., Benke, K.K., Grimbacher, P.S., Miller, S.E., Novotny, V., Samuelson, G.A., Stork, N.E., Weiblen, G.D. & Yen, J.D.L. (2010) Quantifying uncertainty in estimation of tropical arthropod species richness. *American Naturalist*, **176**, 90.

Hammond, P. (1992) Species inventory. *Global biodiversity: status of the earth's living resources* (ed. by B. Groombridge), pp. 17-39. Chapman & Hall, London, UK.

Heil, M. & McKey, D. (2003) Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology Evolution and Systematics*, **34**, 425-453.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Harvard University Press, Cambridge.

Hunt, J.H. (2003) Cryptic herbivores of the rainforest canopy. *Science*, **300**, 916-917.

Huxley, C.R. (1978) The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology. *New Phytologist*, **80**, 231-268.

Janda, M. & Konecna, M. (2011) Canopy assemblages of ants in a New Guinea rain forest. *Journal of Tropical Ecology*, **27**, 83-91.

Janda, M., Klimes, P. & Borowiec, M. (2007) Ecology of New Guinea ants (Hymenoptera: Formicidae) - exploring an unknown fauna. *Myrmecological News* **10**, 109.

Janda, M., Kotrla, J., Borowiec, M., Riha, P., Klimes, P. & Alpert, G. (2011) *The Ants of New Guinea: species checklist and database of melanesian ant fauna* http://www.newguineants.org (accessed July 2011).

Johns, R.J. (1993) Biodiversity and conservation of the native flora of Papua New Guinea. *Papua New Guinea Conservation Needs Assessment* (ed. by J.B. Alcorn). Biodiversity Support Program, Washington, D. C.

Lach, L., Parr, L.C. & Abbott, K.L. (2010) *Ant Ecology*. Oxford University Press Inc., New York.

Leponce, M., Roisin, Y. & Pasteels, J. (1999) Community interactions between ants and arboreal-nesting termites in New Guinea coconut plantations. *Insectes Sociaux*, **46**, 126-130.

Leston, D. (1973) The ant mosaic - tropical tree crops and the limiting of pests and diseases. *PANS (Pest Artic. News Summ.)*, **19**, 311-341.

Letourneau, D.K., Arias, G.F. & Jebb, M. (1993) Coping with enemy-filled space: herbivores on *Endospermum* in Papua New Guinea. *Biotropica*, **25**, 95-99.

Majer, J.D. (1993) Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia - its structure and influence on ant diversity. *Hymenoptera and biodiversity* (ed. by J. Lasalle and I.D. Gauld), pp. 115-141. CAB International, Oxford.

Majer, J.D., Camer-Pesci, P. (1991) Ant species in tropical Australian tree crops and native ecosystems. Is there a mosaic? *Biotropica*, **23**, 173-181.

Mittermeier, R., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., Da Fonseca, G. & Kormos, C. (2003) Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences*, **100**, 10309.

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, **312**, 101-104.

Morris, R.J., Lewis, O.T. & Godfray, H.C.J. (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature*, **428**, 310-313.

Narendra, A., Gibb, H. & Ali, T.M.M. (2011) Structure of ant assemblages in Western Ghats, India: role of habitat, disturbance and introduced species. *Insect Conservation and Diversity*, **4**, 132–141.

NGBRC (2011) The New Guinea Binatang Research Center: Research – Plant-herbivore food webs in primary and secondary rainforests. Available at http://www.entu.cas.cz/png/parataxoweb.htm (accessed June 2011).

Novotny, V. (2010) Rain Forest Conservation in a Tribal World: Why Forest Dwellers Prefer Loggers to Conservationists. *Biotropica*, **42**, 546-549.

Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G.D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*, **313**, 1115-1118.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., Kasbal, M., Isua, B., Kutil, R., Manumbor, M. & Molem, K. (1999) Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. *Australian Journal of Ecology*, **24**, 477-483.

Ozanne, C., Anhuf, D., Boulter, S., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A., Nakashizuka, T. & Dias, P. (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science*, **301**, 183.

Pfeiffer, M., Cheng Tuck, H. & Chong Lay, T. (2008) Exploring arboreal ant community composition and co occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. *Ecography*, **31**, 21-32.

Philpott, S.M. & Foster, P.F. (2005) Nest-site limitation in coffee agroecosystems: Artificial nests maintain diversity of arboreal ants. *Ecological Applications*, **15**, 1478-1485.

Powell, S., Costa, A.N., Lopes, C.T. & Vasconcelos, H.L. (2011) Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *Journal of Animal Ecology*, **80**, 352-360.

