Journal of Tropical Ecology

www.cambridge.org/tro

Distance–decay patterns differ between canopy and ground ant assemblages in a tropical rainforest

Reuber Antoniazzi[1,*], Arleu B. Viana-Junior[2], Jaime Pelayo-Martínez[3], Liliana Ortiz-Lozada[3], Frederico S. Neves[4], Maurice Leponce[5,6] and Wesley Dáttilo[1,*]

[1]Red de Ecoetología, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico; [2]Programa de Pós-graduação em Biodiversidade e Evolução, Coordenação de Zoologia, Museu Paraense Emílio Goeldi, 66077-530, Belém, Pará, Brazil; [3]Servicios Especializados en Estudios Integrales Ambientales, Xalapa, Veracruz, Mexico; [4]Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; [5]Biodiversity Monitoring & Assessment, Royal Belgian Institute of Natural Sciences, Brussels, Belgium and [6]Evolutionary Biology & Ecology, Université Libre de Bruxelles, Brussels, Belgium

Research Article

Cite this article: Antoniazzi R, Viana-Junior AB, Pelayo-Martínez J, Ortiz-Lozada L, Neves FS, Leponce M, and Dáttilo W (2020) Distance–decay patterns differ between canopy and ground ant assemblages in a tropical rainforest. *Journal of Tropical Ecology* **36**, 234–242. https://doi.org/10.1017/S0266467420000188

Received: 17 July 2019
Revised: 22 September 2020
Accepted: 5 November 2020
First published online: 18 January 2021

Keywords:
ant diversity; arboreal ants; beta diversity; habitat-niche partitioning; vertical stratification; spatial distribution

Author for correspondence:
*Reuber Antoniazzi and Wesley Dáttilo, Email: reuberjunior@gmail.com; Wesley Dáttilo, Email: wesley.dattilo@inecol.mx

Abstract

Both decreases in compositional similarity with increasing geographic distances between sites (i.e. distance–decay relationship) and vertical stratification of species composition are key issues in ecology. However, the intersection between these two trends has scarcely been investigated. Here we use identical sampling methods in the canopy and at ground level in a tropical rainforest remnant on the coast of the Gulf of Mexico to evaluate, for the first time, a distance–decay relationship within vertical strata in insect assemblages. We found that the ant assemblage was vertically stratified; ant species richness was higher at ground level than in the canopy, and the species composition differed between the two vertical strata. Moreover, we observed that β-diversity increased with geographic distance at ground level, but not in the canopy strata. However, contrary to our prediction, there was less species turnover (lower β-diversity) between vertical strata than between trees. These findings may reflect differences in the dispersal capacity and nest habit of ants from each vertical stratum, and also habitat heterogeneity on the horizontal scale, e.g. the species of sampled trees. Our results illustrate the importance of sampling more than one vertical stratum to understand the spatial distribution patterns of biological diversity in tropical rainforests.

Introduction

Tropical rainforests host a huge diversity of life forms, even at small spatial scales (Carson & Schnitzer 2011, Turner & Corlett 1996). Much of this diversity is related to the vertical stratification of these environments (Oliveira & Scheffers 2019). For instance, different groups of animals forage on trees, using their leaves, exudates, bark and other plant structures for feeding and nesting (Antoniazzi *et al.* 2019, Power 1992, Shaw 2004). Distribution of these plant resources varies across vertical strata, and biotic communities respond to that variation (Shaw 2004). Moreover, abiotic conditions change among different strata, since in the canopy sunlight incidence and temperatures are higher and humidity is lower than at ground level (Fetcher *et al.* 1985, Madigosky 2004, Parker 1995). Hence, in tropical rainforests, vertical stratification is a well-known pattern for the spatial distribution of a wide number of taxa from plants to animals (Basset *et al.* 2003, Gregorin *et al.* 2017, Oliveira & Scheffers 2019, Popma *et al.* 1988, Smith 1973). In addition, species composition also changes across horizontal space as community similarity generally declines with increasing distance; this is known as the distance–decay relationship (Nekola & White 1999). The distance–decay relationship is mainly due to the decrease in similarity of environmental features with distance, leading to changes in the biotic community since species have different niche requirements (Nekola & White 1999). The distance–decay relationship can be found over large distances (Nekola & White 1999, Soininen *et al.* 2007), but also occurs at smaller scales, such as within a single forest (Basham *et al.* 2018). At small scales within forests, environmental conditions such as canopy openness (Brown 1993, Schnitzer & Carson 2001) or terrain slope (Lang *et al.* 2012) can change over relatively short distances, driving rapid turnover. Thus, horizontal (i.e. geographic) and vertical (i.e. tree height) components combine to form a three-dimensional structure with a variety of microhabitats and microclimates in which a high diversity of life forms coexist (Oliveira & Scheffers 2019).

Among all the arthropods in tropical forests, ants form a notable group since they exhibit great abundance (Wilkie *et al.* 2010) and account for a considerable proportion of total arthropod biomass (Fittkau & Klinge 1973, Tobin 1995). Ants are also ecologically dominant, both behaviourally and numerically (Davidson 1998), and they perform several roles in ecosystem

© The Author(s) 2021. Published by Cambridge University Press

CAMBRIDGE UNIVERSITY PRESS

functioning, including nutrient cycling and contributing to energy flow (Folgarait 1998). Moreover, ants are highly responsive to microclimatic changes, both on the forest floor (Soares & Schoereder 2001) and in the canopy (Basset *et al.* 2015). So, ant species distribution and activity are shaped by differential use of the available microhabitat at each stratum as well as by biotic interactions, e.g. competition (Basset *et al.* 2015, Soares & Schoereder 2001, Tavella *et al.* 2018, Theunis *et al.* 2005). Although previous studies state that ant species composition changes among vertical strata, there is no consensus in the literature about ant species richness. Some studies have found that ant species richness was quite similar between canopy and ground (Brühl *et al.* 1998, Wilkie *et al.* 2010), while others have found greater ant species richness in vertical strata below the canopy (Longino & Nadkarni 1990, Vasconcelos & Vilhena 2006). Differences in these studies' conclusions are likely related to the sampling methods used not being standardized between strata, a well-known bias in ecological studies with ants (Gotelli *et al.* 2011). Thus, investigation of the spatial distribution of ants in highly diverse environments, such as tropical forests, remains an exciting theme in ecology, whether concerning vertical stratification or horizontal distance.

Changes in species composition among different environments can be quantified using β-diversity (i.e. spatial species turnover and nestedness; Whittaker 1960). However, β-diversity is highly context-dependent in terms of the organism and habitat type (Soininen *et al.* 2007). For instance, in a temperate forest, β-diversity in lepidopteran communities is higher between vertical strata than among sites, while the pattern is reversed in coleopteran communities (Hirao *et al.* 2009). Furthermore, a recent study showed that the distance–decay relationship of amphibian communities differs among vertical strata in a tropical rainforest (Basham *et al.* 2018). Specifically, within-stratum comparisons show a classic distance–decay relationship for canopy and understorey communities, but not for ground communities (Basham *et al.* 2018). This study hypothesized that amphibians can more easily disperse at ground level than in the canopy, because the canopy lacks continuity in physical structure compared with the ground level (Basham *et al.* 2018). However, distinct organisms exhibit differences in their dispersal abilities across vertical strata (Schnitzer *et al.* 2015).

