

Spatio-temporal variation in ant (Hymenoptera: Formicidae) communities in leaf-litter and soil layers in a premontane tropical forest

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Abstract

Nearly half of the ant species present in a tropical forest are directly in contact with the ground for nesting or foraging, with evidence of vertical stratification among ground layers (i.e., surface, litter, and soil). How ants in each layer respond to environmental factors and to seasonality remains little studied. We hypothesized that ant species distribution varied spatially and seasonally among the three ground layers and that their distribution was distinctly affected by various abiotic and biotic factors.

Ants were collected in an Ecuadorian premontane tropical forest and their distribution was analyzed spatio-temporally: vertically (between the ground surface, leaf-litter, and mineral soil, using pitfalls, Winkler, and soil cores), horizontally (every meter along a 100 m transect) and seasonally (between the dry and the rainy seasons). Four environmental parameters were measured every meter along the transect: canopy openness, slope, leaf-litter depth, and leaf-litter volume. Correlations between species distribution, richness, abundance, and environmental variables were calculated.

Species richness was high, with 176 species collected along the transect. Our results show a clear vertical stratification, with distinct faunal composition in each layer and a strong seasonal effect. Stable distribution of several dominant species between seasons suggests a low nest relocation rate. During the dry season, higher ant richness and abundance were found in pitfall traps suggesting higher activity on the surface of the forest floor. Similarly, higher ant richness and abundance found in the soil during the dry season suggest the migration of drought-sensitive species downwards deeper into the soil. Species richness and dominant species distribution were related to distinct factors according to the layer considered; we found strong correlations between the quantity of leaf-litter and dominant ant species distribution and species richness in the leaf-litter layer, while no correlation was found with any factor in the soil layer.

Our results show that ant faunal composition and the response of ants to environmental factors vary vertically at small spatial scale and seasonally, which emphasizes the importance of distinguishing layers in the ground matrix.

Key words: Tropical mountain forests, ant biodiversity, Ecuador, Andes, ant community, vertical stratification.

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Introduction

Heterogeneity is a dominant feature of tropical forests. Heterogeneity of the spatial and temporal distribution of arthropods is driven by various biotic and abiotic processes varying both spatially and temporally. Resources such as food and habitat are scarcely distributed and vary seasonally, as do predation pressure and competition. Species are also limited by their range of tolerance to abiotic conditions or their physiological requirements (DIDHAM & SPRINGATE 2003, BERG & BENGTTSSON 2007, WARDHAUGH 2014). Evidence of vertical stratification, spatial heterogeneity, and seasonal variation in distribution patterns has been demonstrated for various arthropod taxa in tropical and subtropical

environments (ROISIN & al. 2006, KARASAWA & HUIJ 2008, RYDER WILKIE & al. 2010). How the distribution pattern of ants in a diverse assemblage varies spatio-temporally and which processes drive the observed patterns remains little studied (but see MUNYAI & FOORD 2015).

In tropical forests, ants are found in all strata, from the soil to the upper canopy (HÖLLDOBLER & WILSON 1990, RYDER WILKIE & al. 2010). Previous studies highlighted a distinct assemblage composition between the ground and the canopy strata (YANOVIK & KASPARI 2000, RYDER WILKIE & al. 2010), with occasionally intermediate strata such as trunks (HASHIMOTO & al. 2006) or lower vegeta-

tion (BRÜHL & al. 1998, VASCONCELOS & VILHENA 2006). Furthermore, several studies gave evidence of vertical stratification within the ground stratum itself, with distinct ant faunas in the leaf-litter layer and in the underlying soil layer (FOWLER & al. 2000, ANDERSEN & BRAULT 2010, RYDER WILKIE & al. 2010). Nearly half of the ant species present in a tropical forest are directly in contact with the ground stratum, including the leaf-litter and the mineral soil layers, for nesting or foraging (RYDER WILKIE & al. 2010, FLOREN & al. 2014). It is a structurally complex habitat with leaves and other organic particles decreasing in size with increasing depth, due to decomposition processes. The distribution of ground-dwelling ants within this profile is related to their ecology, with, for instance, long-legged hunters running on the surface of the leaf-litter, while litter-specialists will nest and forage in the leaf-litter layer, and small cryptic species tending coccids on roots will be found in the mineral stratum (KASPARI & WEISER 2007, RYDER WILKIE & al. 2007, 2010). Although not constituting a physical layer but rather an interface between the leaf-litter / soil and the understory / canopy strata, the ground surface supports the foraging activity of a mixed fauna, originating from lower or upper strata (DONOSO & RAMÓN 2009).

Besides vertical heterogeneity, ground-dwelling ant distribution in tropical ecosystems is also highly heterogeneous horizontally, at a small spatial scale (m). Local diversity (CAMPOS & al. 2003), density (LEVINGS 1983, KASPARI 1996a, KASPARI 1996b) and specific composition (LEPONCE & al. 2004, THEUNIS & al. 2005, JACQUEMIN & al. 2012) can vary greatly within a few meters. A series of environmental factors can also potentially influence the ant distribution and richness at the local scale, as they are heterogeneous themselves: slope and topography through their effect on local leaf-litter accumulation and soil drainage (VASCONCELOS & al. 2003), canopy openness influencing local litterfall, ant-plant interactions (DÁTILO & DYER 2014), local moisture and temperature through incident light and sunflecks (MEZGER & PFEIFFER 2010), and leaf-litter quantity. Leaf-litter constitutes both the habitat and food reservoir of most ground-dwelling ants (KASPARI & YANOVIK 2008), and its effect on ant diversity and assemblage structure has been demonstrated (CAMPOS & al. 2003, VARGAS & al. 2007, SILVA & al. 2011). Interspecific competition has also been shown to affect ant community structure (SAVOLAINEN & VEPSÄLÄINEN 1988, see review in CERDÁ & al. 2013) and species diversity (ANDERSEN 1992, ANDERSEN & PATEL 1994).