Primack, R.B. & Corlett, R. (2005) *Tropical rain forests: an ecological and biogeographical comparison*. Blackwell Publishing Ltd.

Ribas, C.R. & Schoereder, J.H. (2002) Are all ant mosaics caused by competition? *Oecologia*, **131**, 606–611.

Ribas, C.R., Schoereder, J.H., Pic, M. & Soares, S.M. (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, **28**, 305-314.

Room, P.M. (1975) Relative distributions of ant species in cocoa plantations in Papua New Guinea. *Journal of Applied Ecology*, **12**, 47-61.

Sanders, N.J., Crutsinger, G.M., Dunn, R.R., Majer, J.D. & Delabie, J.H.C. (2007) An ant mosaic revisited: dominant ant species disassemble arboreal ant communities but co-occur randomly. *Biotropica*, **39**, 422-427.

Schulz, A. & Wagner, T. (2002) Influence of forest type and tree species on canopy ants (Hymenoptera: Formicidae) in Budongo Forest, Uganda. *Oecologia*, **133**, 224-232.

Shearman, P. & Bryan, J. (2011) A bioregional analysis of the distribution of rainforest cover, deforestation and degradation in Papua New Guinea. *Austral Ecology*, **36**, 9-24.

Shearman, P.L., Ash, J., Mackey, B., Bryan, J.E. & Lokes, B. (2009) Forest conversion and degradation in Papua New Guinea 1972-2002. *Biotropica*, **41**, 379-390.

Snelling, R. (1998) Social Hymenoptera of the Lakekamu Basin. A biological assessment of the Lakekamu Basin*,* Papua New Guinea. *RAP Working Papers*, **9**, 10-39.

Soares, S.M. & Schoereder, J.H. (2001) Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil. *Insectes Sociaux*, **48**, 280-286.

Tanaka, H.O., Yamane, S. & Itioka, T. (2010) Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. *Population Ecology*, **52**, 147-157.

Weiser, M.D., Sanders, N.J., Agosti, D., Andersen, A.N., Ellison, A.M., Fisher, B.L., Gibb, H., Gotelli, N.J., Gove, A.D., Gross, K., Guenard, B., Janda, M., Kaspari, M., Lessard, J.P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Yanoviak, S.P. & Dunn, R.R. (2010) Canopy and litter ant assemblages share similar climate-species density relationships. *Biology Letters*, **6**, 769-772.

Whitfeld, T.J.S., Novotny, V., Miller, S.E., Hrcek, J., Klimes, P. & Weiblen, G.D. (2011) Predicting the impact of tropical rain forest conversion on insect herbivore abundance from plant traits and phylogeny. *Ecology* (In press).

Wilson, E.O. (1959) Some ecological characteristics of ants in New Guinea rain forests. *Ecology*, **40**, 437-447.

Wilson, E.O. (1987) The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica*, **19**, 245-251.

Yusah, K.M., Fayle, T.M., Harris, G. & Foster, W.A. (2011) Optimizing Diversity Assessment Protocols for High Canopy Ants in Tropical Rain Forest. *Biotropica* (In press). DOI: 10.1111/j.1744-7429.2011.00775.x.

CHAPTER 1

Whole-forest diversity of arboreal ants: Why are there more species in primary than secondary tropical forests?

Klimeš P., Novotný V., Idigel C., Rimandai M.,
Janda M. & Weiblen G.D. (2011)

Manuscript
(to be submitted to *Diversity and Distributions*)

Whole-forest diversity of arboreal ants: Why are there more species in primary than secondary tropical forests?

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ABSTRACT

Aim Species diversity of arboreal ants tends to increase during rainforest succession so that their communities in primary forests comprise more species than those on secondary vegetation, but it is not well understood why. Primary forests differ from secondary forests in a wide array of factors whose relative impact on ant diversity has not yet been quantified.

Location Tropical lowland forest, Papua New Guinea.

Methods We used a complete census of 1,332 ant nests from all trees with DBH ≥ 5 cm occurring within two 0.32 ha plots, one in primary and one in secondary forest, to assess effects of succession-related determinants on ant diversity. In particular, we measured the ant species richness on sets of primary forest trees randomly selected to match a 0.1 ha set of secondary trees in their density, size distribution, and taxonomic diversity.

