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Distribution of epigeic and hypogeic ants (Hymenoptera: Formicidae) in ombrophilous forests in the Brazilian Amazon

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Abstract

In the Amazon basin, ants are often associated with environmental or edaphic factors. However, these associations may vary between the epigeic and hypogeic strata. Here, we investigated differences in richness and composition of epigeic and hypogeic ant assemblages along an environmental gradient in the Brazilian Amazon. The four studied sites cover different topographic and soil characteristics. We sampled 25 plots of 250 m^2 using 10 samples of epigeic pitfalls and 10 samples of hypogeic pitfalls installed at two depths (10 and 30 cm). The pitfalls remained in the field for 48 hours. In the same plots, soil clay content and terrain altitude were also measured. We collected 219 species or morphospecies, of which 14 were exclusively hypogeics. We found higher local richness in the epigeic compared to hypogeic assemblages. We also found an interaction between clay content and strata for ant species composition. Overall, the species turnover was related to clay content, but the effect depended on the strata, with hypogeic fauna being more heterogeneous, compared with epigeic fauna. Despite the relationship between clay content and ant´s assemblage's composition, we did not find strong environment predictors for both strata, which suggests that other factors may structure ant assemblages in these sites. This reinforces the need for studies to define which environmental gradient determines the distribution of Amazonian epigeic and hypogeic ants.

Introduction

The soil harbors a large diversity of invertebrates that coexist in small areas, utilizing resources and occupying microhabitats above and below the surface (Lavelle, 1996; Ettema & Wardle, 2002; Nielsen et al., 2010). Most soil invertebrates have relatively short life spans and respond to slight changes in edaphic environments, such as soil humidity and physical properties (Stork & Eggleton, 1992; Moldenke et al., 2000; Bardgett, 2002). In addition, the soil fauna can modify the surrounding environment and increase its value to other organisms (Stork & Eggleton, 1992; Lavelle et al., 1997).

Among invertebrates, ants are considered good indicators of changes in terrestrial environments (Folgarait, 1998; Andersen & Majer, 2004; Underwood & Fisher, 2006),

and are relatively easy to collect and identify (Majer, 1983; Alonso & Agosti, 2000). Ant diversity and abundance can be affected locally by food resource availability and microhabitat specificities for colony establishment, which, with few exceptions, are stationary (Kaspari & Weiser, 2000; Armbrecht et al., 2004). The distribution of nests in the tropical forest leaflitter is often gregarious, where ground-dwelling ants concentrate their activities on resource patches and may respond to variation in edaphic factors, litter cover, humidity, vegetation cover and composition (Levings & Franks, 1982; Kaspari & Weiser, 2000; Soares & Schoereder 2004; Vasconcelos et al., 2003). However, these environmental factors may not affect all ant species in a similar manner. For instance, hypogeic ant species usually nest, forage and migrate in below ground (Silva & Silvestre; 2004; Rabeling et al., 2008),

and have a number of characteristics related to low light environments and restricted space for movement (Fowler & Delabie, 1995; Weiser & Kaspari, 2006). These features include small body size, relatively short legs and narrowed body, smaller or absent eyes (often present only in the form of eyespots), and cuticle pallor (Rabeling et al., 2008; Andersen & Brault, 2010; Silva & Brandão, 2010). Hypogeic ants may also respond to variation in soil properties (Oliveira et al., 2009) or soil-related variables, such as water-table fluctuation (Baccaro et al., 2013). However, some studies have not detected any effect of soil properties on underground ants (e.g. Jacquemin et al., 2012).

In central Amazonia the topography is closely-related to soil properties, where the bottomlands (valleys) harbor sandy soils and higher areas (plateaus) have soil with higher clay content (Chauvel et al., 1987). Topographic variation also influences soil moisture and forest cover (Ranzani, 1980; Luizão et al., 2004), which are good predictors of the distribution of epigeic ant assemblages in the Amazon (Vasconcelos et al., 2003; Oliveira et al., 2009) and how ants interact with other organisms (Dáttilo et al., 2013). These edaphic variables are related to primary production and the availability of nesting sites (Vasconcelos et al., 2003; Luizão et al., 2004; Kaspari & Yanoviak, 2008).

Soil type, texture and moisture can structure epigeic and hypogeic myrmecofauna, these factors are linked with soil compaction and gas exchange in soil organisms (Ettema & Wardle, 2002; Decaëns, 2010). However, these factors may have different effects depending on the guild or microhabitat studied (Austin, 1985). Several papers have already indicated strong differences between epigeic and hypogeic ant fauna (Fowler et al., 2000; Andersen and Brault, 2010; Ryder Wilkie et al., 2007; Martins et al., 2020), which could lead to different responses even when subjected to similar environmental gradients (Wilkie et al., 2010). However, most of the information on the effect of environmental gradients comes from ground-dwelling ants (e.g. Vasconcelos et al., 2003; Oliveira et al., 2009; Gomes et al., 2018), so the knowledge regarding how hypogaeic ants are distributed along environmental gradients is still incipient (Jacquemin et al., 2012).

Here, we investigated the responses of epigeic and hypogeic ant assemblages (richness and composition) associated with edaphic gradients in four sites in the Brazilian Amazon. We expected a strong difference between hypogeic and epigeic ant species richness and composition, which could be correlated with different environmental predictors. Specifically, we hypothesized interaction between edaphic factors (clay content and elevation) with strata (epigeic and hypogeic) for ant species richness and composition.

Material and Methods

Study sites

We investigated the distribution of epigeic and hypogeic ant richness and assemblage composition in four sites associated with the Brazilian Biodiversity Research Program (PPBio). These four sites are distributed along ~ 450 km, with a minimum distance of 50 km from one another, covering different topographies, soil characteristics and phytophysiognomies. The Rio Amazonas, separate the UFAM from the other three sites, which are located along the BR-319 highway (Figure 1). All sites have seasonal rainfall, with rain concentrated from October to March (De Marques-Filho et al. 1981). Coordinates, vegetation type, elevation range, rainfall and spatial layout of the study sites are summarized in Table 1.

Fig 1. Location of the four sampling sites in the Brazilian Amazon.

Sampling design

Ants were sampled in permanent plots with ten samples each using the two sampling techniques. In total, we took 500 samples from 25 plots (Table 1). We used the RAPELD sampling design, which is based on a system of trails and permanent plots where a diverse range of taxa can be sampled (Magnusson et al. 2005, 2013; Costa and Magnusson 2010). The permanent plots are 250 m² (250 m x 1 m) and positioned to follow terrain contours to minimize the effects of topographical variation within plots. In each site, plots were 1 km distant from each other. The number of 250-m long sampled plots varied between areas (Table 1), but all had the same standardized spatial design and were subject to the same sampling effort.

Table 1. Vegetation, rainfall, elevation range, number of samples and sampling techniques in four sites in the Brazilian Amazon.

