



# Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest

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The physical characteristics of habitats shape local community structure; a classic example is the positive relationship between the size of insular habitats and species richness. Despite the high density and proximity of tree crowns in forests, trees are insular habitats for some taxa. Specifically, crown isolation (i.e. crown shyness) prevents the movement of small cursorial animals among trees. Here, we tested the hypothesis that the species richness of ants ( $S_a$ ) in individual, isolated trees embedded within tropical forest canopies increases with tree size. We predicted that this pattern disappears when trees are connected by lianas (woody vines) or when strong interactions among ant species determine tree occupancy. We surveyed the resident ants of 213 tree crowns in lowland tropical forest of Panama. On average, 9.2 (range = 2–20) ant species occupied a single tree crown. Average ( $\pm$  SE)  $S_a$  was ca 25% higher in trees with lianas ( $10.2 \pm 0.26$ ) than trees lacking lianas ( $8.0 \pm 0.51$ ).  $S_a$  increased with tree size in liana-free trees ( $S_a = 10.99A^{0.256}$ ), but not in trees with lianas. Ant species composition also differed between trees with and without lianas. Specifically, ant species with solitary foragers occurred more frequently in trees with lianas. The mosaic-like pattern of species co-occurrence observed in other arboreal ant communities was not found in this forest. Collectively, the results of this study indicate that lianas play an important role in shaping the local community structure of arboreal ants by overcoming the insular nature of tree crowns.

A key goal of ecology is to determine the factors that influence local community structure (Agrawal et al. 2007). Both regional and local processes shape local species richness and composition via dispersal filters, habitat limitation, and species interactions (Huston 1999), and effectively predict community structure across a variety of ecosystems (Cornell and Lawton 1992, Caley and Schluter 1997, Myers and Harms 2009). Likewise, habitat area is a fundamental determinant of species richness for insular communities (Preston 1962). In particular, species–area relationships and habitat isolation (MacArthur and Wilson 1963, 1967) are widespread and relatively scale-independent predictors of species richness on islands (Simberloff and Wilson 1969, Ricklefs and Schluter 1993, Losos and Ricklefs 2009). Species richness also increases with habitat heterogeneity and resource availability, especially in combination with increasing total habitat area (Kohn and Walsh 1994, Tews et al. 2004, Kadmon and Allouche 2007, Hortal et al. 2009). However, identifying the most important determinants of local community structure in highly diverse systems such as tropical forests is challenging (Erwin 1982, Godfray et al. 1999, Basset et al. 2012).

The tropical forest canopy – the uppermost forest layer composed of the crowns of mature trees (Nadkarni et al. 2004) – provides a unique opportunity to examine the

determinants of local species richness and community composition. Individual trees frequently are physically isolated within a forest canopy because of ‘crown shyness’, or the tendency for a gap to exist between neighboring crowns (Ng 1977). Although narrow, such gaps can limit animal movement within the canopy (Emmons and Gentry 1983, Yanoviak 2015). Consequently, individual tree crowns function as habitat islands for some taxa (Southwood and Kennedy 1983, Harris 1984, Sverdrup-Thygeson and Midtgaard 1998), especially small, cursorial animals (Moed and Meads 1983, Wardle et al. 2003, Yanoviak 2015). For example, species richness and total biomass of non-volant arthropods that are restricted by crown shyness (including Collembola, Araneae, and wingless Hymenoptera) increase with tree size (Hijii 1986, Ribas et al. 2003, Campos et al. 2006, Klimes et al. 2012), whereas this is not true for many winged taxa (Southwood et al. 1982).

Tree species differ in the resources they contribute to arboreal arthropod communities (Blüthgen et al. 2004, Poelman et al. 2008). As a result, some insect communities are more similar between conspecific trees compared to heterospecifics (Klimes et al. 2012). Tree species identity also affects the local distribution of specialized herbivores (Erwin 1982, Davidson and Epstein 1989, Basset 1992, Basset et al. 1996), many of which are tended by ants (Davidson et al.

2003). Moreover, some arboreal ant species are involved in obligate mutualisms with trees, often occupying specialized domatia (Ward 1999, Rico-Gray and Oliveira 2007). Consequently, at the scale of a forest stand, arboreal arthropod species richness tends to increase with increasing tree diversity (Ribas et al. 2003, Basset et al. 2012).

