Tree size and habitat complexity affect ant communities (Hymenoptera: Formicidae) in the high canopy of Bornean rain forest

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Abstract

Canopies of tropical rain forest host a considerable proportion of the world's biodiversity. However, the factors driving variation in this diversity are poorly known, particularly for the upper-most canopy strata, and for species-rich groups such as arthropods. We surveyed high canopy ants from emergent trees (height 35 - 60 m) in rain forest in Malaysian Borneo and measured a range of aspects of canopy structure that might affect the structure of these communities, including variables relating to tree dimensions and within-tree habitat complexity. We used two methods: a baiting-based method (purse-string trapping), which samples more behaviourally dominant ants foraging on the trunk and on major branches, and canopy insecticide fogging, which samples ants from the entire canopy. As expected, there were positive correlations between measures of tree size and ant abundance and species richness (baiting: abundance-crown width, richness-crown width; fogging: richness-tree height). However, fewer ant individuals were found in fogging samples from trees with larger trunk diameter, and fewer ant species were found at baits in taller trees, suggesting complicated relationships between tree size and ant community size. Habitat complexity also affected ant communities: More ant species were found in trees with more hollows (based on baiting) and with more dead branches (based on fogging). Furthermore, greater numbers of ant individuals were found in fogging samples from tree crowns with greater epiphyte / climber cover. These results suggest that higher levels of habitat complexity increase both the total number of ant workers that a tree canopy can support and the number of species that can co-exist there. There were also more ant individuals in crowns with higher connectivity, based on baiting, potentially as a result of increased foraging rates from nearby trees. Trees of the species *Parashorea malaanonan* supported more species of ants, but lower abundances of ants, than trees of the species *P. tomentella*, indicating the presence of larger numbers of colonies with smaller colony size. Finally, species composition for both fogging and purse-string traps samples were affected by trunk diameter and the presence of epiphytes and climbers, indicating that forests in which these factors are more variable are likely to present a wider range of niches for ants and hence support higher diversity. Taken together, these results demonstrate how variation in canopy structure and complexity can contribute to the high diversity of ants in the canopy of tropical rain forest.

Key words: Formicidae, emergent tree, *Parashorea*, nest sites.

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Introduction

The coexistence of ant species is mediated by various factors, including demand for nesting sites and food availability (DAVIDSON 1998, FLOREN & LINSENMAIR 2000, BLÜTHGEN & al. 2004, ARMBRECHT & al. 2006, FAYLE & al. 2015). In particular, the high diversity and abundance of ants in the canopy of tropical rain forest (FLOREN & al. 2014) may be explained by the complexity of the canopy structure: the epiphytes, trunks, branches, and hollows that provide niches for many species to coexist. In the tropics, the micro-environmental heterogeneity of the three-dimensional structure of trees means that as many as 61 ant species are able to coexist within a single tree (FLOREN & LINSENMAIR 2000, WIDODO & al. 2004, FLOREN & LINSENMAIR 2005). Nevertheless, there is no consensus about which environmental factors allow canopy ant species to coexist (STORK 1987, TANAKA & al. 2010).

Tree size is clearly likely to influence the structure of ant communities. Larger trees should provide a habitat for greater numbers of ant colonies relative to small trees or allow expansion of some colonies in size. In addition to these habitat patch size effects, there may also be turnover of species composition through time, with particular species specialising on older, larger trees, although this effect is less obvious for trees that form mutualistic relationships with ants (DEJEAN & al. 2008a).

Other aspects of the physical structure of the canopy are likely to have a substantial impact on ant community composition. This is partly due to the use of structures as

nest sites. Ants often nest in tree hollows, cavities, and suspended leaf litter (e.g., LIEFKE & al. 1998, KLIMEŠ & al. 2012) because these sites provide humid refuges within the canopy (HÖLLDOBLER & WILSON 1990). Hence variation in the presence of these structures is likely to drive variation in ant communities. However, ants can escape this limitation to some degree by building carton nests from masticated plant fiber mixed with worker secretions or by binding leaves together with larval silk (e.g., DEJEAN & al. 2008b). These physical characteristics are likely to vary within a tree species with age and also between tree species (DEJEAN & al. 2008a). In addition, the distribution of palatable plant exudates and the occurrence of mutualistic homopterans may also differ between tree species (DAVIDSON 1998, BLÜTHGEN & FIEDLER 2004).

Another important feature that contributes to overall canopy structure is the presence of epiphytes. Epiphytes make up 10% of all vascular plants in the world and provide important resources for canopy animals (BASSET 2001, DAROCHA & al. 2015). In Southeast Asia, one of the most dominant epiphytes are bird's nest ferns; the large size, and structural complexity of these ferns means that they provide shelter and organic matter for many of the invertebrates that spend all or part of their time in the canopy (ELLWOOD & FOSTER 2004, TURNER & FOSTER 2009), and in particular for ants (FAYLE & al. 2010, 2013).