Sites	UFAM	Orquestra	Capanã	Jari
Coordinates	02°38'26.51"S	04°59'2.39"S	05°36'36.00"S	05°58'11.99"S
	60°5'44.55"W	61°34'30.00"W	62°12'0.00"W	62°29'24.00"W
Vegetation type (number of 250-m long plots)	Dense ombrophilous forest (27)	Dense ombrophilous forest (5)	Dense ombrophilous forest (5)	Dense ombrophilous forest (5)
Elevation range (m.a.s.l.)	42-130	36-61	70-72	70-72
Mean rainfall (mm)	2362	2200	2200	2200
Sampling-grid area (km2)	24	5	5	5
Number of plots with Pitfall traps	10	5	5	5
Number of plots with hypogeic traps	10	5	5	5
Total of samples	200	100	100	100
Sampling date	September/2011	November/2010	November/2010	November/2010

Ant sampling and identification

Epigeic ants were sampled with pitfall traps, consisting of plastic containers (6.5 cm diameter, 8 cm high, 500 ml volume) installed at ground level. The pitfall traps contained 70% alcohol to preserve the collected material and a few drops of detergent to decrease surface tension. The traps remained in the plots for 48 hours (Souza et al., 2012). One pitfall-trap was installed in the ten sampling points in each plot.

Hypogeic ants were sampled using underground traps with canned commercial sardine oil as bait. These traps shared the basic features of the traps used by Andersen and Brault (2010) and Schmidt and Solar (2010). The underground traps used were composed of a plastic tube, 12 cm long, 3 cm in diameter and 50 ml volume (Figure 2A). All tubes had 12 holes in their sides randomly positioned in their upper portion. Each underground trap had an attractive bait inside. The traps were filled with 15 ml of 70% alcohol mixed with detergent. Using an auger, two underground traps were installed, one above the other. One trap was installed at approximately 10 cm and the other at 30 cm below the soil surface (Figure 2B). Thus, a total of 20 traps were installed, distributed at two different depths, at the 10 sampling points in each plot (Figure 2C). In the data analysis, the underground traps arranged on top of each other were combined and treated as a single sample. In order to standardize the sampling time, these traps remained buried for 48 hours (the same time as the pitfall-traps), according to the technique used by most studies with hypogeic ants (Wong & Guénard, 2017).

Ants were identified at genus level using the keys provided in Baccaro et al. (2015). Later, this material was identified by morphospecies or species whenever possible, using available taxonomic keys, comparison with material previously identified by specialists and deposited in National Institute of Amazon Research (INPA) entomological collections.
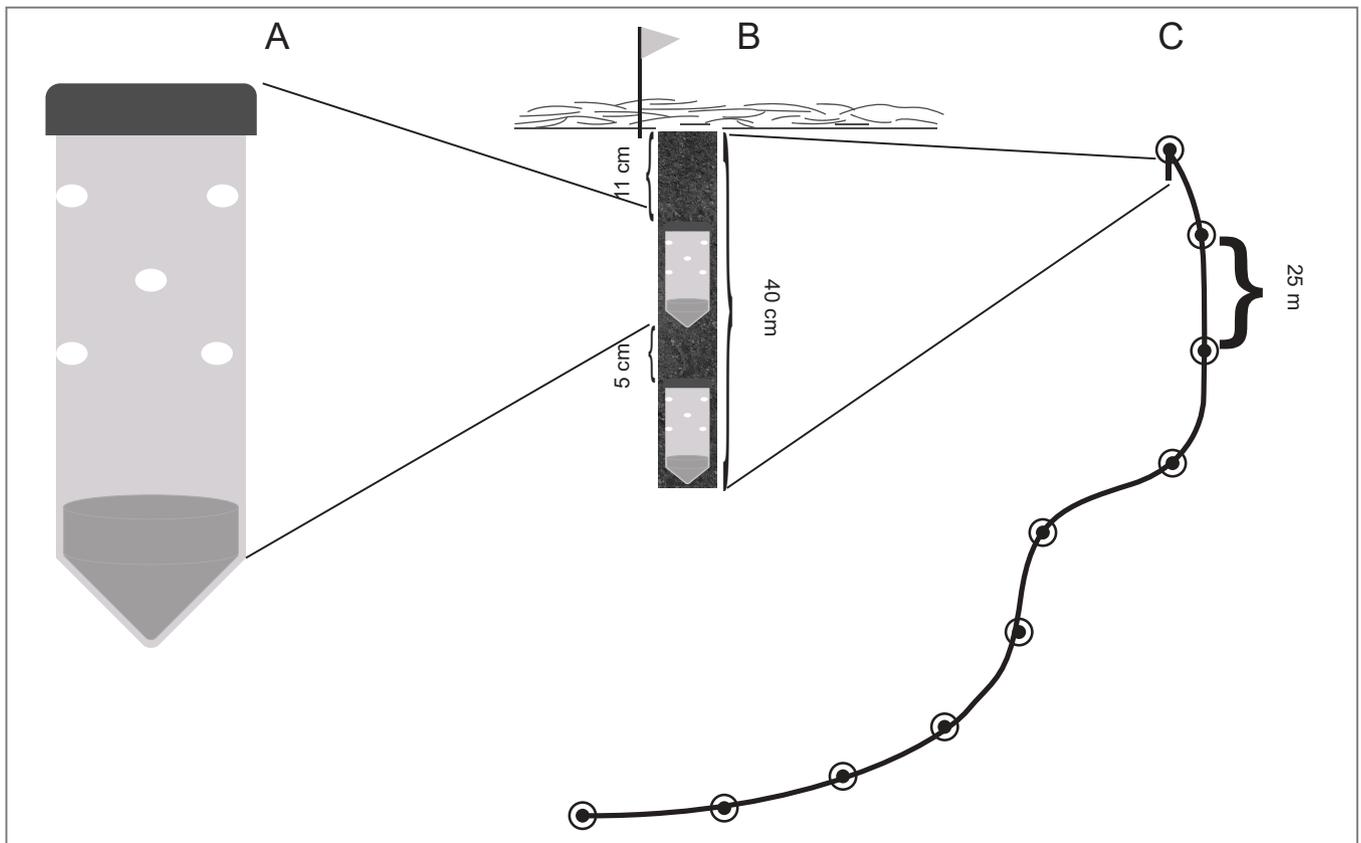
Fig 2. Representation of the collection trap and sampling unit for underground ants collection. (A) Underground trap with lateral holes; (B) Trap positioning below the surface; (C) Plot with 250 m contour line with 10 sub-sampling units installed at ombrophilous forests in the Brazilian Amazon.

Environmental predictors

We used clay content and elevation as environmental predictors due to their influence on the distribution of ground-dwelling ants in previous studies in the Amazon basin (Vasconcelos et al., 2003; Oliveira et al. 2009; Gomes et al., 2018). Along each of the permanent plots, soil samples were collected at six points 50 m apart. The samples were collected up to 20 cm deep after removal of the leaf litter and large roots. The six individual samples were mixed, yielding a sample representing the plot, of which 500 g was separated for particle size analysis. After dispersion with sodium pyrophosphate, the clay percentage was determined by drying 20 μm of the suspension in an oven at 105 ºC (http://ppbio.inpa.gov.br/knb/metacat). The altitude above sea level (m.a.s.l.) of the plots was obtained from GPS (Global Positioning System) data taken at the start of each plot. These data are available on the PPBio website (http://ppbio.inpa.gov.br/repositorio/dados).