Arboreal ants are an ideal focal taxon for exploring the determinants of local community structure in forest canopies (Yanoviak et al. 2012, Yanoviak and Schnitzer 2013). Although forest canopies host a wide diversity of organisms (Lawton 1983, Ozanne et al. 2003), arboreal ants account for up to 50% of the total animal biomass and 90% of total insect abundance (Davidson 1997, Davidson et al. 2003, Blüthgen and Stork 2007). Moreover, ants are relatively easy to collect, and the common arboreal taxa can be identified to species level.

Species interactions and habitat filters shape arboreal ant communities (Majer 1972, Yanoviak 2015). Specifically, competitive exclusion can result in mosaic-like patterns of ant species distributions among tree crowns (Hölldobler and Lumsden 1980, Blüthgen et al. 2004, Dejean et al. 2007, Sanders et al. 2007). Habitat characteristics such as tree size, tree species identity, and crown connectivity are good predictors of arboreal ant community structure in some systems (Tschinkel and Hess 1999, Ribas et al. 2003, Powell et al. 2011, Klimes et al. 2012, Cuissi et al. 2015). Because arboreal ants rarely descend from the canopy (Camargo and Oliveira 2012, but see Hahn and Wheeler 2002), and nearby tree crowns frequently do not touch (Ng 1977), trees likely function as islands for arboreal ant communities (Yanoviak 2015). However, explicit tests of the hypothesis that local arboreal ant communities (i.e. within an individual tree) follow the classical insular species–area relationship (Preston 1962) are lacking.

Apart from trees, lianas (woody vines) are a conspicuous component of lowland tropical forests, where they commonly infest more than 70% of the canopy trees (Pérez-Salicrup et al. 2001, van der Heijden and Phillips 2008, Ingwell et al. 2010, Schnitzer et al. 2012). Lianas provide important resources for arboreal ant communities, including nest sites (Yanoviak and Schnitzer 2013), extrafloral nectaries (Blüthgen et al. 2000), and preferred feeding locations for trophobionts (Tanaka et al. 2010). Lianas also frequently occupy multiple tree crowns (on average, each liana inhabits 1.6 tree crowns, with some connecting up to 49 trees; Putz 1984). Arboreal ants use lianas as physical bridges to travel and forage among neighboring tree crowns (Yanoviak 2015), effectively overcoming isolation induced by crown shyness. Moreover, the number of liana stems in a single tree crown varies from zero to thousands of stems (Schnitzer and Bongers 2002), potentially producing natural gradients in resource availability and connectivity for arboreal ant communities. As such, lianas likely play an important role in determining local arboreal ant community structure. This is especially relevant to ant species that would be most affected by crown isolation – in particular, wide-ranging solitary foragers (*Neoponera* spp. and *Paraponera clavata*) or those that require a large resource base to support large colonies (e.g. *Azteca* spp., *Cephalotes atratus*; Hölldobler and Wilson 1990).

The principal objectives of this study were to determine if local arboreal ant species richness (i.e. the number of resident

species in a single tree crown; hereafter,  $S_a$ ) follows the classical species–area relationship  $S = CA^z$  (Preston 1962), and to explore the role of lianas in this pattern. Specifically, we predicted that  $S_a$  in trees lacking lianas would increase with tree size. We expected such effects to disappear in trees occupied by lianas, and that  $S_a$  would increase with liana density. Our secondary objective was to examine the effects of tree size, identity, and liana occupancy on ant species composition and co-occurrence. Specifically, our goals were to evaluate potential host-specificity between ants and trees, and to determine if ant species in this forest follow mosaic patterns of distribution (Leston 1978). Lianas are defensible, efficient foraging pathways for ants (Clay et al. 2010, Yanoviak et al. 2016), and can expand the foraging space of an ant colony well beyond its home tree. Thus, we expected that trees occupied by lianas would exhibit a higher frequency of behaviorally aggressive ant species with large colonies (e.g. *Azteca* spp.; Adams 1990) and ant species with wide-ranging solitary foragers (e.g. ponerines; Camargo and Oliveira 2012).

## Methods

### Study site

Field work for this study was conducted from 2009 to 2015 within the Barro Colorado Natural Monument in the Panama Canal Zone (09.15°N, 79.85°W; hereafter, BCNM). The BCNM is a lowland, seasonally moist tropical forest. More information about the site is available elsewhere (Leigh et al. 1996). Focal trees were scattered across Barro Colorado Island and the nearby Gigante Peninsula. Many of the Gigante trees were within sixteen 80 × 80 m plots that are part of a larger ongoing liana removal study (Martínez-Izquierdo et al. 2016); however, only non-manipulated trees were used for statistical analyses in this study. All data were collected between 09:00 and 16:00 in the early wet season (May to August) of each year.

