

Environmental determinants of leaf litter ant community composition along an elevational gradient

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Abstract

Ant communities are extremely diverse and provide a wide variety of ecological functions in tropical forests. Here, we investigated the abiotic factors driving ant composition turnover across an elevational gradient at Mont Itoupé, French Guiana. Mont Itoupé is an isolated mountain whose top is covered by cloud forests, a biogeographical rarity that is likely to be threatened according to climate change scenarios in the region. We examined the influence of six soil, climatic, and LiDAR-derived vegetation structural variables on leaf litter ant assembly (267 species) across nine 0.12-ha plots disposed at three elevations (ca. 400, 600, and 800m asl). We tested (a) whether species cooccurring within a same plot or a same elevation were more similar in terms of taxonomic, functional, and phylogenetic composition, than species from different plots/elevations, and (b) which environmental variables significantly explained compositional turnover among plots. We found that the distribution of species and traits of ant communities along the elevational gradient was significantly explained by a turnover of environmental conditions, particularly in soil phosphorus and sand content, canopy height, and mean annual relative humidity of soil. Our results shed light on the role exerted by environmental filtering in shaping ant community assembly in tropical forests. Identifying the environmental determinants of ant species distribution along tropical elevational gradients could help predicting the future impacts of global warming on biodiversity organization in vulnerable environments such as cloud forests.

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KEYWORDS

ants, climate, elevation, environmental filtering, French Guiana, functional traits, soil composition

1 | INTRODUCTION

Determining how environmental factors drive biodiversity patterns is one of the fundamental goals in ecology. Predictable changes in diversity and composition of plant and animal communities are observed along broad elevational or latitudinal gradients (Hillebrand, 2004; McCain & Grytnes, 2010; Willig et al., 2003). Elevational gradients are particularly valuable to study biodiversity patterns, given that they often span sharp gradients in abiotic conditions even over small spatial scales (e.g., Hodkinson, 2005; Hoiss, Krauss, Potts, Roberts, & Steffan-Dewenter, 2012; Kraft et al., 2011). For instance, recurrent patterns observed with increasing elevation involve a continuous decrease of temperature (McCain & Grytnes, 2010) or an increase in soil moisture and organic carbon content (He, Hou, Liu, & Wen, 2016).

Niche models predict that environmental conditions select species with particular traits to establish and persist within an area (Keddy, 1992). The effect of environmental filtering may be studied by comparing observed functional or phylogenetic diversity of communities with those expected under nulls models generated by drawing species at random from a regional species pool (e.g., Gotelli, 2000). At local to landscape scales, homogeneous environmental conditions should generate assemblages of species that are functionally and phylogenetically (if traits are conserved) more similar than expected by chance (i.e., functional/phylogenetic clustering, respectively). Several studies examining biodiversity patterns along elevational gradients reported a functional or phylogenetic overdispersion of species in lowland assemblages, shifting to a functional or phylogenetic clustering of species in highland assemblages (Dehling et al., 2014; Graham, Parra, Rahbek, & Mcguire, 2009; Machac, Janda, Dunn, & Sanders, 2011). These results can be interpreted as the effect of increasing strength of environmental filtering on shaping communities (Purschke et al., 2013), which may be caused by the reduction of temperatures with increasing elevation.

Here, we aim to measure the variations in ant community composition and to determine the environmental factors that shape these variations along a Neotropical altitudinal gradient. Ants (Hymenoptera: Formicidae) represent an ideal model for studying the determinants of species distribution and coexistence because they are abundant and ecologically dominant in terrestrial ecosystems (Hölldobler & Wilson, 1990), and they perform a wide variety of ecological functions such as predation, scavenging, and seed dispersal (Del Toro, Ribbons, & Pelini, 2012; Folgarait, 1998). Furthermore, previous studies have shown that ant community composition can change markedly along environmental gradients (e.g., Arnan, Cerdá, & Retana, 2014; Bihn, Gebauer, & Brandl, 2010; Bishop, Robertson, van Rensburg, & Parr, 2015; Fontanilla et al., 2019; Groc et al., 2014; Silva

& Brandão, 2014; Smith et al., 2014; Yates et al., 2011). Nevertheless, few studies have investigated changes in ant community composition along elevational gradients in tropical regions (Brühl, Mohamed, & Linsenmair, 1999; Dunn et al., 2009; Nowrouzi et al., 2016; Smith et al., 2014). Elevational gradients deserve a special attention because they are characterized by a sharp change of various abiotic conditions, especially temperature and humidity, which are predicted to shape ant species distribution. For instance, Nowrouzi et al. (2016) have emphasized marked species turnovers between 600 and 800m, which in their study site corresponded to a transition between lowland and cloud forests. Considering the rise of the cloud layers that is predicted by climate change scenarios and associated increases in temperature and decreases in relative humidity (Helmer et al., 2019; Los et al., 2019), it is urgent to characterize species distributions in these environments to assess threats to their persistence.

To address this gap, we assess how taxonomic, functional, and phylogenetic composition of Neotropical ant assemblages is shaped by different environmental parameters along an elevational gradient. We focused on leaf litter ants because they are easily sampled with a standardized and generalizable collection protocol, and their taxonomy has been well described in the region (Fichaux et al., 2019; Groc et al., 2009). We collected leaf litter ants at Mont Itoupé (French Guiana), a mountain which represents a particular biogeographic interest, because of its isolation and its relatively high elevation (ca. 800m) in the eastern Guiana Shield. The top of the mountain is covered by cloud forests, a biogeographic rarity that is likely to be threatened according to scenarios of climate change in this region. Climatic parameters, such as temperature and humidity, may represent major drivers of ant species distributions (e.g., Arnan, Cerdá, & Retana, 2015; Dunn et al., 2009; Sanders et al., 2007; Silva & Brandão, 2014). Variation in habitat characteristics such as nutrient availability, vegetation cover, and soil texture may also play an important role (Blatrix et al., 2016; Chen, Adams, Bergeron, Sabo, & Hooper-Büi, 2015; Schmidt et al., 2016; Vasconcelos et al., 2003).

We sampled along these gradients to address two main objectives. First, we assessed whether ant community structure differed from a random distribution of species along the elevational gradient. A stronger effect of environmental filtering is generally observed at highest elevations, leading to a clustered assemblage structure (Dehling et al., 2014; Graham et al., 2009; Machac et al., 2011; Smith et al., 2014). Thus, we expected to observe clustered patterns among the leaf litter assemblages at Mont Itoupé, as a result of the effects of the environmental filtering particularly at high altitude. Second, we identified the main environmental determinants (soil, climate, and vegetation structure as measured by LiDAR) of the taxonomic, functional, and phylogenetic composition of ant assemblages. A decrease in ant diversity along elevational gradients is a common pattern (Brühl et al., 1999; Fontanilla

et al., 2019; Longino, Branstetter, & Colwell, 2014; Machac et al., 2011) which may be explained by the variation in climatic or soil parameters. We therefore expected both climate and soil variables to be strongly correlated with variation in leaf litter ant assemblages' composition. Moreover, ant species turnover has been shown to be highly coordinated with tree species turnover in the region, independently from environmental gradients (Vleminckx et al., 2019). We may therefore expect a change of ant species composition with elevation considering previous evidence that forest structure and composition change along elevational gradients (Swenson et al., 2011).

2 | METHODS

2.1 | Experimental design

We collected ants during the dry season in November 2014, at Mont Itoupé (3°01'10.32"N, 53°04'45.90"W), French Guiana. Mont Itoupé, located in the heart of the National Park of the Amazon in French Guiana, peaks at an altitude of 830m asl, representing one of the highest peaks within 250 km. A total of nine 0.12-ha plots were established at approximately 400 m, 600 m, and 800 m asl, with three plots per elevation

range, spanning a total area of ca. 10 km² (Figure 1). The plots were chosen to span the range of variation in both climatic and soil conditions across the site. Mean annual rainfall in the area reached 2,584 mm (<140 mm of difference across elevations), while mean annual temperature ranged from 23.0 at 400m to 21.6°C at 800m (worldclim.com).

