GfÖ
GfÖ Ecological Society of Germany,
Austria and Switzerland
Basic and Applied Ecology 56 (2021) 32–44

Basic and
Applied Ecology
www.elsevier.com/locate/baae

Spatial and functional structure of an entire ant assemblage in a lowland Panamanian rainforest

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Received 12 September 2020; accepted 13 June 2021
Available online 19 June 2021

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https://doi.org/10.1016/j.baae.2021.06.007
1439-1791/

Abstract

Ants are a major ecological group in tropical rainforests. Few studies in the Neotropics have documented the distribution of ants from the ground to the canopy, and none have included the understorey. A previous analysis of an intensive arthropod study in Panama, involving 11 sampling methods, showed that the factors influencing ant β diversity (i.e., changes in assemblage composition) were, in decreasing order of importance, the vertical (height), temporal (season), and horizontal (geographic distance) dimensions. In the present study, we went one step further and aimed (1) to identify the best sampling methods to study the entire ant assemblage across the three strata, (2) to test if all strata show a similar horizontal β diversity and (3) to analyze the functional structure of the entire ant assemblage. We identified 405 ant species from 11 subfamilies and 68 genera. Slightly more species were sampled in the canopy than on the ground; they belonged to distinct sub-assemblages. The understorey fauna was mainly a mixture of species found in the other two strata. The horizontal β diversity between sites was similar for the three strata. About half of the ant species foraged in two (29%) or three (25%) strata. A single method, aerial flight interception traps placed alongside tree trunks, acting as arboreal pitfall traps, collected half of the species and reflected the vertical stratification. Using the functional traits approach, we observed that generalist species with mid-sized colonies were by far the most numerous (31%), followed by ground- or litter-dwelling species, either specialists (20%), or generalists (16%), and arboreal species, either generalists (19%) or territorially dominant (8%), and finally army ants (5%). Our results reinforce the idea that a proper understanding of the functioning of ant assemblages requires the inclusion of arboreal ants in survey programs.

Keywords: Horizontal β diversity; Vertical stratification; Ant diversity; Canopy; Ant sampling methods; Colony size; Feeding habits; Functional groups; Nesting mode

Introduction

The hot and humid climate of most intertropical areas promotes ecosystem productivity and so the formation of species-rich tropical rainforests characterized by large trees (30-50 m in height) and structured into three main strata (i.e., the canopy, understorey and ground) fostering a high plant diversity, including lianas and epiphytes (Morley, 2002; Nieder et al., 2001; Tymen et al., 2017; Wright, 2002). The canopy is exposed to high insolation and large differences in temperature and humidity between day and night, whereas at ground level climatic conditions are more stable, cooler and wetter (Parker, 1995). This environmental heterogeneity induces a vertically stratified distribution of organisms adapted to local environmental conditions (Shaw. 2004). Stratification in rainforests has been observed in a wide range of organisms, including vertebrates and invertebrates, and is responsible for spatial change in species composition (i.e., vertical β diversity) (Basham et al.. 2019; Basset et al., 2003). Horizontal β diversity is also generalized and, for arthropods at least, is lower than vertical β diversity in continuous vegetation types such as lowland tropical forests (Novotny et al., 2007; Basset et al., 2015). However, what is less well demonstrated is whether horizontal β diversity is similar in the three forest strata. Differences could be generated by differences in habitat continuity, as the ground is continuous while the strata above the ground are discontinuous, which may limit species dispersal (Shaw, 2004). This hypothesis is likely for amphibian assemblages, where a classic distance-decay (decrease in compositional similarity with geographic distance) was observed in the canopy and understorey, but not at ground level, indicating different rates of β diversity between strata (Basham et al., 2019). Alternatively, tolerance to microclimatic changes might also differ, with ground-dwelling species living in a more stable environment than species above ground (Madigosky, 2004). In contrast, when studying ants, Antoniazzi et al., 2021, found only a distance-decay relationship at ground but not at canopy level. This result may have been affected by the sampling method, baits and visual searching, which only capture a fraction of the ant assemblage, especially dominant species with large colonies which differ in their biology and ecology between the ground and the canopy (Dejean, Corbara, Orivel, & Leponce, 2007).

Ants are one of the dominant animal groups in rainforests because of their colony size. Some species have very large colonies (i.e., several thousands to several million individuals) such as, at ground level, leaf-cutting ants which are major defoliators, army ants which are major predators, and at canopy level, territorially dominant arboreal ants (territories distributed in a mosaic pattern) that protect their host trees from defoliators (Brady, Fisher, Schultz, & Ward, 2014; Dejean et al., 2007; Hölldobler & Wilson, 1994, 2011; Majer, 1993). The development of large populations is made possible by the availability of energy-rich resources derived from plants. Most ant species are partly herbivorous (primary consumers) feeding on extrafloral nectar, food bodies, pollen, sap and leaves through fungiculture; they are also ‘cryptic herbivores’ feeding on hemipteran honeydew (Davidson et al., 2003; Rico-Gray & Oliveira, 2007; Tobin, 1994). Most of these ants are generalists as they also scavenge dead animals and feces and capture different kinds of prey. Finally, some species are predators, either generalists or specialists (Cerdá & Dejean, 2011; Hölldobler & Wilson, 1994).

Few studies in the Neotropics have documented ant distribution from the ground to the canopy. Using a single method, baiting 20 trees from the base to the canopy, Yanoviak and Kaspari (2000) recorded 48 ant species. Ryder Wilkie, Mertl, and Traniello (2010) obtained 489 ant species in Ecuador with six methods (i.e., subterranean probes, pitfall traps, hand collecting, Winkler devices, baiting and canopy fogging). Longino and Colwell (2020) noted 539 species with seven methods (i.e., Malaise, light traps, Berlese, Winkler, baiting, hand collecting and fogging). Finally, Antoniazzi et al. (2021) using baits and hand collection in the canopy and at ground level found 43 species on 10 trees. Unfortunately, none of the studies included the understorey stratum, often dominated by palms in the Neotropics (Popma, Bongers, & Meave, 1988).