### Canopy sampling

In total, 738 ant surveys were conducted in 213 trees representing 33 tree species across the BCNM. We accessed the crown of each tree using the single rope technique (Perry 1978) and censused the arboreal ant community using hand collections and baiting. Baits were placed near the main fork of each tree (10–35 m above the ground) and on all accessible branches and liana stems. Baits consisted of a mixture of honey and meat (ham, tuna, or chicken) to provide a combination of carbohydrates, salts, fats, and proteins. Each bait was examined multiple times during each survey to ensure that species were not missed due to turnover. Baiting and hand collecting are commonly used in canopy ant research (Yanoviak and Kaspari 2000, Ribas et al. 2003, Yanoviak et al. 2007). Our collective decades of experience with canopy ant surveys, plus data from destructive sampling combined with baiting for other studies in the BCNM (Yanoviak et al. 2011), indicate that baiting is very effective at identifying resident species.

The collection effort was limited to one hour after baits were placed, and the survey area was limited to one tree crown and its associated lianas (Ellison et al. 2011). The total area sampled per survey varied with tree size such that the relative surveyed area per tree was approximately equal across trees. We collected representatives of all ant species and morphospecies observed in each tree crown throughout the one-hour survey period. If only one worker of a particular species or morphospecies was found in a tree, that ant was recorded as a stray (i.e. a non-resident forager). Collected workers were stored in 95% ethanol for later species identification using online and published keys (Ward 1989, 1993, 1999, Longino 2010). Reference specimens were sent to taxonomists for confirmation. Voucher specimens were deposited at the Univ. of Louisville; the United States National Museum, Washington DC; the Smithsonian Tropical Research Inst., Panama; and the Fairchild Museum at the Univ. of Panama.

For every canopy ant survey, we recorded the date, time of day, air temperature, and relative humidity at the beginning of the collection period. We identified every focal tree to species, measured its diameter at breast height (DBH; used to compute basal area), and determined its liana score on a logarithmic scale from zero to three. The liana score was an estimate of liana abundance in a tree crown, where 0 = no lianas, 1 = 1–10 liana stems, 2 = 11–100 liana stems, and 3 = > 100 liana stems. Liana stems were counted as the number of stems that intercepted an imaginary horizontal plane extending from the main fork of the tree. A single individual liana may have hundreds of stems in a tree crown (Putz 1984); therefore, these counts do not represent individual liana abundance. For all trees with lianas, lianas within the focal tree crown extended into the crown of at least one neighboring tree.

## Analysis

To determine if the whole arboreal ant community of the BCNM was well represented by the collection effort, we created a sample-based species accumulation curve (SAC) using all 738 surveys ( $S_{est}$  function in EstimateS ver. 9.1.0; Colwell 2009). Since many collections represented annual resampling of the same trees, we also created a SAC using only data from the first survey conducted in each tree ( $n = 153$ ). To maintain statistical independence, all subsequent analyses used only these initial survey data.

We used a linear model to determine which factors influence ant species richness in canopy trees. The complete model included liana score, tree species, tree size (using basal area as a proxy variable for crown area; O'Brien et al. 1995), temperature, and all possible interaction terms as fixed effects. We included temperature because it is a key abiotic variable affecting the activity of small ectotherms like ants (Kaspari et al. 2016). We eliminated non-significant terms using stepwise model reduction based on AIC values (Ribas et al. 2003, Johnson and Omland 2004), and used a post-hoc Tukey HSD test to compare groups within liana score and tree species. Finally, to test the predictions that individual trees function as islands and that lianas overcome the isolating effect of crown shyness, we conducted a parallel

analysis in which liana score was replaced with liana presence or absence.

We used PERMANOVA (Anderson et al. 2008) to assess the effects of liana score or liana presence/absence in combination with tree species, tree size, and temperature on ant species composition. The complete model included all possible interaction terms. We converted the continuous variables basal area and temperature into ordered quartiles to meet the data structure requirements of this analysis. We calculated community similarity using the Jaccard index and used 9999 permutations for the analysis. We used post-hoc pairwise PERMANOVA tests to compare groups within liana score and tree species, and indicator species analysis to determine which ant species contributed the most to differences revealed by the PERMANOVA tests (Dufrêne and Legendre 1997, de Cáceres and Legendre 2009).