Each plot represented an area of 30 m × 40 m, within which we established a grid system of 20 sampling points separated by at least 10 m, according to the Ants of Leaf Litter Protocol described in Agosti and Alonso (2000). At each sampling point, we collected leaf litter ants using pitfall traps and the mini-Winkler method (for more details, see Bestelmeyer et al., 2000). Pitfall traps were left in the ground for 72 hr, while the mini-Winkler extractors were installed for 48 hr. Because pitfall traps and mini-Winkler extractors were used as complementary traps, we pooled data from both methods in our analyses. Thus, only a single occurrence was reported for a species collected in both traps at the same sampling point.

2.2 | Ant identification

Ants were identified at the species level whenever possible or assigned to a morphospecies code. Species identification was mainly

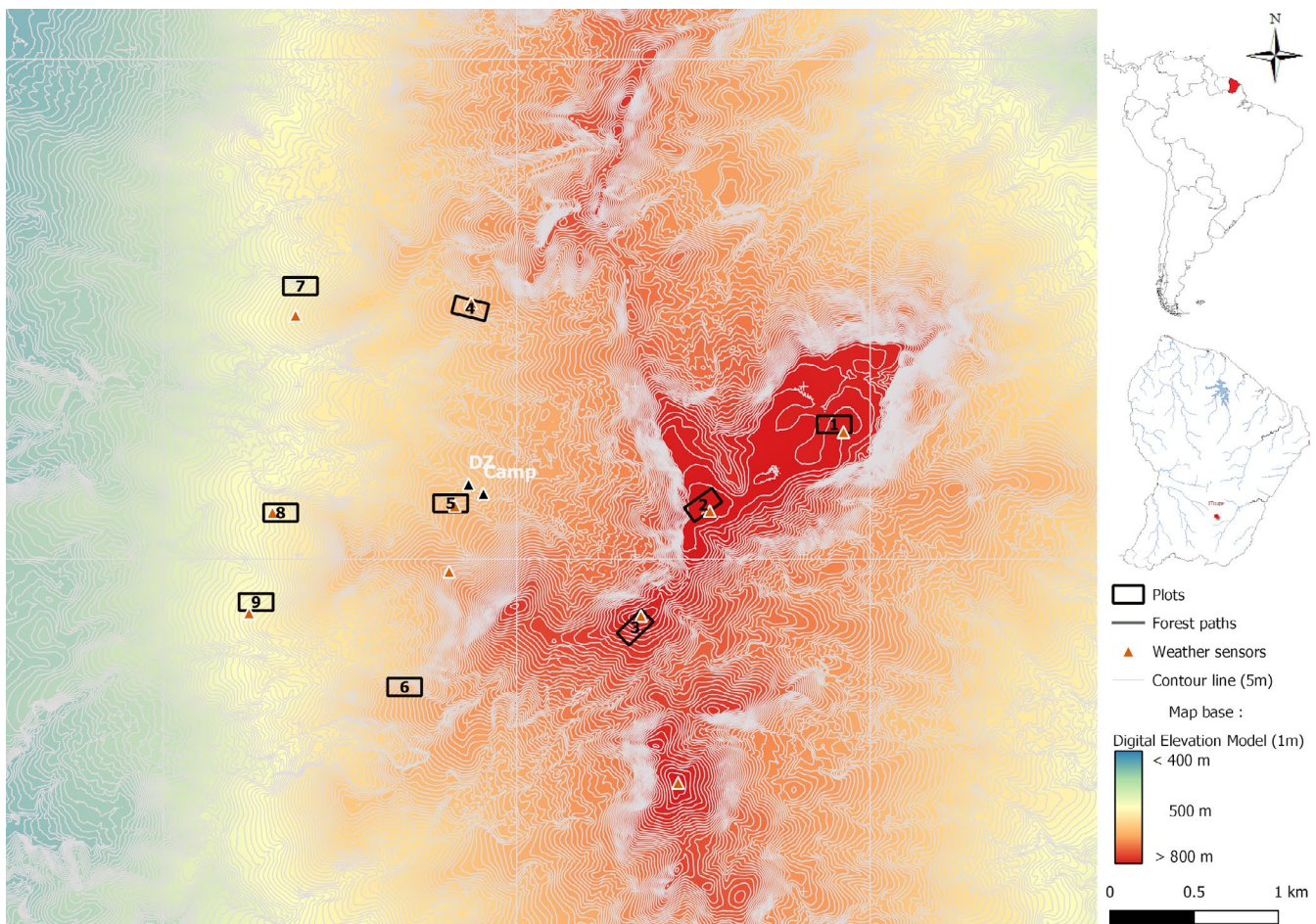


FIGURE 1 Location of the study area and the nine sampling plots and environmental sensors at Mont Itoupé, French Guiana. The weather sensor of Plot 6 was located halfway between Plot 5 and Plot 6 (for more details, see section 2.5.2)

TABLE 1 List of morphological traits measured and their hypothesized ecological functions

Traits	Hypothesized ecological functions
WL	Proxy for body size, related to several physiological and ecological traits, such as habitat use (Kaspari & Weiser, 1999; Weber, 1938).
HW	Indicator of mandibular musculature, related to trophic position (Kaspari, 1993; Weiser & Kaspari, 2006).
HL	Indicator of body size (Kaspari & Weiser, 1999) and body mass which determines the quantity of resources consumed.
PW	Predictor of body mass (Kaspari & Weiser, 1999).
FL	Indicator of foraging speed, related to habitat complexity (Feener Jr. et al., 1998).
SL	Related to sensory abilities (Weiser & Kaspari, 2006), indicative of an ant's ability to navigate and move through its surroundings (Yates et al., 2014).
EL	Indicator of feeding behavior (predatory ants have smaller eyes); hypogaeic ant species have smaller eyes compared to epigaeic ant species (Weiser & Kaspari, 2006; Yates et al., 2014).
CL	Related to liquid absorption abilities (Davidson, Cook, & Snelling, 2004); clypeus length is here used as a surrogate for liquid feeding habits in ants.
ML	Longer mandibles are associated with larger prey consumption (Fowler, Forti, Brandão, Delabie, & Vasconcelos, 1991). In some cases (i.e., trap-jaw ants), sublinear to linear and long mandibles are used as extremely rapid trap for hunting and killing fast preys (Gronenberg, Tautz, & Hölldobler, 1993).

Abbreviations: WL, Weber's length; HW, head width; HL, head length; PW, pronotum width; FL, femur length; SL, scape length; EL, eye length; CL, clypeus length; ML, mandible length.

based on online identification keys published on Antwiki (http://www.antwiki.org/wiki/Category:Identification_key) and keys developed by John T. Longino (<http://ants.biology.utah.edu/AntsofCostaRica.html>). We also used the reference collection of the Laboratory Ecofog (Kourou, French Guiana). For the morphospecies with problematic morphological identification (i.e., species from the genera *Hypoponera*, *Nylanderia*, *Pheidole*, and *Solenopsis*), we also sequenced the 16S rRNA barcode (at least three specimens per morphospecies) using the protocol developed by Kocher et al. (2016). DNA sequences were compared to a local reference barcode library for the ant species of French Guiana (under development; unpublished data). Samples are housed in the Laboratory Ecofog, with voucher specimens deposited in the Laboratório de Mirmecologia, Cocoa Research Centre CEPEC/CEPLAC (Itabuna, BA, Brazil) under the references #5761 (mini-Winkler traps) and #5762 (pitfall traps).

2.3 | Morphological data

We measured nine morphological attributes (Table 1) using an ocular micrometer accurate to 0.01mm mounted on a Leica M80 dissecting microscope (Leica Microsystems). Traits were selected based on their expected link with ecological strategies related to resource use (Table 1). Measures were performed for all the species collected (i.e., 267 species), using at least six randomly selected (minor-caste) workers per species whenever possible (Table S1).

2.4 | Phylogenetic data

We produced a genus-level phylogenetic tree and calculated phylogenetic distances among all inventoried genera ($n = 56$) using

the phylogenetic tree produced in a recent publication (Blanchard & Moreau, 2016). Because two genera sampled in this study (*Gigantiops* and *Rasopone*) were missing in the tree of Blanchard and Moreau (2016), our resulting tree contained 54 genera (Figure S1).