A previous analysis of an intensive arthropod study in Panama, involving 11 sampling methods, showed that species turnover for arthropods, including ants, was driven primarily by vertical and seasonal variation, and less by horizontal variation (Basset et al., 2015). We analyze here this dataset in further detail to determine three approaches related to studying ants. (1) The complementarity and the pertinence of the methods for studying the entire ant assemblage, including the understorey species. (2) The validity of the null hypothesis that all three strata show similar horizontal species turnover based on the best method for studying the ant assemblages in multiple strata. We predicted the following. (a) The turnover will be higher in the arboreal strata (canopy and understorey), representing islands of habitats (Adams et al., 2017), than at ground level, a continuous habitat (Theunis et al., 2005). (b) The local site conditions, whether abiotic or biotic, likely influence local ant species composition (i.e., the non-random distribution of species diversity within-sites will be lower than between sites, or distance-decay). (3) The functional structure of the entire forest ant assemblage based on our survey and on a thorough review of the literature on the biology and ecology of each species. Our prediction is that key ant groups, with large populations, will differ according to the strata considered.

Materials and methods

Study sites

This study was conducted in Panama during the IBISCA-Panama project in the 6,000 ha evergreen seasonal mixed rainforest in the San Lorenzo Protected Area which has been free of major disturbance for the past 200 years (9°16’N, 79°58’W; 130 m a.s.l.). The climate is moist tropical, with a mean annual rainfall of 3,139 mm, and the daily mean temperature is 26 °C (see STRI, 2017 for details). Ants were collected from 11 study sites that were representative of the forest environment of the area, each measuring 40×40 m and centered around a 20×20 m botanical plot (Basset et al., 2012, 2015). The present study was conducted over a total surface area of ≈1.76 ha and the sites were distributed from 24 to 1941 m apart (median: 700 m). Field permits were granted by the Autoridad Nacional del Ambiente of Panama.

Ant sampling methods

During the IBISCA-Panama project four surveys were conducted spanning the dry and the wet seasons (September 2003 - November 2004) (Basset et al., 2012, 2015). Because the San Lorenzo rainforest remains humid and experiences almost no loss of canopy cover during the January-April dry season, the ground-level fauna is not thought to suffer much from drought stress (see Roisin et al., 2006 for termites).

A combination of 11 sampling methods, resulting in an exceptionally large dataset, was used (Table 1; Fig.S1). (1) Berlese funnel. Three trees per site were sampled. For each tree, 16 soil cores of 15 cm^3 were gathered at ground level (n=8) and at the bases of main branches (n=8) and placed in Berlese funnels for 2 days. (2) Winkler. This sampling was conducted on 51 quadrats of 1 m^2 distributed at intervals of 5 m around each 20×20 m plot. The leaf-litter present within each quadrat was sifted and extracted during 48 hours by a Winkler extractor. (3) Pitfall traps. At each study site 15 pitfall traps (424 ml) were buried in a line at 1.3 m intervals. They contained a solution of ethanol, salt and detergent and were examined after 3 days. (4) Aerial composite flight interception traps (aFIT). Each trap consisted of two vertical perspex sheets (60×23 cm) above a collecting funnel; a preserving jar was suspended from canopy branches by sturdy nylon ropes. The funnel functioned as a large arboreal pitfall collecting many ant workers and a few winged sexuals. Six to seven traps were placed in each of five sites at different heights (0, 1.3, 7, 14, 21, 28 m and in some cases 35 m). Because baiting experiments showed that canopy ants are generally present from 7 m above the ground (Leponce et al., 2019, Leponce, Dejean, Mottl, & Klimes, 2021), we considered that the traps installed above this height intercepted ants from the canopy, whereas those placed 1.3 m above the ground rather intercepted ants from the understorey and those placed at 0 m rather permitted ground-dwelling ants to be captured. Left in place for 1 year, these traps were sampled every 10 days yielding 1659 samples from the three forest strata. (5) Understorey Flight Interception Traps (uFIT). Each uFIT consisted of a fine mesh screen (3×1 m that was left at each study site during three consecutive 2-day-long periods). (6) Beating. Ants were dislodged by beating the foliage (three strong strokes using a stick) and collected on a square beating sheet measuring 0.4 m^2. Beating was conducted in the canopy and the understorey at seven sites during the first survey and two sites during the second, third and fourth surveys (10 canopy and 10 understorey samples per site). A total of 560 beating samples were collected. (7) Palm tree inspection. Small Geonoma congesta H. Wendl. ex Spruce (Arecaceae) dominated

Table 1. Sampling effort used to collect ants in the three strata of the San Lorenzo rainforest with the number of samples for each method, the number of samples containing ants (also expressed as a percentage), the number of ant species collected, the number of species occurrences, the number of sites where these methods were used, the number of seasonal replicates, and the total number of trapping days. Abbreviations: aFIT: aerial composite Flight Interception Trap installed every 7 meters along the tree trunk (plus one at 1.3m above ground); uFIT: understorey Flight Interception Trap.

Habitat strata	Method	No. samples	Samples with ants	%	No. of ant species	Occurrences	No. Sites	Replicates	Trapping days
Ground	Berlese funnels	264	151	57.19	72	367	8	2	264
	Winkler	561	543	96.79	150	2197	8	2	561
	Pitfall traps	225	86	38.22	71	244	8	4	900
	aFIT @ 0m	285	147	51.58	147	597	5	6	3,067
Understorey	aFIT @ 1.3m	279	86	30.82	70	176	5	6	3001
	uFIT	170	82	48.24	97	254	8	2	410
	Beating	280	77	27.5	35	137	8	4	280
	Light traps	48	16	33.33	15	24	8	4	54
	Palm tree inspection	391	284	72.63	62	404	5	1	391
	Malaise traps	63	60	95.24	119	504	8	3	645
Canopy	Berlese funnels	264	111	42.05	53	226	8	2	264
	aFIT @ $\geq$7m	1,095	302	27.58	146	579	5	6	11,835
	Beating	280	74	26.43	50	124	8	4	280
	Light traps	48	13	27.08	17	29	8	4	54
	Climbers	174	152	87.36	87	398	5	1	838
	Fogging	120	117	97.5	141	1014	8	3	120
	Total	4,547	2,301	/	405	7274	/	/	22,964

