Canopy assemblages of ants in a New Guinea rain forest

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Abstract: The ant assemblages in two common tree species in primary lowland forest of New Guinea were explored using direct canopy access and tuna bait traps. The 19 trees investigated were occupied by 21 ant species of which 18 were canopy inhabitants. On average only 3.6 ant species per tree and 3 species per bait were found. Height of bait position was positively related to ant species richness, with the upper parts of the canopy being occupied by the highest number of species. On the other hand, tree species and study site did not have any effect on ant species richness nor on structure of the ant assemblages. Ant species appeared to be distributed randomly and we did not detect any effect of distance on similarity of ant assemblage occurring on the trees. The dominant species (*Crematogaster polita*) had certain negative effects on the presence of some species at food sources co-occurring at the same tree, but it did co-occur with the other ants to some extent as well. The majority of species found in the canopy were generalist omnivores (depending mainly on trophobionts or plant exudates).

Key Words: bait traps, canopy, dominance, foraging activity, interspecific interactions

INTRODUCTION

Ants play key ecological roles as predators, cryptic herbivores or mutualists and may influence the abundance and composition of numerous insect taxa in an ecosystem (Hölldobler & Wilson 1990). Many studies have demonstrated that ants dominate the canopy of lowland rain forests (Floren & Linsenmair 1997, Stork 1991, Wagner 1997) and are often considered the most important predators, strongly influencing the composition of arthropod fauna (Floren *et al.* 2002). On the other hand, recent studies have shown that a significant proportion of ecologically dominant ant species are herbivorous, deriving a significant proportion of their nutrients either from plant exudates or through other insects feeding on plants (Blüthgen *et al.* 2003, Davidson *et al.* 2003).

The spatial distribution of some arboreal ants referred to as dominants (i.e. species with traits such as large colonies, high recruitment rate, aggressive behaviour and absolute territories), can be arranged in a three-dimensional mosaic fashion with mutually exclusive territories maintained by interspecific competition (Dejean *et al.* 2007, Leston 1978, Room 1971).

The complex of positive and negative interactions among dominants and other co-occurring ant species is considered to be a major mechanism influencing the structure of the arboreal ant community (Blüthgen & Fiedler 2004, Dejean *et al.* 2007, Majer 1976, Room 1971). However, there is evidence for both non-random (Gotelli & Ellison 2002, Pfeiffer *et al.* 2008, Sanders *et al.* 2003) as well as random co-occurrence patterns in ant assemblages, suggesting that interspecific competition may not always shape their distribution (Sanders *et al.* 2003, 2007). Evidently, ant assemblages may differ markedly in their organizational patterns; the processes which may lead to a mosaic-like distribution are not yet sufficiently understood.

We investigated the composition of ant assemblages living in the canopy of two locally widespread tree species in lowland rain forest of Papua New Guinea. To date few ecological studies of Melanesian ants exist, and this region remains largely unexplored. Some authors (Majer 1993, Room 1975, Wilson 1959) described a mosaic-like pattern of ant distribution for the New Guinea, although the reported ant mosaics were not tested for positive and negative associations among species by adequate methods (Albrecht & Gotelli 2001, Blüthgen & Stork 2007).

The aim of our study was to survey the canopy ant assemblages and focus on the determinants of ant community composition, including the effect of interspecific interactions, tree species and tree height. We

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determined the ecologically dominant ants, assessed their activity and distributional patterns, and their impact on other ant species within the community. We used our data to test the following hypotheses: (1) similarity of ant assemblage will decrease with distance among trees investigated, (2) species occurrence and abundance will vary with height in the canopy, with higher ant species richness and abundance in the upper canopy, (3) presence of dominant ant species will negatively affect the overall richness on particular trees or at the food sources (baits).

METHODS

Study site

The study area was located in the vicinity of Madang town, Madang province, Papua New Guinea. Two study sites were located in primary lowland perhumid forests around Baitabag (145º47′E 5º 08′S, 50–100 m asl) and Ohu (145º41′E 5º 16′S, c. 200 m asl). The two localities are about 30 km apart, but are connected by primary and secondary forests. The area is covered with species-rich evergreen rain forest (152 species of woody plants with dbh $\geq$ 5 cm ha^{-1}, Novotny *et al.* 2002). The primary forest at both sites is occasionally fragmented by 10–30-y-old patches of secondary vegetation on abandoned gardens created as a part of the traditional slash-and-burn agriculture. Average annual rainfall in the Madang area is 3558 mm, with a moderate dry season from July to September. The annual mean air temperature is 26.5 °C.