2.5 | Environmental data

We measured environmental parameters from soil, climatic, and LiDAR data.

2.5.1 | Soil data

In each plot, soil samples were collected at ten locations from three different soil layers (0–10, 10–20, and 20–30 cm), following the procedure described in Baraloto et al. (2011). The 10 samples for each depth were then bulked into a single composite sample of ca. 500 g of soil. Composite sample were then transported to the Laboratory Ecofog and dried to reach constant weight at 25°C, sieved to 2 mm, and sent to the INRA Arras soil analysis laboratory (Arras, France) for physical and chemical analyses. A set of nine physico-chemical properties was measured (Table S2): the percentage of sand, silt and clay, soil pH, the percentage of organic matter (OM), the carbon-to-nitrogen ratio (C/N), and the soil P, Na, and K contents. Particle size analysis of sand, silt, and clay was quantitatively performed by their settling rates in an aqueous solution using a hydrometer. Soil pH was measured in 1 M potassium chloride solution. The organic matter content was determined based on the loss of gases after ignition for 2 hr at 360°C. The total amount of nitrogen (N) and carbon (C) in all forms in soil was quantitatively analyzed using a dynamic flash combustion system coupled with a gas chromatographic separation

system and thermal conductivity detection system. Extractable phosphorus (P) was assayed using the Olsen method (Olsen et al., 1954) based on the extraction of phosphate from the soil by 0.5 N sodium bicarbonate solution adjusted to pH 8.5. A semi-quantitative method was used to determine the amount of soil exchangeable sodium (Na) and potassium (K) residing on the soil colloid exchange sites by displacement with ammonium acetate solution buffered to pH 7.0.

2.5.2 | Climatic data

Air temperature (in °C) and relative humidity (in %) were measured in all plots using micro-environmental sensors (HOBO U23-001) as described in Tymen et al. (2017). The weather sensors were placed within the area of each plot except for Plot 6, for which the sensor was placed halfway between Plots 5 and 6 because of a logistical issue. Since this sensor was not far away for the sampled area and at the same elevation, the climatic data were used as a proxy for environmental data of this plot (see Figure 1).

The two parameters (air temperature and relative humidity) were monitored for one year, from 1 January 2015 to 31 December 2015 with one measurement every 30 min. Using the local micro-environmental data, we defined four climatic variables for each plot (Table S2): T_{MEAN} —mean annual Temperature, RH_{MEAN} —mean annual Relative Humidity, T_{MIN} —minimum temperature of the coldest month, and RH_{MIN} —minimum Relative Humidity of the driest month.

2.5.3 | LiDAR data

LiDAR data were acquired in early August 2014 using a LMS-Q560 RIEGL laser range finder (wave length 1550nm) on board an aircraft flying at ca. 600m above the ground. A total of 64 km² were covered with a scan angle ranging from $\pm 25^\circ$. Point density slightly exceeded 20 pts/m² (pulse density ca. 13 pulses/m²), with a ground point density of 0.31 pts/m². Digital elevation model (DEM) at 1m resolution was interpolated from ground LiDAR points using Lastools (Insenburg n.d.). Digital surface model (DSM) was built using Quick Terrain Modeler (free trial version, <http://appliedimagery.com>) at the same resolution. Canopy height model (CHM) was then calculated as the difference between DSM and DEM. When we ground-surveyed our plots, multiple GPS point positions were acquired for each plot using a hand-held GPS (accuracy 5–10 m). To further improve plot geo-referencing, we adjusted plot locations against LiDAR CHM as in Réjou-Méchain et al. (2015): The location of all surveyed trees (DBH ≥ 30 cm) inferred from ground positioning was first compared to that deduced from CHM. Tree GPS coordinates were then shifted until best match with the CHM, resulting in horizontal shifts typically of <15 m. With the improved plot locations, we then derived three variables for the plots from LiDAR data (Table S2): canopy height (C_H), canopy cover (C_{COV}),

and the gap fraction (gap). Canopy height was calculated as the mean value of CHM pixels inside each plot. Canopy cover was calculated using LAStools (*lascanopy -cov*), with the height threshold set at 5 m for separating canopy and non-canopy points. Gap fraction was also calculated following the approach of Morsdorf et al. (2006), which was defined as the percent of vegetation echoes to all (ground and vegetation) echoes.

2.6 | Data analysis

All analyses were conducted using R 3.5.1 statistical software (R Core Team, 2018). The taxonomic, functional, and environmental datasets are available in supplementary material (Tables S1, S2 and S3).

2.6.1 | Functional heterogeneity among species

The mean value of traits ($n = 9$) per species was normalized by using a Box-Cox transformation, and then, all traits (except Weber's length) were standardized by dividing their values by Weber's length to correct for individual body size (see Table 1). A principal component analysis (PCA) on the species \times traits matrix (hereafter, $\text{PCA}_{\text{TRAITS}}$) was then performed to eliminate trait redundancy (see Figure S2), using the R package "FactoMineR" (Lê, Josse, & Husson, 2008). Subsequent analyses were based on the first three principal components (except for the fourth-corner analysis for which we also used individual traits; see below), which jointly explained 77% of the overall trait inertia (Table S4).

2.6.2 | Environmental heterogeneity among plots

Environmental variables were normalized (using Box-Cox transformation) and standardized (z-score transformation) prior to analyses, using the R package "forecast" (Hyndman et al., 2019; Hyndman & Khandakar, 2008). We then performed a PCA on all environmental variables ($n = 17$), hereafter the PCA_{ENV} , to examine associations among variables and to characterize environmental differences among plots. The difference among the three elevations for each environmental variable was tested using a Kruskal-Wallis test.

2.6.3 | Community-wide taxonomic, functional, and phylogenetic structure

A community that is taxonomically, functionally, or phylogenetically clustered within plot corresponds to a situation where species cooccurring within these plots share more similar taxa, traits, or are phylogenetically closer-related, respectively, than species from different plots. This clustering was quantified using the I_{ST} , τ_{ST} , and Π_{ST} statistics, which calculate the taxonomic, functional, and phylogenetic

turnover among plots, respectively (Hardy & Senterre, 2007). The three indices are calculated as followed:

$$I_{ST} = 1 - TD_w / TD_a \text{ (Taxonomic turnover)} \quad (1)$$

$$\tau_{ST} = 1 - FD_w / FD_a \text{ (Functional turnover)} \quad (2)$$

$$\Pi_{ST} = 1 - PD_w / PD_a \text{ (Phylogenetic turnover)} \quad (3)$$

where TD corresponds to the taxonomic diversity calculated using Simpson index with species occurrence data; FD and PD correspond, respectively, to the mean functional dissimilarity (here, Euclidean) between distinct species and the mean phylogenetic distance (mean divergence time based on the phylogenetic tree) between distinct genera (thus FD and PD are based on species/genus presence-absence), within (w) and among (a) plots. τ_{ST} and Π_{ST} thus quantify the relative increase of the mean functional divergence and phylogenetic distance between species sampled among plots versus within plots, respectively. Species, trait, and phylogenetic clustering are observed if I_{ST} , τ_{ST} , or $\Pi_{ST} > 0$, respectively, while negative values indicate overdispersion (Hardy & Senterre, 2007). The overall clustering within plots was calculated using the mean I_{ST} , τ_{ST} , and Π_{ST} values among all pairs of plots. These mean values were tested by comparing their observed value with 999 null values obtained under a null model where species occurrences are randomized across plots (Hardy, 2008). We then used the pairwise values of these statistics among all pairs ($n = 36$) of different plots in regression models to test the effect of environmental dissimilarity on taxonomic, functional, and phylogenetic turnover (see next section). Turnover values were also quantified and tested among pairs of altitudes (three comparisons, 400–600 m, 400–800 m, and 600–800 m). These indices were calculated using the R package “spacodiR” (Eastman, Paine, & Hardy, 2013).

