

The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems

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Abstract

Recent efforts to understand global patterns of ant diversity have largely neglected the canopy which harbours a diverse ant fauna, particularly in tropical lowland forests. We comprehensively sampled ant diversity and abundance by canopy-fogging in South-East Asian lowland rain forests (99 trees fogged, 151,396 ant individuals, 328 morphotypes) and in Central European temperate forests (375 trees fogged, 9,232 ant individuals, 12 species). We found large differences in taxonomic composition, diversity, and overall abundance of the canopy ant communities in both biomes. Our data suggest that in the tropics approximately 50% of all ant species are at least partially associated with the canopy. Taxonomic work on selected groups of ants suggests that a substantial proportion of these species are new to science. Due to high habitat specificity canopy ants previously were out of reach for ant collectors and have thus largely remained unrecorded. Canopy ants therefore have been neglected in ecosystem analyses or global diversity modelling. In contrast, in temperate forests only 12% of the species are known to be arboreal and ants rarely achieve dominance in the canopy. The large difference in abundance and species numbers in the canopy of temperate and tropical forests suggests major differences in the ecological and functional impact of canopy ants.

Key words: Borneo, Central Europe, Formicidae, fogging, species diversity, stratification.

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Introduction

Tree canopies have been shown to harbour a large proportion of species diversity in forests, particularly in tropical lowland rainforests (STORK & al. 1997, FLOREN & SCHMIDL 2008). Nevertheless, canopy arthropods are only rarely taken into account in ecosystem analyses. Worldwide, in both tropical and temperate regions, forests are heavily exploited and the pressure especially on primary forests is progressively increasing (HANSEN & al. 2008, GIBBS & al. 2010, MASEK & al. 2011, MIETTINEN & al. 2011). However, still far too little is known on how large scale forest destruction affects biodiversity and ecosystem function (DENT & WRIGHT 2009, FOSTER & al. 2011, GIBSON & al. 2011, WARDLE & al. 2011).

Ants are dominant in tropical lowland forest canopies in terms of overall abundance and biomass (HÖLLDOBLER & WILSON 1990). As key-stone species, ants carry out important ecological functions. In tree canopies, for example, they exert a high predation pressure and thus significantly influence the diversity, structure and dynamics of arboreal arthropod communities (FLOREN & al. 2002, PHILPOTT & ARMBRECHT 2006). Less obviously, they are also effective herbivores that obtain carbohydrates and nitrogen from plant-based sources such as extra-floral nectar and homo-

pteran honeydew (DAVIDSON & al. 2003, BLÜTHGEN & FELDHAAR 2009). In temperate forests, ants are less dominant in the canopy and do not build large arboreal nests, but ground nesting species such as *Formica polyctena* FOERSTER, 1850 (Formicinae) who forage in the canopy in large numbers (PUNTILLA & al. 2004, SEIFERT 2007, 2008) can under suitable local conditions still have major effects. These sharp differences between biomes also suggest a different ecological impact. Nevertheless, there are only very few comparative studies of the diversity and ecological impact of arboreal ants in temperate and tropical forests (JAFÉ & al. 2007).

Ants are an ideal model group for biodiversity research due to their moderate species richness with about 15,000 described species of ants occurring worldwide (BOLTON 1994) and due to their large ecological importance (HÖLLDOBLER & WILSON 1990, FOLGARAIT 1998, DEL TORO & al. 2012). In order to understand the mechanisms maintaining species diversity and to aid conservation responses to habitat destruction and climate change, recent attempts have been made to model global patterns of ant distribution and diversity (DUNN & al. 2009, JENKINS & al. 2011, GUÉNARD & al. 2012). However, most studies still only refer to

Tab. 1: Number of trees (by species and families) from which ants were collected by insecticidal knock-down in Central Europe (375 trees) and in Borneo (99 trees).