Results In total, 80 species from 389 trees in primary and 42 species from 295 trees in secondary forest were recorded. Surprisingly, there were no differences between plots in mean species richness per tree and in the relationship of ant diversity to tree size. However, similarity of ant communities was higher among secondary than primary trees. An analogous pattern was observed also for similarity of nest sites suggesting that secondary trees were more uniform in providing nesting opportunities compared to trees in primary forest. There were 49 ant species in the primary forest tree set, which was 24 species more than in the secondary tree set. This difference was partitioned according to the effects of higher tree density (17%), larger tree size (12%), and higher taxonomic diversity of trees (21%) in primary than in secondary forest. The remaining difference of 12 species (50%) was due to higher beta diversity of ant communities between primary forest trees.

Main Conclusions Our study suggests that microhabitat heterogeneity between trees is more important for maintaining ant diversity in tropical forests than plant species diversity. A lower turnover of nesting microhabitats is thus probably main cause of the species loss in secondary forests.

Keywords Formicidae, diversity partitioning, ecosystem conservation, species richness, tree canopies, tropical ecosystems.

CHAPTER 2

Diversity, composition and nesting preferences of arboreal ant communities in a primary and secondary tropical forest

Klimeš P., Idigel C., Rimandai M. & Janda M. (2011)

Manuscript

Diversity, composition and nesting preferences of arboreal ant communities in a primary and secondary tropical forest.

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ABSTRACT

The tropical forest canopies are known for extraordinary abundance and high diversity of ants. However, the factors which structure these communities and enable coexistence of many species within a limited space are not well understood. We sampled the complete arboreal ant fauna within one plot of primary and one plot of secondary forest in Papua New Guinea (0.32 ha each). In the first study of its kind, the diversity and composition of whole forest communities was explored for nesting and foraging ants. All trees with DBH over 5 cm were sampled and the effects of tree size, forest type, strata and nesting preferences on the ant communities were assessed. Multivariate analysis with variation partitioning was applied to test for separate effects of the nest sites and tree species on ants within each forest community.

The effects of forest type and of tree size were significant regardless whether considering foragers, nests, or both combined. The number of recorded species per tree varied from zero to 20 species. In total, 102 species from 389 trees occurred in the primary plot compared with only 50 species from 295 trees in the secondary forest plot. However, there was a rather small difference in mean ant richness per tree between primary and secondary forest (3.8 and 3.3. sp. respectively). Considerably lower richness per tree was found when only nest records were considered (1.5 sp. per tree in both forests). In general, tree crowns were more species rich than trunks, but stratification of species was rather low.

Primary forest was dominated by the native species *Crematogaster polita* Smith F. and *Anonychomyrma* cf. *scrutator*, whereas invasive species such as *Anoplolepis gracilipes* (Smith F.) and *Monomorium floricola* (Jerdon) were common in secondary forest. Nest sites plus tree species explained 26% of the variance in ant community composition in each forest. Nevertheless, most of the variance was linked to nest sites, whereas the effect of tree species was low. The primary forest communities were only slightly more specialized to particular nest sites. However, they used a greater variety of microhabitats than the secondary forest communities.

Our results highlight the importance of nest site diversity and availability for arboreal ants, but rather small effect of rainforest stratification and plant diversity on structuring their communities. The study demonstrates high contribution of foragers to arboreal diversity and the relevance of primary vegetation for the conservation of native fauna.

Keywords: biodiversity, canopy, disturbance, invasive species, foraging activity, microhabitats, nest site selection, New Guinea, rainforest trees.

CHAPTER 3

Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities.

Klimeš P., Janda M., Ibalim S., Kua J. & Novotný V. (2011):

Ecological Entomology 36: 94-103.

Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities

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Abstract

1. Ants are extremely abundant in lowland tropical forests where they are important predators, plant mutualists and herbivores. Their complex role in tropical plant-insect food webs can be best assessed by experimental manipulation of their abundance. Historically, ant exclusion experiments have had a small-scale focus, such as single trees. Here, we test a new 'whole-forest' method of ant exclusion, using treated canopy bait stations, in a diverse tropical rainforest in New Guinea.
2. We conducted a 10-month manipulative experiment in primary and secondary rainforests. In each forest type, a 625 m^2 treatment plot was isolated from the surrounding forest and 135 bait stations treated with fipronil, S-methoprene and hydramethylnon were placed in trees to suppress ants. Ant activity was monitored in the forest canopy and understorey with an additional 65 stations in treatment and control plots.
3. We achieved a dramatic decline in ant abundance in treatment plots compared to controls in both forest types, with an average decrease in ant numbers per station of 82.4% in primary and 91.2% in secondary forest. In particular, native dominant species *Oecophylla smaragdina*, *Anonychomyrma* cf. *scrutator* in primary forest, and invasive *Anoplolepis gracilipes* in secondary forest were greatly affected. In contrast, *Tapinoma melanocephalum* flourished in treatment plots, perhaps benefitting from reduced competition from other ant species.
4. Our study demonstrates that it is possible to selectively eradicate most of the foraging ants in a structurally complex tropical forest. We propose whole-forest manipulation as a novel tool for studying the role of ants in shaping plant-insect food webs.