2.6.4 | Environmental determinants of taxonomic, functional, and phylogenetic composition

We used multiple regression on distance matrices (MRM; Lichstein, 2007) to quantify and test the association between environmental dissimilarity and taxonomic (I_{ST}), phylogenetic (Π_{ST}), and functional (τ_{ST}) turnover of ant assemblages among plots, using the R package “ecodist” (Goslee & Urban, 2007). Statistical significance of each regression coefficient was assessed through residuals permutation tests ($n = 9,999$ permutations). Pairwise τ_{ST} values corresponded more exactly to the functional turnover among plots calculated using the three first axes of the PCA_{TRAITs} together, as well as each of these axes individually. Analyzing the functional turnover based on individual PCA axes can help identifying significant effects on traits that may be obscured when all traits are taken into account in the analysis. The examination of trait loadings on the PCA axes can help identifying those traits (Figure 2). It is worth noting that all of our tests may suffer from a limited statistical power due to the number of pairwise turnover values ($n = 36$) investigated in the

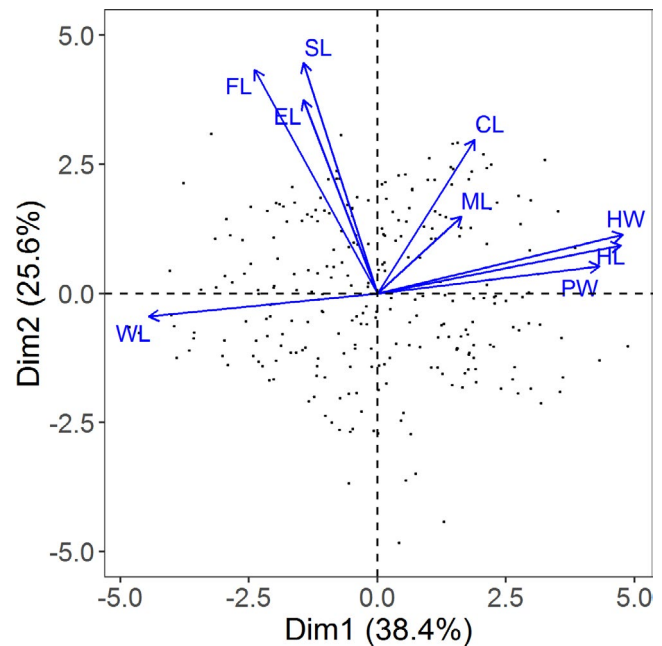


FIGURE 2 Principal component analysis of trait data in each plot. HL = relative head length; HW = relative head width; ML = relative mandible length; CL = relative clypeus length; SL = relative scape length; EL = relative eye length; WL = Weber length; FL = relative femur length; PW = relative pronotum width

MRM. Thus, while the significant signals observed may reflect some ecological reality, the absence of signals should also be taken with caution as they could mean that our sampling design did not allow capturing a significant association.

Three types of MRM models were used for each of the six response variable (I_{ST} , τ_{ST} calculated over the three first axes of the PCA_{TRAITs}, τ_{ST} calculated for each of these three axes, and Π_{ST}). The first model (Model 1) corresponded to a simple regression testing the effect of the overall environmental (Euclidean) dissimilarity (calculated over the 17 environmental variables) on each response variable. Model 2 corresponded to a multiple regression model where we tested the relative effects (regression coefficients) of the dissimilarity of several environmental variables, using a reduced set of variables with limited collinearity to limit the number of tests. To do so, we retained ecologically relevant variables with r -Spearman correlation ≤ 0.6 for climate and soil variables separately (Figures S3–4). In doing so, four soil variables (the percentage of sand, OM, soil pH, and P) and one climatic variable (RH_{MEAN}) were retained for analyses. For LiDAR data, because the variation in the variables “canopy cover” and “gap fraction” remained virtually unchanged across plots (see Table S2), we only retained the variable “canopy height” (C_H) for analyses. This latter variable was positively correlated with the variables “canopy cover” and “gap fraction” (Figure S5). In Model 3, we tested the relative effects of the dissimilarity in the scores of the two first axes of the PCA_{ENV}. In each of the three models, the spatial dependence among plots was taken into account by including spatial distance (Euclidean, untransformed) among the explanatory variables.

Finally, to have more accurate insights regarding the associated pairs of environmental variables and traits, we performed a fourth-corner analysis (Legendre, Galzin, & Harmelin-Vivien, 1997), using the R packages “ade4” (Dray & Dufour, 2007) and “adespatial” (Dray et al., 2019). The fourth-corner analysis combines three matrices—plots \times environmental variables (R), plots \times species occurrences (L), and species \times traits (Q)—into a matrix of trait–environment associations. The latter is then used to quantify and test pairwise associations between traits and environmental variables, using 9,999 randomizations with the so-called model “6” which combines models “2” and “4” as described in Dray et al. (2014), in order to avoid type-I error inflation.

3 | RESULTS

We collected a total of 31,865 ant individuals belonging to 267 species, 56 genera, and 11 subfamilies along the elevational gradient at Mont Itoupé (Table S3). The total number of species slightly decreased with increasing elevation (resp. 198, 176, and 161 species at 400m, 600m, and 800m asl.). Across plots, the number of observed species ranged from 85 (P6; 600m asl.) to 129 (P9; 400m asl.). The average number of species per sample was higher at the lowest elevations (400m: mean \pm SD = 25.45 \pm 2.69; 600m: mean \pm SD = 20.38 \pm 4.48; 800m: mean \pm SD = 20.63 \pm 1.60). We also calculated Simpson's index and found very similar values along the elevational gradient (mean \pm SD = 0.98 \pm <0.01 for each elevation).

3.1 | Functional heterogeneity

The PCA performed on species traits (PCA_{TRAITS}) showed that the first three axes jointly explained 77% of the overall trait inertia (38%, 26%, and 13%, respectively; Figure 2 and S6; Table S4). Plot scores on the first axis were highly positively correlated with HL, HW, and PW and negatively with WL. The second axis was mostly associated with FL, SL, and EL, which were highly positively correlated with each other; the third axis was negatively associated with ML (Figure 2 and Figure S6, Table S4).

3.2 | Environmental heterogeneity

The PCA performed on the matrix of environmental data (hereafter, PCA_{ENV}) revealed that axes 1 and 2 explained 60.5% and 20.7% of the overall environmental inertia across the nine plots, respectively (Figure 3; Table S5). Among the variables retained for analyses, PCA scores indicated that relative humidity (RH_{MEAN}) and canopy height (C_{H}) were strongly correlated with axis 1 (resp. $r = .93$ and $r = -.90$), while pH was strongly correlated with axis 2 ($r = .85$).

We found that the following variables significantly (or almost) varied across elevations (Kruskal–Wallis rank tests): OM ($X^2 = 7.20$, $p = .03$), C_{H} ($X^2 = 6.00$, $p = .05$), P ($X^2 = 2.40$, $p = .06$), and RH_{MEAN} ($X^2 = 5.42$, $p = .07$). In contrast, no significant variation was found

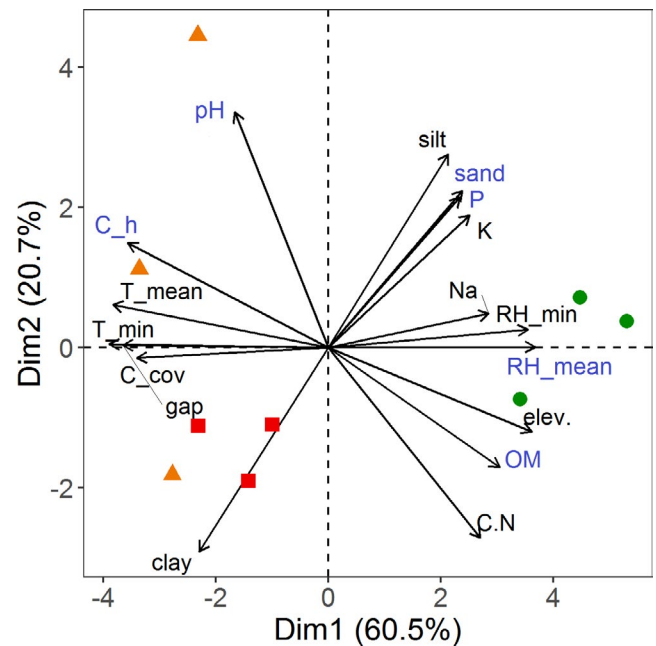


FIGURE 3 Principal component analysis of environmental data in each plot. Plots of the same elevational band are represented by green circles (800m), red squares (600m), and orange triangles (400m). elev = elevation (m); sand = percentage of sand; silt = percentage of silt; clay = percentage of clay; pH = soil pH; OM = percentage of organic matter; C/N = carbon-to-nitrogen ratio; P = Olsen-phosphorus concentration; Na = sodium concentration; K = potassium concentration; T_min = minimum temperature of the coldest month; T_mean = mean annual temperature of the driest month; RH_min = minimum relative humidity of the driest month; RH_mean = mean annual relative humidity; C_cov = canopy cover; C_h = canopy height; gap = gap fraction. Variables retained for analyses are highlighted in blue

in sand ($X^2 = 2.40$, $p = .30$) and soil pH ($X^2 = 0.61$, $p = .74$) across elevations.