Data analysis

Information about ant diversity and environmental factors were summarized to plot level in the analysis. Ant species richness was evaluated in two forms, first considering the observed richness and then by comparing the species accumulation curves (Colwell & Coddington, 1994) of the epigeic and hypogeic strata at each site. The accumulation curves (interpolation and extrapolation) were based on 1000 randomizations and order zero of Hill number (q = 0). A matrix of occurrence of species per plot was generated to minimize the possible effects of ants' colonial habitats. Several ant species have mass foraging strategies and their nests, or foraging/displacement trails (e.g. Dorylinae) may be close to the sampling point (Hölldobler & Wilson, 1990; Brühl et al., 2003). Thus, the number of each species occurrence varied between zero and ten at each plot. We used a Linear Mixed Model (LMM; Laird & Ware, 1982) to investigate the interaction effect of strata (epigeic and hypogeic) with clay content and strata with elevation on observed ant species richness per plot. The study sites were included as a random factor in the model to control for possible spatial autocorrelation of the data. In cases when the interaction term was non-significant, a simpler model without interaction was fitted. Both clay content and elevation were scaled to zero mean and unit variance to increase model convergence. We also calculated the conditional and marginal R^2 for the LMM model to measure the importance of the random variable (site). Conditional R^2 gives the variation explained by fixed and random effects, while Marginal R^2 indicates the variation explained by the fixed effects only (Nakagawa & Schielzeth, 2013).

We used Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001) to investigate

the interaction effect of strata (epigeic and hypogeic) with clay content and the interaction of strata with elevation on ant assemblage composition. We created a stratified permutation procedure to keep the nested structure of the data (plots nested in sites) in the PERMANOVA to control for possible spatial autocorrelation of the data. We also built simpler models when the interaction terms were non-significant. The PERMANOVA probability values were based on 999 permutations.

To further understand the composition patterns, we used the homogeneity of multivariate group dispersions analysis (PERMDISP, Anderson 2006), to test the homogeneity of species composition between strata. PERMDISP is a multivariate analog of Levene's test for homogeneity of variances, based on permutations. The PERMDISP probability values were based on 999 permutations. All analyses were run in the R environment for statistical computing (R Core Team, 2019, version 3.6.1), using the packages vegan 2.5-5 (Oksanen et al., 2019), nlme 3.1-142 (Pinheiro et al., 2019) and iNEXT 2.0.19 (Hsieh et al., 2019).

Results

We sampled 219 species/morphospecies of ants belonging to 52 genera and eight subfamilies. *Ectatomma lugens* was more frequent in epigeic pitfalls, occurring in 20 (80%) plots sampled. *Solenopsis* sp. 04 was the most frequent species sampled in the hypogeic traps, being detected in 10 (40%) plots of the total plots sampled. At the other extreme, 49.3% of the taxa were rare, as they occurred only once

(singleton: 84 taxa), or only twice (doubleton: 36 taxa) in the studied sites (Table 2). At UFAM, 106 taxa (65.7% of the total) were sampled only from the epigeic stratum, five (4.3%) were restricted to the hypogeic stratum and eight taxa (6.8%) were recorded in both epigeic and hypogeic strata. In BR-319 modules, at Orquestra (km 300) 85 taxa (84.5%) occurred exclusively in the epigeic stratum, ten (9.7%) only in the hypogeic stratum and eight (7.8%) were recorded from both strata. At Capanã (km 400) 90 taxa (84.1%) occurred exclusively in the epigeic stratum, nine (8.4%) only in the hypogeic stratum and eight (7.5%) were recorded from both strata, and in Jari (km 450) 85 taxa (78%) occurred exclusively in the epigeic stratum, 15 (13.8%) were found only in the hypogeic stratum and nine (8.3%) were recorded from both strata (Table 2).

Species accumulation curves did not reach the asymptote at the four sites studied for either strata (Figure 3). The epigeic ant richness (112 taxa in the UFAM, 93 taxa in the Orquestra, 98 taxa in the Capanã and 94 in the Jari) was higher than the hypogeic richness (13 taxa in the UFAM, 18 taxa in the Orquestra, 17 taxa in the Capanã and 24 in the Jari).

Ant species richness differed between the epigeic and hypogeic strata (LMM: $p < 0.001$), but was not related to clay content ($p = 0.725$) or elevation ($p = 0.261$). As both interaction terms (strata x clay and strata x elevation) were not significant, both interactions were removed from the analysis. The strata explained a large amount of ant species richness variation (marginal $R^2 = 0.85$), with relatively little variation explained by fixed and random factors, sites in our case (conditional $R^2 = 0.91$).
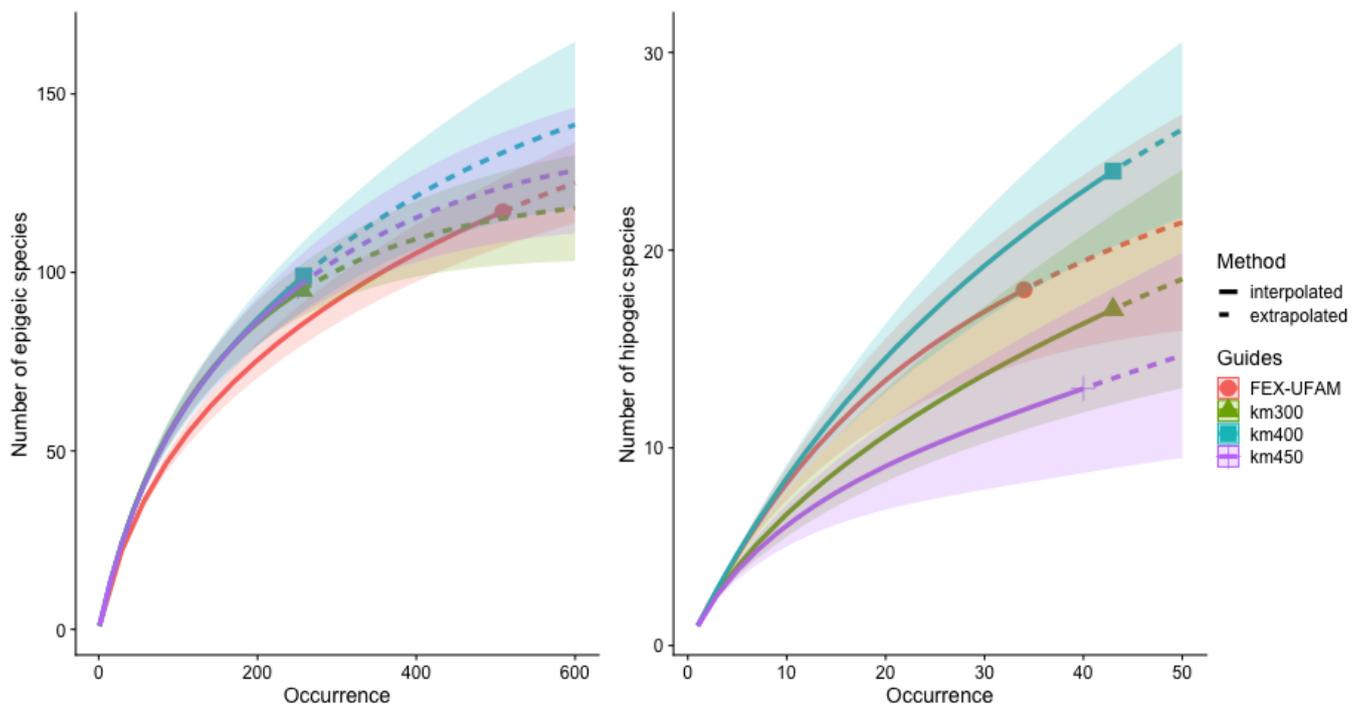

Fig 3. Species accumulation curves based on 1,000 randomization of FEX-UFAM and BR-319 modules samples, representing the epigeic and hypoggeic strata. Shaded area represent the standard deviation of the richness average.