Distinct ant species present differences in home range size and dispersal ability, particularly in relation to the habitat they occupy (Yanoviak & Kaspari 2000). For instance, in tropical rainforest canopies, some ant species have large colonies and move among treetops of contiguous trees or use ground trails to interconnect neighbouring trees (Adams *et al.* 2019, Antoniazzi *et al.* 2020*a*, Dejean *et al.* 2019). However, the drivers of the spatial distribution of ground-dwelling ants tend to operate at small scale, being related to microclimate and microhabitat conditions (Luque & Reyes-López 2007, Theunis *et al.* 2005) or food availability (McGlynn 2006). Although some ant species have large foraging areas, such as ants of the *Atta* genus (Kost *et al.* 2005), most ground-dwelling ant species in tropical forests forage over small spatial distances (restricted to a few metres; Eguchi *et al.* 2004). Furthermore, several ant colonies may co-occur in small areas, with overlapping foraging areas on the ground (Hanisch *et al.* 2018) and in the canopy (Tanaka *et al.* 2010). Therefore, canopy and ground ants present differences in habitat use and distribution in tropical forests, which can lead to distinct patterns of species distributions in the horizontal dimension.

While it has been repeatedly demonstrated that the taxonomic similarity of ground ants decreases with increasing geographic distance, changes in species composition as a function of distance within different vertical strata are relatively unexplored. In this study we evaluated the patterns of vertical stratification of the richness, composition and distance–decay relationship of ant assemblages in a tropical rainforest. We aimed to test whether species richness and composition are similar between ground and canopy strata and whether distance–decay relationships exist within each vertical stratum since these two habitats present differences in abiotic conditions and physical structure. To achieve these aims we sampled ants in the canopy and at ground level in a rainforest remnant on the coast of the Gulf of Mexico using an identical sampling method in both the vertical strata. Firstly, we expected to find strong vertical stratification patterns, in both ant species richness and species composition, since the canopy and ground strata present marked differences in abiotic conditions and resource availability (Shaw 2004, Yanoviak & Kaspari 2000). Secondly, we expected β-diversity to be higher between vertical strata (canopy strata and ground level) than among individual trees, considering both strata together, because changes in abiotic and biotic conditions are generally more extreme in the vertical than in the horizontal dimension within a forest (Shaw 2004, Smith 1973). Thirdly, we expected β-diversity to increase with geographic distance at ground level, since tropical environments are very heterogeneous in microhabitats and microclimatic conditions at short spatial distances (Benson 1985), but less so in the canopy, mainly because canopy ants can move through the treetops and often present large dominant colonies spread over large territories (Dejean *et al.* 2007).

Methods

Study area

The study was conducted in a 130-ha forest fragment located in the municipality of Ixhuatán, Veracruz, Mexico (18°2′22.99″N, 94°21′27.61″W, 20–60 m asl). The fragment is located inside a private protected area (*Área de Protección y Desarrollo de Ceratozamia*) established in 2015 by the Braskem Idesa Company as a Management Unit for Wildlife Conservation (Retes López *et al.* 2010). The climate in the study area is warm and humid with a mean annual temperature of 27°C and an annual rainfall of 1800 mm. The driest months of the year (less than 200 mm of rainfall/month) are between January and May, while the rains are concentrated from June to December (more than 500 mm of rainfall in September). About 50% of the fragment consists of grasslands with some isolated trees and the other 50% is composed of a remnant of secondary lowland tropical rainforest, with some representative species: *Bursera simaruba* (L.) Sarg. (Burseraceae), *Cecropia obtusifolia* Bertol. (Urticaceae), *Coccoloba hondurensis* Lundell (Polygonaceae), *Cupania dentata* Moc. & Sessé ex DC. (Sapindaceae), *Guazuma ulmifolia* Lam. (Malvaceae), *Miconia argentea* (Sw.) DC. (Melastomataceae) (Ortiz-Lozada *et al.* 2017).

Ant sampling

We selected 10 trees separated by 339.9 m on average (SD: 161.4 m, min: 94.0 m and max: 767.9 m) which we considered the tallest (height around 20 m) and safest to climb. To sample ants in the tree crowns (here called canopy), we used the 'single rope climbing technique' (Perry 1978). We also sampled ants on the ground around the trunk of each tree climbed (here called the ground level). Sampling in both strata was performed between 9 a.m.

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

and 4 p.m. in May 2016. To sample ants, we used tuna bait, honey bait and hand collection (Adams *et al.* 2017, Antoniazzi *et al.* 2020*b*, Yanoviak & Kaspari 2000), each deployed independently and simultaneously for each stratum. Bait was placed near the main fork at the highest point that could be safely reached in the canopy (10–15 m above the ground, depending on the tree height) and on the ground by each tree. Samples were collected after 60–90 min in individual plastic bags (Bestelmeyer *et al.* 2000). Hand collection was carried out in the canopy, on the trunk, and from branches as high and as far as the climber could safely reach, and at the level of ground vegetation, e.g. herbs and small shrubs, always close to the focal tree, in an area similar to that of the canopy survey to make comparisons possible. Hand collection was limited to 10 min for each stratum. All samples were stored in 70% ethanol and transported to the laboratory for sorting, mounting, and identification to the lowest taxonomic level possible. For genus identification, we used a genus guide (Baccaro *et al.* 2015) and for species identification we used the databases AntWeb (Fisher 2002), AntCat (Bolton 2012), Ants of Costa Rica (Longino 2007) and Mexico ants (Dáttilo *et al.* 2020). All material was deposited in the Entomological Collection (IEXA) of the Instituto de Ecología, A. C. (INECOL), Mexico.

Data analysis

To determine whether our sample effort was sufficient we constructed accumulation curves for the ant species with our number of samples (n = 10), i.e. trees combining all sample methods. For this, we used rarefaction and extrapolation curves, in which the number of samples was extrapolated to double the sample size as suggested by Chao *et al.* (2014). We implemented these methods using the package *iNEXT* (Hsieh *et al.* 2016) in R software (R Core Team 2017).

To test whether the ant species richness was different between strata we used Generalized Linear Mixed Models (GLMM; Bolker *et al.* 2009, Zuur *et al.* 2009), following the data exploration procedures proposed by Zuur *et al.* (2010). Specifically, we built the fixed-effect model structure using ant species richness as a function of the vertical strata (canopy and ground level). We used the tree as a random effect intercept (n = 10). All models followed a Poisson error distribution and logarithmic link function, frequently used for count data (O'Hara & Kotze 2010, Zuur & Ieno 2016). We analysed the residual distribution to verify the adequacy of the assumed error distribution.