Some of those factors vary spatially at the local scale, but also seasonally. Leaf-litter quantity is balanced between litterfall input and decomposition rate, both being seasonally variable according to temperature, rainfall and nutrient availability (KASPARI & YANOVIK 2008). Canopy openness varies seasonally according to tree phenology, which in turn influences leaf-litter quantity and microclimate on the ground (SMITH & al. 1992). A seasonal effect has been shown on ant species density, activity and composition in Cameroon (DEBLAUWE & DEKONINCK 2007) and Brazil (COELHO & RIBEIRO 2006). However, these studies focused on ants caught in pitfall traps, i.e., reflecting the ant activity on the surface of the leaf-litter. How ground-dwelling ants of the leaf-litter layer and the underlying soil respond to seasonality is poorly known. Seasonal differences have

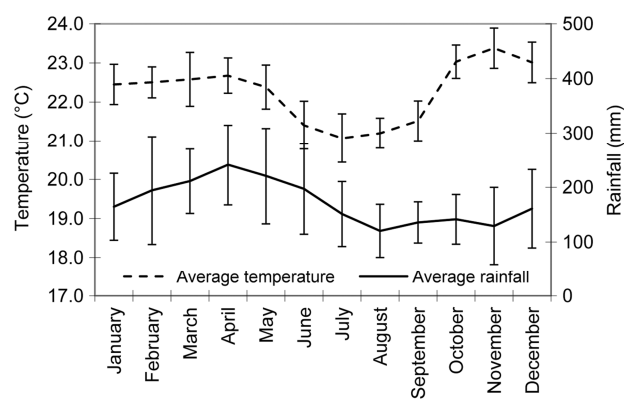


Fig. 1: Average monthly temperature (°C) (\pm SD) and average rainfall (mm) (\pm SD) in Copalinga, from 2003 to 2011. On average, November is the warmest month, and April the rainiest.

been observed in the vertical distribution of several macro-invertebrate taxa, from top leaf-litter layer to deep mineral soil (DOBLAS-MIRANDA & al. 2009). Similarly, collembolans have been shown to migrate from top to deeper soil layers during the dry season (HASSALL & al. 1986, DETSIS 2000). The hypothesis of a seasonal migration of ants from leaf-litter to mineral soil during the dry season to avoid drought has been little investigated.

Our hypotheses were (1) that ant species distribution (i.e., abundance, richness, and composition) varies spatially and seasonally among the three ground layers (i.e., surface, leaf-litter and soil), and (2) that distinct abiotic and biotic factors explain the observed distribution according to the ant species and the ground layer considered.

Materials and methods

Study site

The study was conducted in an evergreen premontane forest located in Copalinga (4.0912° S, 78.9607° W), a private reserve on the eastern slope of the Ecuadorian Andes, 1030 m a.s.l. High levels of precipitation occur from February to June, while August to December is drier (average annual rainfall: 2000 mm \pm 387 SD; average annual temperature: 22.3°C \pm 0.9 SD; C.Vits, pers. comm., period: 2003 - 2011) (Fig. 1). In March, the average temperature is 22.6°C \pm 0.7 SD and average rainfall is 212 mm \pm 63 SD. In November, the average temperature is 23.3°C \pm 0.5 SD and average rainfall is 139 mm \pm 76 SD.

Sampling design

During the dry season (November 2009), we delineated a 100 m long transect. Ants were collected every meter along the left side of the transect by using three complementary sampling methods adapted from the A.L.L. protocol (AGOSTI & ALONSO 2000) and appropriate to study the vertical stratification of ant distribution in the three ground layers. (1) Ants running on the ground surface were caught by pitfall traps, consisting in 200 ml cups (diameter: 7 cm) containing water and detergent, left to operate for 48h (Appendix S1, as digital supplementary material to this article, at the journal's web pages). (2) The leaf-litter ant fauna was collected inside ¼ m² quadrats (50 × 50 cm) and extracted with mini-Winkler apparatus for 48h. (3) Subterranean ants were collected in 15 × 15 × 10 cm (length ×

width \times depth) soil blocks. Each soil sample was roughly crumbled on a tray and observed for 20 person-minutes to capture the associated ant fauna (DELABIE & al. 2000). In the present paper the three layers are designated as "surface", "leaf-litter" and "soil", and their related ant fauna as "surface-running ants", "leaf-litter ants" and "soil-dwelling" or "subterranean ants". We repeated the sampling design in the beginning of the rainy season (March 2010) along the right side of the transect, so that the new sampling points were distant by 1 m from those of the dry season. Subterranean ant data were missing for quadrat 92 in March 2010. Ants were preserved in 96% ethanol until identification to species or morphospecies level (BOLTON 1994, 2003, 2014, LONGINO 2007). A table with all the morphospecies collected and their occurrences is available in Appendix S2.

Environmental variables

Four environmental parameters were measured every meter along the transect ($n = 100$) in both seasons: canopy openness, land slope, leaf-litter depth and leaf-litter volume. The percentage of canopy openness was measured from hemispherical photographs shot 1.5 m above ground in the center of each quadrat, and analyzed with the Gap Light Analyzer 2.0 software (FRAZER & al. 1999). Land slope was measured in the field at the center of each quadrat with a clinometer. Leaf-litter depth was measured by pushing a ruler in the leaf-litter until reaching the soil (we performed three measurements per quadrat and used the average value). Leaf-litter siftate volume, to be submitted to mini-Winkler extraction, was measured in a bucket with a measurement scale, after sifting (1 cm mesh).

Data analyses

Seasonal variability of the ant assemblage structure: Analyses of similarity (ANOSIM) were performed to test for significant differences in the ant faunal composition between the dry season (November 2009) and rainy season (March 2010). ANOSIM were performed between pairs of layers and for all three layers (surface, leaf-litter, soil) combined. ANOSIM is a non-parametric test of difference between groups of samples, using permutation procedures applied to Bray-Curtis similarity matrices based on rank similarities between samples. ANOSIM returns an R statistic ranging between 0 and 1, and indicating the degree of discrimination between the treatments. The closer the R value is to 1, the more different the groups are. If R is close to 0, the null hypothesis cannot be rejected, so the faunas can barely be separated. But even if R values may be low, these values may be significantly different from zero (p value ≤ 0.05 , Bonferroni corrected) (CLARKE & WARWICK 2001). ANOSIM were carried out using 999 permutations, and we worked with log-transformed abundance data ($\log_{10}(n + 1)$ with n = raw abundance of ant workers only).