The interaction between strata and clay content explained most of ant species composition variation (PERMANOVA: $F_{3,46}$ = 6.471; R^2 = 0.22; p < 0.001, Figure 4), compared with elevation alone ($F_{3,46}$ = 6.471; R^2 < 0.01; p = 0.995). The interaction term between strata and elevation was not significant and was removed from the analysis. The homogeneity of group dispersion was also different between strata, with epigeic fauna being more heterogeneous, compared with pigaeic fauna (PERDISP: $F_{1,45}$ = 26.936, P < 0.001; Figure 4).
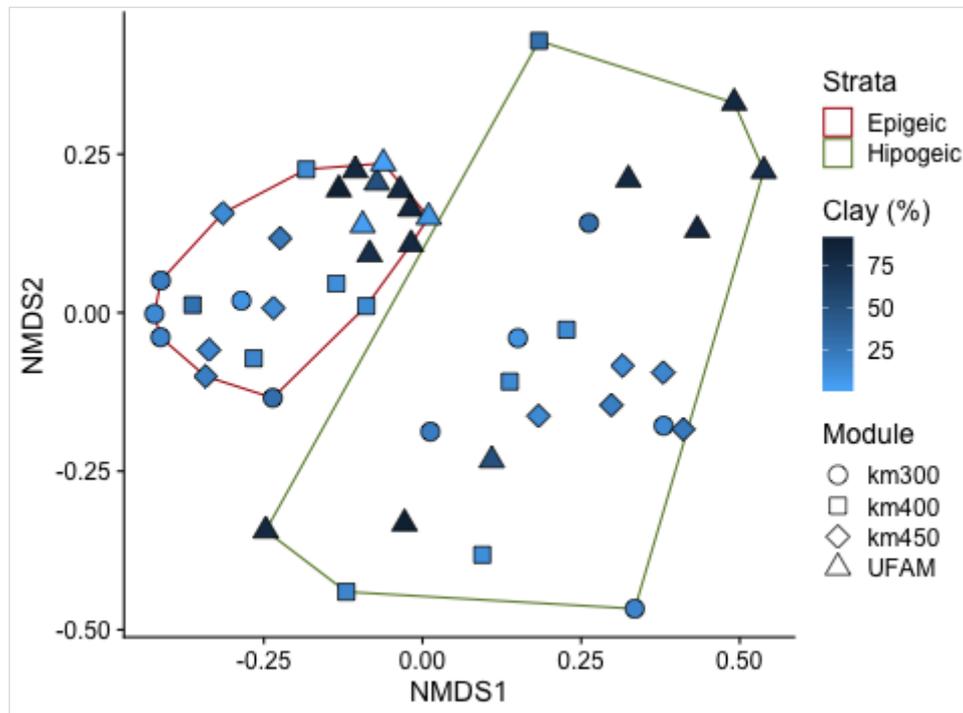

Fig 4. An NMDS ordination (Stress = 0.151) plot indicating the congruence in ant assemblages associations among sudied sites and the sampling strata in 47, 250-m long plots in ombrophilous forests in the Brazilian Amazon. Polygons delimit the epigeic and hypogeic strata and the color variation represents the clay gradient.

Discussion

Even with a minimum distance greater than 50 km and possible geographic barriers (Amazon and Negro rivers) between the sampling sites, the ant richness and composition of the epigeic strata were more similar when compared to those collected in different strata (epigeic and hypogeic) separated by only 20 to 30 cm. Due to the particularities of each stratum, differences in ant richness were expected. Previous studies in an Ombrophilous Forest near Manaus (Vasconcelos & Delabie, 2000), in the Ecuadorian Amazon (Wilkie et al., 2010) and in Southern Region of Brazil (Martins et al., 2020) found higher number of ant species on the soil surface. However, this pattern is not always present. Studies in a tropical forest in Borneo (Berghoff et al., 2003) and in Araucaria forest fragments in southern Brazil (Silva & Silvestre, 2004) did not detect differences in number of species between the strata. This may indicate that other factors such as soil type and vegetation may affect ant richness.

The rarefaction curves show the low contribution of the hypogeic ants to total species richness. Thus, hypogeic ants need more samples to reach the expected number of species when compared to epigeic ants. In addition, the large variance around the mean and the low average richness values per plot indicate that hypogeic ants were relatively more under sampled compared to epigeic ants. More plots or more subsamples per plot could increase the record of more cryptic species, which would lead to an increase in the average richness of hypogeic species. In addition, the lower local hypogeic richness of each site may be related to the bait (sardine oil) used in the underground traps. This bait generally mobilizes dominant ants, which exclude other species of subordinate ants, thus limiting a more accurate richness estimation (Baccaro et al., 2012). In this context, *Solenopsis geminata* and *Solenopsis* sp. 04 dominated four of the five plots in the Capanã site (km 450 of the BR-319 highway), preventing another subordinate species from reaching the underground traps. In addition, the bait may not have mobilized ants with more restricted and/or distinct foraging habits (Delabie & Fowler, 1995; Berghoff et al., 2003). An example of restricted behavior is the *Acropyga* species, which was recorded only once (at Orquestra); species from these genera are associated with specialized root Hemiptera and are not attracted to sardine

bait (Delabie & Fowler, 1995; LaPolla et al., 2002). Thus, the species assemblage captured underground in our samples were probably the most abundant, opportunistic, generalist and active in this stratum (Fowler et al., 2000; Andersen & Brault, 2010).

The difference in species composition between the epigeic and hypogeic strata of the four sampling sites indicates a strong stratification of the ant assemblage. Partitioning of ant assemblages into epigeic and hypogeic strata is often reported (Fowler et al., 2000; Vasconcelos & Delabie, 2000; Silva & Silvestre, 2004; Wilkie et al., 2010; Wong & Guénard, 2017). As well as stratification between leaf litter and canopy assemblages, this difference in epigeic-hypogeic composition may be one of the causes of the high local diversity of ants in tropical forests (Benson & Harada, 1988; Brühl et al., 2003). Assemblage stratification is one dimension of resource partitioning among species in the environment (Schoener, 1974). For ants, stratification is related to nesting and foraging sites (Vasconcelos & Vilhena, 2006; Delabie & Fowler, 1995). However, there is an overlap in the exploitation of these resources, where ants that are usually associated with the epigeic stratum can fetch below-ground resources, and vice versa. The small fraction of species that occurs in both strata, 4.3% at UFAM, 9.7% at Orquestra (km 300), 8.4% at Capanã (km 400) and 13.8% at Jari (km 450), indicates that the overlap between epigeic and hypogeic assemblages is small. Even with a small overlap between these strata, some records are at least curious. *Azteca* sp. 01; *Ectatomma lugens* and *Crematogaster flavosensitiva* have characteristics of specimens that live on the surface and were recorded in both strata. *Prionopelta punctulata*, is a typically hypogeic species and was recorded only in the surface pitfall. Conversely, *Crematogaster* sp. 07 is a species with epigeic characteristics and was recorded only in the hypogeic stratum. These records suggest some type of contamination when installing the traps in the field.