the understorey. The clustering of their leaf petioles gathers litter, favoring the installation of ant nests (crown base at ≈1.5 m in height). During the first survey, 391 palm trees were monitored at three sites and the ants sheltered therein were collected using aspirators. (8) Light traps. At each study site, three traps were installed in the understorey 2 m above the ground and three others in the canopy at a height of 25-35 m. Replicated one night during four seasonal periods they resulted in a total of 96 samples. (9) Malaise traps. A Malaise trap (2×1 m) was operated during 10 days at eight sites during the first survey and occasionally during the three other surveys yielding a total of 63 samples. (10) Climbers (branch-clipping). During the first survey, climbers cut off two to four branches (diameter >10 cm) from the crown of 174 canopy trees situated in the vicinity of seven plots. Just after the branches had fallen to the ground, the ants crawling on them or hiding in parts of nests were collected using aspirators and forceps. Note that this method is particularly useful for capturing territorially dominant arboreal ants (Dejean et al., 2018, 2019). (11) Fogging. A knockdown insecticide (natural pyrethrum quickly broken down by UV rays) was sprayed up into the tree crowns. Stunned arthropods fell onto six collecting sheets (5×4 m). This method was used during the three surveys on 120 of the 174 previously mentioned trees.

Ant identification and voucher conservation

The ants were identified by comparing them with the collection kept at the Myrmecology Laboratory, Cocoa Research Center, in Ilhéus, Bahia, Brazil and by consulting specialized literature. Bolton's catalogue nomenclature was used (Bolton, 2019). Representative samples ("vouchers") of each species were deposited in this collection and at the Royal Belgian Institute of Natural Sciences (RBINS). This study focused on ant workers, but winged sexuals were identified when possible to increase taxonomic coverage but were excluded from the analyses on the stratification of ant assemblages.

Complementarity of each sampling method and its pertinence for studying the entire ant assemblage

To estimate the rate of species accumulation by each method (all strata pooled) or by strata (all methods pooled), species rarefaction curves were plotted on the species occurrences data matrices using the Mao Tau algorithm in EstimateS 9.1.0 software (Colwell, 2016) with 100 randomizations of the sampling order without replacement. Methods were grouped based on their compositional similarity according to the UPGMA algorithm with the Bray-Curtis similarity index available in the PAST 3.26 software.

Vertical stratification of the local ant assemblage

To show differences and overlaps in species composition and richness between the three strata, we used proportional

Venn diagrams in which the area of each shape is proportional to the number of species it includes.

Horizontal β diversity within strata

To measure how species composition changed horizontally, we performed an additive partition of the species richness of each horizontal stratum (Barton et al., 2013, Veech et al., 2002): $\gamma = \alpha + \beta$ where γ is the total species richness, α the average species richness within sites and β the average difference in species richness between sites. This analysis was based on datasets from the three most efficient multi-strata sampling methods: aFITs (three strata), Berlese (two strata) and beating (two strata). We used the software PARTITION3 (Veech, & Crist, 2009) to compare the observed diversity value to a corresponding null distribution (individual-based randomization method, 1000 randomizations). The mean observed richness is equal to the expected richness if the distribution of richness is spatially homogeneous. This allows us to test the significance of the observed value as either a significantly high or low value. In addition, we followed the approach developed by Baselga (2010) to separate β diversity into its turnover (species change) and nestedness (species gain/loss) components. The total compositional variation between assemblages was calculated using the Jaccard pairwise dissimilarity index. For each combination of strata and method, pairwise β diversity measures were calculated using the "betapart" package (Baselga, & Orme, 2012) in R software (R core Team, 2015).

Functional traits of the ant species distributed across strata

Based on previous studies of the nesting and feeding preferences of Neotropical rainforest ant species and the results obtained here on the distribution of morphospecies throughout the three forest strata (Appendix A1), we defined nominal categories for three functional traits (sensu largo, see Wong, Guénard, & Lewis, 2019): (1) size of the colony (five categories: <300 individuals; 300-1,000; 1,000-10,000; 10,000-100,000; and >100,000); (2) nesting habits (seven categories: bivouac; subterranean; leaf-litter; plant-ants associated with myrmecophytes; arboreal nesting in hollow twigs; arboreal nesting in tree cavities; and arboreal building carton or silk nests); and (3) feeding habits (six categories: consumers of plant nectar or food bodies; honeydew feeders; fungus-growing leaf-cutters and debris collectors; scavengers; generalist predators; specialized predators), the whole resulting in 18 categories of functional traits.

We added the nesting strata (i.e., ground and litter, understorey and canopy) as three more traits obtaining a matrix of [405 ant species x 21 categories of traits]. The scores corresponding to the functional traits ranged from "0", indicating "no affinity" for a given trait category, to "3", indicating "high affinity". Information on the traits was structured using a Fuzzy-Coding technique (Chevenet, Dolédec, & Chessel, 1994). A Fuzzy Correspondence Analysis (FCA) was conducted on this [ant species x traits] matrix. We determined the optimal number of clusters (low variance within clusters and high variance between clusters) based on the majority rule after computing 23 clustering indices (Euclidean distance; K-means clustering method). To ease interpretation, bar plots were used to show the distribution of the samples from the different forest strata within clusters. These analyses were conducted with the ADE4, NbClust and ggplot2 packages in R software (R Development Core Team, 2015).

Results

Complementarity of each sampling method and its pertinence for studying the entire ant assemblage

The combination of methods allowed us to record 405 ant species (11 subfamilies and 68 genera) in the ≈1.76 ha of rainforest surveyed (Table 1, Appendix A1). The rarefaction curve for the 11 sampling methods used indicates a near asymptote (Fig. 1A) as ≈81% of the estimated local species richness was recorded (Chao2 = 498, CI95% 459-564). The curves corresponding to the different methods used accumulated species at different rates, those for aerial and understorey FITs being similar, whereas palm trees accumulated the fewest species and light traps attracted only a few winged sexuals (Fig. 1B).