To visualize the overlap of species composition between vertical strata we used non-metric multidimensional scaling (NMDS) plotted on a two-dimensional graph. For this, we used a data matrix of presence/absence data and the Jaccard dissimilarity index. Then, we tested if ant species composition differed between the ground and canopy strata using Permutation Multivariate Analysis of Variance (PERMANOVA). Since our sample design was nested (i.e. 'two vertical strata' within 'tree individuals'), we considered the tree individual as a block factor to ensure that randomizations were made only within trees and not among all trees combined. Then, we estimated significance based on 9999 permutations within each tree individual to account for the differences in species composition among all tree individuals. For this, we used the argument *strata* in the *adonis* function of the vegan R package (Oksanen *et al.* 2018).

To test whether species composition changed more between vertical strata or over horizontal distance, we evaluated the contribution of diversity at different spatial scales. Then, we used additive partitioning of diversity ($\gamma = \alpha + \beta1 + \beta2$), where γ is total species richness, α is species diversity of each sampling point (a given vertical stratum of a tree), $\beta1$ is β-diversity between vertical strata within a tree, and $\beta2$ is β-diversity among trees within the forest fragment (Lande 1996, Veech *et al.* 2010), as used by several studies, for instance, to investigate habitat-level patterns (Dáttilo *et al.* 2019, Devries *et al.* 1997). We tested the statistical significance of the observed β-diversity values relative to the expected values using a null model that fixes each of the diversity components (i.e. α, $\beta1$, $\beta2$), with 999 randomizations (Crist *et al.* 2003). In this case, the null hypothesis is that the mean observed diversity is equal to that expected by the null model, and this should occur if the distribution of diversity is spatially homogeneous. On the other hand, if the mean observed diversity is greater than expected by the null model, this could be the result of strong variation within one of the diversity components (i.e. α, $\beta1$, $\beta2$). Moreover, to understand the processes that regulate the spatial variation in ant diversity, we separated the β-diversity of the whole community into two components: (i) nestedness (species gain/loss) and (ii) turnover (species change). In addition, we deconstructed β-diversity into these two components, the Sørensen (β_{SOR}) and Simpson (β_{SIM}) indexes (Baselga 2010, 2012). β_{SOR} is a measure of the total β-diversity and includes species composition variation, in terms of both nestedness and turnover. β_{SIM} does not depend on species richness variation and only measures turnover. Thus, the percentage of β-diversity contributed by nestedness alone (β_{NES}) can be calculated using the difference between index values: $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$ (Baselga 2010, 2012). Finally, we tested whether β-diversity increases with the geographic distance between sampling points (i.e. distance–decay relationship) using the β_{SOR} of the canopy, ground level, and both strata together. For this, we performed a Mantel test (Smouse *et al.* 1986) using the Jaccard dissimilarity index as a function of the linear distance (in metres) between individual trees in the canopy, at ground level, and in both strata together. In calculating and representing the Mantel significance graphically, we employed linear models using the Euclidean distances between sampling points and species composition dissimilarity ('Jaccard'). All analyses were performed using R software (R Core Team 2017) with the *vegan* (Oksanen *et al.* 2018), *lme4* (Bates *et al.* 2015), and *betapart* (Baselga & Orme 2012) packages.

Results

We recorded 43 ant species belonging to 17 genera and five subfamilies (Table 1). The subfamily Myrmicinae had the highest species richness (41%, 18 ant species), followed by Pseudomyrmecinae (18%, eight species), Dolichoderinae (16%, seven species), Formicinae (14%, six species), and Ponerinae (11%, five species; Table 1). Rarefaction analysis showed that the sample coverage estimate was similar in the canopy (76.9%) and at ground-level (78.5%) since the 95% confidence intervals overlapped (Figure S1). Ant species richness was lower in the canopy (mean ± SD: 1.7 ± 2.1) than at ground level (3.3 ± 2.9; $\chi^2 = 15.9$; df = 1; $P < 0.001$; Figure 1). Moreover, we found that ant species composition differed between the canopy and ground level (PERMANOVA: $F = 3.1$, df = 1, $P < 0.001$; Figure 2).

Additive partitioning of the total ant diversity showed that local ant species (α-diversity) accounted for 15.4% of the total species richness (γ), β-diversity between strata ($\beta1$) accounted for 11.5%, and the β-diversity among the sample points ($\beta2$) accounted for 73% (Figure 3). The observed β diversity between

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

Table 1. Occurrences of ground and canopy ant species in a lowland tropical forest fragment on the coast of the Gulf of Mexico

Subfamily	Species	Canopy	Ground
Dolichoderinae			
	Azteca alfari Emery, 1893	3	0
	Azteca forelii Emery, 1893	6	1
	Azteca nigra Forel, 1912	0	2
	Dolichoderus bispinosus (Olivier, 1792)	2	10
	Dolichoderus lutosus (Olivier, 1792)	1	0
	Linepithema sp1	0	2
Formicinae			
	Camponotus brettesi Forel, 1899	6	1
	Camponotus linnaei Forel, 1886	1	1
	Camponotus mucronatus Emery, 1890	1	2
	Camponotus novogranadensis Mayr, 1870	3	4
	Camponotus planatus Roger, 1863	0	3
	Nylanderia sp1	0	3
Myrmicinae			
	Carebara sp1	0	1
	Cephalotes basalis (Smith, 1876)	1	0
	Cephalotes minutus (Fabricius, 1804)	0	2
	Cephalotes scutulatus (Smith, 1867)	2	2
	Cephalotes umbraculatus (Fabricius, 1804)	2	1
	Crematogaster curvispinosa Mayr, 1862	1	1
	Crematogaster torosa Mayr, 1870	1	0
	Nesomyrmex pleuriticus (Kempf, 1959)	0	1
	Pheidole absurda Forel, 1886	1	1
	Pheidole flavens Roger, 1863	0	9
	Pheidole punctatissima Mayr, 1870	0	1
	Pheidole simonsi Wilson, 2003	0	1
	Pheidole susannae Forel, 1886	0	4
	Pheidole sp1	0	1
	Solenopsis geminata (Fabricius, 1804)	0	8
	Solenopsis sp1	0	1
	Trachymyrmex intermedius (Forel, 1909)	0	2
	Wasmannia rochai Forel, 1912	9	4
Ponerinae			
	Neoponera carinulata (Roger, 1861)	1	1
	Neoponera unidentata (Mayr, 1862)	0	2
	Neoponera villosa (Fabricius, 1804)	1	0
	Odontomachus ruginodis Smith, 1937	0	1
	Pachycondyla harpax (Fabricius, 1804)	0	2
Pseudomyrmecinae			
	Pseudomyrmex boopis (Roger, 1863)	0	7
	Pseudomyrmex cubaensis (Forel, 1901)	1	0
	Pseudomyrmex elongatulus (Dalla Torre, 1892)	2	5
	Pseudomyrmex elongatus (Mayr, 1870)	2	3
	Pseudomyrmex gracilis (Fabricius, 1804)	2	3
	Pseudomyrmex oculatus (Smith, 1855)	1	1
	Pseudomyrmex salvini (Forel, 1899)	0	3
	Pseudomyrmex subater (Wheeler & Mann, 1914)	2	2