Tree species	Family	Number of trees		
		Poland (Białowieża)	Germany (Leipzig, Steigerwald)	Sum
<i>Alnus glutinosa</i> (L.) GAERTN.	Betulaceae	13		13
<i>Betula pendula</i> ROTH	Betulaceae	12		12
<i>Carpinus betulus</i> L.	Betulaceae	18		18
<i>Fagus sylvatica</i> L.	Fagaceae	6	9	15
<i>Quercus robur</i> L.	Fagaceae	156	22	178
<i>Fraxinus excelsior</i> L.	Oleaceae		18	18
<i>Abies alba</i> MILL.	Pinaceae	2		2
<i>Picea abies</i> (L.) H.KARST.	Pinaceae	39		39
<i>Pinus sylvestris</i> L.	Pinaceae	51		51
<i>Populus tremula</i> L.	Salicaceae	6		6
<i>Acer pseudoplatanus</i> L.	Sapindaceae	1	18	19
<i>Tilia cordata</i> MILL.	Tiliaceae	1		1
<i>Ulmus laevis</i> PALL.	Ulmaceae	1	2	3
Total		306	69	375
Borneo, Malaysia		Kinabalu NP	Crocker Range	Sum
<i>Melanolepis</i> sp.	Euphorbiaceae		21	21
<i>Saraca dentate</i> RUIZ & PAV.	Fabaceae		1	1
<i>Clerodendron</i> sp.	Lamiaceae		1	1
<i>Vitex pinnata</i> L.	Lamiaceae	23		23
<i>Melochia umbellata</i> (HOULT.) STAPF	Malvaceae	11		11
<i>Aporusa lagenocarpa</i> SHAW	Phyllantaceae	22		22
<i>Aporusa subcaudata</i> MERR.	Phyllantaceae	14		14
<i>Xanthophyllum affine</i> KORTH.	Polygalaceae	6		6
Total		76	23	99

ground living species and neglect the remarkable diversity of ants in tropical canopies (e.g., FLOREN & LINSENMAIR 1997, STORK & al. 1997, RYDER-WILKIE & al. 2010).

Our work aims at closing these knowledge gaps by providing large datasets from tree canopies in two major biomes, Central European (CE) temperate forests and South-East (SE) Asian tropical lowland rainforests. We provide general information about the diversity and taxonomic composition of the studied canopy ant communities and discuss their ecological impact. The main questions addressed in this study are: (I) How does the canopy ant fauna differ in respect to diversity and to taxonomic composition between tropical and temperate forests? (II) What proportion of the ant fauna can be considered arboreal in these biomes and how can we explain the differences? (III) What can be inferred about the impact of arboreal ants on the arthropod fauna in these biomes?

Material and Methods

Study sites: We analyzed data that were collected by insecticidal knock-down ("canopy-fogging") of 474 trees during the last 20 years in several types of old-world tropical and temperate forests. In CE, 375 trees were fogged (Tab.

1), mostly in the Białowieża forest in East Poland (52° 30' - 53° 00' N, 23° 30' - 24° 15' E) from 2001 to 2004 summing up to 306 trees in total. More than 50% of the trees were *Quercus robur* L. (Fagaceae), which harbors a particularly diverse fauna of arthropods (BRÄNDLE & BRANDL 2001). The forest is situated in the transitional zone between the temperate and the cold-temperate climate zones, and is predominately a mixed oak-linden-hornbeam forest (*Tilio carpinetum*) with a natural contribution of *Picea abies* (L.) H. KARST. (Pinaceae) (FALINSKI 1986). For more details on the study sites we refer to FLOREN & al. (2008). Another 60 trees were fogged in the Leipzig flood plain forest, Germany, in 2006 and 2008 (51° 20' N, 12° 22' E). Nine beech trees (*Fagus sylvatica*, L., Fagaceae) were fogged in the Steigerwald in Northern Bavaria, Germany, in 2009 (50° 4' N, 10° 26' E). In all cases we studied lowland deciduous forests where trees reached up to 40 meters height.

In the tropics, we sampled 99 trees from different lowland forests in Sabah, Malaysian Borneo, from 1992 to 2001 (Tab. 1). In or around the Kinabalu National Park (size: 754 km², 6° 3' N, 116° 42' E) 76 trees were fogged. Most trees belonged to the genus *Aporusa* (Phyllantaceae) and to *Vitex pinnata* (Lamiaceae). Another 21 trees, mostly

Melanolepis sp. (Euphorbiaceae) were fogged close to the Crocker Range National Park (size 1,399 km², 5° 24' N, 116° 7' E). No myrmecophytic tree species were chosen for this study. All sampled forests were located between 500 and 700 meters above sea-level in the Crocker Mountain Range where a natural mixed dipterocarp hill forest is growing. For a comprehensive description of all SE-Asian study sites, including a map, please see FLOREN & al. (2011).

Collecting method: Canopy arthropods were collected by insecticidal knock-down. Methodical details are discussed in full length in FLOREN (2010). We used natural pyrethrum, a poison which attacks the nervous system of insects, as insecticide. Arthropods react immediately after contact, and drop into the collecting sheets installed beneath the tree crown. Fogging was always carried out early in the morning or late in the afternoon when there was little wind drift, insuring that the insecticidal fog could reach the top of the trees. A dropping time of two hours was allowed before the arthropods were brushed together and stored in 70% ethanol. Ants were sorted to morphotypes and checked by specialists in doubtful cases. Voucher specimens of all species are stored in the collection of the first author. For further information on the species we refer to the taxonomic ant picture-base of Asia and Europe (<http://www.antbase.net>) maintained by M. Pfeiffer and K. Enkhtur from the Department for Ecology, Mongolian National University, where pictures of many of the species in question are published.