Altogether 19 mature individuals of two locally widespread tree species, *Ficus subtrinervia* Lauterb. & K. Schum. (Moraceae) and *Pouteria maclayana* (F. Muell.) Baehni (Sapotaceae), were selected for our study. Ten individual trees, five from each species, were surveyed at Ohu and five individuals of *F. subtrineriva* and four of *P. maclayana* in Baitabag. The surveyed trees ranged from 22 to 32 m in height (mean $\pm$ SD = 26 $\pm$ 2.39) with dbh of 50–200 cm. All trees were located within primary forest and separated by at least 300 m from each other. The overall area across which the trees were distributed was approximately 9 km^2 at each site. All trees were surveyed from June to October 2004.

Sampling methods

A combination of bait trapping and direct searching for any foraging and nesting ants was used to investigate ant fauna. The single-rope climbing technique (Perry 1978) was used to move along the trees. We attracted ants using crushed tuna meat with vegetable oil. Baits were set on small square pieces of gauze (two teaspoons of bait on 5 × 5-cm gauze) and these were tacked down to bark or leaves on every tree. Baits were, as far as possible, set at 2, 5, 10 and 15 m height from the tree base on the main trunk and lateral branches at every suitable occasion. Above 15 m, baits were placed at 2-m intervals until the highest accessible section of the crown was reached, which was typically 3–4 m below the top of the tree canopy. In cases where more traps were set at the same height on the lateral branches, they were always spaced at least 2 m from each other in all directions. From 5 to 15 (mean = 10.5, SD = 2.39) baits were set on individual trees, depending on tree height, size, and branching pattern of the crown. All baits were checked after 1 and 3 h. We recorded the number of ant species and number of individuals for each species present at the baits (or estimated for numbers above 100 approximately). Ants were always counted only within a 10 × 10-cm square, measured from the centre of the bait. Several ant individuals were removed by forceps and stored in 95% ethanol for identification.

Protein-and-oil-based bait traps were used as a collecting method as it was assumed that this would attract a large proportion of the ants occurring in the canopy. This is because arboreal ants are known to be nitrogen-limited, in contrast to terrestrial ants which are more carbohydrate-limited (Davidson 1997, Tobin 1994, Yanoviak & Kaspari 2000). Moreover, tuna baits usually capture a wider spectrum of ant species than sugar (CHO) baits, such as many general-scavengers or opportunists (Bestelmeyer *et al.* 2000, Kaspari & Yanoviak 2001). For example Bestelmeyer *et al.* (2000) reported no difference in ant species composition attracted to protein- and sugar-based baits (but see Yanoviak & Kaspari 2000).

To overcome eventual selectivity of bait traps, we also thoroughly investigated trees (including associated epiphytes, lianas and dry branches) before and after baiting and hand collected every ant species found foraging or nesting on the tree. If the species had not been previously recorded on bait traps they were included into the analyses as well.

Two trees a day were explored at most; usually one in the morning and one during early afternoon. Ant specimens were mounted and sorted into species; voucher specimens were determined by the use of literature or comparison with museum collections. All voucher specimens are deposited in the Ant Reference Collection at the Biology Center, Czech Academy of Sciences, Czech Republic, under Accession Numbers: MJ00236-MJ4288. Photographs of the voucher specimens are accessible at the open-access database 'Ants of New Guinea' on www.newguineants.org.

Data analysis

The effect of environmental factors (site, tree species and height) on ant species richness was tested using

Generalized Linear Models (GLM) in STATISTICA 7.0 for Windows (StatSoft, Inc.; Tulsa, OK, USA). Our data set was unbalanced due to different numbers of baits exposed at various heights on every tree, as determined by tree architecture. To ensure a balanced design for statistical analyses, tree height was divided into three intervals (0–10, 10–20 and > 20 m) and the average number of ant species per bait in a particular height interval was calculated. Data were square-root transformed to achieve normal and homoscedastic distribution.

The composition of ant assemblages was analyzed by methods of gradient analysis using CANOCO 4.0 (ter Braak & Šmilauer 1998, Microcomputer Power, Ithaca, USA).