Tree size (basal area in  $m^2$ ) was log transformed to improve normality. Tree species represented by < 5 individuals in the data set were excluded from pairwise PERMANOVA tests. We used a Bonferroni adjustment for multiplicity where necessary. Linear models and indicator species analyses were conducted using the R statistical package ver. 3.2.3 along with packages 'lsmeans', 'multcomp', 'MASS', and 'indicpecies' (R Core Team). We performed PERMANOVA analyses using PRIMER ver. 6.1.14 including the PERMANOVA+ package ver. 1.0.4 (PRIMER-E).

## Species co-occurrence

Patterns of co-occurrence are commonly used to assess potential mosaic structures in canopy ant communities (Majer 1976, Blüthgen and Stork 2007, Sanders et al. 2007). The C-score is an index that compares patterns of co-occurrence in natural systems against a null model with a random distribution (Gotelli 2000). As described above, we limited the dataset to the first survey for each tree ( $n = 153$ ), and then used EcoSimR 1.0 (Gotelli and Ellison 2013) to generate a C-score for the whole community of canopy-dwelling ants of the BCNM. We used 9999 randomized matrices and applied a fixed-fixed algorithm to both ant species and individual tree survey. We assumed that ant species differ in their frequency of tree occupation, and that different individual trees harbor different potential habitats for ants (Tschinkel and Hess 1999, Gotelli 2000). We tested pairwise species associations using PAIRS software with the same parameters listed above (9999 randomizations and a fixed-fixed algorithm; Gotelli and Ulrich 2012). All species were accounted for in pairwise analyses but only results for species that occurred in at least 15 surveys ( $\geq 10\%$  of the focal trees) are reported.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.b34d2>> (Adams et al. 2016).

## Results

We found 128 species and morphospecies of ants representing 30 genera and 8 subfamilies in the BCNM forest canopy. The species accumulation curve predicted a maximum of

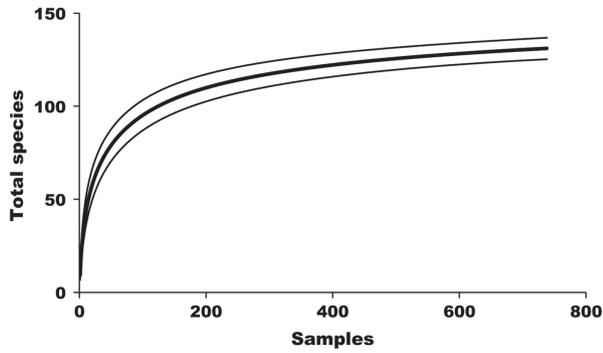


Figure 1. A species accumulation curve (SAC) based on the total collection data set ( $n = 738$ ). Dotted lines indicate 95% confidence intervals. The total number of species collected was 128 with a maximum of 136 predicted.

136 species in the canopy (Fig. 1), thus, our collection effort captured 94% of the expected species richness at this site.

### Local ant species richness ( $S_a$ )

Using data from all tree surveys (including repeated surveys of the same trees;  $n = 738$ ), canopy trees contained an average ( $\pm$  SD) of  $9.3 \pm 3.2$  ant species, with 20 ant species in the most diverse tree and two ant species in the least diverse tree. Limiting the data set only to the initial survey of each tree produced similar results ( $9.8 \pm 3.1$  species;  $n = 153$  surveys).  $S_a$  was significantly influenced by liana score, tree size, and air temperature ( $F_{5,147} = 4.55$ ;  $p = 0.0007$ ;  $R^2 = 0.10$ ). Specifically,  $S_a$  increased with increasing liana score ( $F_{3,147} = 2.97$ ;  $p = 0.03$ ; Fig. 2), tree size ( $F_{1,147} = 9.12$ ;  $p = 0.003$ ), and air temperature ( $F_{1,147} = 4.71$ ;  $p = 0.03$ ; Fig. 3). Although air temperature was a significant predictor of  $S_a$ , it spanned the normal range of thermal conditions at which canopy ants are active in this forest (25–34°C; Kaspari et al. 2016) and its effect was very small ( $R^2 = 0.03$ ).