The extent of connectivity between the host tree and the surrounding forest vegetation may affect canopy animals in general (EMMONS & GENTRY 1983), and specifically ant communities, because foragers regularly cross between adjacent tree crowns (KLIMEŠ & al. 2015) with connectivity potentially increasing the number of co-existing species in a tree (POWELL & al. 2011). For example, in sub-humid forest (5 - 10 m high) in Veracruz, Mexico, arboreal ants are less abundant in isolated trees (GOVE & al. 2009). However, terrestrial ant species tend to forage in the canopy of isolated trees more often and those trees had different ant assemblages due to the specialised microclimate and biophysical variables of the trees. The diameter of connecting vegetation can also filter ants in terms of body size, with larger species being less likely to use small diameter stems (YANOVIAK & al. 2012). In Southeast Asia, ants such as *Camponotus gigas* are known to be highly mobile, and therefore the degree of connectivity might affect their foraging patterns within the canopy (PFEIFFER & LINSENMAIR 2000).

Although the effects of canopy structure and complexity have been investigated in various systems, the drivers of ant community structure in the uppermost strata of tropical rain forest are still not clear, at least in part due to the difficulties of accessing and working in the high canopy. Here we assess how variation in these factors affects ant communities of high canopy rain forest trees in Malaysian Borneo. Specifically, we ask how ant abundance, species richness, and species composition are affected by tree dimensions, microhabitat complexity, connectivity, and tree species identity.

Material and methods

Field site: Field work was carried out in primary lowland dipterocarp rain forest around Danum Valley Field Centre in Sabah, Malaysia (117° 49' E, 5° 01' N, altitude 170 m) part of one of the largest remaining areas of continuous

pristine lowland forest in Southeast Asia (Danum Valley Conservation Area, 43,800 ha) between September 2007 and October 2009. Ant communities were surveyed from twenty trees, which were also assessed for a range of environmental variables to which ants might respond. Trees were accessed using rope-based methods, specifically climbing a static line using mechanical ascenders to reach the crown, and then arborists' technique to move around the canopy (DIAL & TOBIN 1994).

Ant surveys: Ants were collected from the twenty trees using two methods: a bait-based method, called purse-string trapping, and canopy insecticide fogging. Purse-string trapping allows retrieval of bait platforms from branches without disturbing attendant ants (YUSAH & al. 2012). Two pairs of traps were used per tree, one pair directly adjacent to the trunk and one pair 7 - 15 m from the trunk on large lateral branches. In each pair, one trap was baited with tuna in oil, and one with sugar water. Bait-based sampling allows assessment of the behaviourally dominant ant species present (ANDERSEN 1992). Canopy fogging was conducted exclusively within the crown of the focal tree, with trays (10×1 m^2 circular) and fogging machine being suspended within the crown, following ELLWOOD & FOSTER (2004). Fogging in this manner minimises drift from trees nearby thus ensuring that all ants sampled are from the focal tree (Appendix S1, video available as digital supplementary material to this article, at the journal's web pages). Canopy fogging collects greater numbers of species than bait-based methods, and gives an overall impression of the canopy ant community. Ants were identified by reference to published keys and online image databases, first to genus (BOLTON 1994, HASHIMOTO 2007), and then to species (BOLTON 1974, BROWN 1978, RIGATO 1994, SCHÖDL 1998, FISHER 2010, PFEIFFER 2013). See YUSAH & al. (2012) for further details of tree locations and survey methods. Data from replicated purse-string traps (from both bait types) were combined within each tree to yield a single community for that tree, with the same being done for fogging samples.

Measurement of environmental variation: Trees were selected from two species of *Parashorea* in order to assess how tree species might affect ant communities (*Parashorea tomentella*, N = 5 and *P. malaanonan*, N = 15). A total of 11 other environmental variables were measured for each of these trees: tree diameter (DBH) and height, crown diameter, degree of connectivity, number of live branches, dead branches, hollow cavities, large and small bird's nest ferns (*Asplenium* spp.), and percentage cover of epiphytes and climbers on both the trunk and the crown of the tree (Tab. 1). We chose to use three different measures of tree size, since these should assess different measures of the dimensions of the tree, which are not always completely correlated (Appendix S2, available as digital supplementary material to this article, at the journal's web pages).

Statistical analyses: A series of linear models (LMs) was used to assess the effects of environmental variables on ant abundance and species richness. Predictor variables with the least significant P-value were removed from the analysis in a stepwise manner until only significant environmental variables were left. Response and predictor variables that were not normally distributed were transformed using log10(x + 1) and arcsine square-root (for proportion data) to achieve normality. We created partial regression

Tab. 1: Environmental variables measured for the 20 study trees. Variables 5 - 12 were measured by full inspection of trees, both from ground level and from within the canopy during sampling for ants.