The effect of the environmental variables on the species composition of ant assemblages was tested using redundancy analysis (RDA). RDA is a method of direct gradient analysis that identifies multidimensional axes explaining most of the variation in the response variables by the explanatory environmental and spatial variables (ter Braak & Prentice 1988). The contribution of each environmental variable was tested by Monte Carlo permutation test (MCP). The effect of tree species and locality on the composition of ant species was tested using the average abundance of each ant species per tree, regardless of height. RDA with split-plot design was used to assess the effect of height and collecting time on the composition of ant assemblages recorded at baits. Tree identity (1–19) and collecting times (T1, T3) were used as covariables when testing the effect of height, while only tree identity was used as a covariable to test the effect of time. The number (log-transformed) of canopy species on all baits was used as input data. Non-canopy species (*Leptomyrmex puberulus*, *Pachycondyla* sp. 1, *Diacamma rugosum*), and species found foraging outside the baits (*Camponotus* sp. 3, *Camponotus* sp. 6 and *Camponotus chloroticus*), were omitted from both the RDA as well as the GLM analyses. Similarity of species composition among individual trees was assessed by the Sørensen index (Koleff *et al.* 2003) and the effect of tree distance on assemblage similarity was assessed by regression.

Repeated-measures ANOVA was used to assess the effect of interspecific interactions on the abundance of ants, which co-occurred at the same bait. Co-occurrence was considered in cases where more than one species were recorded on a particular bait during both time intervals. Only species with more than five incidents of co-occurrences were included in the analyses (i.e. *Crematogaster polita*, *Camponotus vitreus*, *Tapinoma melanocephalum* and *Paratrechina longicornis*). All of the other species were combined into one category ('other species'). If more than two such species occurred simultaneously at a bait, the abundances of these non-target species were pooled and tested against the abundance of the target species.

We defined dominant species as those that reached very high abundance (over 50 individuals per bait) over the course of observations at the baits and had some direct effect on the abundance of one or more co-occurring species and/or have been observed to interact aggressively with other species on baits. We used the Monopolization Index (MI) (Andersen 1992, LeBrun 2005), as a measure of dominance. The MI represents proportion of baits monopolized by a particular species of the total number of baits occupied by this species. Any species monopolized bait if it was in sole possession of the bait (by at least three workers) during the second sampling period.

Null model analyses (Gotelli 1996) were used to test statistical significance of the patterns of species co-occurrence at surveyed trees. Our small samples size (19 trees) and large distance among trees did not allow us to test for presence or absence of ant mosaic as such. Following the approach of Gotelli & Ellison (2002), we could however test whether ant communities are randomly assembled, and whether any positive or negative interactions occur among ant species inhabiting individual trees. A presence–absence matrix was constructed (21 rows × 19 columns), with all recorded ant species as rows and individual trees as columns. C-scores (Stone & Roberts 1990) were calculated as a metric for co-occurrence within the matrices. Observed C-scores were then compared with 5000 C-scores generated from randomly constructed null assemblages using a fixed-equiprobable null model (SIM2, Gotelli 2000). A mean C-score significantly greater than that expected by chance, indicates assemblages structured by competition. C-scores not significantly larger indicate random species distribution, and C-scores smaller than expected by chance indicate species aggregation. All analyses were performed using EcoSim 7.0 (Gotelli & Entsminger 2005, Acquired Intelligence Inc. & Kesey-Bear).

Trophic position of each ant species was assigned on the basis of literature (Blüthgen *et al.* 2003, Davidson *et al.* 2003, Shattuck 1999). Unidentified species were classified into trophic groups on the basis of their generic identity.