3.3 | Taxonomic, functional, and phylogenetic structure of ant assemblages

The leaf litter ant assemblages displayed significant taxonomic and trait clustering at the plot level (Table 2). Trait clustering was mostly explained by a significant clustering observed for the scores of the second axis of the PCA_{TRAITS} (Table 2), which accounted for 26% of the overall functional inertia. The latter axis (i.e., axis 2 of the PCA_{TRAITS}) was mostly associated with relative femur and scape length (Figure 2; Table S4). In contrast, we did not find any significant phylogenetic clustering (Table 2). We further found that the taxonomic clustering was mostly due to differences in species composition between 800 and 600m elevation plots and that the functional clustering was mostly due to differences in trait composition between the most elevated plots (800m) and the other plots (Table 2). No phylogenetic clustering signal was found at the plot or the elevation level.

3.4 | Effect of environmental variables on taxonomic, functional, and phylogenetic composition

To facilitate the reading hereafter, we will sometimes omit to use the term “dissimilarity” when describing that the “dissimilarity of A significantly explains the dissimilarity of B” and will simply write that “A significantly explains B”; but we must keep in mind that we only deal with dissimilarity values among plots in our regression models. The overall environmental dissimilarity significantly explained the taxonomic (I_{ST}) and the overall functional (τ_{ST}) turnover among plots (Table 3)

TABLE 2 Taxonomic, functional, and phylogenetic turnover of ant assemblages, averaged over all pairs of plots (Global turnover) or for each pair of elevations (in m: 800–600, 800–400, 600–400)

	Global turnover	800–600	800–400	600–400
I_{ST}	40.98***	36.31*	31.83	17.26
τ_{ST}	19.31**	14.51**	30.88*	-5.46
$\tau_{ST}PC1$	10.18	-10.44	-9.28	-7.79
$\tau_{ST}PC2$	36.24**	39.62**	92.41*	0.76
$\tau_{ST}PC3$	3.20	-9.20	-2.01	-9.44
Π_{ST}	1.05	9.10	7.52	-4.68

Note: I_{ST} = taxonomic turnover (species level); τ_{ST} = functional turnover (species level); Π_{ST} = phylogenetic turnover (genus level). The functional turnover was calculated using the three first axes of PCA_{TRAITS} (τ_{ST}) and each of these axes separately ($\tau_{ST}PC1$; $\tau_{ST}PC2$; $\tau_{ST}PC3$). Turnover values were multiplied by 10^4 to facilitate the reading.

Significant values are emphasized in bold and with asterisks (** $p \leq .001$; ** $p \leq .01$; * $p \leq .05$).

but not the phylogenetic (Π_{ST}) turnover. Moreover, the scores of the first axis (strongly associated with Weber's length, the relative head length, the relative head width, and the pronotum width) and second axis (strongly associated with the relative scape and the relative femur lengths) of the PCA_{TRAITS} were significantly explained by the overall environmental dissimilarity.

Meanwhile, the plot scores of the first axis of the PCA_{ENV} (which was strongly associated with temperature, relative humidity, and vegetation structure; Table S5) significantly explained the variation in the overall taxonomic and functional composition, as well as the variation in the plot scores of axes 1 and 2 of the PCA_{TRAITS} (Table 3). When examining the relative effects of each of the six selected environmental variable (sand, pH, OM, P, RH_{MEAN} , and C_H), we found that soil phosphorus content and canopy height significantly explained the taxonomic composition (I_{ST}) but not the overall functional composition (τ_{ST}), the latter being only explained by the percentage of sand (with a marginal significance; $p = .081$). Although the second axis of the PCA_{TRAITS} displayed the strongest association with environment and with the first axis of the PCA_{ENV} , it was not significantly explained by any individual environmental variable, despite a relatively high coefficient value obtained with C_H , which may result from a lack of power. Axes 1 and 3 of the PCA_{TRAITS} , however, were both significantly explained by soil phosphorus, while axis 1 was also significantly explained by pH and axis 3 by the percentage of sand. The phylogenetic (Π_{ST}) turnover was (marginally) significantly explained by soil pH only.

The fourth-corner analysis indicated that the percentage of sand was negatively related to the relative scape, eye, and femur lengths and to the second and third axes of the PCA_{TRAITS} (Table 4) which

	I_{ST}	τ_{ST}	$\tau_{ST}PC1$	$\tau_{ST}PC2$	$\tau_{ST}PC3$	Π_{ST}
Model 1						
Global env. effect	0.08*	0.20***	0.17*	0.47***	-0.06	-0.02
Model 2						
Sand	1.55	10.17†	-0.54	17.08	14.55*	-2.83
pH	-6.95	0.22	14.59†	-14.40	-1.03	10.41†
OM	0.91	-2.08	-0.32	4.93	-7.64	-5.90
P	7.90†	9.42	35.61**	3.22	-13.59†	2.14
RH_{MEAN}	-7.62	7.75	21.61	11.26	-11.51	13.15
C_H	21.99*	15.34	-8.14	43.75	3.40	-13.49
Model 3						
PC1	34.18†	96.57**	67.75†	233.89***	-24.70	-8.90
PC2	9.82	-7.09	28.34	-53.53	-2.23	-0.37

Note: For the functional turnover, the effect of environmental variables was evaluated for the three first axes of PCA_{TRAITS} (τ_{ST}) together and for each of these axes separately ($\tau_{ST}PC1$; $\tau_{ST}PC2$; $\tau_{ST}PC3$). Sand = percentage of sand; pH = soil pH; OM = percentage of organic matter; P = Olsen-phosphorus concentration; RH_{MEAN} = mean annual relative humidity; C_H = canopy height). Regression coefficients are multiplied by 10^4 to facilitate the reading as they sometimes reach very low yet significant values. Significant coefficients are emphasized in bold (** $p \leq .01$; *** $p \leq .001$; * $p \leq .05$; † $p \leq .1$). The regression coefficients were obtained by including the spatial distance in each of the three models in order to remove spatial effects (see methods).