A cluster analysis showed that the methods fell into four groups according to the ant species collected (Fig. 2). The first group consists of soil and leaf-litter samples from the ground or the canopy collected with Berlese funnels and Winkler devices. The second group consists of understorey or canopy samples collected with Malaise traps, beating, fogging and by climbers. The third group consists of samples from all three strata obtained with aerial and understorey flight interception traps (aFITs and uFITs), pitfall traps and through palm tree inspection. Finally, the fourth group consists of light traps, less effective than the other methods.

The 10 most species-rich genera make up 50.9% of the occurrences of the 405 species recorded, whereas 11 ant species out of 405 account for more than one quarter of the occurrences (exactly 25.3% of 7,274 occurrences; Appendix A1). We collected few winged sexuals (100 occurrences) for 48 species of which eight were the sole sample of their species (Appendix A1).

Vertical stratification of the local ant assemblage

Winged sexuals were excluded from this analysis resulting in 397 ant species studied here. Ant species composition showed a moderate vertical stratification.

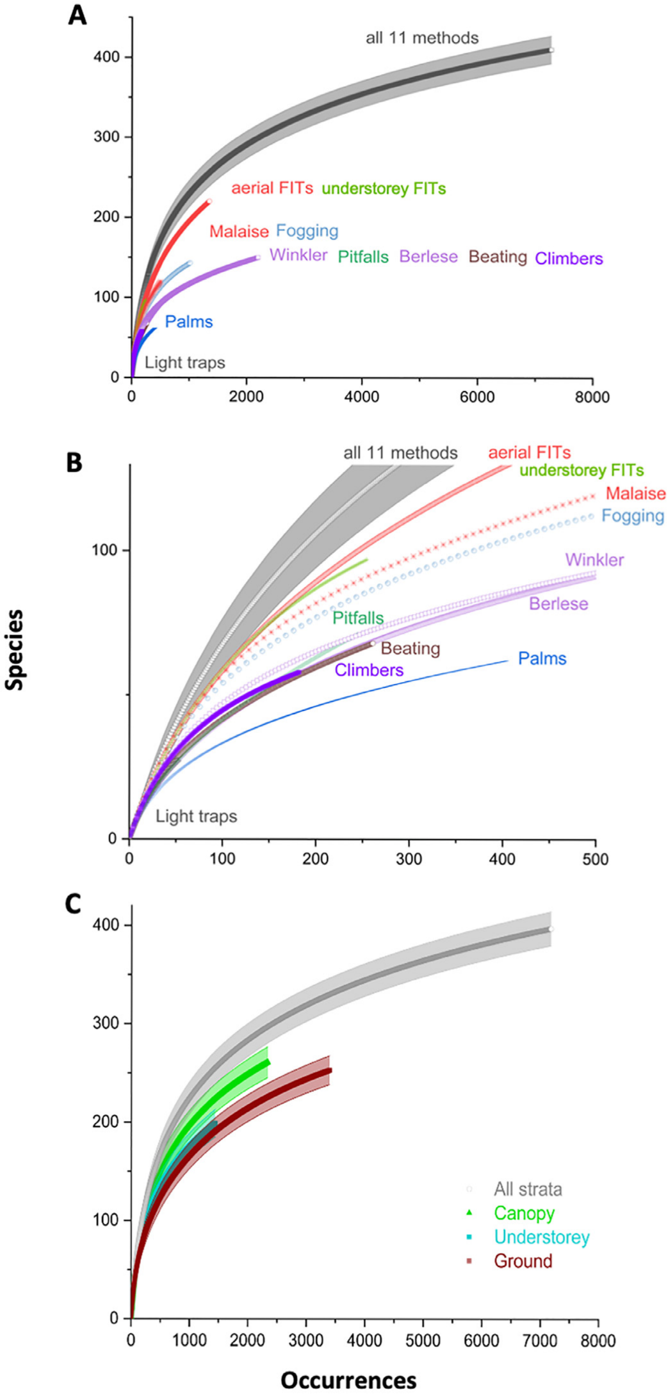

Fig. 1. Sample-based rarefaction curves for the 11 sampling methods used in the San Lorenzo protected area (405 ant species and 4,547 samples). (A) Global view, all strata combined; (B) Close-up; (C) Individual-based rarefaction (all methods pooled, winged sexuals excluded; 397 species) showing the number of species found in each stratum.

Globally, a total of 253 species out of 397 were recorded on the ground, 199 in the understorey and 261 in the canopy. The slightly higher presence of ants in the canopy compared to the ground and understorey was confirmed by rarefaction (standardized richness for 1000 occurrences; ground: 176±13 species; understorey: 166±13; and canopy: 198±14) (Fig. 1C). However, 87 species (22%) were sampled exclusively on the ground, 23 in the understorey (6%), and 72 (18%) in the canopy (Fig. 3A). Overall, this indicates that certain species can patrol in two or three strata, as confirmed by individual multi-strata collection methods

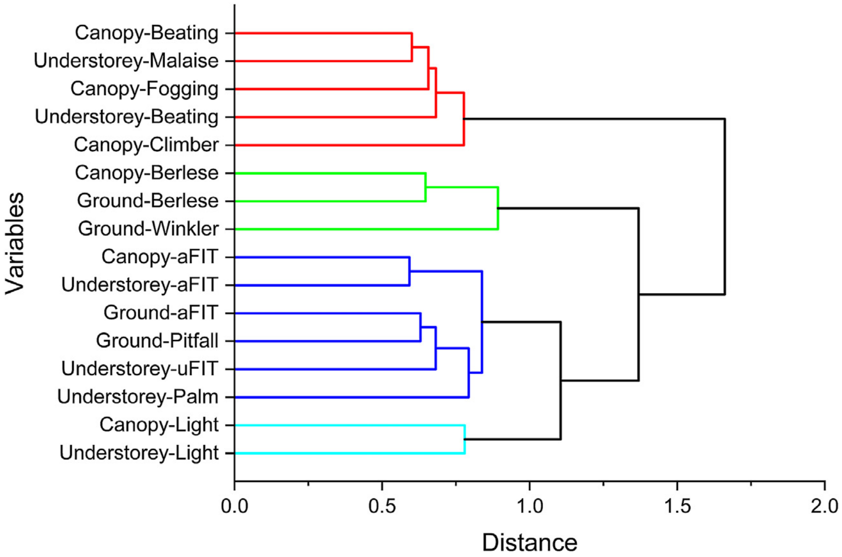

Fig. 2. Faunal similarity between the ant species captured using the different sampling methods for the three forest levels.