RESULTS

There were 17 ant species recorded on baits, and an additional four species were found foraging or nesting in dead branches and epiphytes (Figure 1). The complete list of the species is given in Appendix 1. Of these 21 species, 18 can be considered as canopy inhabitants including 15 visiting baits (based upon information from the literature and our observations at both sites). Abundance and presence–absence data of these 15 species were therefore included into the analyses. Two
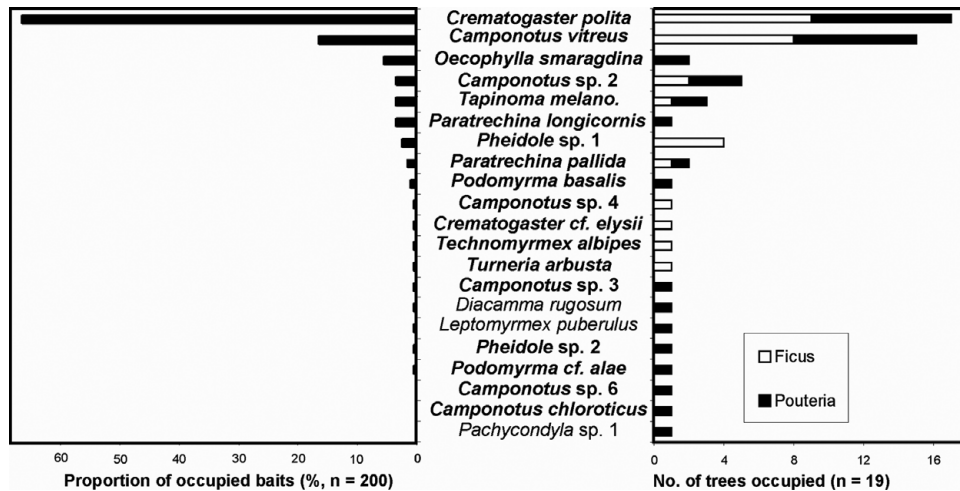
Figure 1. Proportion of baits occupied by all ant species recorded at the study trees (left) and number of trees at which particular species were present (right). White columns represent *Ficus subtrinervia*, black represent *Pouteria maclayana*. Arboreal ant species are in bold.

hundred baits were exposed on 19 trees, of which 169 (84.5%) were visited by ants. On average, there were (mean $\pm$ SD) 3.6 ± 1.46 ant species present per tree and 3 ± 1.2 species per bait. The number of ant species present at each bait increased with height above the ground, while the effect of individual trees, tree species and study site were not significant (Table 1, Figure 2).

The two tree species differed in bait occupancy (ANOVA, F = 23.6, P < 0.001, df = 4). On *Ficus* 22% of baits were empty, while only 7% of baits were empty on *Pouteria*. More than 77% of the baits on *Pouteria* were visited by only one ant species, compared with 55% of baits on *Ficus*. Furthermore, baits placed at a lower position on the trunk (<15 m) were less occupied than baits placed higher in the tree crown (both tree species analysed together, Fisher's exact test, $\chi^2 = 22.7$, P < 0.001).

According to the RDA analyses of average species abundances per tree, the locality and the tree species did not have any significant effect on ant assemblage structure (MCP, 499 permutations; locality: F = 1.45, P = 0.22, df = 1; tree species F = 1.36, P = 0.21, df = 1). In contrast, height did have a significant effect and explained 19.7% of the variability in ant assemblage composition (RDA, MCP, 499 permutations, F = 94.1, P = 0.002, df = 1). There was no significant relationship between similarity of ant assemblage composition (expressed by
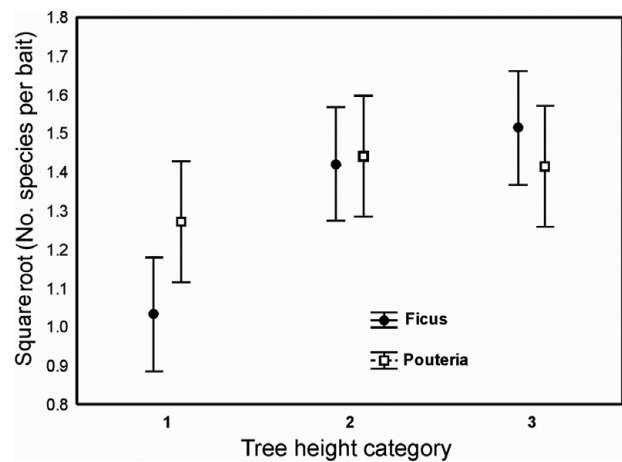

Figure 2. Relationship between bait height (divided into three categories: 1 = 0–10 m; 2 = 10–20 m; 3 = 20–30 m from a tree base) and ant species richness per bait (square root-transformed). *Ficus subtrinervia* is represented by the black circles and *Pouteria maclayana* by the white squares. Vertical bars denote 95% confidence intervals.

the Sørensen index) and distance among individual trees (R = 0.007, P = 0.9, n = 171). Faunal similarity among trees separated from 0.3 to 3 km was not distinguishable from those separated by 30 km of rain forest.