TABLE 3 Regression coefficients quantifying the effect on the turnover in community composition (I_{ST} = taxonomic turnover; τ_{ST} = functional turnover; Π_{ST} = phylogenetic turnover), of the overall environmental dissimilarity (Model 1), the dissimilarity of individual environmental variables (Model 2) and the dissimilarity in the scores of the two first axes of the PCA_{ENV} (PC1, PC2; Model 3)

TABLE 4 Results from the fourth-corner analysis quantifying the strength of pairwise trait-environment associations

	sand	pH	OM	P	RH _{MEAN}	C _H
HL	0.03	0.05	-0.02	.07*	0.04	-0.00
HW	0.01	0.04	-0.02	.05	0.01	-0.02
ML	0.03	0.04	-0.01	.02	0.01	-0.01
CL	-0.03	0.02	-0.03	.01	-0.02	0.03
SL	-0.07*	0.02	-0.05	-.05	-0.07*	0.07
EL	-0.10**	0.00	-0.06	-.08	-0.10*	0.09
WL	-0.03	-0.04	0.01	-.08**	-0.05	0.00
FL	-0.08†	0.01	-0.05	-.10	-0.10**	0.09
PW	0.01	0.04	-0.02	.5	0.01	-0.01
PC1	-0.04	-0.04	0.01	-.08*	-0.05	0.01
PC2	-0.08*	0.03	-0.06	-.06	-0.08	0.09
PC3	-0.05*	-0.02	-0.02	-.02	-0.02	0.02

Note: Abbreviations: HL, relative head length; HW, relative head width; ML, relative mandible length; CL, relative clypeus length; SL, relative scape length; EL, relative eye length; WL, Weber's length; FL, relative femur length; PW, relative pronotum width; PC1/PC2/PC3: axes 1, 2 and 3 of the PCA_{TRAITs}; sand, percentage of sand; pH, soil pH; OM, percentage of organic matter; P, Olsen-phosphorus concentration; RH_{MEAN}, mean annual relative humidity; C_H, canopy height. Significant relationships are highlighted in bold (** $p \leq .01$; * $p \leq .05$; † $p \leq .07$).

were highly associated with the variation of these three traits, while the third axis was also strongly correlated with the relative mandible length (Table S4). Phosphorus concentration was positively related to relative head length, whereas it was negatively related to Weber's length and the first axis of the PCA_{TRAITs}. Mean annual relative humidity was negatively related to relative scape, eye, and femur lengths of ants (Table 4).

4 | DISCUSSION

This study highlights the existence of associations between key abiotic environmental variables and the distribution of species and functional traits among Neotropical ant assemblages at a local (i.e., 10 km²) scale. Ant species and functional composition were mostly explained by canopy height and the first axis of the PCA_{ENV} which was strongly associated with the relative humidity and temperature (and thus elevation) and to a lesser extent by soil phosphorus concentration, sand, and pH (Table 3). The observed within-plot and within-elevation functional clustering (Table 2) likely arose from the filtering of these environmental conditions.

Climate represents a major environmental filter and restricts the number and identity of species that can survive and establish at different locations. Among climatic filters, temperature has been shown to be a key parameter influencing patterns of ant species distributions (e.g., Dunn et al., 2009; Sanders et al., 2007; Silva & Brandão, 2014). Other studies have also reported a relationship

between temperature and ant functional composition (Arnan et al., 2014; Stuble et al., 2013). Relative humidity may be even more constraining for leaf litter ants than temperature (Kaspari & Weiser, 2000; Menke & Holway, 2006). These studies reported results that were consistent with our findings. Indeed, we found that the variation in the dissimilarity of plot scores along the first axis of the PCA_{ENV}, which was highly explained by variation in soil relative humidity, temperature, and elevation (Figure 3; Table S5), significantly explained the taxonomic and functional turnover. As highlighted by the PCA generated on environmental data (PCA_{ENV}; Figure 3), the top of the mountain (ca. 800m asl), which is covered by cloud forests, is characterized by slightly higher levels of humidity (mean_{RH} = 99.3%) compared to lower elevations (between ca. 400 and 600m asl; mean_{RH} = 96.5%). The top forests may therefore provide a refuge area for certain species preferring relatively colder and more humid conditions. Changes in species and functional composition may thus reflect the presence of climate specialists at higher elevations. More specifically, our results suggest that smaller ant species, as well as species with relative smaller eyes or smaller legs, were found in sites with higher levels of humidity (thus at higher elevation). These traits are characteristics of hypogaecic ant species, that is, ant species that nest and forage within the litter or into the soil (Weiser & Kaspari, 2006).

Along Mont Itoupé, turnovers in species and functional composition were also associated with variation in phosphorus concentration (Table 3). Phosphorus limitation may explain variation in plant diversity (Vleminckx et al., 2017; Wright et al., 2011), which in turn is likely to influence the diversity and density of leaf litter-associated invertebrates (McGlynn & Salinas, 2007; Vleminckx et al., 2019). In their study, McGlynn and Salinas (2007) found that environments richer in phosphorus had greater litter invertebrate densities (mostly detritivores). Thus, the association between phosphorus availability and the species and functional composition of ant communities may be indirectly explained by the variation in the density of prey for predatory ant species. The fourth-corner analysis performed in this study reveals that phosphorus concentration was positively related to the relative head length and negatively related to body length (i.e., Weber's length), features that are characteristics of small hypogaecic ant species belonging to genera such as *Carebara*, *Solenopsis*, and *Strumigenys*. These predatory ant genera may thus benefit from the higher phosphorus concentrations that may favor the abundance of small prey. Such results contrast with those obtained in a study conducted by Jacquemin, Maraun, Roisin, and Leponce (2012), in which they found a decrease of predatory ant species in plots enriched in carbon, nitrogen, and phosphorus. In their study, predatory ants seemed to be limited by habitat loss due to the increased litter decomposition. The positive effect of higher levels of phosphorus for small predatory ant species found in our study may have been counterbalanced by habitat loss in their study, since the amount of leaf litter at the highest elevation, that is, at high levels of phosphorus, was much more important than at the lowest ones.

In addition to climatic factors, nutrient availability and soil texture can also influence invertebrate composition by imposing constraints

on species living in ground habitats (Costa-Milanez, Majer, Castro, & Ribeiro, 2017; Schmidt et al., 2016; Vasconcelos et al., 2003), but also indirectly via an effect of these variables on tree community assembly (Vleminckx et al., 2019). In our study, a significant association was found between the functional composition and the soil texture (percentage of sand) turnover across plots (Table 3), especially for the third axis of the PCA_{TRAITS}, which was mostly associated with the relative mandible length (Table S4). We lack hypotheses to explain that result. In addition, the percentage of sand was negatively related to individual functional traits of ants (i.e., the relative scape and femur lengths). Particular functional traits of ant species rather than the global functional space of ant assemblages may thus be linked to soil texture. Short scape and eye, relative to body size, are typical of hypogaecic ant species (Brandão, Silva, & Delabie, 2012), foraging and nesting inside the leaf litter. Sandy soils may thus favor movements and nest establishment of hypogaecic species within the litter, compared to clay-rich soils.

5 | CONCLUSIONS

Elevational gradients stretching from lowland forests to lower mountain cloud forests represent a major source of environmental variation in tropical regions, which, in our study, has been shown to influence the distribution of leaf litter ants. In particular, the taxonomic and functional turnover of ant communities was mostly explained by soil phosphorus content, climatic (temperature, relative humidity) variables, and vegetation structure, while trait variation seemed to be also influenced by soil texture and pH. Our results shed light on the unique biodiversity value of cloud forests, a particularly rare ecosystem in the eastern Guiana Shield, likely to be threatened by climate change, with scenarios predicting an intensification of drought events and an increase of temperature across the region (Esquivel-Muelbert et al. 2019). Indeed, the congruence between species and functional turnover along the humidity gradient highlights that a loss of species and functional diversity represent real threats in this regional biodiversity hotspot.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.612jm641m> (Fichaux et al., 2020).