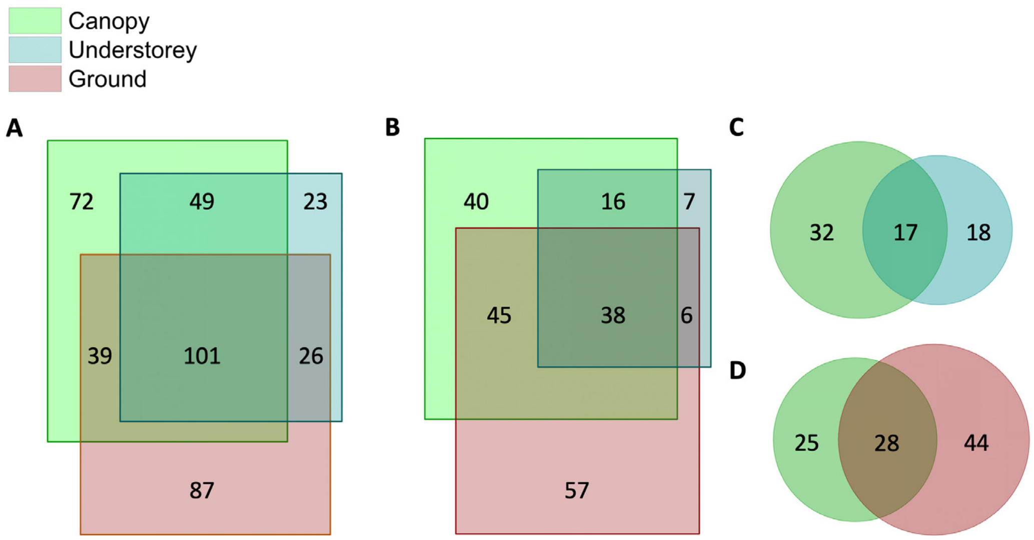

Fig. 3. Proportional Venn diagram of the number of species collected from the ground, understorey and canopy levels showing both differences and overlaps between the three strata (based on workers; winged sexuals excluded). (A) The combined 11 sampling methods resulted in 397 ant species being captured. (B) Aerial FITs, acting as pitfall traps, captured 209 species combined from the ground (traps at 0 m, with buried collector funnel), the understorey (traps suspended 1.3 m above the ground) and the canopy (traps at 7, 14, 21, 28, 35 m). (C) Beating enabled 67 species to be sampled. (D) Berlese funnels resulted in 97 species being captured. Values indicate the number of ant species in each category.

(Fig. 3B-D). Aerial FITs alone captured 53% of the species present and reflected species stratification (Fig. 3B). The ground stratum was dominated by the Myrmicinae, Ponerinae and Ectatomminae, while the canopy had a higher proportion of Formicinae, Dolichoderinae and Pseudomyrmicinae (Fig 4). An intermediate situation was found in the understorey.

Differences in horizontal β diversity between strata

Whatever the method considered, there was no significant difference between strata in horizontal β diversity between sites, (aFIT: F $_{(2,12)}$=0.39, P=0.69; Berlese: t=-0.84, P=0.41; beating: t=0.29, P=0.78) (Fig. 5). Furthermore, the observed β diversity between sites was significantly higher than

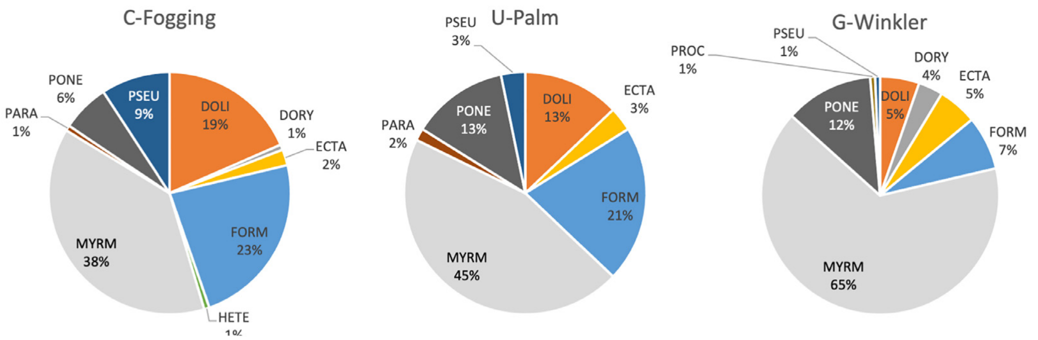

Fig. 4. Proportion of ant subfamilies observed in the three strata and by stratum-specific methods (Winkler, palm inspection, fogging, respectively). Subfamily abbreviations: DOLI: Dolichoderinae, DORY: Dorylinae, ECTA: Ectatomminae, FORM: Formicinae, HETE: Heteroponerinae, MYRM: Myrmicinae, PARA: Paraponerinae; PONE: Ponerinae; PROC: Proceratiinae; PSEU: Pseudomyrmecinae.