In addition, the similarity percentage analysis (SIMPER) was used to determine which species accounted for seasonal differences in the composition of the ant fauna. SIMPER measures the contribution of each taxa, in terms of percentage, to the seasonal dissimilarity (CLARKE 1993, CLARKE & WARWICK 2001). In the Results section we cite only the three species contributing the most to the dissimilarity.

Seasonal shift in layer preference was tested for each common species (present in $\geq 20\%$ of samples, at least in

one layer and during one season) with a Chi-square test using PAST software version 2.14 (HAMMER & al. 2001).

Spatial variability of the ant assemblage structure:

We also performed ANOSIM to test for differences of faunal composition between the different layers. ANOSIM and SIMPER were performed using PAST software version 2.14 (HAMMER & al. 2001).

For each season we calculated the horizontal species turnover within a layer by averaging the Jaccard index calculated between contiguous samples (i.e., distant by 1 m, $n = 99$).

The estimated species richness of each layer and of the whole transect (i.e., all layers pooled) was calculated using the Chao2 estimator (CHAO 1987). Species turnover and Chao2 were calculated with EstimateS version 9.1 (COLWELL 2013).

We tested the spatial fidelity of ant nests from dry to rainy season on the common ant species (i.e., present in $\geq 20\%$ of samples in both seasons), in the leaf-litter layer and in soil. We only tested the species presenting an aggregation pattern, considering patches as a surrogate of colonies (8 species in total: 7 in leaf-litter, and 1 in soil). For each species, we calculated a Pearson's correlation coefficient between its log-transformed abundances along the transect during the dry and the rainy season. The correlation was computed after 999 toroidal randomizations preserving the spatial structure of the data (see Results) (TOROCOR software, HARDY 2009).

Association between environmental variables and ant species richness, abundance, and distribution:

We suspected the occurrence of non-random spatial patterns (aggregation) in the distribution of the environmental factors distribution along the transect. For this reason, for each season, the spatial autocorrelation of environmental variables was investigated using Moran's I statistic with TOROCOR software (HARDY 2009). Most environmental factors showed a significant spatial autocorrelation pattern (i.e., aggregated pattern) during the dry (Moran's I tests, $p \leq 0.01$ for slope, canopy openness and leaf-litter volume) and rainy season (Moran's I tests, $p \leq 0.01$ for slope, canopy openness and leaf-litter volume; $p \leq 0.05$ for leaf-litter depth). Only leaf-litter depth during the dry season did not show a spatial autocorrelation pattern. Ant distribution in each layer has also been verified for spatial autocorrelation.

For each season, the correlation was tested between each environmental variable and (1) the ant species richness; (2) the log-transformed abundance of all ant species ($\log_{10}(n + 1)$ with n = raw abundance of workers, in order to reduce the weight of populous samples); and (3) the log-transformed abundance of each common ant species. We used $p \leq 0.05$ as threshold of significance for (1) and (2), and $p \leq 0.0125$ for (3) in order to avoid Type I error due to the high number of pairs tested (i.e., 0.05 divided by the number of environmental variables tested, i.e., 4). Because the spatial distribution of several environmental variables and of several ant species was autocorrelated, the correlation tests were computed after toroidal randomizations preserving the spatial structure of the data (TOROCOR software, HARDY 2009). TOROCOR characterizes the association between variables by Pearson's correlation coefficient. To avoid bias due to the spatial autocorrelation, significance of the observed values is established from their

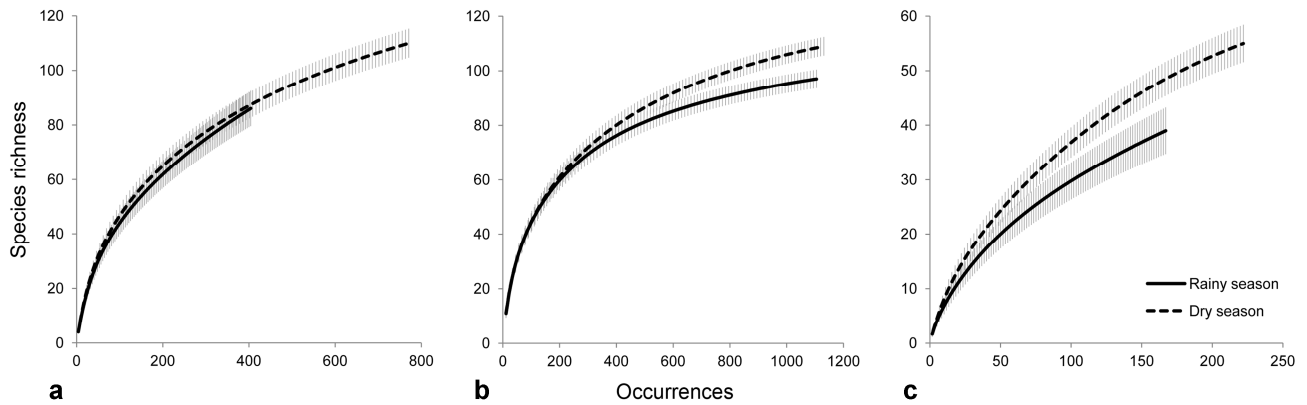


Fig. 2: Occurrence-based rarefaction of species richness in surface (a), leaf-litter (b), and soil samples (c).

Tab. 1: Seasonal characteristics of the ant fauna sampled on the ground surface, in the leaf-litter layer, and in the mineral soil.

	Study site (pooled layers and seasons)	Pooled layers		Surface		Leaf-litter		Soil	
		Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
Number of individuals	24626	14611	10015	4453	748	9359	8720	799	547
Number of occurrences		1829	1498	771	404	1131	1105	222	167
Number of sampled species	176	161	134	110	86	109	97	55	39
Mean number species / quadrat \pm SD		18.29 \pm 3.82	14.98 \pm 3.66	17.73 \pm 2.51	4.13 \pm 2.18	11.46 \pm 4.07	111.07 \pm 3.25	2.79 \pm 1.32	1.99 \pm 1.15
Estimated species richness \pm SD (Chao2)	199 \pm 10	194 \pm 14	177 \pm 19	148 \pm 17	166 \pm 37	122 \pm 7	110 \pm 8	70 \pm 8	72 \pm 21

distributions obtained from 4999 torus-translation randomizations. The goal of torus-translation randomizations is to break down the association between variables while keeping their respective spatial autocorrelation patterns intact, minimizing the risk of having false positives when applying tests of association. A torus translation randomization consists of translating all the samples within each transect by a random number of steps in each direction. Because all samples move in parallel, their spatial relationships, hence the spatial structure of the variables, are preserved. When samples are translated beyond one extremity of the transect, they are re-introduced through the opposite extremity, as if the transect was inscribed on the surface of a torus or a circle.