Replacing liana score with liana presence/absence in the model resulted in a significant interaction between liana presence and tree size ( $F_{4,148} = 6.80$ ;  $p < 0.0001$ ;

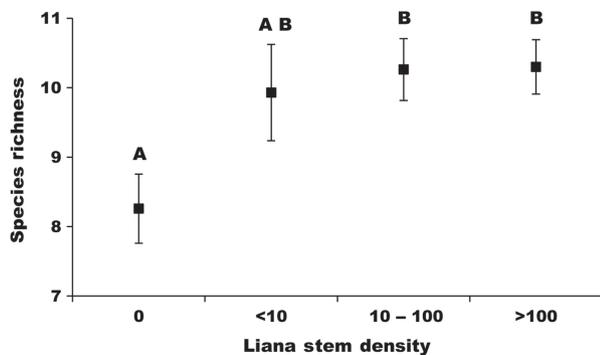


Figure 2. Average ( $\pm$  SE) ant species richness vs approximate liana stem density in focal tree crowns. Means were calculated from 153 independent tree samples ( $n = 35, 18, 43$  and  $57$  trees in liana density categories 0,  $<10$ , 10–100, and  $>100$ , respectively). Similar letters indicate means that do not differ based on Tukey HSD tests.

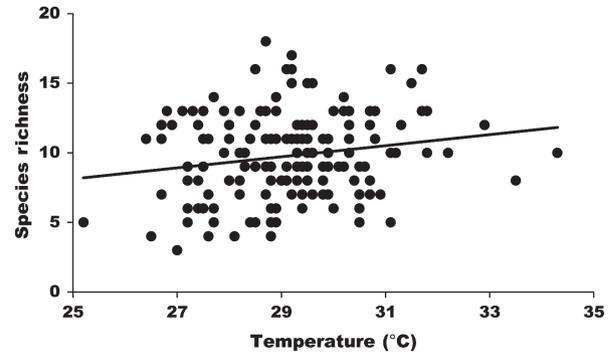


Figure 3. Species richness ( $S_a$ ) of arboreal ants vs air temperature ( $T$ ) at the time of collection for the liana score model. The equation for the regression is  $S_a = 0.399T - 1.86$  ( $R^2 = 0.03$ ;  $p = 0.03$ ).

$R^2 = 0.13$ ), supporting the hypothesis that arboreal ant communities are functionally different in liana-free trees versus trees with lianas. Subsequent analysis of  $S_a$  vs tree size and temperature separately for trees with and without lianas revealed a positive linear relationship between  $S_a$  and tree size (basal area in  $m^2$ ;  $A$ ) in trees without lianas ( $F_{2,32} = 19.27$ ;  $p = 0.0001$ ;  $R^2 = 0.36$ ). This relationship followed the power function  $S_a = 10.99A^{0.256}$ . The observed value of  $Z$  (0.256) lies within the expected range predicted for other insular habitats (Rosenzweig 1995). In contrast, there was no species–area relationship in trees with lianas present ( $F_{2,115} = 3.03$ ;  $p = 0.08$ ; Fig. 4). Temperature at the

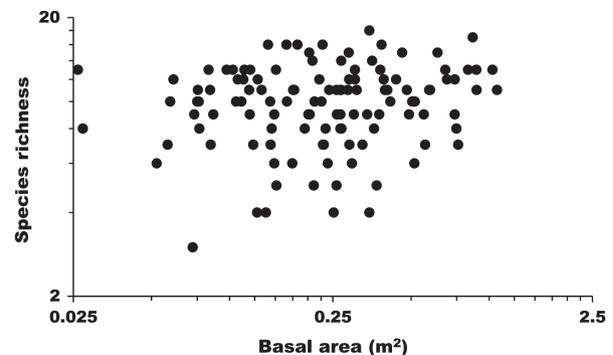
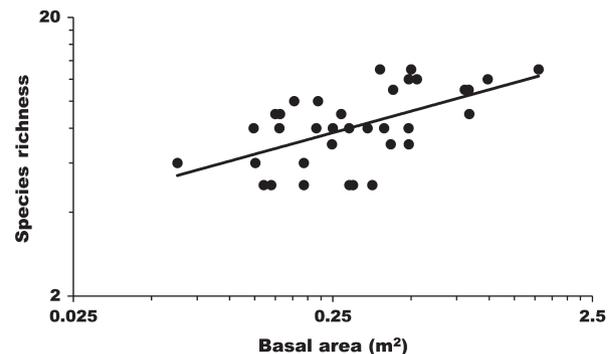


Figure 4. Arboreal ant species richness vs tree size (as basal area) in trees lacking lianas (top panel) and trees with lianas (bottom panel). Ant species richness ( $S_a$ ) increases with tree size ( $A$ ) in trees lacking lianas as described by the equation  $S_a = 10.99A^{0.256}$  ( $R^2 = 0.36$ ;  $p = 0.0001$ ). Tree size does not correlate with ant species richness in trees with lianas.

time of collection was not a significant predictor of species richness in either of these models.