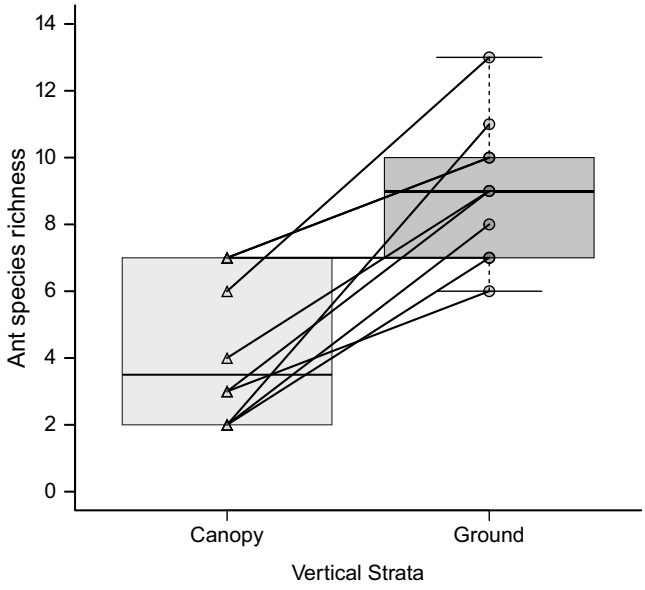


Figure 1. Ant species richness in the canopy (left) and at ground level (right) in trees from a tropical rainforest fragment in Mexico. Lines show the same tree at different vertical strata.

vertical strata within trees ($\beta 1_{obs} = 11.5$) and among trees within the forest fragment ($\beta 2_{obs} = 73.0$) were not different from those expected by the null hypothesis (mean value from the 999 randomizations: $\beta 1_{exp} = 12.0$, $P = 0.54$; $\beta 2_{exp} = 74.0$, $P = 0.23$). On the other hand, the contribution made by local ant species ($\alpha_{obs} = 15.5$) was greater than that expected by the null model simulations ($\alpha_{exp} = 14.1$, $P = 0.001$; Figure 3). Species turnover was the main contributor to β-diversity (93.5%), while nestedness contributed 6.5%. We found a positive relationship between total β-diversity and geographic distance when the ant assemblages of both strata were combined (Mantel test: $r = 0.37$, $P = 0.02$; Figure 4A; Table 2) and when ground-layer assemblages were analysed alone (Mantel test: $r = 0.29$, $P = 0.05$; Figure 4C; Table 2).

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

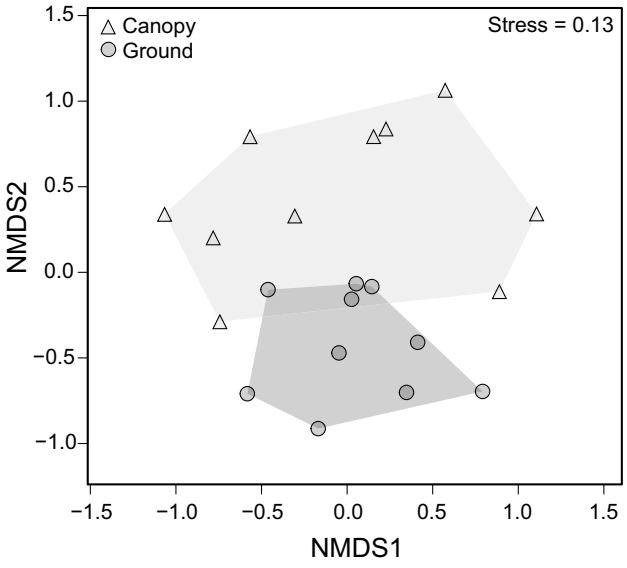


Figure 2. Non-metric multidimensional scaling plot of species composition divided by stratum (canopy = light grey, ground-level = dark grey) in a tropical rainforest fragment on the coast of the Gulf of Mexico.

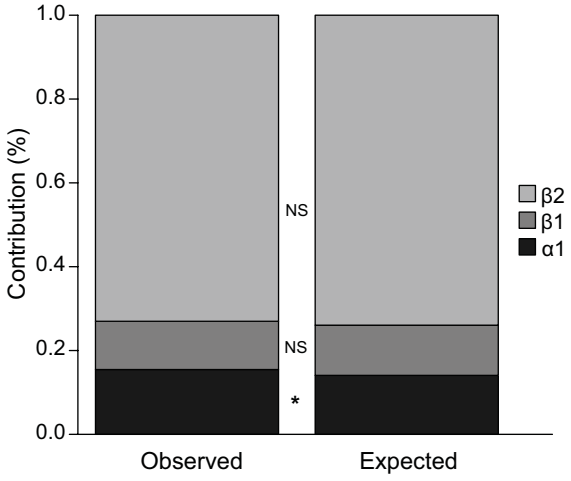


Figure 3. Observed and expected contribution (%) of alpha (α_1; local species), β_1 (β-diversity between canopy and ground level), and β_2 (β-diversity between trees considering both ground and canopy strata) of a tropical rainforest fragment on the coast of the Gulf of Mexico. 'NS' refers to non-significant and asterisk to significant differences ($P < 0.05$) between observed and expected values, given by 999 simulations using null models.

However, we found no relationship between β-diversity and geographic distance when considering the canopy assemblages alone (Mantel test: $P = 0.46$; Figure 4B; Table 2).

Discussion

We found that although ant species richness and composition differed between canopy and ground level, there was greater β-diversity between individual trees than between vertical strata. Moreover, we also showed a clear distance–decay relationship between individual trees, i.e. with canopy and ground-layer combined. However, analysing ant assemblages of each stratum separately, we only found a distance–decay relationship for ground ant