Association between species: Associations between the common ant species were tested pair by pair, by calculating a Pearson's correlation coefficient, in both seasons, and in the leaf-litter and in the soil layers only (pitfalls were excluded from this analysis because they capture species that may never encounter due to distinct foraging times). The correlation was computed after 4999 toroidal randomizations in TOROCOR software with a threshold of significance of $p \leq 0.05$ (HARDY 2009). As we expected 5% of the combinations to be significant by chance, we performed a one-tailed binomial test providing the maximum number of pairs expected to be significant by chance, and

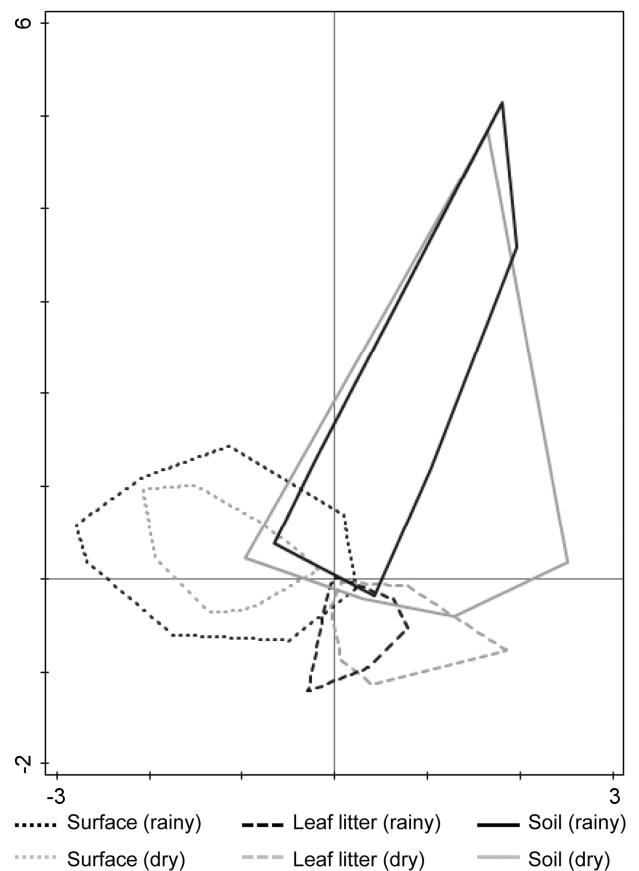


Fig. 3: CCA-ordination plot showing the separation between sample classes defined by season and layer of collection (surface, leaf-litter, soil). Each class of samples is delimited by minimum enclosing polygon. Diagrams were plotted in CANOCO 5.0.