## Species composition

*Pseudomyrmex*, a widespread arboreal specialist (Ward 1999), was the most common genus in our collections, and *Pseudomyrmex gracilis* was the most frequently encountered species, occurring in 69% (106 trees) of initial tree surveys. Only two other species occurred in more than 50% of initial surveys: *Camponotus linnaei* and *Pseudomyrmex oculatus* (56 and 52%, respectively). Nearly 40% of species (50 species) were relatively rare, appearing in less than 1% of the initial surveys (Supplementary material Appendix 1, Table A1).

Ant species composition differed among trees based on liana presence (Pseudo- $F_{1,128} = 1.50$ ;  $p = 0.05$ ). Cumulatively, 92 species occurred in trees with lianas and 58 species occurred in trees without lianas. Species with solitary foraging strategies (e.g. *Neoponera villosa*) occurred more frequently in trees with lianas; however, contrary to our prediction, species with large colony sizes (e.g. *Azteca* spp. and *Cephalotes atratus*) occurred with equal frequency in trees with and without lianas. *Solenopsis picea*, an open habitat specialist (Pacheco et al. 2013), occurred 10 times more frequently in trees lacking lianas. Indicator species analyses revealed four species that were associated with liana-free tree crowns (*Crematogaster crinosa*, *Pseudomyrmex simplex*, *Pseudomyrmex tenuissimus*, and *Solenopsis picea*) and three ant species from trees with lianas (*Crematogaster carinata*, *Neoponera villosa*, and *Pheidole caltrop*; Table 1).

Tree species identity also influenced the composition of local arboreal ant communities (Pseudo- $F_{22,128} = 1.17$ ;  $p = 0.003$ ). However, post-hoc pairwise tests of tree species indicated that ant community composition differed between only two trees: *Dipteryx panamensis* ( $n = 83$ ) and *Apeiba membranacea* ( $n = 13$ ;  $t = 1.52$ ;  $p = 0.008$ ). Specifically, the ant species *Neoponera striatinodis* and *Acromyrmex volcanus* were positively associated with *A. membranacea* trees, whereas *Camponotus cameroni* was positively associated with *D. panamensis* trees (Table 2).

## Species co-occurrence

Unlike similar arboreal ant communities that exhibit mosaic patterns of distribution, the canopy ant community in the

Table 1. The list of indicator species of arboreal ants in trees with and without lianas. Values are the indicator value (IndVal) and adjusted p-value (p). Separate analyses were conducted for trees with and without lianas. See the text and de Cáceres and Legendre (2009) for more details about indicator species analysis.

Liana presence	Ant species	IndVal	p
Present	<i>Crematogaster carinata</i>	0.401	0.0436
Present	<i>Neoponera villosa</i>	0.519	0.0252
Present	<i>Pheidole caltrop</i>	0.357	0.0474
Absent	<i>Crematogaster crinosa</i>	0.364	0.0311
Absent	<i>Pseudomyrmex simplex</i>	0.420	0.0114
Absent	<i>Pseudomyrmex tenuissimus</i>	0.670	0.0021
Absent	<i>Solenopsis picea</i>	0.429	0.0009

Table 2. The list of indicator species of arboreal ants for *Apeiba membranacea* and *Dipteryx panamensis* trees with their indicator value (IndVal) and adjusted p-value (p). A separate analysis was conducted for each tree species.