Key words. Ant exclusion, canopy, bait traps, Formicidae, food webs, tropical forests

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SUMMARY

SUMMARY

Tropical forest canopies are known to host an extraordinary abundance and high diversity of ants, one of the most ecologically important animal groups in the tropics. However, the factors that structure their communities and enable the coexistence of many species within a limited space are not well understood. Such knowledge is crucial as tropical forests are being degraded into structurally simpler habitats with lower species diversity.

This thesis explored the diversity and ecology of arboreal ant communities in a diverse tropical rainforest in Papua New Guinea. Unlike previous studies that focused on communities sampled from just a few trees, a novel and complex approach was designed to study whole patches of forest. Both foraging ants and those nesting in tree trunks and canopies were extensively sampled from 684 felled trees (DBH > 5 cm) and 260 bait stations in plots of primary and early successional secondary forest. The first two chapters of the thesis were based on the results from trees sampled in two 0.32 ha plots, one being established in primary and one in secondary forest. The final chapter focused on the results from a large scale manipulative experiment where ant communities were actively suppressed from two 625 m^2 plots using combination of arboreal bait stations treated with insecticides and isolation from surrounding vegetation.

Main findings

The first chapter focused on the question ‘Why are ant communities more species rich in primary than in secondary forests?’ and explored the main environmental traits that might influence nesting diversity on tropical trees. In agreement with our prediction, the species diversity in the primary forest plot was considerably higher than in the secondary plot. In total, 80 species from 752 nests on 389 trees in primary but only 42 species from 580 nests on 295 trees in secondary forest were recorded. However, at the level of individual trees, there were no significant differences in species and nest site diversity between plots. Although the tree size and taxonomic diversity varied greatly between primary and secondary forest, the correlation with tree size did not vary between plots. Similarly, plant taxonomy also had little effect on ant communities in both forest types. Using a random selection of trees from each plot, analysis demonstrated that disparities in vegetation between plots accounted for only half of the difference in ant species richness between forest types, while the residual variance was due to higher beta diversity of ant species among primary than secondary forest trees. As secondary forest trees were more similar to each other in the nesting opportunities they provided compared to primary trees, a lower turnover of nesting microhabitats is likely to be the main cause of species loss in secondary forest.

The focus of *the second chapter* was to explore the diversity, taxonomic composition and nesting preferences of entire ant communities, and to assess the relative differences between the primary and secondary forest ecosystem. The effects of forest type and tree size were found to be significant whether considering ant foragers, nests, or both combined. The secondary forest was much more dominated by invasive species. However, there was a rather small difference in mean ant richness per tree between primary and secondary forest (3.8 and 3.3. sp. respectively). For nesting ants alone, a considerably lower richness per tree was observed (1.5 sp. per tree in both forests). The results highlighted the importance of tree canopies, as opposed to trunks, for species and nest diversity. Furthermore, the effects of tree species and forest stratification were low at the species level. Considerable proportion of variation in communities was explained by variability in nest sites, but the primary forest species were not significantly more specialized in their nesting preferences than secondary species. The findings greatly support the results of the previous

chapter that the availability of nest microhabitats and their turnover between forest trees is the main factor structuring arboreal ant communities.

The results of the ant manipulation experiment presented *in the third chapter* demonstrated that it is possible to selectively suppress the activity of ants foraging on tropical vegetation, including tree canopies. A dramatic decline in ant abundance in treated plots, compared to controls, in both forest types, with an average decrease in ant numbers per station of approx. 80 % in primary and 90 % in secondary forest, was achieved. Moreover, the results revealed that community species composition was altered significantly as a result of the manipulation. Given the multiple roles ants play in tropical plant-insect food webs, such as predators of herbivorous insects and/or 'cryptic herbivores', the method could prove to be useful for future studies aiming to assess the influence of ants on plant and insect communities at scale of 'whole forest'.