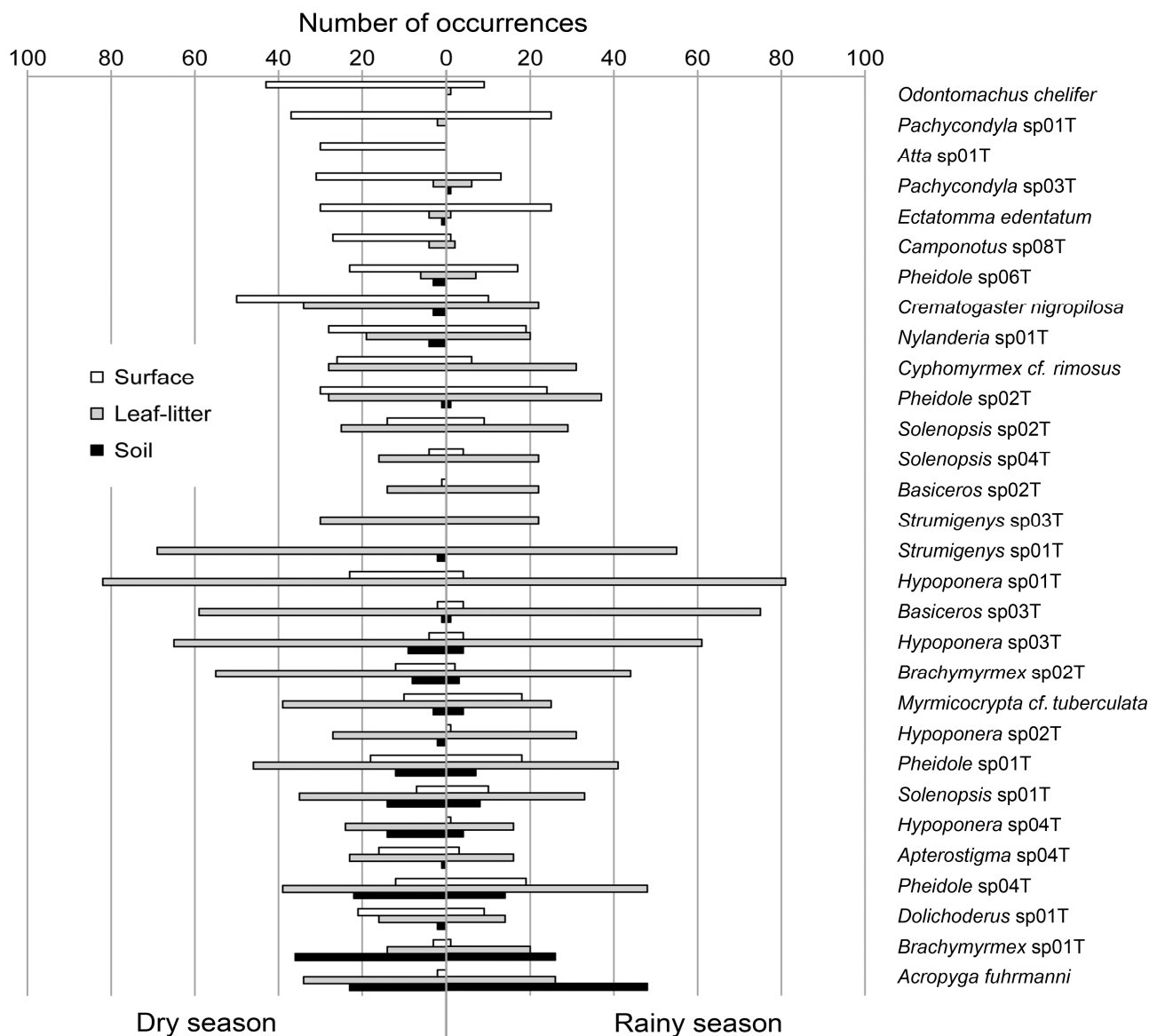


Fig. 4: Number of occurrence of the most common species (present in $\geq 20\%$ of samples, at least in one layer and during one season), during the dry and rainy seasons. Species in the upper part were mostly found on the ground surface, species in the middle mostly in the leaf-litter layer and species in the lower part were predominant in the soil layer.

compared that value to the observed number of significant results.

Results

Seasonal variability of the ant assemblage structure

We observed 161 ant species and 1829 occurrences along the transect during the dry season and 134 species and 1498 occurrences during the rainy season, all layers pooled. We sampled more species in each layer, and also when pooling all layers, during the dry season than during the rainy one (Tab. 1). Rarefaction curves show that, for a similar number of occurrences, species richness was higher during the dry season than during the rainy one, in both leaf-litter and soil layers (Fig. 2).

ANOSIM revealed a significant seasonal difference regarding the specific composition of the ant fauna caught on surface ($R = 0.13$, $p \leq 0.0001$), in leaf-litter ($R = 0.04$,

$p \leq 0.0001$), in soil ($R = 0.07$, $p \leq 0.0005$), and when the three layers were pooled ($R = 0.09$, $p \leq 0.0001$) (Fig. 3).

The species contributing the most to the faunal dissimilarity in surface samples between dry and rainy season were *Atta* sp01T, *Crematogaster nigropilosa*, and *Ectatomma edentatum* (17.3% contribution to dissimilarity, three species pooled, SIMPER analysis). The occurrence of *Atta* sp01T and *C. nigropilosa* decreased strongly during the rainy season compared to the dry season (Fig. 4). The species contributing the most to the faunal dissimilarity in leaf-litter samples between seasons were *Hypoconera* sp03T, *H. sp01T*, and *Basiceros* sp03T (16.1% contribution, pooled). In soil samples, *Brachymyrmex* sp01T, *Acropyga fuhrmanni*, and *Pheidole* sp04T contributed together to 48% of the faunal dissimilarity observed between dry and rainy season. The occurrence of *A. fuhrmanni* doubled from dry to rainy season (Fig. 4).

Tab. 2: R and p values of the ANOSIM performed to test for vertical variation of the ant fauna: between all the layers (R and p global) and between the layers taken pair by pair (surface vs. leaf-litter, leaf-litter vs. soil, surface vs. soil), for both dry and rainy season.

	Dry season	Rainy season
R (global)	0.54	0.46
p (global)	0.0003	0.0003
R (surface vs. leaf-litter)	0.61	0.48
p (surface vs. leaf-litter)	0.0003	0.0003
R (leaf-litter vs. soil)	0.54	0.62
p (leaf-litter vs. soil)	0.0003	0.0003
R (surface vs. soil)	0.52	0.34
p (surface vs. soil)	0.0003	0.0003

Higher occurrences of species dominant on the ground surface were observed during the dry season. Similarly, higher occurrences of species dominant in the soil layer were observed during the dry season, except for *Acropyga fuhrmanni*, the dominant subterranean ant during the rainy season. Contrastingly, leaf-litter species occurrences were similar during both seasons. Some species, such as *Pheidole* sp04T, are ubiquitous, while other species are layer-specialist, such as *Strumigenys* sp03T found exclusively in the leaf-litter layer, and *Pachycondyla* sp01T caught mostly on the ground surface. No significant seasonal shift in layer preference was observed, except for *Crematogaster nigropilosa*, occurring mostly on ground surface during the dry season and in the leaf-litter layer during the rainy season ($df = 2$, $\chi^2 = 8.7$, $p = 0.013$), and *A. fuhrmanni*, predominant in the leaf-litter layer during the dry season, and in the soil during the rainy season ($df = 2$, $\chi^2 = 10.31$, $p = 0.006$) (Fig. 4).

Spatial variability of the ant assemblage structure

Vertical variation across layers: ANOSIM revealed distinct specific composition of the ant fauna between the layers, taken globally and pair by pair (surface vs. leaf-litter, leaf-litter vs. soil, and surface vs. soil), in both seasons (Tab. 2, Fig. 3).

Horizontal variation along the transect: Horizontal species turnover was more important during the rainy season compared to dry season on surface (One-way ANOVA: $F_{1,192} = 12.48$, $p = 0.0005$), and it was more important during the dry season in the soil (One-way ANOVA: $F_{1,140} = 10.58$, $p = 0.0014$) (Fig. 5).

The inter-seasonal spatial fidelity of the ant colonies was significant for two out of eight common and aggregated species in leaf-litter and soil. In leaf-litter, the spatial fidelity of the patches was verified for *Cyphomyrmex* cf. *rimosus* ($R = 0.25$, $p \leq 0.05$) and *Hypoponera* sp03T ($R = 0.53$, $p \leq 0.01$), and in soil for *Brachymyrmex* sp01T ($R = 0.38$, $p \leq 0.05$) (Fig. 6).