It has already been shown that fogging collects arboreal ant species efficiently (FLOREN 2005, YUSAH & al. 2012). Intensive hand collections and bait samples in the tree crowns proved that most species in Borneo nest in the trees and form long lasting communities (FLOREN & LINSSENMAIR 2000). The data used for the comparison of total ant diversity of Borneo are those published by PFEIFFER & al. (2011), which also consider the fogging data analyzed here. Information for CE is based on the work of SEIFERT (2007, 2008) which allowed us to distinguish truly arboreal species that nest in the canopy from those species that nest on the ground but forage in the canopy. For the comparison of species numbers we refer to the 114 species recorded from Germany (SEIFERT 2007) as all ant species that we collected in Poland can also be found in Germany. Besides the key provided by SEIFERT (2007) we used BOLTON (1994) who also helped during the process of morpho-species classification in dubious cases.

Data analysis: Data were analyzed using R, version 2.15.1 (R DEVELOPMENT CORE TEAM 2012). Mann-Whitney U-tests were used to compare the abundance, diversity, and proportion of ants in fogging samples. We used the vegan-package for R (OKSANEN & al. 2011) to calculate the species estimators Chao, first order jackknife (jack1), and second order jackknife (jack2) for both biomes. Individual-based rarefaction curves were used to test for completeness of sampling.

Results

Diversity and taxonomic composition of canopy ant communities: The data collected comprise a total of 474 fogged trees and reveal clear differences between temperate and tropical forests (Tab. 2). In the 375 European samples we found 9,232 ant individuals from 12 species. In the Białowieża forest we collected 7,253 ant specimens, but

Tab. 2: Number of ant species and individuals collected by insecticidal knock-down from trees in Borneo and Central Europe. The tropical forests clearly show higher numbers at both levels. Arthropod community sizes for the proportion calculations are based on studies of FLOREN & LINSSENMAIR (1997) and FLOREN (2008). SD = standard deviation.

		Number of ant species per tree	Number of ant individuals per tree	Proportion of ants in arboreal arthropod communities (%)
Borneo	Mean ± SD	24.4 ± 11.7	1529.3 ± 1536.1	38.1 ± 20.8
	Median	23	1025	39.3
	Range	7 - 53	13 - 8231	2.2 - 82.3
Central Europe	Mean ± SD	2.7 ± 1.2	44.8 ± 81.5	2.4 ± 7.0
	Median	3	16	0.7
	Range	1 - 7	1 - 675	0 - 59.8

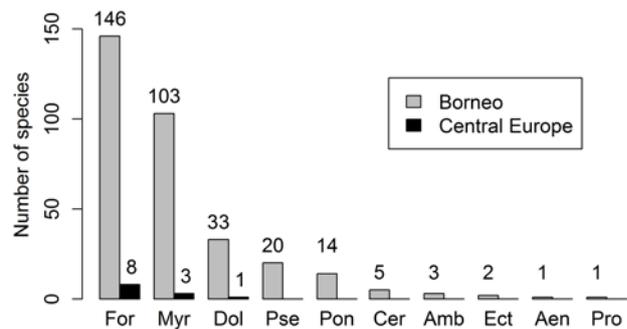


Fig. 1: Subfamily-composition of the canopy ant fauna collected by insecticidal knock-down in Borneo and Central Europe. The number of species per subfamily is indicated on top of the bars. Formicinae (For), Myrmicinae (Myr), and Dolichoderinae (Dol) dominate both in tropical and temperate forests. Pseudomyrmecinae (Pse), Ponerinae (Pon), Cecropachyinae (Cer), Amblyoponinae (Amb), Ectatomminae (Ect), Aenictinae (Aen), and Proceratiinae (Pro) were found in lower species numbers in tropical canopies only.

almost half of the trees harbored no ants at all (44.8% or 137 out of 306 trees). In Leipzig and in the Steigerwald ants were found on all trees with 1,737 and 242 individuals, respectively. Mean proportion of ants in all canopy arthropods was 2.4% but the number of ants varied largely between trees, with a maximum of 675 individuals representing 59.8% of all arthropods on that particular tree. Only 24 trees had more than 100 individuals. The average number of ant species per tree was three, while the maximum number was seven. In the tropical forests we collected 151,396 ants from the 99 trees. In contrast to the temperate forests, ants were clearly the dominant group here representing on average 38.1% of all arthropods per tree (ranging from 2.2% - 82.3%). The proportion of ants and the number of individuals was highly significantly larger in tropical canopies (Mann-Whitney U-test, both $p < 0.0001$). Ants were fogged from all trees but numbers var-

Tab. 3: Species diversity of canopy ants in temperate forests collected by insecticidal knock-down. Information on colony size and feeding habits after SEIFERT (2007, 2008) with additions from HIGASHI & al. (1987), BLACKER (1992), and HANSEN & KLOTZ (2005). Of the twelve species, four are arboreal specialists (*) which nest and forage solely in the canopy. The four canopy specialists known from Germany that we did not collect are listed for completeness. All other species nest in the ground and enter trees to forage. Abbreviations: z = zoophagous, t = trophobiont, n = nectarivor.