In summary, the results of the thesis demonstrated high beta diversity of ant assemblages between individual tropical trees, evidently supported by great microhabitat heterogeneity in forest canopies. This result seems to contradict the assumption that inter-species interactions, plant diversity, tree size and density are the main factors structuring ant communities at local scales. Instead, it suggests the importance of nesting microhabitat availability and diversity. The results further showed the high contribution of foragers to arboreal diversity and raised the possibility that the diversity of canopy ants in previous studies has been over-estimated. As secondary forest highly was characterized by the presence of opportunistic and invasive species and was significantly species-poorer, it is clear that primary vegetation is very important when considering conservation of the native ant fauna.

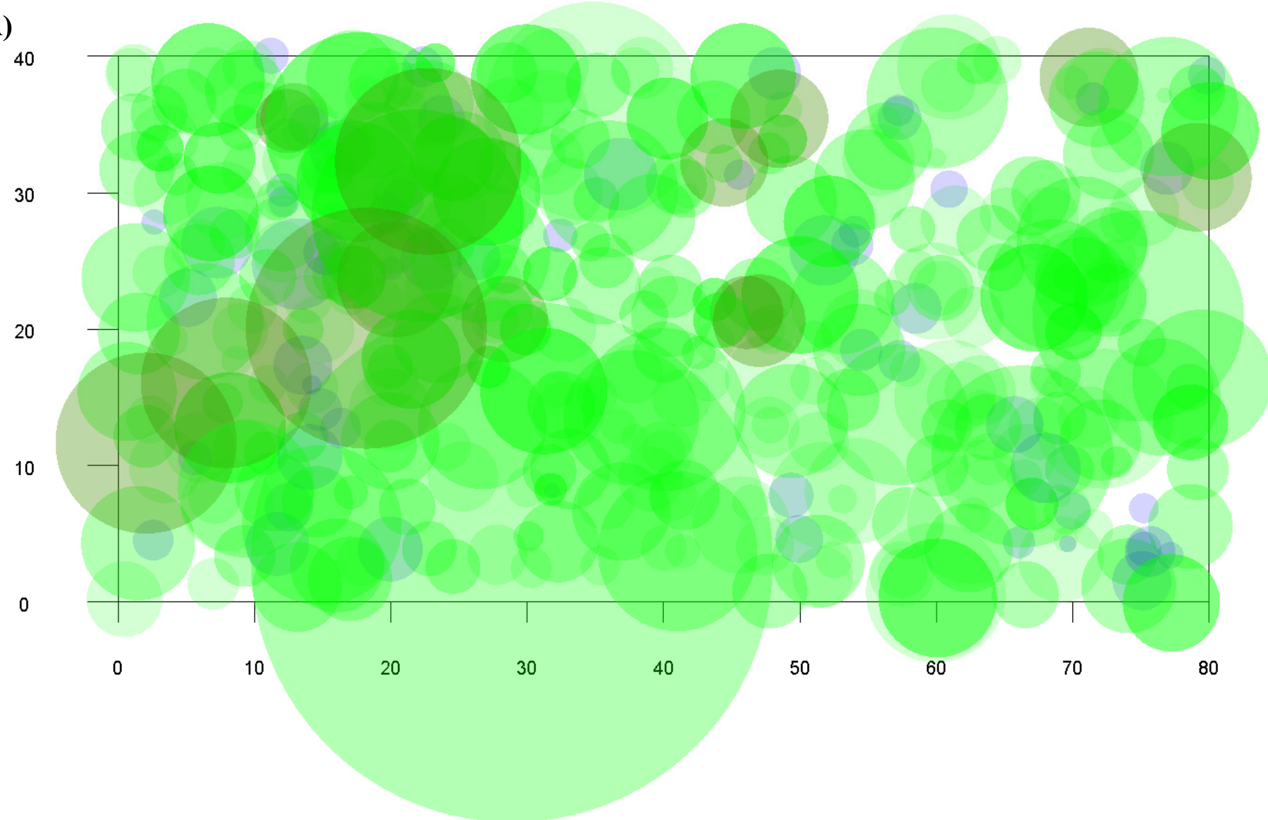
Future directions

The thesis provided interesting insights into the factors responsible for structuring ant communities on tropical trees. In particular, the study focused on ant diversity, their activity patterns and nesting ecology. However, as the available data also includes unique spatial information on the trees, there are other directions to be explored. In particular, the datasets could be used to test for the presence of 'ant mosaic' in the New Guinean rainforest and to explore possible correlations between spatial distribution of ant species and their insect symbionts and other herbivorous insects occurring on the same vegetation. These research topics were not included in the current work as material for non-ant taxa are being processed. The novel method employing large-scale suppression of ant communities could be used in a replicated design that also will focus on other insect or arthropod taxa in order to assess the importance of ants in tropical plant-insects food-webs. The author hopes that this thesis will serve as a template for ambitious future studies.