	Environmental variables	Description
1	Tree species	Trees were identified by local experts in the field. Two of the most common species of *Parashorea* were chosen, *P. tomentella* and *P. malaanonan*. *P. malaanonan* is listed as a "critically endangered" species under the IUCN Red List (ASHTON 1998).
2	Tree diameter	Diameter at breast height (DBH) in meters. Measured using tape measure.
3	Height of trees	Measured using a laser rangefinder (Impulse 200 LR, Laser Technology Incorporated, Englewood, CO, U.S.A.)
4	Crown diameter	Tree crown diameter was measured from the ground. Measurements were taken twice at 90° angles to each other and averaged.
5	Connectivity	Percentage of connectivity of the focal tree crown with other trees through 360° estimated from within the canopy. Crowns surrounded and completely touching other trees were scored as 100% while those that were completely isolated were scored as 0%.
6	Live branches	Number of live branches on the tree > 30 cm in diameter.
7	Dead branches	Number of dead branches on the tree > 30 cm in diameter.
8	Tree hollows (cavity)	Number of hollows in the tree crown on both the main trunk and side branches, caused by branches falling off, recorded for the sides of all branches > 10 cm in diameter visible from the accessible canopy (some outwards facing cavities on outer branches may have been missed).
9	Large *Asplenium nidus*	Number of *Asplenium nidus* with core diameter approximately > 25 cm.
10	Small *Asplenium nidus*	Number of *Asplenium nidus* with core diameter approximately < 25 cm.
11	Epiphytes and climbers (trunk)	Percentage cover of ant plants, orchids, stags horn ferns, mosses, climbers and rattans on the trunk.
12	Epiphytes and climbers (crown)	Percentage cover of ant plants, orchids, stags horn ferns, mosses, climbers and rattans in the crown.

plots to visualise the impacts of individual variables. All univariate analyses were conducted in Minitab v10. The three measures of tree size, were correlated ($0.45 < r < 0.63$), as were connectivity and crown diameter ($r = -0.58$, see Appendix S2), which raises concerns about multicollinearity, i.e., that the identity of predictors in final models is arbitrary. To test for this, in all final models for which at least one of the size-related predictors was included, or where one of connectivity or crown size were included, we looked at the effects of swapping these variables. Usually this resulted in the newly-included variable being non-significant in the model. Nine of ten instances for the three size variables resulted in non-significant P-values for the size-related predictor(s), and for the remaining instance the P-value was larger than in the original model. For connectivity / crown size, P-values also became non-significant (two instances) or were less significant (one case). Hence we conclude that the different measures of tree size assess distinct aspects of tree architecture, and also that the negative relationship between crown size and connectivity is not sufficiently strong to cause multicollinearity.

Ordinations were used to assess the relationship between environmental variables and species composition. Ant abundance data from both purse-string trapping and fogging were square-root transformed and species that were represented by fewer than ten individuals in total across all samples for a particular sampling method were excluded from the ordination analysis, meaning that a subset of 72 species from both purse-string trapping and fogging combined were used. Detrended Correspondence Analysis (DCA) gave a maximum axis length of 3.99 for purse-string trapping and

3.79 for fogging, indicating relatively high levels of species turnover. Thus, a direct gradient Canonical Correspondence Analysis (CCA) was used to assess the relationship between species composition and environmental variables (TER BRAAK & ŠMILAUER 2003). This analysis assumes a unimodal response of the abundance of individual species to environmental variables. In these analyses, the predictive power of each environmental variable was tested using an unrestricted Monte Carlo permutation test with 999 runs. Environmental variables which were significant were introduced into the model in a stepwise manner until no further significant predictors remained. All ordinations were conducted in CANOCO v.4.51.

Results

Effects of environmental variation on ant species richness and abundance: A total of 171 species from 37 genera (35,642 individuals) were collected from the canopies of the twenty trees (Appendix S3). Insecticide fogging caught greater numbers of ant individuals and ant species than purse-string trapping (for further description of differences between sampling methods see YUSAH & al. 2012).