Differences between assemblages collected in the epigeic and hypogeic strata were greater than dissimilarities caused by distance or geographical location. In our study, the sampling sites are separated by at least 50 km. In addition, one of the study sites (UFAM) is separated from the others (along the BR-319 highway) by the Amazon and Negro rivers at a distance greater than 300 km. A similar result was reported between secondary and primary forests in the Amazon and Atlantic Forest in Bahia (Fowler et al., 2000; Wilkie et al., 2007). This reinforces the role of soil as a dominant vertical barrier in the separation of ant assemblages between strata. Large geographical barriers such as sizeable rivers in the Amazon basin are often cited to support hypotheses about limiting dispersal for birds, primates, amphibians and squamates (Dias-Terceiro et al., 2015; Moraes et al., 2016). However, a recent study refutes this hypothesis for a wide variety of taxa in the Amazon region, suggesting that other processes are also acting on dispersion processes (Santorelli Jr et al., 2018). Our results are in line with the latter, suggesting that large rivers are not strong barriers to ant species. However, further studies using molecular data are needed to unravel the evolution of ant assemblages between riverbanks.

The altitude of the terrain was not able to explain the variation in the richness and species composition of the ants in the studied sites and strata. However, the clay content associated with the strata explained some variation (22%) in the ant assemblage composition. Clay content in the central Amazon, is often related to other environmental properties, such as soil moisture retention, vegetation composition and leaf cover, which may support different numbers of ant species in both the epigeic and hypogeic strata (Ranzani, 1980; Luizão et al., 2004, Oliveira et al., 2009). The influence of clay content and altitude on the assemblage composition of epigeic ant fauna is relatively well documented for the Amazon region (Vasconcelos et al., 2003; Oliveira et al., 2009; Gomes et al., 2018). The lack of effect of altitude on species richness and composition or the finding that an effect of clay content is only detected when associated with the strata at these study sites may be the result of the low variation in these predictors in our study. Studies of the Amazon basin that have detected an effect of clay content on the richness and composition of ants record greater amplitudes in this environmental variable (e.g. Vasconcelos et al., 2003; Souza et al., 2012; Gomes et al., 2018). Even though the four sites were distributed across ~ 450 km, we found low variation in clay content and altitude that may have attenuated the changes in ant's species richness and composition between plots.

The various soil types of the Amazonian forests are directly correlated with forest architecture and altitude gradient (Guillaumet, 1987; Costa & Magnusson, 2010). These environmental predictors are often associated with changes in ant assemblage structure (Vasconcelos et al., 2003; Oliveira et al., 2009, Gomes et al., 2018), and may have great practical importance, going beyond showing correlations between the numbers of taxonomic entities (Souza et al., 2016). Environmental predictors can be used to evaluate management decisions about sampling techniques employed (Souza et al., 2012, 2018) or the use of surrogates as a shortcut to assessing species diversity (Souza et al., 2016) or to optimize ant research protocols. However, their lack of effect on ant fauna indicates that there is still no universal distribution pattern. As the distribution of ants is quite different between strata (Andersen & Brault, 2010; Ryder Wilkie et al., 2010; Martins et al., 2020), it is probable that the factors determining the distribution of ants in the epigeic stratum are distinct from those that do so in the hypogeic stratum. This reinforces the relevance of future studies to clarify if and what environmental or biological factors affect the epigeic and hypogeic ant fauna, thus facilitating better prediction of the distribution of ants.

Table 2. Occurrence and frequency of ant species and morphospecies sampled in the hypogeic (10 plots) and epigeic (7 plots) strata at UFAM and on BR 319 modules Orquestra, Capanã and Jari (5 plots in both strata for each site).

Subfamilies / Taxon	FEX-UFAM		Orquestra (km 300)		Capanã (km 400)		Jari (km 450)		Frequence (%)
	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	
Amblyoponinae									
Prionopelta punctulata Mayr, 1866	2								4
Dolichoderinae									
Azteca sp. 01	1		1	1	1		2	1	14
Azteca sp. 02							1		2
Dolichoderus bidens (Linnaeus, 1758)			1						2
Dolichoderus bispinosus (Olivier, 1792)			2		2		2		12
Dolichoderus decollatus Smith, 1858							1		2
Dolichoderus sp. 02							1		2
Dolichoderus sp. 03			4		2				12
Dolichoderus sp. 05							1		2
Dolichoderus sp. 07					1		2		6
Dolichoderus sp. 10					1				2
Linepithema sp. 01			1						2
Dorylinae									
Acanthostichus sp. 02								1	2
Eciton burchellii (Westwood, 1842)	1								2
Eciton dulcium Forel, 1912	1								2
Labidus coecus (Latreille, 1802)	3	5						1	18
Labidus praedator (Smith, 1858)	4		2	1	1	1	3	2	28
Labidus spininodis (Emery, 1890)		1		1					4
Neivamyrmex sp. 03		1					1		4
Neivamyrmex sp. 07				2		2		2	12
Neivamyrmex sp. 08	1					1			4
Neivamyrmex sp. 09		1							2
Nomamyrmex esenbeckii (Westwood, 1842)					1				2
Ectatomminae									
Ectatomma edentatum Roger, 1863	8						1		18
Ectatomma lugens Emery, 1894	8	1	4		3		5	1	44
Gnamptogenys acuminata (Emery, 1896)	1		1		2		1		10
Gnamptogenys haenschi (Emery, 1902)	1								2
Gnamptogenys horni (Santschi, 1929)	6				1		1		16
Gnamptogenys moelleri (Forel, 1912)	1						1		4
Gnamptogenys tortuolosa (Smith, F., 1858)	4				1				10
Gnamptogenys sp. 06			1		3				8
Gnamptogenys sp. 11	1								2
Formicinae									
Acropyga sp. 02			1						2
Brachymyrmex longicornis Forel, 1907	1								2
Brachymyrmex sp. 02			2		1		2		10
Camponotus atriceps (Smith, 1858)					1				2
Camponotus balzani Emery, 1894			4		3		4		22
Camponotus femoratus (Fabricius, 1804)	2		2		2		2		16
Camponotus novogranadensis Mayr, 1870	1		1		3		2		14
Camponotus rapax (Fabricius, 1804)	1				1				4
Camponotus renggeri Emery, 1894			2		1		3		12