Table 1. Results of GLM analysis of the effect of environmental factors and their interactions (site = Locality, tree species = *Pouteria maclayana* or *Ficus subtrinervia*, and height = Height R) on ant species richness. Only height of bait position had a significant effect on species richness.

Variable (environmental factors)	Effect	df	F	Explained variability (%)	P
Height R	Fixed	2	10.7	1.07	0.0002
Locality	Fixed	1	0.02	0.00	0.891
Tree species	Fixed	1	1.39	0.07	0.256
Tree indiv. (Locality × Tree)	Random	16	1.02	0.81	0.463
Tree sp. × Height R	Fixed	2	2.68	0.27	0.083
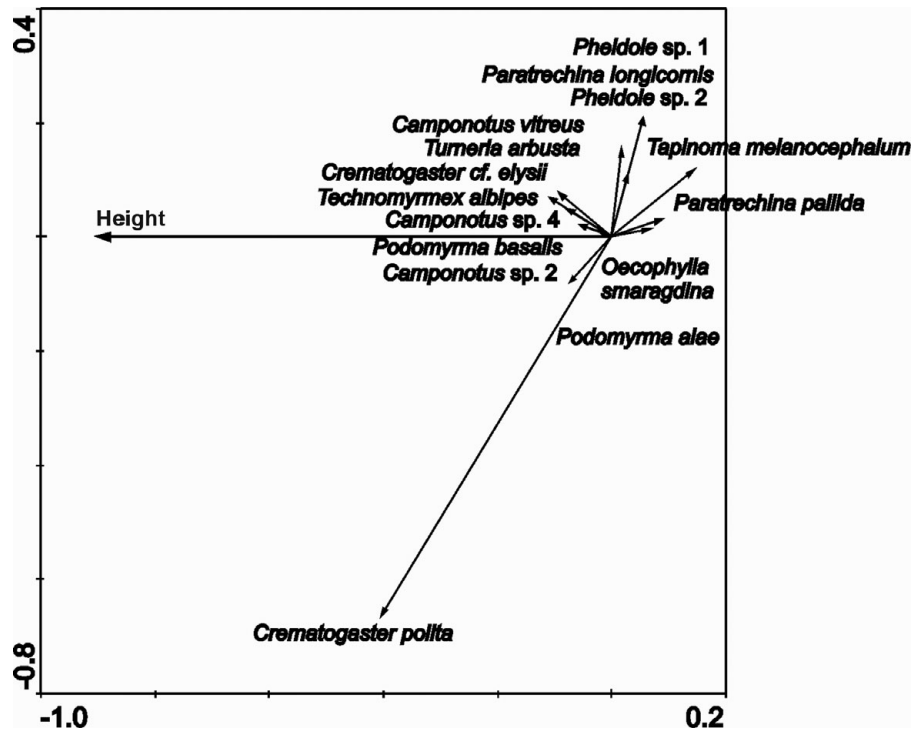
Figure 3. RDA ordination diagram of the effect of bait height position on composition of canopy ant assemblages. The abundance of *Crematogaster polita* and several *Camponotus* species increased with height. Bait height explained 19.7% of the variability in ant assemblage composition.

Some ant species increased, while others decreased, in abundance with height above the ground (Figure 3). The abundance of *Crematogaster polita* in particular, and to a lesser extent also of all *Camponotus* spp. increased with height (x-axis, Figure 3), while the abundance of *Pheidole* sp. 1 and *Oecophylla smaragdina* decreased. RDA further illustrates the avoidance of most species towards *Crematogaster polita*. This effect was not dependent on height and is represented by the y-axis of Figure 3. On the baits where *Crematogaster polita* was absent, the other species e.g. *Pheidole* spp. and *Paratrechina* spp., as well as *Tapinoma melanocephalum*, occurred in higher abundances. The abundance-height response of the remaining species, although appearing positive or negative, is difficult to assess as they were mostly found on only a few baits.