Ant species recorded by fogging	Number of ant individuals	Species constancy	Potential size of colonies [workers]	Feeding guild
<i>Camponotus fallax</i> (NYLANDER, 1856)*	583	38	< 300	z, t
<i>Formica fusca</i> LINNAEUS, 1758	110	18	< 2000	z, t
<i>Formica polyctena</i> FOERSTER, 1850	17	7	several millions	z, t
<i>Formica rufa</i> LINNAEUS, 1761	924	11	max. 25% of <i>F. polyctena</i>	z, t
<i>Lasius alienus</i> (FOERSTER, 1850)	19	8	several 1000	z, t, n
<i>Lasius brunneus</i> (LATREILLE, 1798)*	2537	115	< 200	z, t
<i>Lasius fuliginosus</i> (LATREILLE, 1798)	185	4	< 2 millions	z, t
<i>Lasius plathythorax</i> SEIFERT, 1991	1870	28	several 10000	z, t
<i>Myrmica rubra</i> (LINNAEUS, 1758)	62	26	< 300	z, t
<i>Myrmica ruginodis</i> NYLANDER, 1846	487	101	< 2000	z, t
<i>Temnothorax corticalis</i> (SCHENK, 1852)*	1611	126	< 300	z
<i>Dolichoderus quadripunctatus</i> (LINNAEUS, 1771)*	827	65	< 300	z
Sum	9232			
Not collected by fogging				
<i>Camponotus herculeanus</i> (LINNAEUS, 1758)*			> 10000	z, t
<i>Camponotus truncatus</i> (SPINOLA, 1808)*			< 500	z, t
<i>Crematogaster scutellaris</i> (OLIVIER, 1792)*			populous	z, t
<i>Temnothorax affinis</i> (MAYR, 1855)*			< 200	z

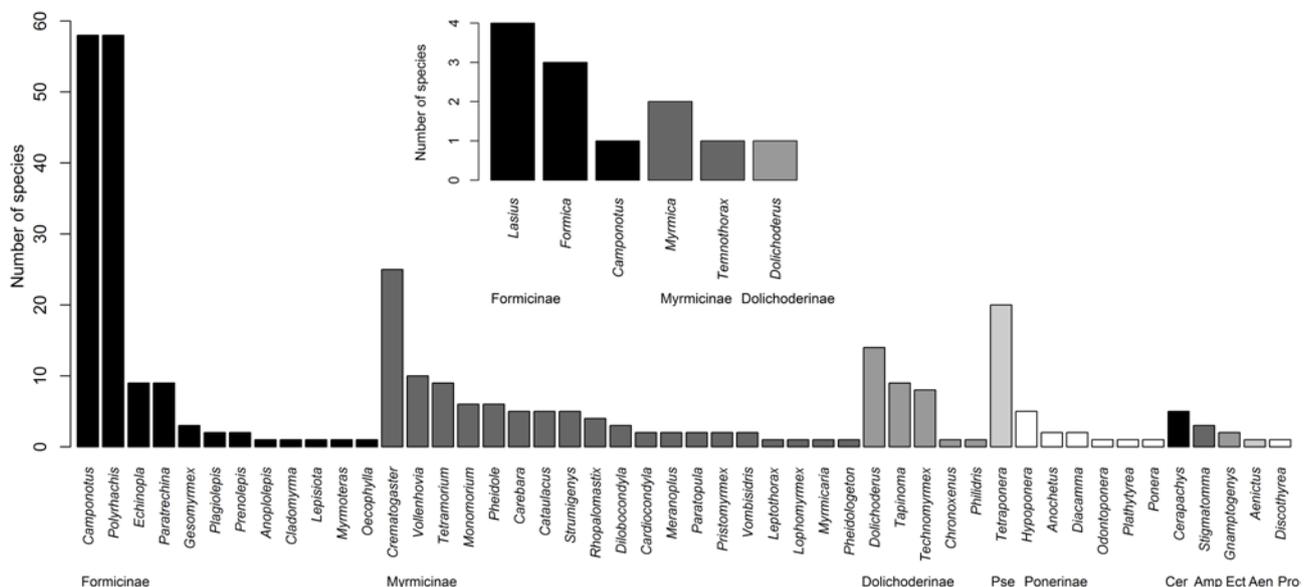


Fig. 2: Ant species per genus collected in tropical (large figure) and temperate forests (embedded figure). Generic and species diversity is much larger in the tropics but different genera contribute to overall diversity in both types of forests. Abbreviations as in Figure 1.

ied largely (Tab. 2). Only from nine trees we fogged less than 100 ant individuals.