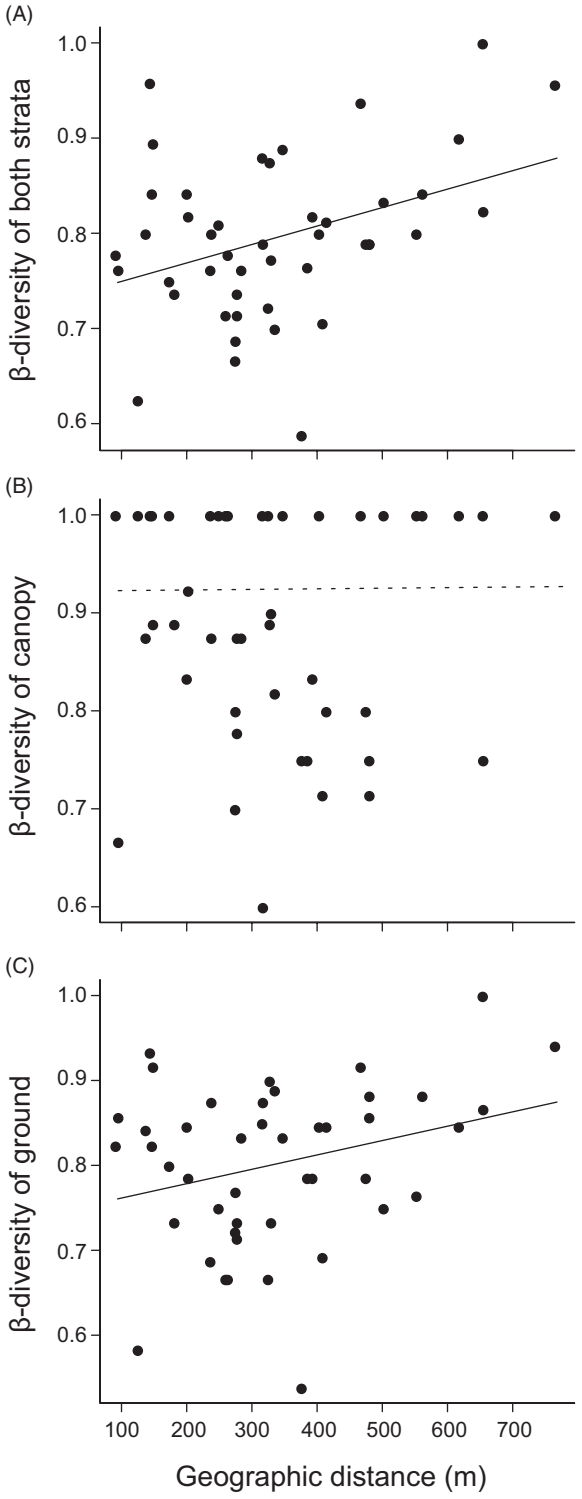


Figure 4. Mantel test regression of β-diversity (Jaccard dissimilarity) with geographic distance among sampling points for (A) both strata combined, (B) canopy and (C) ground level, in a tropical rainforest fragment on the coast of the Gulf of Mexico. For model statistics, see Table 2.

assemblages. Our results make clear that different rules determine the organization of ant assemblies in each stratum, probably as a result of the conditions that these habitats impose and, consequently, of the limitations to the dispersal capacity of the species that occupy them (Soininen *et al.* 2007). Importantly, a potential

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

Table 2. Linear model and Mantel test statistics presented in Figure 4 for sampling scale comparisons (both vertical strata together, only canopy, and only ground-layer) of dissimilarity between samples (Jaccard index) against geographic distance among samples. Values with asterisks denote $P < 0.05$

Sampling scale	SS†	%	*F*	df	P	r_{mantel}	P_{mantel}
Both strata	0.04	15.7	6.7	1	0.01*	0.37	0.02*
Canopy	0	0	0	1	0.95	0.01	0.48
Ground-layer	0.03	0.09	3.8	1	0.05*	0.29	0.05*

†SS refers to the sum of squares of each model.

limitation of our findings could be the low number of trees sampled, which could reduce the inference of our results. However, we observed 76.9% and 78.5% of estimated sampling coverage for canopy and ground level, respectively (Figure S1). A previous study involving local inventories of the Lepidoptera from an isolated Pacific island has reviewed under-sampling and the measurement of β-diversity (Beck *et al.* 2013) and found that biases were low when sample coverage was ~80% using the Jaccard index, as used in this study. Moreover, in the β-diversity analyses we performed 90 comparisons between all possible pairs for each stratum (Figure 4), and employed the same sampling effort and method in each vertical stratum. Therefore, despite the apparently low number of trees sampled, for the first time our study enables us to show empirically a distance–decay relationship in ant assemblages separately for canopy and ground strata. Nonetheless, a better understanding of how insects are distributed in tropical forests would benefit from greater sampling coverage (Basset *et al.* 2015). In particular, future studies should evaluate in detail the distance–decay relationship at different spatial and temporal scales. In addition to improving the sampling effort, investigating other insect taxa with different dispersal abilities and life histories in different environments should broaden the debate started here.

We found fewer ant species per tree than other arboreal ant surveys that also used hand collecting and baiting sampling methods (Adams *et al.* 2017, Yanoviak *et al.* 2007). However, in such studies ants were surveyed for a longer period than in our study (a minimum of 2 h over 1–3 days) and in a primary rain forest (Yanoviak *et al.* 2007). Here, we sampled for 10 min at each sampling site and our sampling sites were in a secondary rainforest, and these are known to host fewer species than primary forests (Klimes *et al.* 2012). Related to vertical strata, we found fewer ant species in the canopy than in the forest floor, as reported in previous studies in tropical systems (Neves *et al.* 2013, Schmidt *et al.* 2013). Sampling bias is considered to be one of the main issues that must be taken into account when making comparisons among biological communities in general (Gotelli *et al.* 2011). Using intense and diverse sampling methods in distinct tropical rainforests, Brühl *et al.* (1998) and Wilkie *et al.* (2010) found similar ant species richness between canopy and ground level, while other studies have found that the ground level has greater richness than higher strata (Longino & Nadkarni 1990, Vasconcelos & Vilhena 2006), as we found here. While many studies use different sampling methods in each vertical stratum, here we have used the same (complementary) sampling methods in both strata — namely, hand collecting, tuna bait, and honey bait (Adams *et al.* 2017, Antoniazzi *et al.* 2020*b*, Yanoviak & Kaspari 2000). We are therefore confident that our richness data were collected in a way that makes them comparable between strata.

Climate, habitat and resources are markedly different between the canopy and the ground level (Madigosky 2004), and ants that occupy these habitats endure these conditions and use these resources differentially (Yanoviak & Kaspari 2000). While at ground level microhabitat conditions and nutrient availability are the main determinants of the ant community (McGlynn & Kirksey 2000), in the canopy nest availability, tree height and surrounding conditions promote changes in ant diversity (Antoniazzi *et al.* 2019, Campos *et al.* 2006, Friedrich & Philpott 2009, Klimes *et al.* 2012). In this study, although some of the ant species we collected on the ground are known to nest strictly in the canopy (e.g. most *Camponotus* spp. and *Pseudomyrmex* spp., all *Cephalotes* spp., and *Neoponera carinulata*), we found a distinct species composition in each vertical stratum (Figure 2). These findings are consistent with a broad pattern in the literature dealing with the vertical stratification of ants (Antoniazzi *et al.* 2020*a*, Arruda *et al.* 2015, Brühl *et al.* 1998, Hashimoto *et al.* 2006, Vasconcelos & Vilhena 2006, Wilkie *et al.* 2010). Typical ant species in each vertical stratum must respond to distinctive abiotic conditions and resources for feeding and nesting (Folgarait 1998, Klimes 2017). For instance, arboreal ants are often associated with carbohydrate sources that are provided by plant structures or insects, e.g. extrafloral nectaries and sap-sucking trophobiont insects (Del-Claro *et al.* 2016), while at ground level ants have more nitrogen sources in the form of available prey (Yanoviak & Kaspari 2000). Therefore, ants' use of multiple available microhabitats and resources in tropical rainforests supports their high diversity (Cloudsley-Thompson 2003, Ellwood & Foster 2004, Sarty *et al.* 2006, Tobin 1995).