More ant species were found in purse-string traps in trees with wider crowns ($F_{1,19} = 5.53$, $P = 0.032$), and those with more hollows ($F_{1,19} = 4.65$, $P = 0.047$), while fewer species were found in taller trees ($F_{1,19} = 4.74$, $P = 0.045$; Figs. 1a - c, Tab. 2). For fogging samples, more species were found in trees of the species *Parashorea malaanonan* than in those of *P. tomentella* ($F_{1,19} = 4.93$, $P = 0.041$), in taller trees ($F_{1,19} = 7.22$, $P = 0.016$) and in those with more dead branches within the crown ($F_{1,19} =$
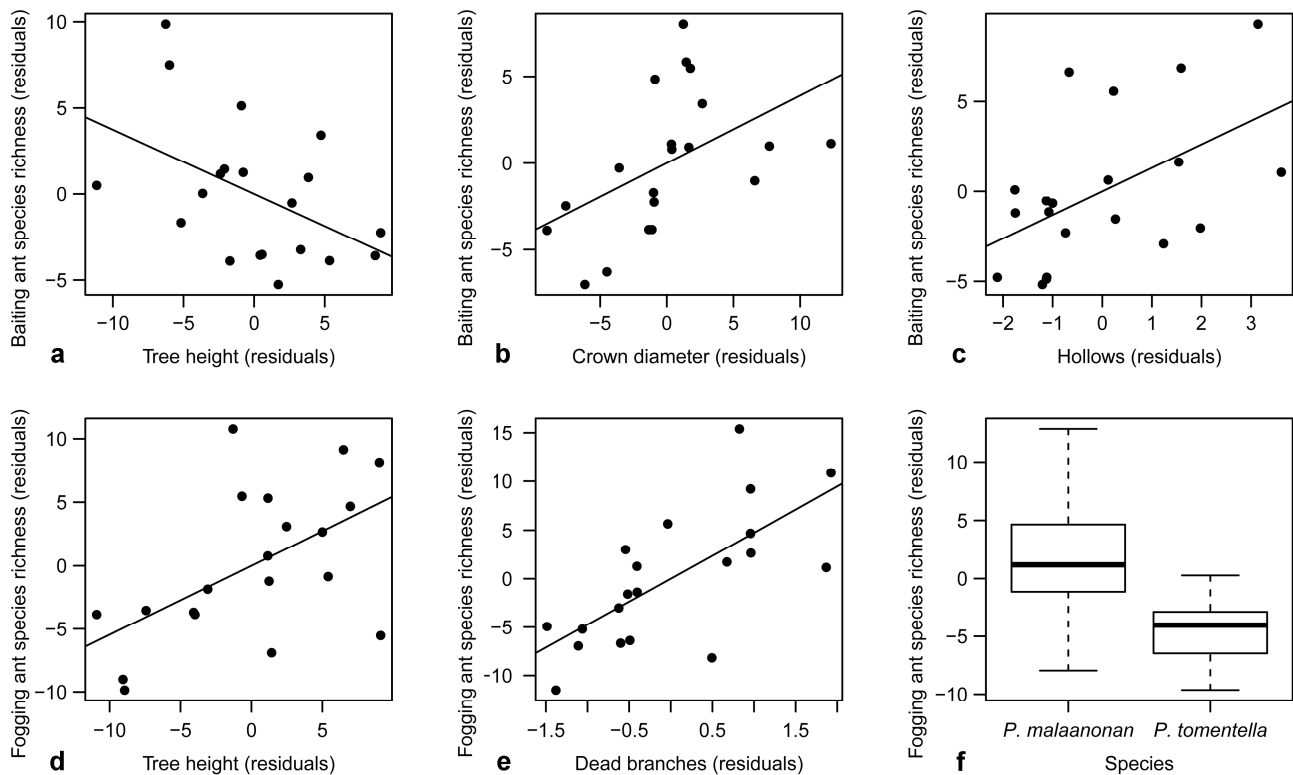
Fig. 1: A number of environmental variables predicted ant species richness as assessed using purse-string trapping (a - c) and fogging (d - f). All plots are of partial regressions, with only the effect of that predictor being plotted, while holding all other predictors from the final model constant. Only significant predictors are plotted here; for all predictors see Table 2.

Tab. 2: LM results for species richness data from purse-string trapping and fogging. Statistics for significant variables (in bold) are presented from final reduced models and those for non-significant variables from the full models. The "Effect" column indicates the direction of statistically significant relationships (m+ indicates that the tree species P. *malaanonan* had more ant species).

Environmental variables	Purse-string trapping			Fogging		
	F-value	P-value	Effect	F-value	P-value	Effect
Tree species	0.19	0.67		**4.93**	**0.04**	**m+**
Tree size (DBH) (m)	0.08	0.78		0.26	0.63	
Tree size (height) (m)	**4.74**	**0.04**	–	**7.22**	**0.01**	+
Crown diameter (m)	**5.53**	**0.03**	+	0.00	0.97	
Connectivity (%)	0.02	0.88		0.00	0.95	
Live branches	0.00	0.95		0.34	0.58	
Dead branches	1.05	0.34		**14.64**	**0.001**	+
Hollows	**4.65**	**0.04**	+	0.21	0.66	
Large *Asplenium nidus*	0.07	0.80		0.02	0.88	
Small *Asplenium nidus*	0.11	0.75		0.70	0.43	
Epiphytes, climbers on trunk (%)	0.22	0.65		0.37	0.56	
Epiphytes, climbers in crown (%)	0.27	0.62		0.11	0.75	

14.64, P = 0.001; Figs. 1d - f, Tab. 2). No other environmental variables predicted ant species richness for either trapping method.