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REFERENCES

- Agosti, D., & Alonso, L. (2000). The ALL Protocol. In D. Agosti, J. Majer, L. Alonso & T. Schultz (Eds.), *Ants: Standard methods for measuring and monitoring biodiversity* (pp. 204–206). Washington, DC: Smithsonian Institution Press.
- Arnan, X., Cerdá, X., & Retana, J. (2014). Ant functional responses along environmental gradients. *Journal of Animal Ecology*, 83, 1398–1408. <https://doi.org/10.1111/1365-2656.12227>
- Arnan, X., Cerdá, X., & Retana, J. (2015). Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ*, 3, e1241.
- Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., ... Fine, P. V. A. (2011). Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, 17, 2677–2688. <https://doi.org/10.1111/j.1365-2486.2011.02432.x>
- Bestelmeyer, B. T., Agosti, D., Alonso, L. E., Brandão, C. R. F., Brown, W. L. Jr, Delabie, J. H. C., & Silvestre, R. (2000). Field techniques for the study of ground-dwelling ants: An overview, description, and evaluation. In D. Agosti, J. Majer, L. Alonso, & T. Schultz (Eds.), *Ants: Standard methods for measuring and monitoring biodiversity* (pp. 122–144). Washington, DC: Smithsonian Institution Press.
- Bihn, J. H., Gebauer, G., & Brandl, R. (2010). Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*, 91, 782–792. <https://doi.org/10.1890/08-1276.1>
- Bishop, T. R., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, 42, 1776–1786. <https://doi.org/10.1111/jbi.12537>
- Blanchard, B. D., & Moreau, C. S. (2016). Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. *Evolution*, 71, 315–328. <https://doi.org/10.1111/evo.13117>
- Blatrix, R., Lebas, C., Galkowski, C., Wegnez, P., Pimenta, R., & Morichon, D. (2016). Vegetation cover and elevation drive diversity and composition of ant communities (Hymenoptera: Formicidae) in a Mediterranean ecosystem. *Myrmecological News*, 22, 119–127.
- Brandão, C. R. F., Silva, R. R., & Delabie, J. H. C. (2012). Neotropical ants (Hymenoptera) functional groups: Nutritional and applied implications. In J. R. P. Parra (Ed.), *Insect bioecology and nutrition for integrated pest management* (pp. 213–236). Boca Raton, IL: CRC.
- Brühl, C. A., Mohamed, M., & Linsenmair, K. E. (1999). Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, 15, 265–277. <https://doi.org/10.1017/S0266467499000802>

- Chen, X., Adams, B., Bergeron, C., Sabo, A., & Hooper-Büi, L. (2015). Ant community structure and response to disturbances on coastal dunes of Gulf of Mexico. *Journal of Insect Conservation*, *19*, 1–13. <https://doi.org/10.1007/s10841-014-9722-9>
- Costa-Milanez, C. B. D., Majer, J. D., Castro, P. D. T. A., & Ribeiro, S. P. (2017). Influence of soil granulometry on average body size in soil ant assemblages: Implications for bioindication. *Perspectives in Ecology and Conservation*, *15*, 102–108. <https://doi.org/10.1016/j.pecon.2017.03.007>
- Davidson, D. W., Cook, S. C., & Snelling, R. R. (2004). Liquid-feeding performances of ants (Formicidae): Ecological and evolutionary implications. *Oecologia*, *139*, 255–266. <https://doi.org/10.1007/s00442-004-1508-4>
- Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. *Ecography*, *37*, 1047–1055. <https://doi.org/10.1111/ecog.00623>
- Del Toro, I., Ribbons, R. R., & Pelini, S. L. (2012). The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*, *17*, 133–146.
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., ... Wagner, H. H. (2019). *adespatial*: multivariate multiscale spatial analysis. R package version 0.3-4. Retrieved from <https://CRAN.R-project.org/package=adespatial>
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & Ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, *95*, 14–21. <https://doi.org/10.1890/13-0196.1>
- Dray, S., & Dufour, A.-B. (2007). The *ade4* package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.
- Dunn, R. R., Agosti, D., Andersen, A. N., Arnan, X., Bruhl, C. A., Cerdá, X., ... Sanders, N. J. (2009). Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, *12*, 324–333. <https://doi.org/10.1111/j.1461-0248.2009.01291.x>
- Eastman, J., Paine, T., & Hardy, O. (2013). *spacodiR*: spatial and phylogenetic analysis of community diversity. R package version 0.13-0115. Retrieved from <https://CRAN.R-project.org/package=spacodiR>
- Esquivel-Muelbert, A., Baker, Timothy R., Dexter, Kyle G., Lewis, Simon L., Brienen, Roel J. W., Feldpausch, Ted R., ... Vieira, Ima Célia Guimarães, (2019). Compositional response of Amazon forests to climate change. *Global Change Biology*, *25*, 39–56.
- Feener, D. H. Jr, Lighton, J. R. B., & Bartholomew, G. A. (1988). Curvilinear allometry, energetics and foraging ecology: A comparison of leaf-cutting ants and army ants. *Functional Ecology*, *2*, 509–520.
- Fichaux, M., Béchade, B., Donald, J., Weyna, A., Delabie, J. H. C., Murielle, J., ... Orivel, J. (2019). Habitats shape taxonomic and functional composition of Neotropical ant assemblages. *Oecologia*, *189*, 201–513. <https://doi.org/10.1007/s00442-019-04341-z>
- Fichaux, M., Vleminckx, J., Courtois, E. A., Delabie, J. H. C., Galli, J., Tao, S., ... Orivel, J. (2020). Data from: Environmental determinants of leaf-litter ant community composition along an elevational gradient. Dryad Digital Repository, <https://doi.org/10.5061/dryad.612jm641m>
- Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodiversity and Conservation*, *7*, 1221–1244. <https://doi.org/10.1023/A:1008891901953>
- Fontanilla, A. M., Nakamura, A., Xu, Z., Cao, M., Kitching, R. L., Tang, Y., & Burwell, C. J. (2019). Taxonomic and functional ant diversity along tropical, subtropical, and subalpine elevational transects in Southwest China. *Insects*, *128*, 1–15.
- Fowler, H. G., Forti, L. C., Brandão, C. R. F., Delabie, J. H. C., & Vasconcelos, H. L. (1991). *Ecologia nutricional de formigas*. In A. R. Panizzi & J. R. P. Parra (Eds.), *Ecologia nutricional de insetos e suas implicações no manejo de pragas* (pp. 131–223). São Paulo, Brazil: Editora Manole.
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, *22*, 1–19.
- Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, *81*, 2606–2621. [https://doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2)
- Graham, C. H., Parra, J. L., Rahbek, C., & McGuire, J. A. (2009). Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences*, *106*, 19673–19678. <https://doi.org/10.1073/pnas.0901649106>
- Groc, S., Delabie, J. H. C., Fernández, F., Leponce, M., Orivel, J., Silvestre, R., ... Dejean, A. (2014). Leaf-litter ant communities (Hymenoptera: Formicidae) in a pristine Guianese rain-forest: Stable functional structure versus high species turnover. *Myrmecological News*, *19*, 43–51.
- Groc, S., Orivel, J., Dejean, A., Martin, J.-M., Etienne, M.-P., Corbara, B., & Delabie, J. H. C. (2009). Baseline study of the leaf-litter ant fauna in a French Guianese forest. *Insect Conservation and Diversity*, *2*, 183–193. <https://doi.org/10.1111/j.1752-4598.2009.00060.x>
- Gronenberg, W., Tautz, J., & Hölldobler, B. (1993). Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science*, *262*, 561–563. <https://doi.org/10.1126/science.262.5133.561>
- Hardy, O. J. (2008). Testing the spatial phylogenetic structure of local communities: Statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology*, *96*, 914–926. <https://doi.org/10.1111/j.1365-2745.2008.01421.x>
- Hardy, O. J., & Senterre, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology*, *95*, 493–506. <https://doi.org/10.1111/j.1365-2745.2007.01222.x>
- He, X., Hou, E., Liu, Y., & Wen, D. (2016). Altitudinal patterns and controls of plant and soil nutrient concentrations and stoichiometry in subtropical China. *Scientific Reports*, *6*, 24261. <https://doi.org/10.1038/srep24261>
- Helmer, E. H., Gerson, E. A., Baggett, L. S., Bird, B. J., Ruzycski, T. S., & Voggesser, S. M. (2019). Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. *PLoS One*, *14*(4), e0213155.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, *163*, 192–211. <https://doi.org/10.1086/381004>
- Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, *80*, 489–513. <https://doi.org/10.1017/S1464793105006767>
- Hoiss, B., Krauss, J., Potts, S. G., Roberts, S., & Steffan-Dewenter, I. (2012). Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4447–4456.
- Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. Cambridge, Massachusetts: Harvard University Press.
- Hyndman, R., Athanasopoulos, G., Bergmeir, C., Caceres, G., Chhay, L., O'Hara-Wild, M., ... Yasmeen, F. (2019). *forecast*: forecasting functions for time series and linear models. R package version 8.7. Retrieved from <http://pkg.robjhyndman.com/forecast>
- Hyndman, R. J., & Khandakar, Y. (2008). Automatic time series forecasting: The forecast package for R. *Journal of Statistical Software*, *27*, 1–23.
- Insenburg, M. (n.d.) *LAStools*—efficient LiDAR processing software (version 160921, academic). Retrieved from <http://rapidlasso.com/LAStools>.
- Jacquemin, J., Maraun, M., Roisin, Y., & Leponce, M. (2012). Differential response of ants to nutrient addition in a tropical Brown Food Web.