We found that most of the changes in ant species occurred horizontally, among individual trees, rather than between vertical strata, highlighting the great variation of ant assemblages in a tropical environment, even at a very small scale (Theunis *et al.* 2005). This was an especially interesting result given the small spatial scale of our sample (the maximum horizontal distance between trees was around 700 m). Moreover, since β-diversity between vertical strata (β1) and between trees (β2) was not significantly different from the expected value, ant assemblages are subsamples of the same species pool. However, the differences observed between the local ant species (α-diversity) and those expected by the null model suggest structural differences in the ant community between trees (Figure 3). Part of this variation may be explained by host tree species, a factor influencing associated ant species composition (Dejean *et al.* 2019, Klimes 2017). Other factors that may influence ant species composition, e.g. tree development stage (Antoniazzi *et al.* 2019, Dejean *et al.* 2008), were comparable among the trees we sampled, but other axes of variation may exist, caused by factors such as epiphytes or tree-bark structure. Future studies should incorporate these tree characteristics as much as possible, because they may have a significant influence on small-scale turnover. Indeed, we found that turnover (93.5%) was the main component of β-diversity when considering the whole community.

Despite the differences in ant species composition and richness between the canopy and ground level and contrary to what we had expected, we found lower β-diversity between vertical strata (β2) than over horizontal dimension (β1). Several factors can have led to the lower vertical stratification we found, such as the successional stage of the forest, the ant foraging patterns, and seasonality (i.e. dry vs. wet season). Secondary forests have lower structural complexity than primary forest, which may result in a lack of clear vertical stratification (Brokaw & Lent 1999, Pinotti *et al.* 2012). Previous studies have shown that some species are able to traverse the vertical axis, from ground to canopy, particularly in secondary forests (Antoniazzi *et al.* 2019, Marques *et al.* 2017). Indeed,

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

secondary forests often benefit generalist species, since these species may be more thermotolerant, allowing them to move between ground and canopy strata, e.g. some *Pseudomyrmex* species (Spicer *et al.* 2017), agreeing with our results. Further, seasonality is an important factor that affects the vertical stratification of animals, as shown by previous studies with amphibians (Basham & Scheffers 2020) and spiders (Quijano Cuervo *et al.* 2019), in which vertical stratification declined in the dry season. Here, we sampled in the dry season, and future sampling in the wet season may provide additional insight into seasonal variation in vertical stratification.

In addition to the higher β-diversity of ant assemblages among trees than between vertical strata when we combined both strata, we also found a positive correlation between β-diversity and geographic distance, known as the distance–decay relationship. However, when we analysed this relationship within each stratum, the classic distance–decay relationship only occurred at ground level. The dissimilarity of ant species composition in the canopy was uniformly high ($\beta > 0.6$) and not related to geographic distance. This uniformity may be due to the ability of ants to traverse the canopy using lianas and other structures that facilitate movement (Adams *et al.* 2019), with many canopy species forming large territories spread across multiple trees (Dejean *et al.* 2007). Thus, canopy ants tend to exhibit higher territoriality (Adams 2016) while at ground level the territories of ground ants often overlap in space and time (Morrison 1996), possibly due to the greater heterogeneity of microhabitats and conditions on the forest floor (McGlynn 2006, Soares & Schoereder 2001).

Overall, we found a strong pattern of vertical stratification, since species composition and richness changed significantly across vertical strata and species richness was higher at the ground level. We would caution against sampling for ants in only one stratum to avoid under-sampling the total community, since our results show that the distance–decay relationship was not consistent between canopy and ground level assemblages, exhibiting a classic distance–decay relationship for the ground assemblage but not the canopy assemblage. The patterns we observed here describe the inverse of the trend seen in Basham *et al.* (2018), where canopy dwelling amphibians showed high turnover in horizontal space, but ground amphibians showed no turnover. Thus, this study illustrates how taxa may differ in their patterns of spatial distribution, making it difficult to generalize patterns of horizontal and vertical trends without further taxon-specific studies.

Acknowledgements. We are grateful to Lynna Kiere, Tatiana Joaqui, and Daniel González Tokman for helpful discussion and comments on previous versions of the manuscript. We also thank Erick Corro, Diana Ahuatzin, Brenda Rattoni, Felipe Aoki and João Penna for ideas and comments in the early stages of this study and Braskem Idesa for the support provided to carry out this study in the Ceratozamia Area of Protection and Development, and especially Roberto Velasco (Industrial Director), Antonio Santos Souza Galvão (Sustainability), Ana Luisa Martínez López and Ana Paulina Deméneghi Calatayud (Environment). We are also grateful to José Alberto Toto Hernández for support in the field. We would like to thank two anonymous reviewers for their valuable suggestions and comments that significantly improved the manuscript. We also thank CONACYT, which provided support for RA's PhD studies (CONACYT scholarship, CVU 771787), and Biodiversity Research Consortium Brazil-Norway (Hydro-Alunorte) for ABVJr. postdoctoral scholarship.

Financial support. RA was supported by CONACYT PhD scholarship CVU 771787.

Supplementary materials. For supplementary material for this article, please visit https://doi.org/10.1017/S0266467420000188

Literature cited

Adams ES (2016) Territoriality in ants (Hymenoptera: Formicidae): a review. *Myrmecological News* **23**, 101–118.

Adams BJ, Schnitzer SA and Yanoviak SP (2017) Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. *Ecography* **40**, 1067–1075.

Adams BJ, Schnitzer SA and Yanoviak SP (2019) Connectivity explains local ant community structure in a Neotropical forest canopy: a large-scale experimental approach. *Ecology* **100**, 1–11.

Antoniazzi R, Garro RNS, Dáttilo W, Ribeiro SP and Neves FS (2019) Ant species richness and interactions in canopies of two distinct successional stages in a tropical dry forest. *The Science of Nature* **106**, 20.

Antoniazzi R, García-Franco J, Janda M, Leponce M and Dáttilo W (2020a) Diurnal foraging ant–tree co-occurrence networks are similar between canopy and understorey in a Neotropical rain forest. *Biotropica* **52**, 717–729.

Antoniazzi R, Ahuatzin D, Pelayo-Martínez J, Ortiz-Lozada L, Leponce M and Dáttilo W (2020b) On the effectiveness of hand collection to complement baits when studying ant vertical stratification in tropical rainforests. *Sociobiology* **67**, 213–222.

Arruda FV, Pesquero MA, Marcelino DG, Leite GA, Delabie JHC and Fagundes R (2015) Size and condition of bamboo as structural factors behind the vertical stratification of the bamboo-nesting ant community. *Insectes Sociaux* **63**, 99–107.