Ant abundance, when measured using purse-string traps, was higher in *Parashorea tomentella* than in *P. malaanonan*

($F_{1,19}$ = 9.75, P = 0.007), and in trees with larger crown diameter ($F_{1,19}$ = 27.54, P = 0.017) and greater connectivity ($F_{1,19}$ = 7.15, P < 0.001; Fig. 2, Tab. 3). Meanwhile in fogging samples, ant abundance increased with the percentage of epiphytes / climbers within the crown ($F_{1,19}$ =
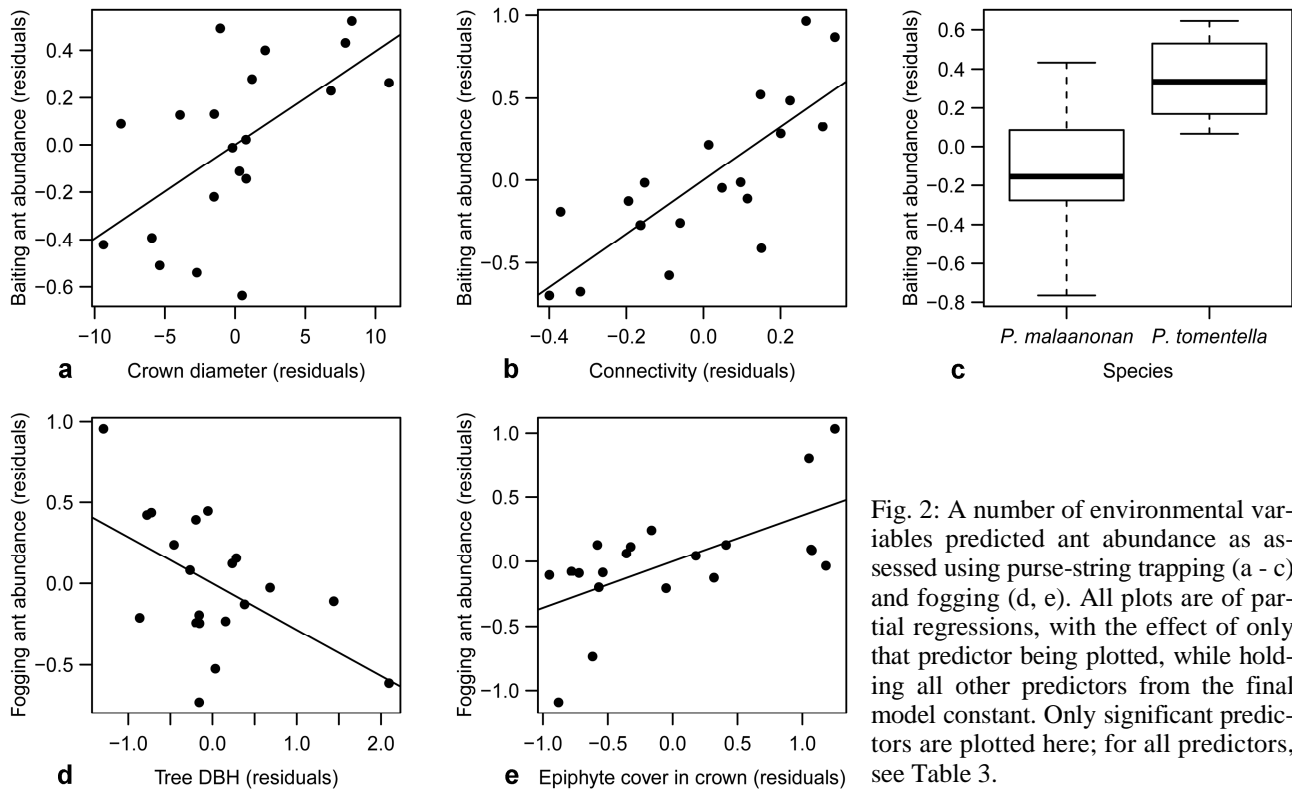
Fig. 2: A number of environmental variables predicted ant abundance as assessed using purse-string trapping (a - c) and fogging (d, e). All plots are of partial regressions, with the effect of only that predictor being plotted, while holding all other predictors from the final model constant. Only significant predictors are plotted here; for all predictors, see Table 3.

Tab. 3: LM results for abundance data from purse-string trapping and fogging. Statistics for significant variables (in bold) are presented from final reduced models and those for non-significant variables from the full models. The "Effect" column indicates the direction of statistically significant relationships (t+ indicates that the tree species *P. tomentella* had more ants).