Association between environmental variables and ant species richness, abundance and distribution

The environmental factors did not differ significantly between the dry season and rainy season (One-way ANOVA:

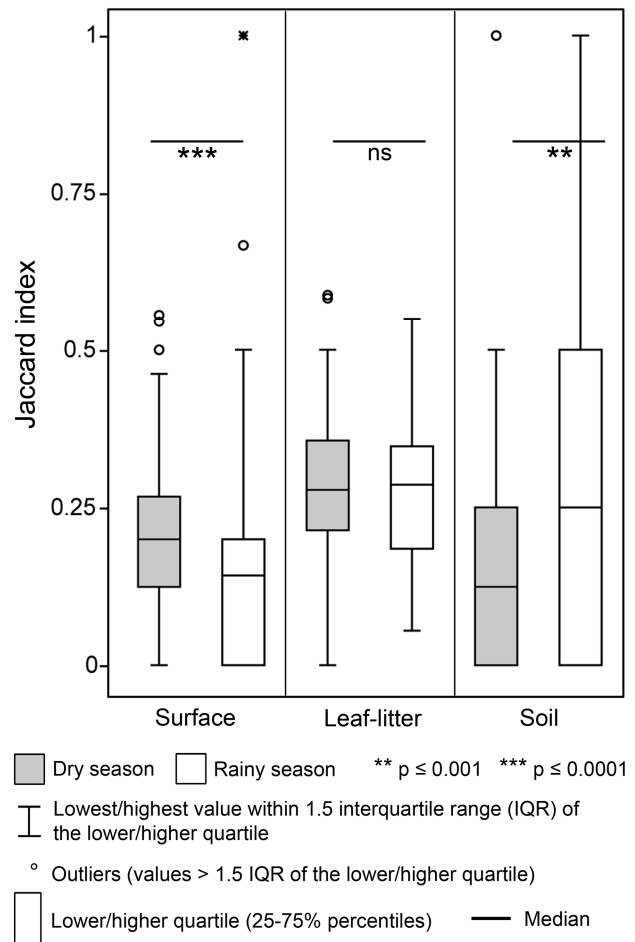


Fig. 5: Average species turnover (Jaccard index) within each layer during dry and rainy season. Species turnover is less important on ground surface and stronger in the soil layer during dry season.

$df = 1, 198$, $p > 0.05$ for slope, canopy openness (%), leaf-litter depth and leaf-litter volume).

Leaf-litter quantity (depth and volume) was strongly correlated with ant species richness and abundance collected in leaf-litter, in both seasons (Tab. 3). In soil samples, we found no correlation between ant species richness and abundance with any factors in any season. Ant species richness on the surface showed a negative correlation with canopy openness during the rainy season.

For the common ant species caught on the surface, we observed a negative correlation between the abundance of *Pheidole* sp02T and canopy openness both during the dry season ($R = -0.29$, $p \leq 0.0125$).

For leaf-litter ants, a series of positive and negative correlations was observed. During the dry season, three top-dominant species (i.e., occurring in $\geq 50\%$ samples, namely *Hypoconera* sp01T, *Strumigenys* sp01T, and *H.* sp03T) were all positively correlated with leaf-litter depth and volume ($0.35 \leq R \leq 0.52$, $p \leq 0.0125$). *Myrmicocrypta* cf. *tuberculata*, *Apterostigma* sp04T, and *Strumigenys* sp03T were also positively correlated to leaf-litter depth or volume ($0.29 \leq R \leq 0.48$, $p \leq 0.0125$). During the rainy season, only *H.* sp01T, *Strumigenys* sp01T, *Solenopsis* sp04T, and *Nylanderia* sp01T were positively correlated to leaf-litter volume ($0.38 \leq R \leq 0.45$, $p \leq 0.0125$). One species was

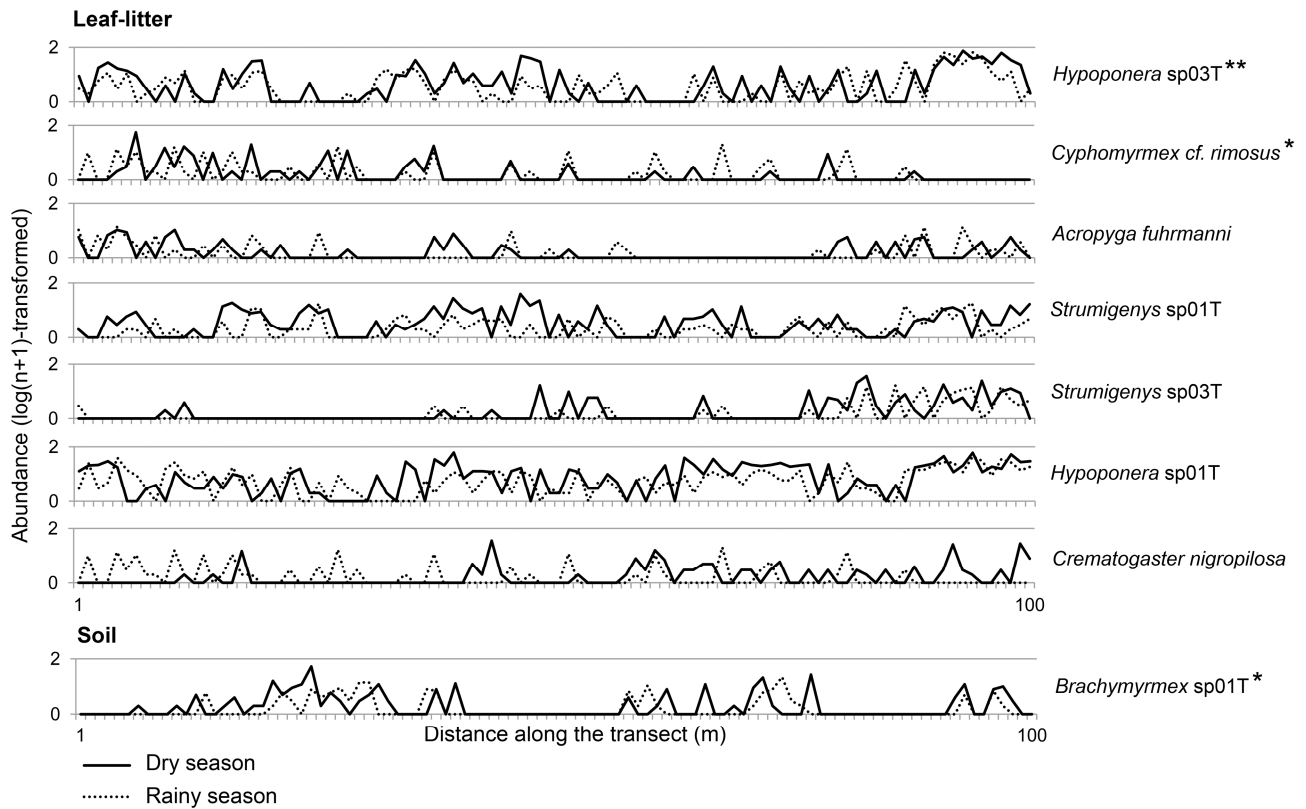


Fig. 6: Horizontal distribution of log-transformed abundance of common ant species foraging in leaf-litter and in soil, during the dry and the rainy season. Spatial fidelity of ant distribution from dry to rainy season was verified for the species marked with an asterisk (* $p \leq 0.05$, ** $p \leq 0.01$).