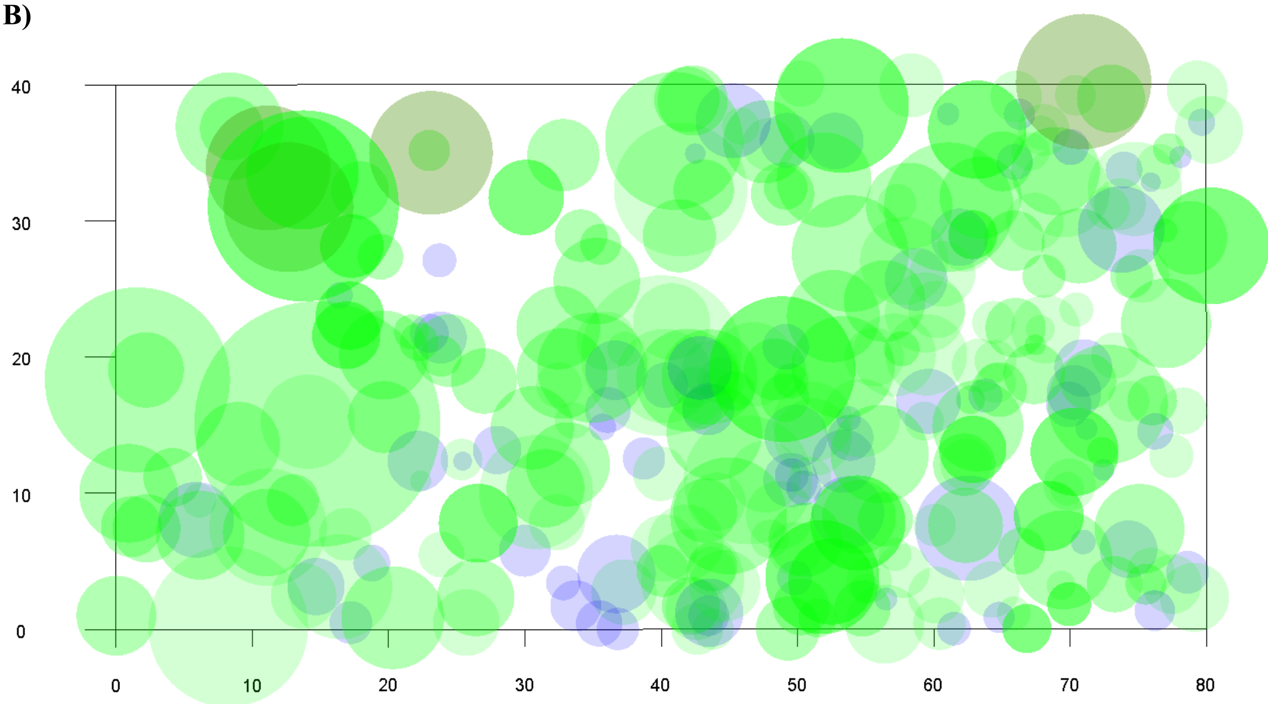
APPENDICES

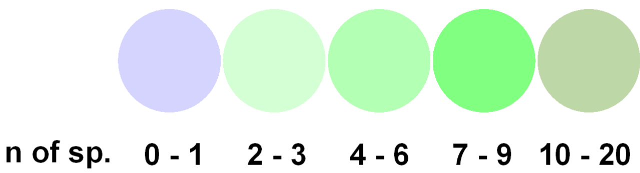
Appendix 1. Two-dimensional map of the primary (A) and the secondary (B) forest plot (0.32 ha, 80 x 40 metres). Each circle represents one tree and its position within the plot. Size of the circle indicate the crown width (in m) and colour the total number of ant species per tree (nesting and foraging occurrences together) for each tree. Figures were constructed using a customized script kindly provided by J. Hrček (University of South Bohemia) run in R software version 2.6.1.