Environmental variables	Purse-string trapping			Fogging		
	F-value	P-value	Effect	F-value	P-value	Effect
Tree species	**9.75**	**0.007**	t+	0.54	0.48	
Tree size (DBH) (m)	0.29	0.60		**-2.89**	**0.01**	–
Tree size (height) (m)	0.10	0.76		0.34	0.57	
Crown diameter (m)	**7.15**	**0.01**	+	0.30	0.60	
Connectivity (%)	**27.54**	**< 0.001**	+	1.23	0.30	
Live branches	0.26	0.63		0.00	0.95	
Dead branches	0.51	0.49		1.49	0.26	
Hollows	3.80	0.07		0.33	0.58	
Large *Asplenium nidus*	0.00	0.98		0.14	0.72	
Small *Asplenium nidus*	0.01	0.91		0.60	0.47	
Epiphytes, climbers on trunk (%)	0.04	0.85		0.01	0.93	
Epiphytes, climbers in crown (%)	0.29	0.61		**3.28**	**0.004**	+

10.76, P = 0.004) but was lower in trees with a larger diameter at breast height ($F_{1,19}$ = 8.33, P = 0.010; Fig. 2, Tab. 3). No other environmental variables predicted ant abundance for either trapping method.

The effects of environmental variation on ant species composition: Species composition was influenced by tree size (DBH) (for both ants from purse-string trapping and fogging), presence of large *Asplenium* (purse-string trapping) and percentage of epiphytes and climbers in the crown (fogging) (Fig. 3, Tab. 4). Results for particular species were reasonably consistent between the two methods: For example, *Camponotus reticulatus* was found more often in trees with large DBH, but with average amount of epiphyte cover, while *Polyrhachis ypsilon* was found in trees with smaller DBH and lower epiphyte cover (Fig. 3). However, some species did not show such consistency:
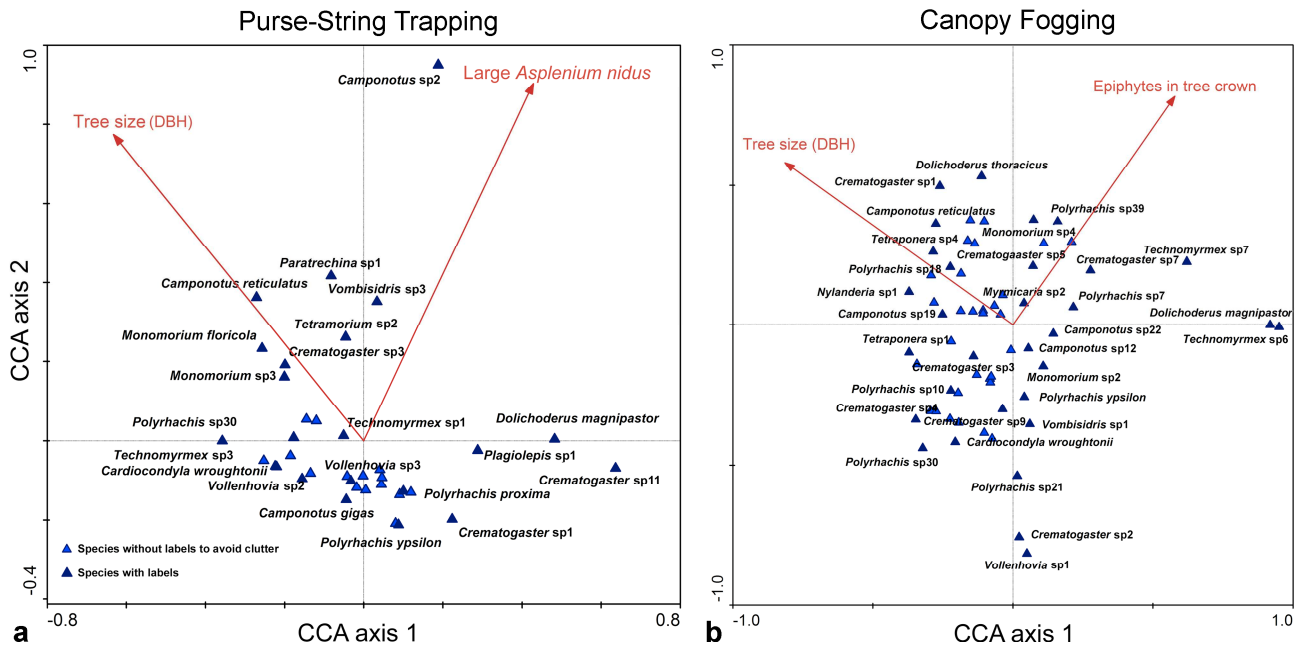
Fig. 3: Constrained ordination plots (Canonical Correspondence Analyses) on square-rooted species abundances showing the variables predicting ant community composition as sampled using (a) purse-string trapping and (b) canopy fogging. Light blue triangles are species close to the origin (hence not strongly correlated with any of the environmental variables) that were not labelled to avoid clutter.