Table 2. Occurrence and frequency of ant species and morphospecies sampled in the hypogeic (10 plots) and epigeic (7 plots) strata at UFAM and on BR 319 modules Orquestra, Capanã and Jari (5 plots in both strata for each site). (Continuation)

Subfamilies / Taxon	FEX-UFAM		Orquestra (km 300)		Capanã (km 400)		Jari (km 450)		Frequence (%)
	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	
Formicinae									
Camponotus sp. 04			1						2
Camponotus sp. 06	2		1		1				8
Camponotus sp. 10					1				2
Camponotus sp. 16			3		2		3		16
Gigantiops destructor (Fabricius, 1804)			2						4
Nylanderia sp. 01	2		1		3		3		18
Nylanderia sp. 02	4		2		3		1		20
Nylanderia sp. 03	9		4		2		2		34
Nylanderia sp. 04		1			1	1			6
Nylanderia sp. 05	1		1						4
Myrmicinae									
Acromyrmex sp. 01					2		1		6
Acromyrmex sp. 03			4		5		5		28
Adelomyrmex sp. 01					1				2
Allomerus septemarticulatus Mayr, 1878							1		2
Apterostigma sp. 01	1				1				4
Atta sp. 01	2								4
Basiceros sp. 01	2								4
Blepharidatta brasiliensis Wheeler, 1915	8								16
Carebara urichi (Wheeler, 1922)	3	2				2		2	18
Carebara sp. 01	2	1	2	1		2		2	20
Carebara sp. 04						1			2
Cephalotes atratus (Linnaeus, 1758)	1		1		1				6
Cephalotes marginatus (Fabricius, 1804)					1				2
Cephalotes pusillus (Klug, 1824)			1						2
Cephalotes sp. 08							1		2
Crematogaster brasiliensis Mayr, 1878	9		2	1	1		1		28
Crematogaster flavomicrops Longino, 2003					1		1		4
Crematogaster flavosensitiva Longino, 2003			1		1	1	4		14
Crematogaster limata Smith, 1858	7		4		4		2		34
Crematogaster rochai Forel, 1903	1								2
Crematogaster sotobosque Longino, 2003	5		3		2		2		24
Crematogaster stollii Forel, 1885			1	1	1		1		8
Crematogaster tenuicula Forel, 1904	2	1							6
Crematogaster sp. 07								1	2
Cyphomyrmex sp. 01	1						2		6
Hylomyrma immanis Kempf, 1973			1						2
Megalomyrmex balzani Emery, 1894	2		1						6
Megalomyrmex cuatiara Brandão, 1990	1								2
Megalomyrmex goeldii Forel, 1912	3								6
Megalomyrmex leoninus Forel, 1885	1								2
Megalomyrmex sp. 01			2		3		1		12
Megalomyrmex sp. 02					1		3		8
Megalomyrmex sp. 03					1				2
Monomorium floricola (Jerdon, 1851)	1								2

Table 2. Occurrence and frequency of ant species and morphospecies sampled in the hypogeic (10 plots) and epigeic (7 plots) strata at UFAM and on BR 319 modules Orquestra, Capanã and Jari (5 plots in both strata for each site). (Continuation)

Subfamilies / Taxon	FEX-UFAM		Orquestra (km 300)		Capanã (km 400)		Jari (km 450)		Frequence (%)
	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	
Myrmicinae									
Myrmicocrypta sp. 01	2				1		1		8
Ochetomyrmex semipolitus Mayr, 1878	6		3		3	1	2		30
Octostruma balzani (Emery, 1894)			1		1		1		6
Octostruma iheringi (Emery, 1888)				1					2
Pheidole vorax (Fabricius, 1804)			1	1	1		1		8
Pheidole sp. 01			2						4
Pheidole sp. 02			2						4
Pheidole sp. 03			1						2
Pheidole sp. 04			1						2
Pheidole sp. 05			1				1		4
Pheidole sp. 06	3		4	1	3		4		30
Pheidole sp. 07			1		1				4
Pheidole sp. 08	2		2		3		1		16
Pheidole sp. 09			1						2
Pheidole sp. 10	7		3		2		2		28
Pheidole sp. 11	4		2				1		14
Pheidole sp. 12	1		2		1				8
Pheidole sp. 13			2						4
Pheidole sp. 14	1		3		3		2		18
Pheidole sp. 15	1		2		1		1	1	12
Pheidole sp. 16	1	1		2	1				10
Pheidole sp. 17			1						2
Pheidole sp. 18			1						2
Pheidole sp. 19	2		2						8
Pheidole sp. 20	6		4		3		3		32
Pheidole sp. 21						2			4
Pheidole sp. 22	1								2
Pheidole sp. 23			1		1				4
Pheidole sp. 26			1		4		3		16
Pheidole sp. 27	3		3		1		2		18
Pheidole sp. 28	3			1					8
Pheidole sp. 29	3								6
Pheidole sp. 30				2					4
Pheidole sp. 31	1							1	4
Pheidole sp. 32			2		1		1	1	10
Pheidole sp. 33	2		1		1				8
Pheidole sp. 35	2		1						6
Pheidole sp. 36					1				2
Pheidole sp. 37	1		2		2		2		14
Pheidole sp. 37a			1						2
Pheidole sp. 41					1				2
Pheidole sp. 42	7	1	3		3		4	1	38
Sheidole sp. 44							1		2
Pheidole sp. 46	1								2
Pheidole sp. 47			2				1		6
Pheidole sp. 48			1						2

Table 2. Occurrence and frequency of ant species and morphospecies sampled in the hypogeic (10 plots) and epigeic (7 plots) strata at UFAM and on BR 319 modules Orquestra, Capanã and Jari (5 plots in both strata for each site). (Continuation)

Subfamilies / Taxon	FEX-UFAM		Orquestra (km 300)		Capanã (km 400)		Jari (km 450)		Frequence (%)
	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	
Myrmicinae									
Pheidole sp. 49	1				1				4
Pheidole sp. 51	1		2		1		1		10
Pheidole sp. 52					1				2
Pheidole sp. 54	1	2	1					1	10
Pheidole sp. 56				1					2
Pheidole sp. 57								1	2
Pheidole sp. 59			1						2
Pheidole sp. 60	3		1		1				10
Pheidole sp. 71			1						2
Pheidole sp. 75			1				1		4
Pheidole sp. 76			2		2		1		10
Pheidole sp. 83					1				2
Pheidole sp. 87	1		2		1		3		14
Pheidole sp. 90	1								2
Pheidole sp. 91	2				1		1		8
Pheidole sp. 93	1								2
Pheidole sp. 94	2								4
Pheidole sp. 95	2								4
Pheidole sp. 96	1								2
Pheidole sp. 97	1				1		1		6
Pheidole sp. 98	2								4
Pheidole sp. 99	1								2
Pheidole sp. 100	1								2
Pheidole sp. 102	1								2
Pheidole sp. 105					1				2
Pheidole sp. 107	1								2
Pheidole sp. 120					1				2
Pheidole sp. 121							1		2
Pogonomyrmex sp. 02							1		2
Rogeria sp. 01							1		2
Rogeria sp. 02			2						4
Sericomyrmex sp. 01	1		3				2		12
Solenopsis geminata (Fabricius, 1804)			2	3	1	4	2	2	28
Solenopsis sp. 01		1		1				2	8
Solenopsis sp. 02							1		2
Solenopsis sp. 03	4		1		2		1		16
Solenopsis sp. 04	2			3		4	2	3	28
Solenopsis sp. 05	6			1	3	1	3	1	30
Solenopsis sp. 06			1		1		3		10
Solenopsis sp. 07	1								2
Solenopsis sp. 08					3		2		10
Solenopsis sp. 09	8								16
Solenopsis sp. 11						1		1	4
Solenopsis sp. 14	4					2		2	16
Solenopsis sp. 15					1	1	1		6