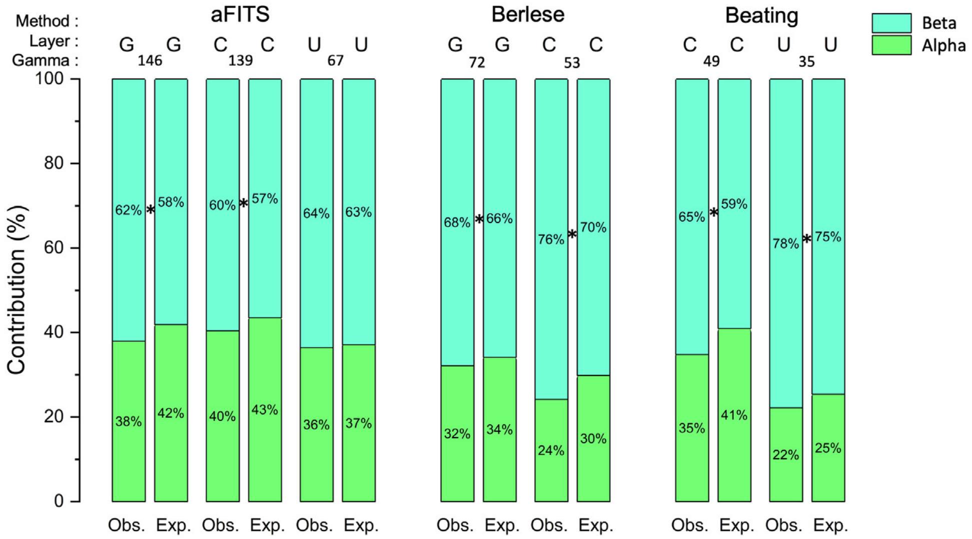

Fig. 5. Comparison of the horizontal species turnover within each stratum for species collected either with aFITs, Berlese or beating. Total (gamma) diversity for each stratum was decomposed into average alpha (local) diversity of 40×40m sites and the β diversity between sites. The observed and expected contribution of alpha and β diversity are provided. An asterisk (*) refers to significant differences between observed and expected values based on 1000 randomizations of the dataset.

expected with randomized datasets, except in the understorey for aFITs (Fig. 5), suggesting some site effect on horizontal species distribution. Species turnover was the main contributor to β diversity (88 ± 6%, n= 7) while nestedness contributed to 12 ± 6%.

Ant functional traits

The FCA analysis based on the functional traits of the 405 ant species clearly delimited six clusters (Fig. 6A). Cluster 1 groups together 83 ground- and litter-nesting species with specialized feeding habits (e.g., specialized predators and fungus-growers) and small colonies except for some fungus-growing species that have large to very large colonies. The 66 species in Cluster 2 are mostly ground and litter nesters with small to slightly larger colonies (i.e., up to 1,000 individuals) and generalist feeding habits (e.g., scavenging, predatory and feeding on sugary substances). Cluster 3 is comprised of 127 species most of which are ground and litter nesters (e.g., *Pheidole* spp.) but some are arboreal that nest in preformed cavities (e.g. *Procryptocerus* spp.; *Pseudomyrmex* spp.). Compared to the previous clusters they are generalist feeders that most frequently feed on sugary substances, whereas the size of the colonies can be relatively large (i.e., up to 10,000 individuals).

Comparatively, Cluster 4 groups together 77 arboreal species with mid-sized colonies that nest in preformed cavities in the trees. Generalist feeders, they mostly exploit sugary substances, particularly honeydew from the hemipterans they tend. By comparison, most of the 31 species in Cluster 5 are characterized by their ability to build carton or silk nests, many of them being territorially dominant arboreal ants with very large colonies. Exceptionally, *Wasmannia*