The composition of ant assemblages changed significantly between 1 and 3 h after bait exposure (RDA, MCP, 499 permutations, F = 12.4, P = 0.002, df = 2), although this change over time explained only a small proportion of the overall variability among the samples (2%). This was primarily due to the abundance of *Crematogaster polita*, which increased over time, while there was no significant change in other species.

Crematogaster polita was the most widespread species in terms of occupied trees (17) as well as baits (66.5% of all baits), followed by *Camponotus vitreus* (15 trees, 16.5% of all baits). *Camponotus* sp. 2 and *Pheidole* sp. 1 were

markedly less abundant on baits, but still present on five and four trees respectively.

Crematogaster polita was also found on the highest absolute number of solely occupied baits (n = 101, out of 133 at which it was present, monopolization index MI = 0.76). Although it occurred on fewer baits (11), *Oecophylla smaragdina* was the most successful species in dominating baits (n = 9, MI = 0.82). *Camponotus vitreus* was recorded alone on seven baits, while it co-occurred with other species on 26 baits (MI = 0.27). Of these three species occurring on more than ten bait traps, *Cr. polita* and *O. smaragdina* can be considered as dominants on the basis of their considerably high MI values.

The two most common species, *Crematogaster polita* and *Camponotus vitreus*, differed in their pattern of abundance change with the collecting time on baits where they co-occurred (repeated-measures ANOVA, n = 20, F = 34.9, P < 0.001) (Figure 4). As abundance of *Crematogaster polita* increased from T1 to T3 (t-test, t = 6.1, P < 0.001) the abundance of *Camponotus vitreus* decreased (t-test, t = 3.5, P < 0.001).

On the other hand, when *Crematogaster polita* co-occurred with other ant species, no difference in abundance change was detected (repeated-measures ANOVA, n = 9, F = 3.5, P = 0.089). *Camponotus vitreus* (n = 6, F = 0.33, P = 0.5), *Paratrechina longicornis* (n = 4, F = 3.77, P = 0.09) and *Tapinoma melanocephalum* (N = 6, F = 2.17, P = 0.17) did not significantly change their
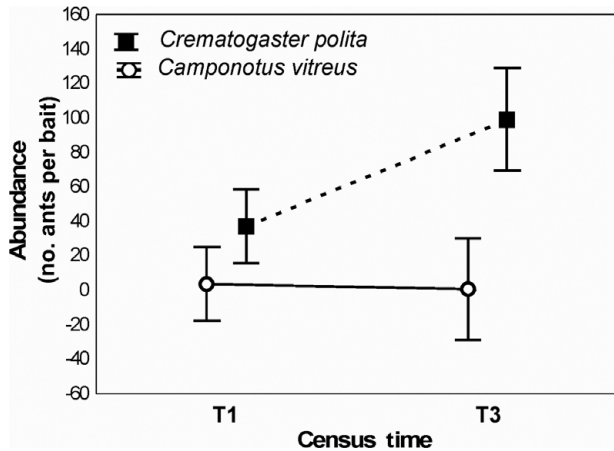
Figure 4. Relationship between census time (1 and 3 h) and abundance (number of ants per bait) of *Camponotus vitreus* and *Crematogaster polita* co-occurring at the same baits. The number of *Camponotus vitreus* decreased with increasing number of *Crematogaster polita* workers at the baits.

abundance when co-occurring with other species (not including *Crematogaster polita*), although the number of interactions used in the analyses was rather low.

Co-occurrence analysis based on a null model did not detect any non-random patterns in species composition of canopy fauna. Ant assemblages from all trees appeared to be random subsets of the overall species pool. The observed C-score in our data for the fixed-equiprobable model did not significantly differ from the mean C-score of simulated matrices (observed (all spp.): 2.81, simulated: 2.65, SD = 0.04; $P_{(obs. \leq exp.)}$ = 0.78).

DISCUSSION

We found lower ant species richness per tree in comparison with the majority of other canopy studies in lowland tropical forests (e.g. 7–20 spp. per tree in Borneo, fogging, Floren *et al.* 2002; 10 spp. per tree, Schonberg *et al.* 2004; 14–20 spp. per tree, Armbrecht *et al.* 2001). On the other hand, several authors described canopy assemblages with similar species richness as in our study (Majer *et al.* 1994; 32 spp. at 20 trees). Although we recorded rather low ant species richness, we believe that our consistent results and minimum of species yielded by additional exhaustive hand collecting (3 spp.) reflect the general pattern of ant richness in the rain-forest canopy at both localities. Furthermore, past investigations at one of the localities (Novotny *et al.* 1999) using termite baits yielded a similar diversity i.e. 17 ant species foraging on 43 trees in the understorey.