Table 2. Occurrence and frequency of ant species and morphospecies sampled in the hypogeic (10 plots) and epigeic (7 plots) strata at UFAM and on BR 319 modules Orquestra, Capanã and Jari (5 plots in both strata for each site). (Continuation)

Subfamilies / Taxon	FEX-UFAM		Orquestra (km 300)		Capanã (km 400)		Jari (km 450)		Frequence (%)
	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	Epigeic	Hypogeic	
Myrmicinae									
Strumigenys beebei (Wheeler, 1915)							1		2
Strumigenys denticulata Mayr, 1887	7		1		1		2		22
Strumigenys elongata Roger, 1863	1								2
Strumigenys trudifera Kempf & Brown, 1969							1		2
Strumigenys villiersi (Perrault, 1986)					2				4
Strumigenys zeteki (Brown, 1959)	2				1		2		10
Strumigenys sp. 01			3		5		2		20
Strumigenys sp. 05	1						1		4
Strumigenys sp. 11							1		2
Paratrachymyrmex sp. 01	4		1		2	1		1	18
Paratrachymyrmex sp. 02	1								2
Paratrachymyrmex sp. 03	2								4
Paratrachymyrmex sp. 05	2								4
Paratrachymyrmex sp. 06	4								8
Paratrachymyrmex sp. 07	1								2
Tranopelta sp. 01								1	2
Wasmannia auropunctata (Roger, 1863)	6				1		1		16
Wasmannia scrobifera Kempf, 1961	1								2
Ponerinae									
Anochetus diegenis Forel, 1912	2				1				6
Anochetus horridus Kempf, 1964	1								2
Centromyrmex sp. 01					1				2
Hypoponera sp. 01			1						2
Hypoponera sp. 07					1				2
Hypoponera sp. 08			1				1		4
Hypoponera sp. 09					3		3		12
Hypoponera sp. 11							1		2
Leptogenys wheeleri Forel, 1901	1								2
Mayaponera constricta (Mayr, 1884)	1		2		3		4	1	22
Neoponera apicalis (Latreille, 1802)	5		3		3		1		24
Neoponera commutata (Roger, 1860)	2								4
Neoponera obscuricornis (Emery, 1890)			3				2		10
Neoponera unidentata (Mayr, 1862)					1				2
Odontomachus caelatus Brown, 1976	1								2
Odontomachus haematodus (Linnaeus, 1758)	1						1		4
Odontomachus laticeps Roger, 1861			1		1		3		10
Odontomachus opaciventris Forel, 1899					1				2
Odontomachus scalptus Brown, 1978	1								2
Pachycondyla crassinoda (Latreille, 1802)	4		4		4		4		32
Pachycondyla harpax (Fabricius, 1804)	7						1		16
Pachycondyla impressa (Roger, 1861)			2				1		6
Mayaponera arhuaca (Forel, 1901)	1						1		4
Pseudomyrmicinae									
Pseudomyrmex sp. 02					1				2
Pseudomyrmex sp. 10			2		4		1		14

Acknowledgements

References

Alonso, L.E. e Agosti, D. 2000. Biodiversity studies, monitoring, and ants: An overview. In D. Agosti, J.D. Majer, L.E. Alonso e T.R. Schultz (Eds.), Ants: standard methods for measuring and monitoring biodiversity (pp. 1–8). Washington, D.C.: Smithsonian Institution Press.

Andersen, A.N. & Majer, J.D. (2004). Ants show the way down under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment, 2(6): 291–298. doi: 10.1890/1540-9295(2004)002[0292:ASTWDU]2.0.CO;2

Andersen, A.N. & Brault, A. (2010). Exploring a new biodiversity frontier: subterranean ants in northern Australia. Biodiversity and Conservation, 19(9): 2741–2750. doi: 10.1007/s10531-010-9874-1

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26: 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J. (2006). Distance-based tests for homogeneity of multivariate dispersions. Biometrics, 62: 245–253. doi: 10.1111/j.1541-0420.2005.00440.x

Armbrecht, I., Perfecto I. & Vandermeer. J. (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science, 304 (5668): 284–286. doi: 10.1126/science.1094981.

Austin, M.P. (1985). Continuum concept, ordination methods, and niche theory. Annual Review of Ecology and Systematics, 16: 39-61

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, R.I.O., Izzo, T.J., Souza, J.L.P. & Solar, R. (2015). Guia para os gêneros de formigas do Brasil. Manaus: Editora INPA, 388p. doi:10.5281/zenodo.32912

Baccaro, F.B., Souza, J.L.P., Franklin, E., Landeiro, V.L. & Magnusson, W.E. (2012). Limited effects of dominant ants on assemblage species richness in three Amazon forests. Ecological Entomology, 37: 1–12. doi: 10.1111/j.1365-2311.2011.01326.x

Baccaro, F.B., Rocha, I.F., del Aguila, B.E.G., Schietti, J., Emilio, T., do Veiga Pinto, J.L.P., Lima, A.P. & Magnusson, W.E. (2013). Changes in ground-dwelling ant functional diversity are correlated with water-table level in an Amazonian Terra Firme forest. Biotropica, 45: 755–763. doi: 10.1111/btp.12055.

Bardgett, R.D. (2002). Causes and consequences of biological diversity in soil. Zoology, 105: 367–374. doi: 10.1078/0944-2006-00072.

Benson, W.W. & Harada, A.Y. (1988). Local diversity of tropical and temperate ant faunas (Hymenoptera, Formicidae). Acta Amazonica, 18: 275–289.

Berghoff, S.M., Maschwitz, U. & Linsenmair, K. E. (2003). Hypogaeic and epigaeic ant diversity on Borneo: evaluation of baited sieve buckets as a study method. Tropical Zoology, 16: 153–163. doi: 10.1080/03946975.2003.10531192.

Brasil. (1978). Projeto RADAM BRASIL. Folha SB.20 Purus; geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Rio de Janeiro: Mineral, D.N.P., 566 p.

Brühl, C.A., Eltz T. & Linsenmair, K.E. (2003). Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation, 12(7): 1371–1389. doi: 10.1023/A:10236 21609102.

Chauvel, A., Lucas, Y. & Boulet, R. (1987). On the genesis of the soil mantle of the region of Manaus, central Amazonia, Brazil. Experientia, 43: 234–241. doi: 10.1007/BF01945546.