The 12 ant species collected from trees in CE belong to three subfamilies and six genera (Tab. 3, Fig. 2). Rarefaction analysis as well as the species estimators Chao, jack1

and jack2 suggest complete sampling, assuming that the number of 12 recorded species is actually close to the number of species occurring regularly in the canopy (Appendix S1, as digital supplementary material to this article, at the journal's web pages). The genera *Lasius* (4 species), *For-*

mica (3) and *Myrmica* (2) constituted most of the species. *Camponotus fallax* (NYLANDER, 1856), *Temnothorax corticalis* (SCHENCK, 1852) and *Dolichoderus quadripunctatus* (LINNAEUS, 1771) were the sole representatives of their genera. In the combined fogging samples *L. brunneus* (LATREILLE, 1798), *L. plathythorax* SEIFERT, 1991 and *T. corticalis* were numerically dominant (Tab. 3). *L. brunneus*, *T. corticalis*, and *M. ruginodis* NYLANDER, 1846 were fogged from at least 100 of all 208 ant-harboring trees and showed the highest constancy. Constancy of the other species was significantly lower (median of 18). Of the eight species considered as truly arboreal in Germany (SEIFERT 2007) we collected four, namely *C. fallax*, *L. brunneus*, *T. corticalis* and *D. quadripunctatus* (Tab. 3). The remaining four canopy specialists not sampled by fogging were *Crematogaster scutellaris* (OLIVIER, 1792), a synantropes species found in urban environments, *Camponotus truncatus* (SPINOLA, 1808), *C. herculeanus* (LINNAEUS, 1758) and *T. affinis* (MAYR, 1855). The latter three species do not occur in Białowieża or in the Leipzig forest but are known from the Steigerwald where sample effort was low.

Ant diversity per tree was larger in the tropical canopy than in the temperate canopy by several orders of magnitude (Mann-Whitney U-test, $p < 0.0001$). The 328 species and morphotypes represent ten subfamilies and 48 genera (Figs. 1 and 2, and Appendix S2, as digital supplementary material to this article, at the journal's web pages). We found 58 species of both *Camponotus* and *Polyrhachis*, each representing 17.7% of the total species number. We found 25 *Crematogaster* species (7.6%), 20 *Tetraponera* species (6.1%), and 14 *Dolichoderus* species (4.3%). Altogether these five genera contributed 175 species or 53.4% of all species. We collected more than 10,000 individuals of each of the five most abundant species which belong to *Dolichoderus*, *Technomyrmex*, and *Crematogaster*. There were 77 singletons, species which are represented by one individual, representing 23.5% of all species. Rarefaction analysis revealed an incomplete sampling, as illustrated by the strongly unsaturated species accumulation curve (Appendix S1). Based on Chao, jack1 and jack2 estimators, 447, 435, and 493 species respectively were estimated to live in the investigated canopies, with a mean of 458 expected arboreal ant species.

Ranking of subfamilies in both biomes was similar (Fig. 1). Formicinae were most species rich followed by Myrmicinae, and Dolichoderinae. Diversity of Formicinae was 18 times higher in Borneo, and the diversity of Myrmicinae and Dolichoderinae were 34 and 33 times higher, respectively. Pseudomyrmecinae, Ponerinae, Cerapachyinae, Amblyoponinae, Ectatomminae, and Aenictinae do not occur in CE. The taxonomic composition of the canopy ant fauna is shown in Figure 2. Diversity on the generic level in the rain forests is very high, and the overlap between tropical and temperate biomes on this taxonomic level is low.