Alternatively, the low diversity of ants detected could be a consequence of the short collecting period and eventual selectivity of tuna baits (Bestelmeyer *et al.* 2000). A low epiphyte load on the trees and relatively open

canopy may be other contributing factors. It is unlikely that precipitation and temperature seasonality played an important role as seasonal changes in activity and occurrence of insect herbivores are small at both study sites (Novotny & Bassett 1998, Novotny *et al.* 2002).

Our study showed that tree species cannot be used as an indicator of the composition and species richness of ant communities. This is not surprising, because ants are known to be unspecialized to particular plants, with the exception of several myrmecophytic species. However, surprising is the high similarity of the ant fauna between the two sampling sites, which are located 30 km apart. Although both localities shared only six (29%) ant species, the same two most abundant species occupied the majority of trees at both sites. Our findings thus did not support our original hypothesis (1) that distance among trees will have a negative effect on similarity of ant assemblages, and suggest that trees at our study sites can be dominated by just several ant species distributed over large distances.

In concordance with our hypothesis (2), the effect of height on ant species richness and abundance emerged as the most important factor in our study. Height had a strong positive effect on the abundance of *Crematogaster* spp. (mainly *C. polita*), as well as several other species including all *Camponotus* spp., both *Podomyrma* spp., *Technomyrmex albipes* and *Turneria arbusta*. All of them represent ants typically nesting in the upper part of the canopy. In contrast, it had a negative effect on the abundance of *Pheidole* spp., *Paratrechina* spp. and *Oecophylla smaragdina*. Except for *O. smaragdina*, the other species are known to nest mainly in tree bark or under lianas in the understorey at the study sites (Janda 2007). The higher abundance of *O. smaragdina* in the lower parts of trees at our sites contrasts with the situation described from other areas, where this species is most abundant in upper parts of the canopy (Blüthgen & Fiedler 2002). Since *O. smaragdina* has been found only on two trees in our study it is not possible to assess whether this might be a general trend or rather spurious result.

Several explanations are possible for the higher richness and abundance of ants in the upper canopy. Most likely, the upper parts of trees offer numerous nesting and feeding opportunities, or may have more favourable microclimatic conditions; therefore, nests of arboreal species are located mostly in the upper or middle portions of the crown (Basset *et al.* 2001).

We predicted that communities are structured by competition and thus species co-occurrence patterns will be segregated. However, we did not find any evidence of an ant mosaic in our data. This is a consequence of a combination of an insufficient sample size, a large spatial scale at which the trees were investigated and highly homogeneous distribution of the most abundant species, which occupied the majority of trees investigated (17 out

19), whereas the remaining species were rare and with patchy distribution.

Although it was not possible to discern any influence of dominant ants decreasing the overall species richness on tree, we did detect a negative effect of presence of dominant ants on occurrence and abundance of other species visiting food resources. Several species (*Paratrechina* spp., *Pheidole* spp., *Tapinoma melanocephalum*) tended to avoid baits at which *Crematogaster polita* was present (Figure 3). At the same time when co-occurring with other species, their numbers did not decrease significantly. On the other hand, although increasing abundance of *C. polita* had a negative effect on the abundance of *C. vitreus*, both species were able to coexist to some extent (Figure 4). This pair seems to be an example of a dominant–subordinate relationship among ant species. Both ants live in a relationship of competitive coexistence (Tokeshi 1999), in which *Camponotus* can occupy the same trees, as well as food sources, with *Crematogaster*, until the local abundance of the dominant reaches a certain threshold. *Camponotus vitreus* specializes on quickly locating and using food sources, before they are monopolized by the dominant *Crematogaster polita*. The higher level of tolerance between *Crematogaster* spp. and *Camponotus* spp. has been repeatedly reported from other tropical areas (Dejean *et al.* 2007), leading in some cases into symbiotic associations (Menzel *et al.* 2008). Furthermore, we did not detect any effect of *C. polita* on the abundance of several other species co-occurring at the baits (e.g. *Podomyrma alae*). This suggests that few species were able to coexist with the dominant not only within its territory, but also to some extent at the food sources. Such coexistence may be facilitated by a sufficient abundance and diversity of alternative food sources in the canopy or due to temporal partitioning in resources (Bestelmeyer 2000, Briese & Macauley 1980, Campos *et al.* 2006, Cerda *et al.* 1997, Dejean *et al.* 2007).