Tree species	Ant species	IndVal	p
<i>A. membranacea</i>	<i>Acromyrmex volcanus</i>	0.447	0.0279
<i>A. membranacea</i>	<i>Neoponera striatinodis</i>	0.457	0.0169
<i>D. panamensis</i>	<i>Camponotus cameroni</i>	0.601	0.0196

BCNM showed no general trends towards non-overlapping species occurrence (observed C-score = 112.1; simulated mean C-score = 112.3; variance of simulations = 0.15; observed  $\leq$  simulated  $p = 0.36$ ; observed  $\geq$  simulated  $p = 0.64$ ). However, the pairwise tests revealed 16 species pairs that tended towards exclusion, and 19 species pairs that tended to co-occur (Supplementary material Appendix 1, Table A2 and Table A3). Using the biological characteristics established by Majer (1972, 1976; numerical abundance, polydomy, and exclusion of or aggression towards other ants at baits), and the tendency for dominant species to not co-occur (Gotelli and Ulrich 2012), we identified five 'dominant' ant species from the 16 segregated species pairs: *Azteca instabilis*, *Azteca trigona*, *Azteca forelii*, *Crematogaster curvispinosa*, and *Dolichoderus bispinosus*. *Azteca instabilis* and *A. trigona* co-occurred with each other less frequently than predicted by the null model, and *Azteca forelii* never co-occurred with *A. instabilis*. Finally, the occurrence of both *C. curvispinosa* and *D. bispinosus* was negatively associated with *A. trigona*.

## Discussion

Here we show that the species richness of resident ants in isolated tree crowns follows the classical species–area relationship (Preston 1962), and that the presence of lianas, a connective element of habitat structure, removes that pattern. The most parsimonious explanation for this effect is that the persistent physical contact among multiple tree crowns provided by lianas makes the area of a single tree crown a poor predictor of effective arboreal habitat area. The conclusion that individual tree crowns function as isolated islands for arboreal ants is further supported by the lower frequency of ant species that rely on wide-ranging solitary foragers in trees lacking lianas. Alternatively, lianas also provide nest sites and nutritional resources for arboreal ants (Blüthgen et al. 2000, Tanaka et al. 2010, Yanoviak and Schnitzer 2013). However, such resources by themselves should not eliminate species–area relationships in trees with lianas (Nilsson et al. 1988, Ricklefs and Lovette 1999).

The idea that individual trees and other forest structures function as islands is not new (Janzen 1968, 1973, Southwood and Kennedy 1983, Frank and Lounibos 1987), and evidence for increasing  $S_a$  with increasing tree size exists for other arboreal ant communities (Majer and Delabie 1999, Tschinkel and Hess 1999, Powell et al. 2011, Klimes et al. 2012). However, such examples come from forests with relatively isolated tree crowns (e.g. pine plantations, Brazilian cerrado, and dipterocarp forests), or were conducted at smaller temporal and spatial scales than this study.

The close correspondence between species–area relationships predicted by theory (Preston 1962) and the results of this study have interesting ecological implications. Specifically, the value of  $C$  in the equation  $S_a = CA^z$  predicts that very small trees (i.e. saplings ranging from ca 1–4 cm DBH) will support one ant species. Indeed, our observations in the BCNM suggest that this prediction is realistic, especially in myrmecophytic trees, which are often occupied by ants as seedlings (Janzen 1966). Given the density of trees in the BCNM forest (2000–2700 stems > 2.5 cm DBH ha<sup>-1</sup>; Leigh et al. 1996), and the frequency of liana occupancy in BCNM trees (75%; Schnitzer et al. 2012), we expect at least 500 tree crowns per hectare to function as small islands for ants in this forest.

Crown isolation also should contribute to the clearly delimited territories that characterize ant mosaic distributions (Majer 1976, Leston 1978) in other arboreal systems (e.g. tropical agroecosystems, the dipterocarp forests of Borneo, the coastal forests of Australia, and the Brazilian cerrado; Majer et al. 1994, Ribas and Schoereder 2004, Blüthgen and Stork 2007, Sanders et al. 2007, Klimes et al. 2012). For territorial animals, the cost of maintaining exclusive territories decreases when shared boundaries between neighbors are minimized (Eason 1992, Adams 2001, 2016). For arboreal ants, high liana frequency should increase the cost of maintaining territories by forcing dominant ant colonies to defend multiple pathways among tree crowns, effectively increasing shared boundary length. Thus, forests in which lianas are common should be less likely to exhibit well defined ant mosaics, and forests with low liana frequency should be more likely to exhibit ant mosaics. Indeed, apart from this study, there is some evidence for this pattern. Specifically, the forests with strong evidence of ant mosaics mentioned above either have lower frequencies of lianas compared to other tropical forests, are agricultural systems managed to reduce liana frequency, or are tropical savannas with widely dispersed trees (Emmons and Gentry 1983, Ratter et al. 1997, Schnitzer and Bongers 2002). Furthermore, in primary forests in the Neotropics and Africa – where liana frequencies are high – ant mosaics are either absent or less well defined (Ribas and Schoereder 2002, Schulz and Wagner 2002, but see Dejean et al. 1999, 2000).