Stratification of ant communities: Figure 3 compares the extent of stratification of the ant species in tropical and temperate forests. Using the recently published list of Borneo ants by PFEIFFER & al. (2011) as basis for comparison of species richness, the 328 canopy-dwelling morphotypes represent approximately half (45.7%) of the hitherto 717 ant species found on Borneo. In contrast, the 12 fogged temperate species represent only 6.9% of the total 173

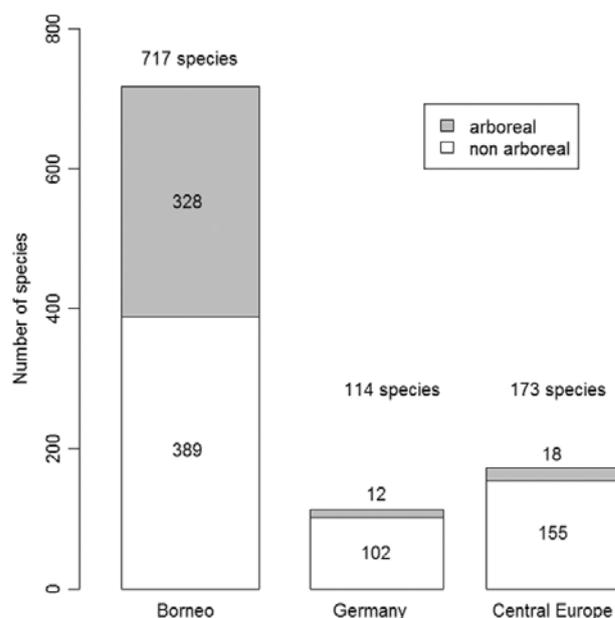


Fig. 3: Comparison of species richness of canopy and ground living ants. In Borneo, 717 ant species are currently known (PFEIFFER & al. 2011) of which 328 (45.7%) can be found in the canopy. In Germany, 12 species (10.5%) were fogged from the trees of which eight (7.0%) are considered true canopy dwellers (SEIFERT 2007). In CE, for comparison with Germany, 173 ant species are known of which 18 (10.4%) are truly arboreal (SEIFERT 2008).

species in CE, and 10.5% of the 114 German species. All species collected in Poland are also common in Germany (SEIFERT 2007, 2008). In total, 18 truly arboreal species can be found in CE, representing 10.4% of the total ant community (SEIFERT 2008). The respective numbers for Germany are eight truly arboreal species or 7% of the total diversity.

Discussion

Based on two large data sets collected over the last 20 years in tropical rain forests in SE-Asia and temperate forests in CE our data document very clearly the large differences in the taxonomic composition, the diversity and the overall abundance of canopy ant communities between these biomes. We also have clear indications of a higher proportion of stratum-specific species in the tropics, where canopy ants account for about 50% of all ant species. This proportion is reduced to about 10% in CE. All ants which were used in this analysis were collected by insecticidal knock-down which has been shown to be highly efficient in sampling arboreal ants (FLOREN 2005, YUSAH & al. 2011). In addition, bait sampling and observations in the trees show that fogging greatly underestimates the abundance of species nesting in tree trunks or wood cavities which are protected due to their sheltered location. As stem nesting species, such as *Pheidole* or *Crematogaster* or rather unobvious species like *Monomorium* can be particularly abundant in tropical trees the true numbers of canopy ants must be assumed to be significantly higher than indicated by the mere numbers of collected specimens (FLOREN & al. 2002).

Diversity of canopy ants in tropical and temperate forests: Our results show that arboreal ants contribute significantly to overall species diversity in the tropical forests of Borneo which is well known for its high generic and endemic diversity (GUÉNARD & al. 2012). With 328 ant morphotypes identified from 99 samples (Appendix S2), this is by far the richest dataset of canopy ants available today (compare YUSAH & al. 2011). Sampling was not sufficient to represent the complete species pool and species estimators predict that the canopy community is comprised of more than 450 species in total. This indicates that canopy ants are highly specialized to arboreal life (see WILSON & HÖLLDOBLER 2005) and do usually not forage on the ground. Hence, they are unsampled with collection methods that focus on lower strata. Efficient habitat separation explains the high number of unknown species in the canopy which remains difficult to access. As explained further below, mainly the climatic conditions in the young post-glacial temperate forests prevent the permanent colonisation of the canopy where only few species have adapted canopy life (Tab. 3). It was surprising to us that, despite the available knowledge, high species richness of the canopy ants has hitherto received so little attention in the analysis of global ant diversity (DUNN & al. 2009, WEISER & al. 2010, JENKINS & al. 2011, GUÉNARD & al. 2012).