A)

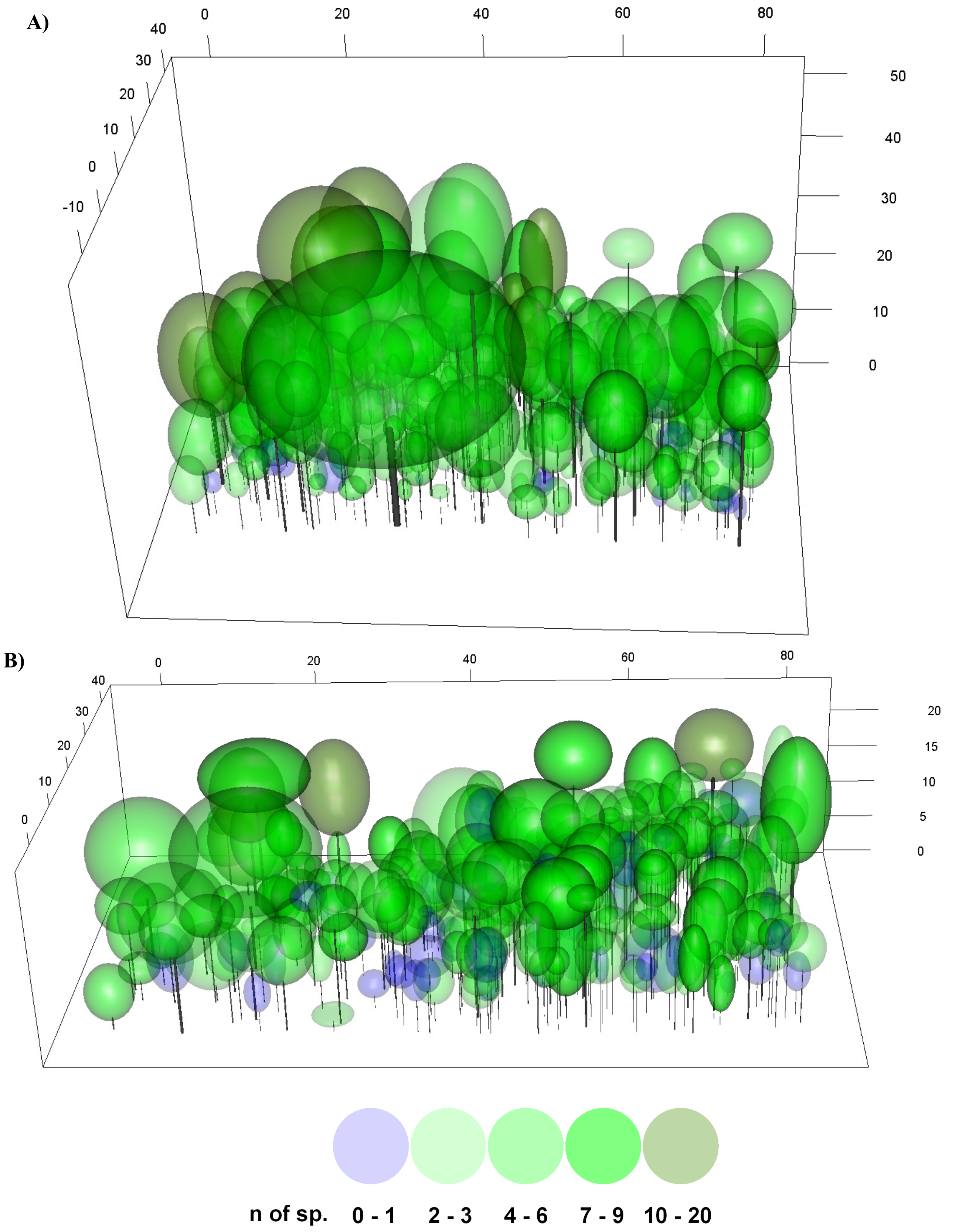


B)





Appendix 2. Three-dimensional map of the primary (A) and the secondary (B) forest plot (0.32 ha, 80 x 40 metres). Each circle represents one tree and its position within the plot. Size of the circle indicate the crown width (in m), width of the bars the DBH (in m) and colour the total number of ant species per tree (nesting and foraging occurrences together) for each tree. Figures were constructed using a customized script kindly provided by J. Hrček (University of South Bohemia) run in R software version 2.6.1.



Appendix 3. Pictures from the field (by P. Klimeš): (1) Research field station in Wanang with the primary rainforest canopy behind. (2) Primary forest. (3) Secondary forest. (4) Assistant Fidelis Kimbang sampling ant nest in a hollow live branch. (5) Paraecologists while searching for arthropod fauna from a felled tree and measuring its height.

Appendix 4. Examples of the common arboreal ants and their nests (photos by NGBRC and/or by 'www.newguineants.org' team).