This study is the largest (in terms of spatial scale) structured survey of arboreal ants in a natural ecosystem. Other regional estimates of arboreal ant richness conducted fewer total surveys (Montgomery 1985, Wilson 1987, Longino et al. 2002, Schulz and Wagner 2002, Ribas et al. 2003, Blüthgen and Stork 2007, Powell et al. 2011), covered smaller forest plots (Klimes et al. 2012), or focused on tropical agroecosystems (Majer et al. 1994, Sanders et al. 2007). The regional ant species richness recorded here (128 species) and average species per tree (9.3) are within the range of other large scale surveys in natural ecosystems (73–169 total species and averages between 3–20 ant species per tree). Compared to a study with a similar total number of surveys (Klimes et al. 2012), the regional ant species richness in the BCNM is higher (99 vs 128 species, respectively). We attribute the higher species richness recorded here in part to the difference in sampling area (ca 5 km<sup>2</sup> in this study vs < 0.01 km<sup>2</sup> in the Bornean forest), but also to biogeographical differences

in ant diversity between the Neotropics and southeast Asia. Specifically, the regional ant species richness reported by Klimes et al. (2012) is comparable to that observed in other studies of Asian and Australian forests (Blüthgen and Stork 2007), whereas the total ant species richness we observed in the BCNM is similar to that found in Peru and Brazil (Wilson 1987, Ribas et al. 2003).

Although increased tree species richness was positively associated with ant species richness in other plot-level surveys (Ribas et al. 2003), we found little evidence of tree species effects on the structure of local arboreal ant communities. The patchy distribution of relatively uncommon ant species (especially *Acromyrmex volcanus* and *Neoponera striatinodis*, which appeared in 5 and 6% of samples, respectively) likely inflated the compositional differences found between *Dipteryx panamensis* and *Apeiba membranacea* trees. Furthermore, ant species predicted to be most influenced by tree species richness, specifically those involved in obligate ant-plant mutualisms (Ward 1993, Rico-Gray and Oliveira 2007), were poorly represented in this study (we collected only one such species, *Cephalotes setulifer*; de Andrade and Baroni Urbani 1999).

Ant body size differences provide a potential explanation for some of the patterns of co-occurrence among the ‘dominant’ ants of the BCNM. All three *Azteca* species overlap in head width (Longino 2007), a morphological trait associated with diet and resource use (Weiser and Kaspari 2006). As such, these ants likely compete for similar resources resulting in less frequent co-occurrence than expected. Similarly, *A. trigona* and *Crematogaster curvispinosa* (Longino 2003), also greatly overlap in head width and tend not to co-occur. Although our community-wide analyses do not support the predictions of an ant mosaic, these pairwise findings suggest that further study of the effects of interspecific interactions on local species richness in arboreal ant communities is needed.

The results of this study raise additional questions that are potentially useful avenues for future investigation. First, does tree size predict arboreal ant species richness in smaller, non-canopy trees? The results of this study suggest that even very small trees will harbor arboreal ants; however, the range of tree sizes sampled in this study did not include that lower limit. Second, how do tree traits (e.g. deciduousness, dioecy, crown architecture, and canopy status), plot characteristics (e.g. forest stand age), or species identity of lianas or epiphytes (Yanoviak et al. 2011) affect ant community structure in individual tree crowns? Finally, why do certain ant species tend to co-occur more or less frequently than expected? Body size appears to explain some of the patterns of exclusion between species; however, territory mapping and aggression assays are still needed to fully evaluate the potential presence of ant mosaics (Majer 1976, Dejean et al. 2007, Adams 2016) in this forest. Ultimately, understanding patterns of local species richness in forest canopies is important because tropical tree crowns harbor ca 40% of extant species (Ozanne et al. 2003), but factors affecting local variation in diversity remain poorly studied. We show that for one of the most abundant members of the tropical forest canopy – arboreal ants – tree crowns function as islands in the absence of lianas.

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Supplementary material (Appendix ECOG-02608 at <[www.ecography.org/appendix/ecog-02608](http://www.ecography.org/appendix/ecog-02608)>). Appendix 1.