There are more than 1,100 estimated ant species in Borneo (PFEIFFER & al. 2011). However, there is an enormous gap between scientifically known species and those still awaiting discovery and formal description. This does not only concern cryptic or rare species – 109 species (33%) in our sample were collected from a single tree or by one individual – but is mainly caused by the high proportion of strictly arboreal species. Even common or large-bodied arboreal species were historically unattainable for ant collectors and may still wait for discovery and scientific description. In our dataset this is reflected in the many potential new species collected over the course of our studies. We found new species even in conspicuous and prominent taxa like *Polyrhachis*. Ongoing taxonomic evaluation has already identified 15 species new to science, which is 26% of all *Polyrhachis* species collected in this study (data by R. Kohout). Among these are a number of species in the canopy nesting subgenus *Myrmatopa* which was long considered not to occur on Borneo. Notably, the amount of new species is difficult to assess in large genera like *Crematogaster* or *Camponotus* where future molecular work is expected to bring greater clarity (BLAIMER 2012). Species richness in CE and particularly in temperate zone trees is much lower; only 12 species were collected from 375 trees. The differences in species diversity between the tropical and the temperate forests become even more striking when land area is taken into account. Borneo covers an area of 73,619 km² and we found over 300 species in tree canopies while sampling in the Malaysian state of Sabah only. In contrast, in all of CE (covering one million square kilometers) 173 known ant species occur in all habitats combined, of which only 18 are considered arboreal (SEIFERT 2008).

Explaining arboreal ant diversity: We propose that a great part of the success of canopy ants in tropical forests is due to their ability to build additional nesting forms which are lacking in temperate forests. Favorable climatic conditions (YANOVIK & KASPARI 2000, DUNN 2004, KAS-

PARI 2004, WEISER & al. 2010) allow the construction of a large variety of nesting types, including silk, carton and leaf nests that are not possible in temperate forests (LIEFKE & al. 1998, BLÜTHGEN & FELDHAAR 2009). The expansion of nesting space into the canopy explains not only the much higher diversity but also the dominance of the species rich genera *Camponotus*, *Polyrhachis*, and *Crematogaster* which are known for their extreme adaptability of nesting sites (LIEFKE & al. 1998; R. Kohout, pers. comm.). In addition, the many mutualistic relationships between ants and plants, as well as the presence of rainforest specific habitats like epiphytic ferns promote species diversity (ELLWOOD & al. 2002, OLIVER & al. 2008, SCHEMSKE & al. 2009, NESS & al. 2009). In temperate forests the climatic conditions are much more unfavorable and force more than 90% of the ant species to nest in or on the ground. The only viable arboreal nest types are in dead wood or under bark (SEIFERT 2007, 2008). According to SEIFERT (2008) the "probability of nesting in canopies is positively correlated with thermophily, cold hardiness and resistance against desiccation and is negatively correlated with nesting space required, ability to excavate solid wood material, foraging range and position in dominance hierarchies of ant communities". The colder conditions in the more continental Białowieża forest relative to the German sites, can explain why ants were absent from approximately half of the trees at this site.

The dominance of phylogenetically old *Camponotus* and *Polyrhachis* in tropical trees has led to the hypothesis that their lack of a metapleural gland was a special adaptation to the life in the canopy (YEK & MUELLER 2011). The metapleural gland has largely antibiotic and antimycotic functions and is one of the autapomorphies of the Formicidae. It evolved as an adaptation to social colonies in the soil. A lack of this gland was hypothesized to be an adaptation to the life in the canopy where pathogen pressure was assumed to be lower than on the ground (HÖLLDOBLER & ENGEL-SIEGEL 1984). Current experimental studies provide little evidence for such a difference in pathogen pressure, however (GRAYSTOCK & HUGHES 2011, WALKER & HUGHES 2011).

Stratification: Our data suggest surprisingly that tropical ant diversity is nearly equally divided between the canopy and the ground. This is in contrast to the currently accepted assumption that ant diversity in the tropics is highest in the soil and leaf-litter (WILSON & HÖLLDOBLER 2005, MOREAU & al. 2006). We think this is due to the much greater sampling effort that has been invested in the more easily accessible ground-dwelling ants and expect that the number of arboreal ant species will greatly increase with future research effort. Although we do not know which species of ants live exclusively in the canopy, comprehensive ant surveys in the trees suggest that canopy and ground habitats are more effectively separated in tropical rainforests than in temperate forests (YAMANE & al. 1996, FLOREN & LINSENMAIR 2000). Similar results were found in a recent survey in Ecuador (RYDER-WILKIE & al. 2010), where intensive sampling (including canopy fogging) collected 282 arboreal ant species, 71.6% of which were only found in the canopy.

Taxonomic differences in canopy ants of tropical and temperate forests: Canopy ant communities differ significantly from the ground fauna in subfamily composition

with a dominance of Formicinae and Dolichoderinae that have risen in numbers relative to Myrmicinae (WILSON & HÖLLDOBLER 2005). Their success is considered a consequence of a change in diet which, in addition to predator and scavenger behavior, includes the usage of liquid exudates of sap-feeding insects (DAVIDSON & al. 2003). However, more recent results suggest that also ground ant communities are characterised by a wide range of trophic modes including "cryptic herbivores" (PFEIFFER & al. 2014).