Baccaro FB, Feitosa RM, Fernandez F, Fernandes IO, Izzo TJ, Souza JLP and Solar R (2015) *Guia para os gêneros de formigas do Brasil*. Manaus: Editora INPA, 388 pp.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**, 1223–1232.

Baselga A and Orme CDL (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**, 808–812.

Basham EW and Scheffers BR (2020) Vertical stratification collapses under seasonal shifts in climate. *Journal of Biogeography* **47**, 1888–1898.

Basham EW, Seidl CM, Andriamahohatra LR, Oliveira BF, Scheffers BR, Seidl CM and Scheffers BR (2018) Distance–decay differs among vertical strata in a tropical rainforest. *Journal of Animal Ecology* **88**, 114–124.

Basset Y, Hammond PM, Barrios H, Holloway JD and Miller SE (2003) Vertical stratification of arthropod assemblages. In Basset Y, Novotny V, Miller SE and Kitching RL (eds), *Arthropods of Tropical Forests*. Cambridge: Cambridge University Press, pp. 17–27.

Basset Y, Cizek L, Cuénoud P, Didham RK, Novotny V, Ødegaard F, Roslin T, Tishechkin AK, Schmidl J, Winchester NN, Roubik DW, Aberlenc HP *et al.* (2015) Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. *PLoS ONE* **10**, 1–22.

Bates D, Mächler M, Bolker B and Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.

Beck J, Holloway JD and Schwanghart W (2013) Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution* **4**, 370–382.

Benson WW (1985) Amazon ant–plants. In Prance GT and Lovejoy TE (eds), *Amazonia*. Oxford: Pergamon Press, pp. 239–266.

Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL, Delabie JHC and Silvestre R (2000) Field techniques for the study of ground-dwelling ant: an overview, description, and evaluation. In Agosti D, Majer J, Alonso LE and Schultz TR (eds), *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Washington, DC: Smithsonian Institution Press, pp. 122–144.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH and White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**, 127–135.

Bolton B (2012) AntCat: An online catalog of the ants of the world. http://antcat.org.

Brokaw NVL and Lent RA (1999) Vertical structure. In Hunter ML (ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge: Cambridge University Press, pp. 373–399.

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

Brown N (1993) The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology* **9**, 153–168.

Brühl CA, Gunsalam G and Linsenmair KE (1998) Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology* **14**, 285–297.

Campos RI, Vasconcelos HL, Ribeiro SP, Neves FS and Soares JP (2006) Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography* **29**, 442–450.

Carson W and Schnitzer S (2011) *Tropical Forest Community Ecology*. Chichester: John Wiley & Sons.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK and Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* **84**, 45–67.

Cloudsley-Thompson JL (2003) Microclimates and the distribution of terrestrial arthropods. *Annual Review of Entomology* **7**, 199–222.

Crist TO, Veech JA, Gering JC and Summerville KS (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *American Naturalist* **162**, 734–743.

Dáttilo W, Vizentin-Bugoni J, Debastiani VJ, Jordano P and Izzo TJ (2019) The influence of spatial sampling scales on ant-plant interaction network architecture. *Journal of Animal Ecology* **88**, 903–914.

Dáttilo W, Vásquez-Bolaños M, Ahuatzin DA, Antoniazzi R, Chávez-González E, Corro E, Luna P, Guevara R, Villalobos F, Madrigal-Chavero R, Falcão JCFF, Bonilla-Ramírez A *et al.* (2020) Mexico ants: incidence and abundance along the Nearctic–Neotropical interface. *Ecology* **101**, e02944.

Davidson DW (1998) Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology* **23**, 484–490.

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

Dejean A, Djiéto-Lordon C, Céréghino R and Leponce M (2008) Ontogenetic succession and the ant mosaic: an empirical approach using pioneer trees. *Basic and Applied Ecology* **9**, 316–323.

Dejean A, Compin A, Delabie JHC, Azémar F, Corbara B and Leponce M (2019) Biotic and abiotic determinants of the formation of ant mosaics in primary Neotropical rainforests. *Ecological Entomology* **44**, 560–570.

Del-Claro K, Rico-Gray V, Torezan-Silingardi HM, Alves-Silva E, Fagundes R, Lange D, Dáttilo W, Vilela AA, Aguirre A and Rodriguez-Morales D (2016) Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies. *Insectes Sociaux* **63**, 207–221.

Devries PJ, Murray D and Lande R (1997) Species diversity in vertical, horizontal, and temporal dimensions of a hit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* **62**, 343–364.

Eguchi K, Bui TV and Yamane S (2004) A preliminary study on foraging distance and nesting sites of ants in Indo-Chinese lowland vegetation (Insecta, Hymenoptera, Formicidae). *Sociobiology* **43**, 445–457.

Ellwood MDF and Foster WA (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* **429**, 549–551.

Fetcher N, Oberbauer SF and Strain BR (1985) Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology* **29**, 145–155.

Fisher BL (2002) Antweb. http://www.antweb.org.

Fittkau EJ and Klinge H (1973) On biomass and trophic structure of the Central Amazonian rain forest ecosystem. *Biotropica* **5**, 2–14.

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

Friedrich R and Philpott SM (2009) Nest-site limitation and nesting resources of ants (Hymenoptera: Formicidae) in urban green spaces. *Environmental Entomology* **38**, 600–607.

Gotelli NJ, Ellison AM, Dunn RR and Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecological News* **15**, 13–19.

Gregorin R, Bernard E, Lobão KW, Oliveira LF, Machado FS, Gil BB and Tavares VC (2017) Vertical stratification in bat assemblages of the Atlantic Forest of south-eastern Brazil. *Journal of Tropical Ecology* **33**, 299–308.

Hanisch PE, Suarez AV, Tubaro PL and Paris CI (2018) Co-occurrence patterns in a subtropical ant community revealed by complementary sampling methodologies. *Environmental Entomology* **47**, 1402–1412.

Hashimoto Y, Morimoto Y, Widodo ES and Mohamed M (2006) Vertical distribution pattern of ants in a Bornean tropical rainforest (Hymenoptera: Formicidae). *Sociobiology* **47**, 697–710.

Hirao T, Murakami M and Kashizaki A (2009) Importance of the understory stratum to entomofaunal diversity in a temperate deciduous forest. *Ecological Research* **24**, 263–272.

Hsieh TC, Ma KH and Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456.

Klimes P (2017) Diversity and specificity of ant–plant interactions in canopy communities: Insights from primary and secondary tropical forests in New Guinea. In Oliveira PS and Koptur S (eds), *Ant–plant Interactions: Impacts of Humans on Terrestrial Ecosystems*. Cambridge: Cambridge University Press, pp. 26–51.

Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD and Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? *Journal of Animal Ecology* **81**, 1103–1112.