Tab. 4: Summary of predictor variables and their significance values for predicting species composition from Monte Carlo permutation tests carried out in CCA. Significant values ($P < 0.05$) are in bold.

Environmental variables	Purse-string trapping		Fogging	
	F-value	P-value	F-value	P-value
Tree species	1.19	0.244	1.17	0.23
Tree size (DBH) (m)	**1.84**	**0.003**	**1.69**	**0.033**
Tree size (height) (m)	1.13	0.314	1.15	0.266
Crown diameter (m)	1.47	0.057	1.41	0.056
Connectivity (%)	1.34	0.095	1.18	0.239
Live branches	0.83	0.715	1.08	0.337
Dead branches	1.02	0.439	1.01	0.468
Hollows	1.26	0.187	0.74	0.839
Large *Asplenium nidus*	**1.97**	**0.002**	1.15	0.274
Small *Asplenium nidus*	0.83	0.635	0.81	0.744
Epiphytes and climbers on trunk (%)	1.16	0.274	0.94	0.599
Epiphytes, climbers in crown (%)	0.67	0.897	**1.61**	**0.011**

For example, *Crematogaster* sp. 1 was found in trees with smaller DBH using purse-string trapping, but in trees with larger DBH using fogging (Fig. 3).

Discussion

Ant communities that thrive in the canopy of tropical rain forest have always been reported as highly diverse and abundant. We found 171 species on the 20 trees, a comparable number to previous surveys of the canopy in the region, accounting for differences in sampling effort (STORK 1987: 98 spp. on 10 trees, WIDODO & al. 2004: 169 spp. on 9 trees, FAYLE & al. 2010: 120 spp. on 20 trees), with a range of environmental variables driving the structure of the communities present.

The physical dimensions of the host trees played an important role in structuring the resident ant communities. Although taller trees supported more species of ants, as sampled by fogging, taller trees supported fewer of the ant species attendant at baits. The latter result is unexpected, since larger habitat patches are expected to support larger numbers of both individuals and species (PRESTON 1962). Taller trees might be able to photosynthesise more, since they will experience less competition for light (KENZO & al. 2006), and hence could provide more carbohydrate resources for ants, either directly, in the form of extra-floral nectaries or indirectly via sap sucking insects (BLÜTHGEN & al. 2000). If behaviourally dominant canopy ants rely on these carbohydrate resources in order to exclude other species (GROVER & al. 2007), this could explain the decreased richness in taller trees at baits but not in fogging samples (where even species that are unable to compete for baits will be sampled). Alternatively, fogging a tree that is taller will, all other things being equal, sample a larger vertical column of canopy hence resulting in larger numbers of species being sampled, whereas baiting a taller tree will not necessarily sample a larger area.

In addition to affecting the number of ant species, tree dimensions also affected species composition, with diameter at breast height being significantly correlated with composition of both fogged and baited ants. Similar patterns, with species composition varying with tree size, in this case height, have been observed in Papua New Guinean rain forest (JANDA & KONEČNÁ 2011), suggesting that this

is a general pattern. Because larger trees will be older, on average, they are likely to have had longer to accumulate ant colonists, and hence may be more likely to support species that are behaviourally dominant, but poor at dispersing, if ant species show a competition-colonisation trade-off (LEVINS & CULVER 1971). Trees of different sizes might also provide different niches for different ant species, due to differences in microclimate, or differences in the epiphyte communities present on them (or they may be older, and hence have had longer to accumulate such microhabitats).

We found some support for this hypothesis, since the availability of epiphytes as potential nesting sites was the second major factor driving ant community structure (although note that we do not have species-level community data for epiphytes). Greater abundances of ants and different ant communities were present in trees with higher epiphyte / climber cover in the crown (for fogging), and presence of large *Asplenium* ferns also affected community composition (for baiting). Note that it is likely that all the *Asplenium* ferns we surveyed belonged to the species *A. nidus*, since all tree crowns surveyed were above the height of 40 m (FAYLE & al. 2009). Ants are the most numerous occupants of *A. nidus* (apart from termites), accounting for 39% of the total biomass of all invertebrate taxa found to live there (ELLWOOD & al. 2002). Although higher abundances of ants were found in trees with more epiphyte cover in the crown, these trees did not support higher species richness of ants. Thus colonies must be larger in these trees, which might also relate to prey availability. Alternatively, in trees with higher abundances of ants, ant dispersal of epiphyte seeds might be more common (KAUFMANN & al. 2001), and hence ant abundance might drive epiphyte cover, rather than vice versa.