Most ant subfamilies evolved in tropical environments (FISHER 2009). During the Tertiary, CE was covered by dense tropical forests and according to ant records in amber or fossils, harbored most of the modern subfamilies (DLUSSKY & al. 2009, DLUSSKY & RASNITSYN 2009, WEDMANN & al. 2010). The current low species diversity is largely a consequence of the Pleistocene glaciations which resulted in forest ecosystems that are not older than 12,000 years. This is reflected in subfamily composition. Seven of all ten ant subfamilies fogged in the tropics were not collected from the temperate trees (Fig. 1). Pseudomyrmecinae, Cerapachyinae, Amblyoponinae, Ectatomminae, and Aenictinae are exclusively tropical or subtropical. Ponerinae and Proceratiinae occur also in temperate ecosystems but are significantly more diverse in tropical than in temperate regions (BROWN 1975). All temperate ponerines and proceratiines, however, are ground-dwelling (SEIFERT 2007). Dolichoderinae are distributed worldwide but also reach maximum richness in the tropics (SHATTUCK 1995). The subfamily-composition of canopy ants is similar in all large tropical lowland rainforests and has been found also in afrotropical forests (SCHULZ & WAGNER 2002, YANOVIK & al. 2008) and in neotropical forests (e.g., LONGINO & al. 2002, RYDER-WILKIE & al. 2010).

The ecological impact of canopy ants: Ants numerically dominate the canopies of tropical lowland rainforests, often accounting for more than 60% of all arthropods (FLOREN & LINSÉNMAIR 1997, SCHULZ & WAGNER 2002, YANOVIK & al. 2008, RYDER-WILKIE & al. 2010). They have a major effect on arboreal ecosystems by acting as keystone species and ecosystem engineers (HÖLLDOBLER & WILSON 1990, FOLGARAIT 1998, ALONSO & AGOSTI 2000, DEL TORO & al. 2012). Experimental studies demonstrate that ants structure arthropod communities and maintain high tropical diversity due to their high predation pressure (FLOREN & LINSÉNMAIR 2000, FLOREN & al. 2002, YANOVIK & KASPARI 2000). Furthermore, canopy ants are important primary consumers via trophobiotic interactions, and their dominance is reflected in their establishment of mutualistic relationships with many plants and animals (DAVIDSON & al. 2003, OLIVER & al. 2008, NESS & al. 2009). As ecosystem engineers they create habitat for many arthropods (ELLWOOD & FOSTER 2004, ORIVEL & LEROY 2011) and certain species are used by humans to biologically control arthropod pests (PHILPOTT & ARMBRECHT 2006, PENG & CHRISTIAN 2009). In temperate latitudes ants rarely have a pronounced impact on the arboreal arthropod fauna. Only a few species, such as the ground nesting *Formica* spp., are efficient enough as predators to significantly affect arthropod communities in tree crowns (PUNTILLA & al. 2004, SEIFERT 2007, CERDA & DEJEAN 2011, SANDERS & VAN VEEN 2011). Usually the influence of arboreal ants is rather negligible even though some species like *Temnothorax corticalis* may establish hundreds of small nests in single trees (SEIFERT 2008).

In degraded tropical forests ant communities provide reduced ecosystem functions in comparison to undisturbed forests (BIHN & al. 2010), raising concern about whether a degraded ecosystem can still provide the same services (GUÉNARD & al. 2012). As one result of forest degradation for example, invasive species can colonize the forests and severely affect the diversity of the indigenous fauna (HOLWAY & al. 2002, LACH & HOOPER-BUI 2009). Furthermore, FLOREN & al. (2002) showed for tropical canopy ants that ant diversity and predation pressure was lower in young, regenerating forests than in primary forests. These examples suggest that forest destruction has severe negative consequences for ecosystem services mediated by canopy ants and a reduced control of potential pest herbivores. In the temperate forests of CE, canopy ants have only recently become a topic of greater research interest (PALLADINI & al. 2007, SEIFERT 2008, DOLEK & al. 2009). Unlike in tropical countries, however, there are only few primary forests left which could be used as a baseline to assess human impact in managed and degraded forests. This may prove to be critical as tree structure and microclimatic conditions greatly differ between pristine and managed forests and may be more important in determining the distribution of canopy ants than previously assumed (SEIFERT 2008, KLIMES & al. 2012). Particularly we want to encourage more studies in temperate canopies focusing hereby on diverse natural forests with a high proportion of old trees and large amounts of standing deadwood that contain suitable nest habitats for canopy ants. Such studies might change our view of how temperate canopy ant communities are composed and encourage large-scale comparisons between biomes.

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