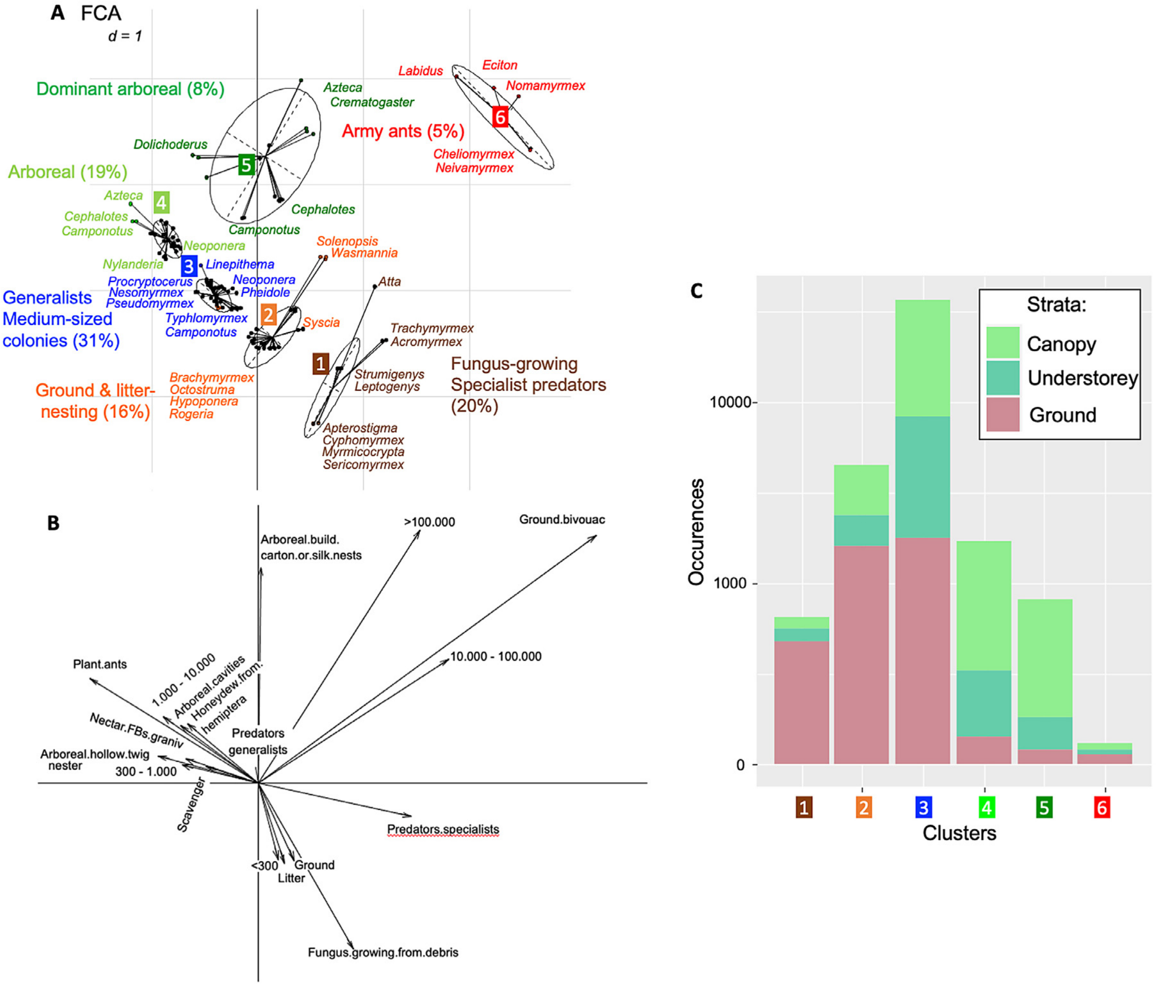

Fig. 6. Fuzzy Correspondence Analysis (FCA) of functional traits composition corresponding to the 405 ant species recorded in this study. (A) Ordination of the ant species on the two first axes of the FCA. The percentage of species in each cluster is indicated in brackets. (B) Ordination of the functional trait modalities on the two first axes of the FCA. (C) Distribution of the ants from the six clusters defined in Fig. 6A among the rainforest strata based on their occurrence in samples.

iheringi has small colonies. Finally, all 21 species in Cluster 6 are highly predatory army ants with very large colonies that nest in bivouacs.

The ant species in these six clusters were noted in all forest strata, but to different degrees as clusters 1, 2 and 3 dominated at ground level, cluster 3 in the understorey and clusters 3, 4 and 5 in the canopy (Fig. 6B).

Discussion

In this Panamanian lowland rainforest, the estimated species richness was between 459 and 564 species (CI 95%). This figure is lower than in Costa Rica and Amazonian Ecuador with 584-636 and 647-736 ant species, respectively (Longino & Colwell, 2020; Ryder Wilkie et al., 2010). We sampled slightly more ant species in the canopy than on the ground (261 vs. 253 species) and their species assemblages were distinct with 87 species observed only on the ground and 72 in the canopy. The understorey ant fauna was mostly a mixture of species from the other two strata, but 23 species were specific to this stratum.

The stratification shown in the San Lorenzo rainforest for various groups of arthropods (Bourguignon, Leponce, & Roisin, 2009; Roisin et al., 2006; Ribeiro, & Basset, 2007; Basset et al., 2015) was also noted for ants for which some species were sampled only in one stratum (Fig. 1C and Fig. 3), in accordance with Ryder Wilkie et al. (2010) and Longino and Colwell (2020).

This stratification results from the following distinct environmental conditions in the three strata. At ground level, fallen leaves, wood and different debris are decomposed by detritivores (Stahl et al., 2013). Their abundance spurs ant diversification through predation involving omnivorous and strictly predatory species (Cerda & Dejean, 2011; Hölldobler & Wilson, 1994; Appendix A1). The ground layer also included leaf-cutting, fungus-growing ants which are preyed upon by specialized army ants (i.e., *Nomamyrmex*; Appendix A1) and detritivorous fungus-growing species preyed upon by other ants (i.e., *Megalomyrmex* as a social parasite of Attina; Appendix A1). Also, certain ant species feed on the honeydew of hemipterans attended on the roots of trees (*Acropyga*; Appendix A1).

The understorey was previously neglected in studies dealing with tropical rainforest ants. This gap is filled by this study showing that 23 species were specific to this stratum, whereas the species richness is intermediate between that for the ground and that for the canopy (176 versus 166 and 198 ant species, respectively, Fig. 1C; Fig. 3). Small palm trees allow several ant species to nest in the litter between the clusters of their leaf petioles (Gibernau, Orivel, Delabie, Barabé, & Dejean, 2007), whereas the workers of several generalist ground- and canopy-nesting species also foraged on understorey plants (Table 1and Appendix A1).

In the canopy, the presence of populous territorially dominant arboreal ant colonies is possible via the presence of large numbers of attended honeydew-producing, sap-sucking hemipterans, whereas extrafloral nectar, rather produced by liana, is mostly exploited by non-dominant ants, the latter forming the core of the species richness in this stratum (Blüthgen et al., 2000; Blüthgen & Stork, 2007; Dejean et al., 2007). Food bodies in the canopy are mostly produced by myrmecophytic *Cecropia* and are the main, if not the only, food source for mutualistic plant-ants specifically associated with these trees such as *Azteca constructor* (Appendix A1).

Contrary to our predictions, which were based on the rationale that ground, understorey and canopy level assemblages were not subject to the same environmental variations because of differences in habitat continuity, we did not find any difference in horizontal β diversity between strata. This result contrasts with the findings of Antoniazzi et al. (2021) who observed that horizontal β diversity was different between the canopy and the ground in a Mexican lowland tropical rainforest. These authors collected ants on a limited number of trees during one-day sessions of baiting and hand collection. Thus, we cannot exclude that our results differ due to a different sampling approach (i.e., different spatio-temporal scale and sampling coverage) (Barton et al., 2013). Furthermore, we observed that the β diversity was greater than expected for a random spatial distribution of species (Veech, 2005). This suggests that general conditions at the local scale (40×40 m site) had a prevailing effect on horizontal species distribution, increasing differences in species composition between sites (Soininen et al., 2007). This could be due to local biotic or abiotic conditions affecting the overall ant species distribution across strata (Hortal et al., 2010; Kaspari et al., 2003; Klimes et al., 2012). Another possibility is that the geographical scale of the study is too small (i.e., sites too close to each other) to show difference in β diversity between strata. The β diversity was mainly driven by species turnover and much less by nestedness, indicating that assemblages at species-poor sites were not subsets of species-rich sites.