Kost C, DeOliveira EG, Knoch TA and Wirth R (2005) Spatio-temporal permanence and plasticity of foraging trails in young and mature leaf-cutting ant colonies (*Atta* spp.). *Journal of Tropical Ecology* **21**, 677–688.

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**, 5–13.

Lang AC, Härdtle W, Bruelheide H, Kröber W, Schröter M, von Wehrden, H and von Oheimb G (2012) Horizontal, but not vertical canopy structure is related to stand functional diversity in a subtropical slope forest. *Ecological Research* **27**, 181–189.

Longino JT (2007) Ants of Costa Rica. Online Publication: http://ants.biology.utah.edu/AntsofCostaRica.html.

Longino JT and Nadkarni NM (1990) A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche* **97**, 81–93.

Luque GM and Reyes-López J (2007) Effect of experimental small-scale spatial heterogeneity on resource use of a Mediterranean ground-ant community. *Acta Oecologica* **32**, 42–49.

Madigosky SR (2004) Tropical microclimatic considerations. In Lowman MD and Rinker HB (eds), *Forest Canopies*. 2nd edition. San Diego, CA: Academic Press, pp. 24–48.

Marques T, Espiríto-Santo MM, Neves FS, Schoereder JH, Espírito-Santo MM, Neves FS and Schoereder JH (2017) Ant assemblage structure in a secondary tropical dry forest: the role of ecological succession and seasonality. *Sociobiology* **64**, 261–275.

McGlynn TP (2006) Ants on the move: Resource limitation of a litter-nesting ant community in Costa Rica. *Biotropica* **38**, 419–427.

McGlynn TP and Kirksey SE (2000) The effects of food presentation and microhabitat upon resource monopoly in a ground-foraging ant (Hymenoptera: Formicidae) community. *Revista de Biología Tropical* **48**, 1–16.

Morrison LW (1996) Community organization in a recently assembled fauna: the case of Polynesian ants. *Oecologia* **107**, 243–256.

Nekola JC and White PS (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**, 867–878.

Neves FS, Queiroz-Dantas KS, DaRocha WD and Delabie JHC (2013) Ants of three adjacent habitats of a transition region between the Cerrado and Caatinga biomes: the effects of heterogeneity and variation in canopy cover. *Neotropical Entomology* **42**, 258–268.

O'Hara RB and Kotze DJ (2010) Do not log-transform count data. *Methods in Ecology and Evolution* **1**, 118–122.

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ and Suggests MASS (2018) vegan: community ecology package. R package version 1.17–4. https://cran.r-project.org/package=vegan.

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press

Oliveira BF and Scheffers BR (2019) Vertical stratification influences global patterns of biodiversity. *Ecography* **42**, 249–249.

Ortiz-Lozada L, Pelayo-Martínez J, Mota-Vargas C, Demeneghi-Calatayud AP and Sosa VJ (2017) Absence of large and presence of medium-sized mammal species of conservation concern in a privately protected area of rain forest in southeastern Mexico. *Tropical Conservation Science* **10**, 11–13.

Parker GG (1995) Structure and microclimate of forest canopies. In Lowman M and Nadkarni N (eds), *Forest Canopies*. San Diego, CA: Academic Press, pp. 73–106.

Perry DR (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica* **10**, 155–157.

Pinotti BT, Pagotto CP and Pardini R (2012) Habitat structure and food resources for wildlife across successional stages in a tropical forest. *Forest Ecology and Management* **283**, 119–127.

Popma J, Bongers F and Meave-Del-Castillo J (1988) Patterns in the vertical structure of the tropical lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74**, 81–91.

Power ME (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**, 733–746.

Quijano-Cuervo LG, Rangel-Acosta J, Martínez-Hernández N and Sabogal-Gonzalez A (2019) Estratificación vertical de arañas tejedoras (Araneae) en fragmentos de bosque seco tropical del Caribe colombiano. *Revista de Biología Tropical* **67**, 224–242.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org.

Retes-López R, Cuevas-González MI, Moreno-Medina S, Denogean-Ballesteros FG, Ibarra-Flores F and Martín-Rivera M (2010) Unidad de manejo para la conservación de la vida silvestre como alternativa para los 'nuevos agronegócios'. *Revista Mexicana de Agronegocios* **27**, 336–346.

Sarty M, Abbott KL and Lester PJ (2006) Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia* **149**, 465–473.

Schmidt FA, Ribas CR and Schoereder JH (2013) How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. *Ecological Indicators* **24**, 158–166.

Schnitzer SA and Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**, 913–919.

Schnitzer SA, Bongers F, Burnham RJ and Putz FE (2015) *Ecology of Lianas*. Chichester: John Wiley & Sons.

Shaw DC (2004) Vertical organization of canopy biota. In Lowman MD and Rinker HB (eds), *Forest Canopies*. 2nd edition. San Diego, CA: Academic Press, pp. 73–101.

Smith AP (1973) Stratification of temperature and tropical forests. *American Naturalist* **107**, 671–683.

Smouse PE, Long JC and Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* **35**, 627–632.

Soares SM and Schoereder JH (2001) Ant-nest distribution in a remnant of tropical rainforest. *Insectes Sociaux* **48**, 280–286.

Soininen J, McDonald R and Hillebrand H (2007) The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

Spicer ME, Stark AY, Adams BJ, Kneale R, Kaspari M and Yanoviak SP (2017) Thermal constraints on foraging of tropical canopy ants. *Oecologia* **183**, 1007–1017.

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

Tavella J, Alvarez-Pringles AP and Cagnolo L (2018) Determinants of ant species spatial distribution in habitats from central Argentina. *Community Ecology* **19**, 300–310.

Theunis L, Gilbert M, Roisin Y and Leponce M (2005) Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. *Insectes Sociaux* **52**, 366–377.

Tobin J (1995) Ecology and diversity of tropical forest canopy ants. In Lowman MD and Nadkarni NM (eds), *Forest Canopies*. San Diego, CA: Academic Press, pp. 129–147.

Turner IM and Corlett RT (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution* **11**, 330–333.

Vasconcelos HL and Vilhena JMS (2006) Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. *Biotropica* **38**, 100–106.

Veech JA, Summerville KS, Crist TO and Gering JC (2010) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* **99**, 3–9.

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 279–338.

Wilkie KTR, Mertl AL and Traniello JFA (2010) Species diversity and distribution patterns of the ants of Amazonian Ecuador. *PLoS ONE* **5**, e13146.

Yanoviak SP and Kaspari M (2000) Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos* **89**, 259–266.

Yanoviak SP, Fisher BL and Alonso A (2007) Arboreal ant diversity (Hymenoptera: Formicidae) in a central African forest. *African Journal of Ecology* **46**, 60–66.

Zuur AF and Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution* **7**, 636–645.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA and Smith GM (eds) (2009) Zero-truncated and zero-inflated models for count data. In *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer, pp. 261–293.

Zuur AF, Ieno EN and Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3–14.

https://doi.org/10.1017/S0266467420000188 Published online by Cambridge University Press