- Soil Biology and Biochemistry*, 46, 10–17. <https://doi.org/10.1016/j.soilbio.2011.11.007>
- Kaspari, M. (1993). Body size and microclimate use in Neotropical granivorous ants. *Oecologia*, 96, 500–507. <https://doi.org/10.1007/BF00320507>
- Kaspari, M., & Weiser, M. D. (1999). The size–grain hypothesis and interspecific scaling in ants. *Functional Ecology*, 13, 530–538. <https://doi.org/10.1046/j.1365-2435.1999.00343.x>
- Kaspari, M., & Weiser, M. D. (2000). Ant activity along moisture gradients in a Neotropical forest. *Biotropica*, 32, 703–711.
- Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164. <https://doi.org/10.2307/3235676>
- Kocher, A., Gantier, J.-C., Gaborit, P., Zinger, L., Holota, H., Valiere, S., ... Muriene, J. (2016). Vector soup: High-throughput identification of Neotropical phlebotomine sand flies using metabarcoding. *Molecular Ecology Resources*, 17, 172–182. <https://doi.org/10.1111/1755-0998.12556>
- Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., ... Myers (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, 333, 1755–1758.
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, 25, 1–18.
- Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology*, 78, 547–562. [https://doi.org/10.1890/0012-9658\(1997\)078\[0547:RBTHS T\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHS T]2.0.CO;2)
- Lichstein, J. W. (2007). Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology*, 188, 117–131. <https://doi.org/10.1007/s11258-006-9126-3>
- Longino, J. T., Branstetter, M. G., & Colwell, R. K. (2014). How ants drop out: Ant abundance on tropical mountains. *PLoS One*, 9, e104030. <https://doi.org/10.1371/journal.pone.0104030>
- Los, S. O., Street-Perrott, F. A., Loader, N. J., Froyd, C. A., Cuni-Sanchez, A., & Marchant, R. A. (2019). Sensitivity of a tropical montane cloud forest to climate change, present, past and future: Mt. Marsabit, N. Kenya. *Quaternary Science Reviews*, 218, 34–48. <https://doi.org/10.1016/j.quascirev.2019.06.016>
- Machac, A., Janda, M., Dunn, R. R., & Sanders, N. J. (2011). Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography*, 34, 364–371. <https://doi.org/10.1111/j.1600-0587.2010.06629.x>
- McCain, C. M., & Grytnes, J.-A. (2010). Elevational gradients in species richness. *Encyclopedia of Life Sciences (ELS)* (pp. 1–10).
- McGlynn, T. P., Salinas, D. J., Dunn, R. R., Wood, T. E., Lawrence, D., & Clark, D. A. (2007). Phosphorus limits tropical rain forest litter fauna. *Biotropica*, 39, 50–53. <https://doi.org/10.1111/j.1744-7429.2006.00241.x>
- Menke, S. B., & Holway, D. A. (2006). Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology*, 75, 368–376. <https://doi.org/10.1111/j.1365-2656.2006.01056.x>
- Morsdorf, F., Kötz, B., Meier, E., Itten, K. I., & Allgöwer, B. (2006). Estimation of LAI and fractional cover from small footprint airborne laser scanning data based on gap fraction. *Remote Sensing of Environment*, 104, 50–61. <https://doi.org/10.1016/j.rse.2006.04.019>
- Nowrouzi, S., Andersen, A. A., Macfadyen, S., Staunton, K. M., VanDerWal, J., & Robson, S. K. A. (2016). Ant diversity and distribution along elevational gradients in the Australian wet tropics: The importance of seasonal moisture stability. *PLoS One*, 11, e0153420.
- Olsen, S., Cole, C., Watanabe, F., & Dean, L. (1954). Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circular Nr 939, US Gov. Print. Office, Washington, D.C.
- Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., ... Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology*, 101, 857–866.
- R Core Team (2018). *R: A language and environment for statistical computing*. R Core Team.
- Réjou-Méchain, M., Tymen, B., Blanc, L., Fauset, S., Feldpausch, T. R., Monteagudo, A., ... Chave, J. (2015). Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest. *Remote Sensing of Environment*, 169, 93–101. <https://doi.org/10.1016/j.rse.2015.08.001>
- Sanders, N. J., Lessard, J.-P., Fitzpatrick, M. C., & Dunn, R. R. (2007). Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, 16, 640–649.
- Schmidt, F. A., Schoederer, J. H., & Caetano, M. D. N. (2016). Ant assemblage and morphological traits differ in response to soil compaction. *Insectes Sociaux*, 64, 219–225. <https://doi.org/10.1007/s00040-016-0532-9>
- Silva, R. R., & Brandão, C. R. F. (2014). Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. *PLoS One*, 9, e93049. <https://doi.org/10.1371/journal.pone.0093049>
- Smith, M. A., Hallwachs, W., & Janzen, D. H. (2014). Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography*, 37, 720–731. <https://doi.org/10.1111/j.1600-0587.2013.00631.x>
- Stuble, K. L., Pelini, S. L., Diamond, S. E., Fowler, D. A., Dunn, R. R., & Sanders, N. J. (2013). Foraging by forest ants under experimental climatic warming: A test at two sites. *Ecology and Evolution*, 3, 482–491. <https://doi.org/10.1002/ece3.473>
- Swenson, N. G., Anglada-Cordero, P., & Barone, J. A. (2011). Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society B*, 278, 1707. <https://doi.org/10.1098/rspb.2010.1369>
- Tymen, B., Vincent, G., Courtois, E. A., Heurtebize, J., Dauzat, J., Marechaux, I., & Chave, J. (2017). Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science*, 74, 32. <https://doi.org/10.1007/s13595-017-0628-z>
- Vasconcelos, H. L., Macedo, A. C. C., & Vilhena, J. M. S. (2003). Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. *Studies on Neotropical Fauna and Environment*, 38, 115–124. <https://doi.org/10.1076/snfe.38.2.115.15923>
- Vlemminckx, J., Doucet, J.-L., Morin-Rivat, J., Biwolé, A. B., Bauman, D., Hardy, O. J., ... Drouet, T. (2017). The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon. *Journal of Ecology*, 105, 354–366. <https://doi.org/10.1111/1365-2745.12707>
- Vlemminckx, J., Schimann, H., Decaëns, T., Fichaux, M., Vedel, V., Jaouen, G., ... Baraloto, C. (2019). Coordinated community structure among trees, fungi and invertebrate groups in Amazonian rainforests. *Scientific Reports*, 9, 11337.
- Weber, N. A. (1938). The biology of the fungus-growing ants. Part 4. Additional new forms. Part 5. The Attini of Bolivia. *Revista De Entomologia*, 7, 154–206.
- Weiser, M. D., & Kaspari, M. (2006). Ecological morphospace of New World ants. *Ecological Entomology*, 31, 131–142. <https://doi.org/10.1111/j.0307-6946.2006.00759.x>
- Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309.
- Wright, S. K., Yavitt, J. B., Wurzbürger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., ... Corre, M. D. (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, 92, 1616–1625.

- Yates, M. L., Andrew, N. R., Binns, M., & Gibb, H. (2014). Morphological traits: Predictable responses to macrohabitats across a 300 km scale. *PeerJ*, 2, e271. <https://doi.org/10.7717/peerj.271>
- Yates, M., Gibb, H., & Andrew, N. R. (2011). Habitat characteristics may override climatic influences on ant assemblage composition: A study using a 300-km climatic gradient climatic gradient. *Australian Journal of Entomology*, 59, 332–338. <https://doi.org/10.1071/ZO11096>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.