Tab. 3: For each season and each layer, we detailed R values of the correlation tests between 1 / ant species richness and each environmental factor; and 2 / ant abundance and each environmental factor. The tested environmental factors were land slope, canopy openness, leaf-litter depth and leaf-litter volume. Slope does not appear in the table because it yielded no significant correlation. Asterisks indicate significance level (* $p \leq 0.05$, ** $p \leq 0.01$), n.s. = non-significant.

		Species richness			Abundance ($\log_{10}(n+1)$ - transformed)		
		vs. canopy openness	vs. litter depth	vs. litter volume	vs. canopy openness	vs. litter depth	vs. litter volume
Surface	Dry season	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Rainy season	-0.297**	n.s.	n.s.	n.s.	n.s.	n.s.
Leaf-litter	Dry season	n.s.	0.412**	0.609**	n.s.	0.514**	0.657**
	Rainy season	n.s.	0.391**	0.470**	n.s.	0.245**	0.520**
Soil	Dry season	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Rainy season	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

positively correlated to canopy openness during the rainy season, *Brachymyrmex* sp01T ($R = 0.22$, $p \leq 0.0125$), and none during the dry season.

In the soil layer, no correlation was observed during the dry or the rainy season.

Associations between species

We found 20 pairs of species being significantly associated in the leaf-litter during the dry season (18 positive associations and two negative ones, $n = 18$ spp., i.e., 153 pairs of species tested; Appendix S3), a maximum of 12 of these associations – either positive or negative – being significant by chance (one-tailed binomial test against the expected 5% Type I error). The strongest positive associa-

tions ($p \leq 0.01$) were observed between *Strumigenys* sp01T and *Hypoponera* sp03T, *Strumigenys* sp01T and *Basiceros* sp03T, *Strumigenys* sp01T and *Apterostigma* sp04T, *H.* sp03T, and *B.* sp03T, *B.* sp03T and *Myrmicocrypta* cf. *tuberculata* and the strongest negative one was observed between *Solenopsis* sp02T and *Solenopsis* sp01T.

We found 22 pairs of species being significantly associated in the leaf-litter during the rainy season (16 positive associations and six negative ones, $n = 20$ spp., i.e., 190 pairs of species tested; Appendix S3), a maximum of 15 of these associations – either positive or negative – being significant by chance (one-tailed binomial test against the expected 5% Type I error). The strongest associations ($p \leq 0.01$) were all positive and were observed between

Strumigenys sp01T and *H.* sp03T, *Nylanderia* sp01T and *Strumigenys* sp01T, and *Strumigenys* sp03T and *Pheidole* sp01T.

We found no significant association (positive or negative) between common soil-dwelling ant species, in both seasons ($n = 3$ and 2 spp., i.e., 3 and 1 pairs of species tested, during the dry and rainy season, respectively).

Discussion

Ant species richness observed in our study site (1030 m a.s.l.) was high, with a total of 176 species collected along a 100 m-long transect (estimated total species richness = 199). In an ant inventory conducted in Ecuadorian mountains (850 m a.s.l.), DONOSO & RAMÓN (2009) collected 103 species and they estimated the richness to 109 species. When focusing exclusively on our $\frac{1}{4}$ m² Winkler samples, we found 97 and 109 species during the rainy and dry season respectively. This is comparable to the species richness of 113 observed by LONGINO & COLWELL (2011) in Costa Rica, at an elevation (1070 m a.s.l.) similar to ours. However, it should be noted that their sampling effort was higher, with 150 Winkler samples of 1 m² of leaf-litter spread over a surface of 1 km². Similarly, SILVA & BRANDÃO (2010), found between 91 and 110 species in southern Brazilian forests located between 700 and 1000 m a.s.l. Again, the surface area sampled was greater than ours, with 1200 m-long transect per forest. A much lower species richness than our study site was observed in Guyana at 1137 m a.s.l. (43 species, LAPOLLA & al. 2007) and in Venezuela at 1100 m a.s.l. (54 species, RODRÍGUEZ & LATTKE 2012). These comparisons emphasize the outstanding species richness of our study area, which is not only true for ants, but also for geometrid moths (BREHM & al. 2005), birds (PAULSCH & MÜLLER-HOHENSTEIN 2008) and plants and which is probably related to the landscape history and the high heterogeneity of the edaphic conditions (RICHTER & al. 2009).

The position of patches of common ant species along the transect changed little after a five month interval, suggesting that our sampling methods were not colony-destructive. This may be due to the small size of the samples ($\frac{1}{4}$ m² of leaf-litter and $15 \times 15 \times 10$ cm of soil), smaller than the colony extent of the common species. This may also be due to low rates of nest relocation. Nest relocation is a regular part of the life history of most ant species in tropical forests, particularly those nesting in leaf-litter (BYRNE 1994). Nest relocation events may be correlated, for instance, with shifts towards more favorable microclimatic conditions, local food depletion, avoidance of competitors or predators such as army ants, or nest deterioration (SMALLWOOD 1982, MCGLYNN & al. 2004, MCGLYNN 2012). The latter process could be slower in our study site because the turnover of organic matter in the organic layer has been shown to be slower in this area than in other tropical mountain forests (WILCKE & al. 2008). Moreover, our study site is located at 1030 m a.s.l., and it has been showed that leaf-litter decomposition rate (i.e., destruction of ant habitat) decreases with increasing elevation (VITOUSEK & al. 1994). An interesting research perspective would be to study the mobility of ant colonies along elevation gradients. However, without genetic data it is difficult to say if the same colony was maintained through time or if a new colony of the same species established in that area

because of local conditions meeting the requirements of the species.