The six clusters corresponding to the ants' functional traits were composed of ant species collected from all three forest strata, but with some notable differences due to the interplay between their nesting and foraging activities, and their colony size (Fig. 6). Cluster 1 is characterized by specialist feeders including all fungus-growing ants of the New World subtribe Attina (subfamily Myrmicinae; tribe Attini) plus specialized predators (e.g., *Acanthognathus* and *Strumigenys* prey on collembollans; *Stegomyrmex*, *Discothyrea* and *Proceratium* on arthropod eggs; *Leptogenys* on diplopods; and *Thaumatomyrmex* on myriapoda of the order Polyxenida) that are ground or litter nesters with small colonies. Yet, some fungus-growing species have large to very large colonies (e.g., *Cyphomyrmex transversus*, *Trachymyrmex cornetzi*, *T. isthmicus* and the leaf-cutting species of the genera *Acromyrmex* and *Atta*) (see details in Appendix A1). Note that leaf-cutting ants are ecological engineers and the main Neotropical defoliator (Hölldobler & Wilson, 2011). Cluster 2 groups ground- and litter-nesting species not belonging to Cluster 1. The exceptions noted in the canopy are colonies nesting in suspended soil (e.g., *Hypoponera* sp.08) or *Solenopsis* from the subgenus *Diplorhoptrum* that are parasites of other ant species from which they steal brood (see Appendix A1), some of them nesting in the forest canopy.

Cluster 3 is species rich because it groups together all generalist ant species with mid-sized colonies, some of which are arboreal (Fig. 6). Cluster 4 corresponds to arboreal ants with medium-sized colonies (Fig. 6), The colonies of *Odontomachus* hastatus noted in this cluster nest in the litter accumulated in understorey palm trees or in association with hemi-epiphytes (Gibernau et al., 2007); other species nest in suspended soils in the canopy (e.g., Pheidole spp.), something facilitated by the presence of epiphytes (DaRocha et al., 2015, 2016, Longino, & Nadkarni, 1990).

Cluster 5 is composed of canopy-dwelling generalist feeders that build carton or silk nests (only *W. iheringi* has small colonies). Most are territorially dominant arboreal ants (e.g., genera *Azteca*, *Cephalotes* and *Crematogaster*) that protect their host trees from defoliators (Majer, 1993). Some workers were collected from the understorey and the ground as they were hunting or forming columns to move from one tree in their territory to another whose crowns were not in contact (Dejean et al., 2007, 2019).

Cluster 6 is composed of typical, nomadic army ants (Dorylinae) that organize raids from the soil to understorey plants, and certain of them (e.g., *Eciton hamatum*) even climb trees to hunt in their crowns, preying on the brood of social wasps and arboreal *Dolichoderus* and *Camponotus* colonies (Brady et al., 2014; Hölldobler & Wilson, 1994, 2011). Although less species-rich than the other clusters, with their large to very large colonies, army ants have a major impact on the rainforest ecosystem as they regulate other arthropods, including other ant taxa (McGlynn & Poirson, 2012). Note that among the subfamily Dorylinae, *Cylindromyrmex meinerti* and *Syscia augustae*, which prey on termites, have small colonies (de Andrade, 1998; Mackay and Mackay, 2002; Appendix 1), so that they belong to Cluster 2.

In conclusion, this study allowed us to link for the first time the diversity and distribution of ants and the functional ecology of the entire above-ground ant community in a lowland Neotropical forest. Generalist species with mid-sized colonies were the most frequent. Ground- or litter-dwelling species with a specialized diet were also species-rich, whereas this was not the case for the ecologically important territorial dominant arboreal ants, leaf-cutting ants and typical army ants. Half of the species foraged in more than one stratum. Slightly more species were present in the canopy than at ground level and an intermediate number of species was found in the understorey. At the scale of a site, local conditions appear to influence the horizontal distribution of species, but there does not seem to be a different horizontal species turnover between strata. Finer-scale studies are needed to determine in more detail which factors may be responsible for this pattern (Klimes et al., 2012). When used for a prolonged period of time, aerial flight interception traps, acting as pitfall traps, collected half of the species in the three forest layers and may be useful for programs monitoring the entire ant assemblage in future studies. By complementing them with subterranean pitfall traps, the hypogeous ant fauna might be even better documented (Wong & Guénard, 2017). Overall, this study emphasizes the importance of comprehensive, multi-strata surveys and thorough reviews of methods to better understand the functioning of ant assemblages in tropical rainforest environments.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

IBISCA-Panama is an initiative of Pro-Natura International, Océan Vert, the University Blaise Pascal, Clermont-Ferrand, France, the University of Panama, and the Smithsonian Tropical Research Institute (STRI). We thank N. Springate, R. Kitching, L. Fagan, F. Odegaard for their contribution to the collection of ant specimens. I. Bachy helped with the design of figures. We are grateful to J. Herrera, E. Andrade, M. Samaniego, S.J. Wright, N. Baiben, S. Bechet, J. Belleguic, T. Aubert, K. Jordan, G. Ebersolt, D. Cleyet-Marrel, L. Pyot, O. Pascal, P. Basset, and E. Bauhaus who helped with logistics in the field and to A. Yockey for proofreading the manuscript. We also wish to thank two reviewers for their useful suggestions and J. Veech for providing the PARTITION 3 software.

Funding

Core funding was provided by SolVin-Solvay SA, STRI, the United Nations Environment Program, the Smithsonian Institution (Walcott Fund), the European Science Foundation, and the Global Canopy Program. YB, a member of the Sistema Nacional de Investigación of the SENACYT in Panama together with HB and EM, acknowledges the help of the Smithsonian Tropical Research Institute and Maestría Centroamericana de Entomología, Universidad de Panamá, during the preparation of the IBISCA-Panama project. YB received financial support through a mobility grant Universidad de Panamá-RBINS, a Czech Science Foundation GAČR grant 20-31295S, the European Social Fund, the Czech Ministry of Education CZ.1.07/2.3.00/20.0064 and the U.S. National Science Foundation DEB-0841885. SPR and JHCD received financial support from the CNPq. JO received financial support from an ‘‘Investissement d’Avenir’’ grant managed by the French Agence Nationale de la Recherche (CEBA, ref. ANR-10- LABX-25-01). The funding institutions had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.06.007. The data that support the findings is openly available at doi:10.5281/zenodo.5018190.

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