The four most abundant species in our study overlapped with those reported by Novotny *et al.* (1999) from understorey trees at one of our study sites (Baitabag). The species exhibited similar abundance patterns on the understorey vegetation as in our study. Such a high overlap of abundant ants found at many different tree species suggest a high spatial and temporal composition stability of the local ant assemblage, at least in terms of dominant species.

Although we did not specifically study food preferences in our study, it was possible to determine the approximate trophic position of the recorded species on the basis of their known dietary preferences and δ^{15}N isotopic levels reported in other studies (Blüthgen *et al.* 2003, Davidson *et al.* 2003). *Tapinoma melanocephalum*, *Paratrechina* spp. and especially *Oecophylla smaragdina* can be considered as species exhibiting high levels of predation in our assemblages. Although these species can generate high predation pressure, it is also known that they obtain a significant proportion of their nutrition from other sources than prey (Dejean *et al.* 2007, Tsuji *et al.* 2004). The genera *Crematogaster* and *Technomyrmex* occupy an intermediate position and utilize mainly honeydew and nectar sources combined to some extent with predation. Low trophic positions are occupied by species of *Camponotus*, which are mainly nectarivorous or trophobiotic (Blüthgen *et al.* 2003, Davidson *et al.* 2003). This proportion of different feeding strategies within an assemblage suggests that predatory ants do not represent a majority of the biomass in the tree canopy (predatory species accounted for 13% of baits inhabited), but that a majority of the fauna consists of generalist and 'cryptically herbivorous' ant species (87% of baits occupied).

In conclusion we found rather low species richness in canopy ant assemblages in the lowland rain forest of New Guinea. These were dominated by only a few abundant species. This might be a consequence of various biotic factors of the local forest, but it seems to be a natural condition of local ant assemblages as parallel direct collecting yielded only three additional species to those found already on the baits. Bait position height had a positive effect on species richness for the majority of the assemblage, although some species did show an opposite response. The highest proportion of ants, in terms of biomass, as well as species occurring in the canopy of the studied trees, was made up of generalist omnivores and ants dependent mainly on trophobiosis. Assemblage structures at closely spaced trees were indistinguishable from those situated 30 km away and appeared to be random subsets of the local species pool. We could not find any evidence of an ant mosaic as one dominant species uniformly occupied the majority of the studied trees. We did however detect several negative interactions among dominant species *Crematogaster polita* and other ant species co-occurring at the same trees. Although most ant species avoided baits occupied by this dominant species, a few species (namely *Camponotus vitreus*) were able to co-exist on the same food resources.

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Appendix 1. List of the ant species recorded during our study and the number of trees at which they were recorded. Occurrence frequencies for both collecting methods (tuna bait traps, hand collecting) and localities are combined.

Ant species	*Ficus subtrinervia*	*Pouteria maclayana*
Camponotus chloroticus Emery, 1897	0	1
Camponotus sp. 2	2	3
Camponotus sp. 3	0	1
Camponotus sp. 4	1	0
Camponotus sp. 6	0	1
Camponotus vitreus (F. Smith, 1860)	8	7
Crematogaster cf. *elysii*	1	0
Crematogaster polita Smith, 1865	9	8
Diacamma rugosum (Le Guillou, 1842)	0	1
Leptomyrmex puberulus Wheeler, 1934	0	1
Oecophylla smaragdina Fabricius, 1775	0	2
Pachycondyla sp. 1	0	1
Paratrechina longicornis Latreille, 1802	0	1
Paratrechina pallida Donisthorpe, 1947	1	1
Pheidole sp. 1	4	0
Pheidole sp. 2	0	1
Podomyrma basalis Smith, 1859	0	1
Podomyrma alae Donisthorpe, 1949	0	1
Tapinoma melanocephalum (Fabricius, 1793)	1	2
Technomyrmex albipes Smith 1865	1	0
Turneria arbusta Shattuck 1990	1	0