Horizontal heterogeneity (i.e., species turnover) along the transect was substantial, with Jaccard index ranging from 0.14 to 0.28 between contiguous samples in each ground layer. We observed a strong vertical stratification in the ant fauna, with distinct specific composition, during both seasons, between the ground surface, the leaf-litter and the underlying soil. The ground surface is an interface between the leaf-litter / soil and the understorey / canopy strata, and pitfall traps reflect ant activity on this interface. The highest species richness was measured on the ground surface in November, parallel with an increase of species occurrences, suggesting an increased activity on the surface of the forest floor during the dry season. When comparing occurrence-based rarefaction curves of surface samples in both seasons, it appears that the dry and rainy season curves are superimposed. It indicates that the higher species richness observed during the dry season on ground surface is due to higher activity of ants and not to a richer pool of species. LEPONCE & al. (2004) observed the same seasonal effect on ant richness in an Argentinean subtropical dry forest and emphasized the importance of comparing the seasonal richness of an ant community for a similar number of occurrences. Parallel to this, for a similar number of occurrences, we observed an increase in species richness in the leaf-litter layer (+ 12.4%) and in the mineral soil (+ 41%) during the dry season. This suggests the migration of sensitive ant species into deeper layers of the ground matrix to avoid drought (LEVINGS 1983). LEVINGS & WINDSOR (1984) showed that ant colonies could move into wetter areas during the dry season, ant brood being prone to desiccation.

We also measured a strong seasonal effect on the taxonomical composition of each layer. This was mainly due to seasonal changes in the occurrence of dominant species, similar to what was shown in a Brazilian secondary forest in the dry and wet season by NEVES & al. (2010). In surface samples, species being dominant during the dry season such as *Crematogaster nigropilosa* and *Odontomachus chelifer* dramatically decreased or totally disappeared during the rainy season. For the subterranean ant fauna, the occurrence of *Acropyga fuhrmanni* doubled from the dry to the rainy season. Although no seasonal shift in layer preference was observed for the majority of species, *C. nigropilosa* and *A. fuhrmanni* occurred predominantly in distinct layers according to season. This may be due to seasonal changes in the availability of resources they rely on for feeding (mainly extra-floral nectaries for *C. nigropilosa* (see LONGINO 2003) and subterranean coccids for *A. fuhrmanni* (see FLANDERS 1957, SCHNEIDER & LAPOLLA 2011)), forcing them to switch to alternative resources in other foraging layers (COOK & al. 2011).

We investigated the relation between the environmental factors and ant richness and abundance along the transect. The negative correlation between ant diversity and canopy openness during the rainy season, and also the lower success of pitfall traps, suggest that the ants foraging on the ground surface are sensitive to heavy rains, as suggested by DEBLAUWE & DEKONINCK (2007). Ant abundance and richness were strongly correlated to leaf-litter depth and volume in leaf-litter samples. Species richness and abundance of subterranean ants was not correlated to any of the

factors we investigated, as has been previously shown (JACQUEMIN & al. 2012).

The common ant species had only a few negative or positive correlations with the environmental factors. On the surface layer, *Pheidole* sp02T was negatively correlated to canopy openness in both seasons, suggesting a preference for shade. Within the leaf-litter layer, the distribution of most dominant species was positively correlated to leaf-litter quantity, which makes sense since leaf-litter provides both food resources and nesting sites for ants (LEVINGS 1983). None of the subterranean species showed any correlation with environmental variables. Our results demonstrated that the ant fauna of each layer responded differentially to the environmental factors considered, and that these factors had a weak structuring effect on ant distribution. Type II error may explain the lack of significance, or other factors that we did not consider may have a structuring effect on ant distribution, such as microclimatic factors (e.g., temperature or moisture content) induced by discontinuity in the canopy cover or soil texture (VASCONCELOS & al. 2003). Nutrients and micronutrients availability may be patchy and play a role in shaping the assemblage distribution through bottom-up effects (MCGLYNN & al. 2007, MCGLYNN & al. 2009). Rather than local favorable abiotic conditions, biological factors may play a structuring role, such as intraspecific competition, reflected by spatial gaps between colonies (THEUNIS & al. 2005). The patchy distribution may be related to the distance of dispersion of sexuals from the natal nest which may differ between species, or to the different mechanism of new colony establishment, e.g., by fission versus independent colony foundation (PEETERS & MOLET 2009). However, the biology of these species has not been studied so far. Interspecific competition has been proposed as a structuring factor in ant communities (see review in CERDÁ & al. 2013), however, we found only one strong negative association (*Solenopsis* sp01T vs. *Solenopsis* sp02T) between ants collected in the leaf-litter. They may exclude each other, or, alternatively, they may exhibit distinct preferences for a factor that we did not measure. Together our data demonstrates little structuring effect of interspecific competition in the ground-dwelling ant assemblage, where foraging ranges may overlap considerably, consistent with SOARES & SCHOEREDER (2001) and THEUNIS & al. (2005). To understand the importance of biotic interactions in determining ant distribution patterns, further studies should focus more on microhabitat and food resources and the role of predators and parasites in limiting ant abundance.

In conclusion, our results showed a strong horizontal (along the transect), vertical (across layers), and seasonal heterogeneity of the ant assemblage. However, several common species showed stable patches through time, suggesting low nest relocation rates for these species. Higher ant species richness and occurrence found on the surface and in the soil suggested a peak of activity on the surface of the forest floor during the dry season and the migration of drought-sensitive species downwards deeper in the soil. Ant richness was related to distinct environmental factors according to the layer considered. Similarly, the distribution of ant species was correlated to distinct factors in each layer, with, for instance, strong correlations between leaf-litter quantity and dominant ant distribution in the leaf-litter layer, while we found no correlation with any factor

in the soil layer. Our results emphasize the importance of distinguishing layers among the ground matrix, since both ant faunas and their response to environmental factors vary vertically and seasonally.

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