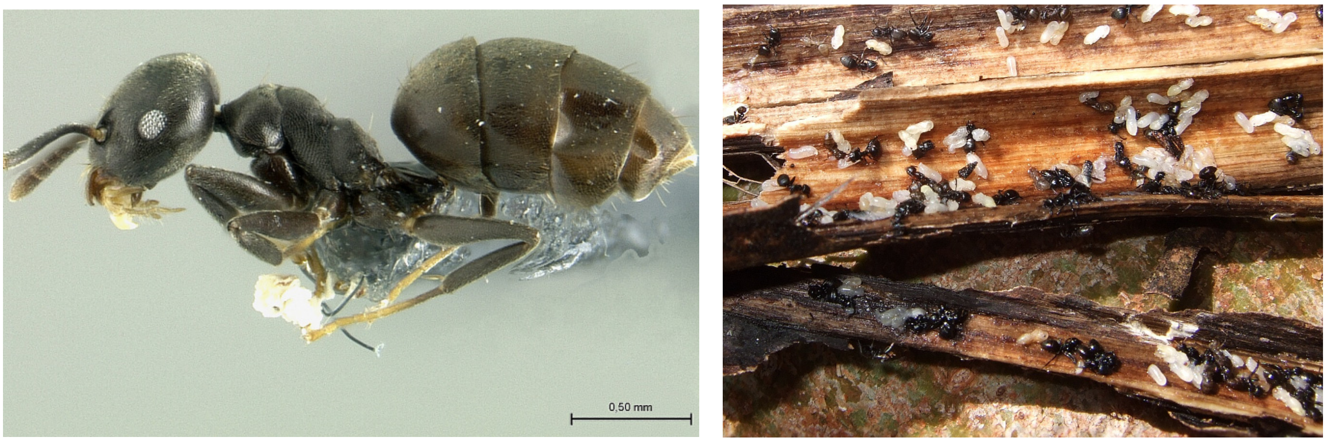
A) Primary forest:


Crematogaster polita (Myrmicinae): wood-carton nest on the bark.

Anonychomyrma cf. scrutator (Dolichoderinae): nest in cavity of live trunk

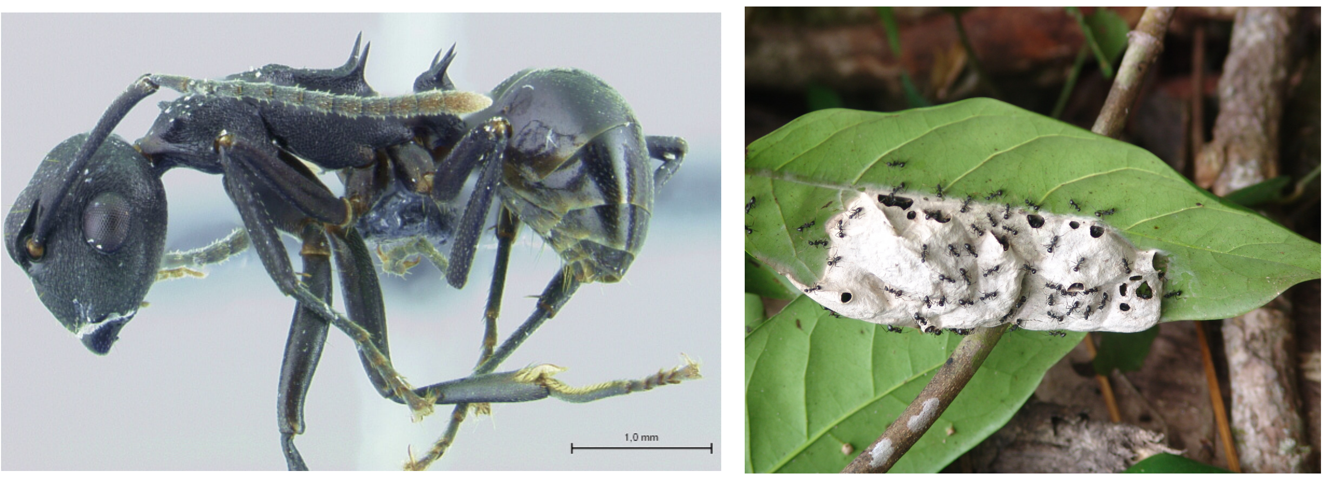
Diacamma rugosum (Ponerinae): nest in aerial soil (i.e. under roots of epiphyte)

B) Secondary forest:



Technomyrmex brunneus (Dolichoderinae): nest under bark of a rotten branch.

Camponotus 010 aff. *macrocephalus* (Formicinae): nest in a dry hollow branch.



Polyrhachis 009 aff. *aequalis* (Formicinae): carton nest on leaf.