More species of ants were also found in trees with more hollows (baiting) and dead branches (fogging). Hence greater availability of these other nesting structures could also increase the probability of colonisation by ant species building nests in dead wood, in the suspended leaf litter found in tree hollows or in the cavities themselves (TANAKA & al. 2010). Alternatively, these structures might provide habitats for prey species, with ants nesting elsewhere in the canopy. It is also possible that older trees (which might not necessarily be larger) have both had longer to accumulate hollows and dead branches (and epiphytes) and for ant succession to occur, hence generating relationships between these variables. Therefore these correlations should not be regarded as necessarily indicating direct causal relationships. It should also be noted that since only cavities in branches > 10 cm diameter were enumerated, smaller cavities, which provide a habitat for many ant species, will have been missed.

Intriguingly, the two tree species harboured significantly different ant abundances (baiting) and species richnesses (fogging), although ant species composition did not differ between the tree species. This was despite the fact that we were unable to detect any differences in environmental variables between the trees (although it should be noted that due to small sample size for *Parashorea tomentella*, the power of these tests is not very high; Appendix S4). Even for two very different species of trees in Papua New Guinea (*Ficus subtrinervia*, Moraceae and *Pouteria maclayana*, Sapotaceae), using canopy baiting JANDA & KO-

NEČNÁ (2011) found similar ant abundance and species richness. Our focal trees might vary in their ability to provide either extra floral or insect derived nectar (DAVIDSON & al. 2003, OLIVEIRA & FREITAS 2004, BLÜTHGEN & al. 2006), or in other structures that we did not measure. This is supported by the fact that the presence of extra-floral nectaries is variable between other members of the genus *Parashorea*, with these structures being present in some species (KOPTUR 1992) and absent in others (MUEHLEISEN 2013).

Ant abundance measured by baiting showed a positive correlation with the connectivity of tree crowns with surrounding trees. Increased connectivity enables the ant fauna to move freely within canopies of trees without having to travel down to the ground, thus providing significant energy savings for foraging canopy ants. YANOVIAK & KASPARI (2000) have shown that within the canopy, interconnected branches (specifically those with relatively smooth surfaces) allow different sizes of ants to coexist. However, the fact that only ant abundance, and not richness, was increased by connectivity, suggests that higher connectivity may allow behaviourally dominant species to invade the focal tree, replacing other species, which might have lower abundances. This is supported by the fact that the relationship between connectivity and abundance was only observed for ants at baits, where behaviourally dominant species are expected to be most abundant, and not for fogging data, and also by previous experiments in which subordinate ants were prevented from removing connections to nearby vegetation, resulting in increased invasion by dominant species (DAVIDSON & al. 1988). Furthermore, post-hoc analysis, using a direct measure of dominance calculated for each tree (probability of selecting at random two individuals of the same species; Simpson's index) shows a positive relationship between connectivity and numerical dominance at baits ($F_{2,17} = 6.81$, $P = 0.007$). Since tropical Asia has a lower density of lianas (a major contributor to canopy connectivity) than either Africa or South America (EMMONS & GENTRY 1983), our results can be interpreted as indicating that Asian canopies may not yet be saturated in terms of ant-relevant liana connectivity, and hence variation in connectivity still alters ant community structure.

Responses of particular ant species to variability in canopy structure are also of interest. The constantly moving, unique "herdsmen ants" (*Dolichoderus* spp.) which farm sap-sucking homopterans are the most prominent ants using dense vegetation and tree cavities as their temporary bivouac nest (MASCHWITZ & HÄNEL 1985). In this study, *Dolichoderus thoracicus* was found more commonly on large trees with a high load of epiphytic cover in the crown (see location in ordination space, Fig. 3). In contrast, *Dolichoderus magnipastor* was found more commonly in the presence of *Asplenium nidus* and thick cover of other plants on the crown: This was probably because they need these plants to raise their herds on (although we did not observe this directly). Another interesting finding was that *Monomorium floricola*, which has been described as a tramp species (NA & LEE 2001), was also found in the canopy (from both baiting and fogging). This species has also been recorded by TANAKA & al. (2010) in the high canopy of Lambir Hills National Park, Sarawak. One possibility is that the presence of this species, which has been

mostly found to date in secondary forests, plantations and urban areas, shows that some tramp species are able to survive in an intact forest high in the canopy, where the microclimate and relatively harsh physical condition imitate their habitats elsewhere. This is of concern, since invasions by non-native species may be taking place unseen, over the heads of earth-bound ecologists. Alternatively, the reverse might be true, and the high canopy of primary rain forest might be the native habitat of *M. floricola*, from which it has subsequently expanded into disturbed habitats, including those modified by humans.

We have demonstrated that the ants from the high canopy of tropical rain forest are structured by a range of influences, including the physical dimensions of the host tree, the availability of nest sites such as dead wood and epiphytes, the species of the host tree, and the degree of connectivity with the rest of the canopy. Variation in these factors between trees hence allows co-existence of multiple ant species, and is likely to be one driver of the high levels of arthropod diversity observed in tropical rain forest.

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