Costa, F.R.C. & Magnusson, W.E. (2010). The need for large-scale, integrated studies of biodiversity – the experience of the Program for Biodiversity Research in Brazilian Amazonia. Natureza & Conservação, 8: 3-10. doi: 10.4322/natcon.00801001.

Colwell, R.K. & Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B, 345: 101–118. doi: 10.1098/rstb.1994.0091.

Dáttilo, W., Rico-Gray, V., Rodrigues, D.J. & Izzo, T.J. (2013). Soil and vegetation features determine the nested pattern of ant-plant networks in a tropical rainforest. Ecological Entomology, 38: 374-380. doi:10.1111/een.12029

Decaëns, T. (2010). Macroecological patterns in soil communities. Global Ecology and Biogeography, 19: 287–302.doi: 10.1111/j.1466-8238.2009.00517.x

Delabie, J.H.C. & Fowler, H.G. (1995). Soil and litter cryptic ant assemblages in Bahiain cocoa plantations. Pedobiologia, 39: 423–433.

Dias-Terceiro, R., Kaefer, I.L., Fraga, R. & Lima, A. (2015). A matter of scale: historical and environmental factors structure anuran assemblages from the upper Madeira river. Biotropica, 47, 259–266. doi: 10.1111/btp.12197.

Ettema, H.C. & Wardle, D.A. (2002). Spatial soil ecology. Trends Ecology and Evolution, 17: 177–183. doi: 10.1016/S0169-5347(02)02496-5.

Folgarait, P.J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity Conservation, 7: 1221–1244. doi: 10.1023/A:1008891901953

Fowler, H.G. & Delabie, J.H.C. (1995). Resource partitioning among epigaeic and hypogaeic ants (Hymenoptera: Formicidae) of an abandoned Brazilian cocoa plantation. Ecologia Austral, 5: 117–124.

Fowler, H.C., Delabie, J.H.C. & Moutinho, P.R.S. (2000). Hypogaeic and epigaeic ant (Hymenoptera: Formicidae) assemblages of Atlantic costal rainforest and dry mature and secondary Amazon forest in Brazil: Continuums or communities. Tropical Ecology, 41(1): 73–80

Franklin, J., Wejnert, K.E., Hathaway, A.S., Rochester, C.J. & Fisher, R.N. (2009). Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. Diversity and Distributions, 15: 167–177. doi: 10.1111/j.1472-4642.2008.00536.x

Gomes, C.B., Souza, J.L.P. & Franklin, E. (2018). A comparison between time of exposure, number of pitfall traps and the sampling cost to capture ground-dwelling poneromorph ants (Hymenoptera: Formicidae). Sociobiology, 65: 138-148. doi: 10.13102/sociobiology.v65i2.1207

Guillaumet, J.L. (1987). Some structural and floristic aspects of the forest. Experientia, 43: 241–251.

Hölldobler, B. & Wilson, E. O. (1990). The Ants. Cambridge: Harvard University Press, 732 p.

Hsieh, T.C., Ma, K.H. & Chao, A. (2019). iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.19

IBGE. 1997. Recursos naturais e meio ambiente: uma visão do Brasil. Rio de Janeiro: Instituto Brasileiro de Geografia e Estatística, 208 p.

Jacquemin, J., Drouet, T., Delsinne, T., Roisin, Y. & Leponce, M. (2012). Soil properties only weakly affect subterranean ant distribution at small spatial scales. Applied Soil Ecology, 62: 163-169. doi:10.1016/j.apsoil.2012.08.008

Kaspari, M. & Weiser, M.D. (2000). Ant activity along moisture gradients in a neotropical forest. Biotropica, 32(4a): 703–711. doi: 10.1111/j.1744-7429.2000.tb00518.x.

Kaspari, M. & Yanoviak, S.P. (2008). Biogeography of litter depth in tropical forests: evaluating the phosphorus growth hypothesis. Functional Ecology, 22(5): 919–923. doi: 10.1111/j.1365-2435.2008.01447.x.

Laird, N.M. & Ware, J.H. (1982). Random-Effects Models for Longitudinal Data. Biometrics, 38: 963–974.

LaPolla, J.S., Cover, S.P. & Mueller, U.G. (2002). Natural history of the mealybug-tending ant Acropyga epedana, with descriptions of the male and queen castes. Transactions of the American Entomological Society, 128 (4): 367-376

Lavelle, P. (1996). Diversity of soil fauna and ecosystem function. Biology International, 33: 3–16.

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. & Dhillion, S. (1997). Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology, 33(4): 159-193.

Levings, S.C. & Franks N.R. (1982). Patterns of nest dispersion in a tropical ground ant community. Ecology, 63: 338–344.

Luizão, R.C.C., Luizão, F.J., Paiva, R.Q., Monteiro, T.F., Sousa, L.S. & Kruijt, B. (2004). Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. Global Change Biology, 10(5): 592–600. doi: 10.1111/j.1529-8817.2003.00757.x.

Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R. & Castilho, C.V. (2005). Rapeld: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica, 5 (2): 1–6.

Majer, J.D. 1983. Ants: bio-indicators of minesite rehabilitation, landuse, and land conservation. Environmental Management, 7: 375–383. doi: 10.1007/BF01866920.

Martins, M.F.O., Thomazini, M.J., Baretta, D., Brown, G.G., Rosa, M.G., Zagatto, M.R.G., Santos, A., Nadolny, H.S., Cardoso, G.B.X., Niva, C.C., Bartz, M.L.C. & Feitosa, R.M. (2020). Accessing the subterranean ant fauna (Hymenoptera: Formicidae) in native and modified subtropical landscapes in the Neotropics. Biota Neotropica. 20(1): e20190782. doi: 10.1590/1676-0611-BN-2019-0782.

Moldenke, A.R.; Pajutee, M. & Ingham, E. (2000). The functional roles of forest soil arthropods: The soil is a living place. In: Powers, R.F., Hauxwell, D.L. and Nakamura, G.M. (Eds.), Proceedings of the California forest soils council conference on forest soils biology and forest management (pp. 7–22). United States Departament of Agriculture. doi: 10.2737/PSW-GTR-178

Moraes, L., Pavan, D., Barros, M.C. & Ribas, C. (2016). Combined influence of riverine barriers and flooding gradient on biogeographical patterns of amphibians and squamates in South-eastern Amazonia. Journal of Biogeography. 43(11), 2113–2124. doi: 10.1111/jbi.12756.

Nakagawa, S. & Schielzeth H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution. 4: 133-142. doi: 10.1111/j.2041-210x.2012.00261.x

Nielsen, U.N., Osler, G. H.R., Campbell. C.D., Neilson R. & Burslem, D.F.R.P. (2010). The enigma of soil animal species diversity revisited: the role of small- scale heterogeneity. PLoS ONE, 5(7): e 11567. doi: 10.1371/journal.pone.0011567

Oliveira, P.Y., Souza, J.L.P., Baccaro, F.B. & Franklin, E.

(2009). Ant species distribution along a topographic gradient in a "terra-firme" forest reserve in central Amazonia. Pesquisa Agropecuária Brasileira, 44: 852–860.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019). Vegan: community ecology package. Version 2.5-5.

Pacheco, R. & Vasconcelos, H.L. (2012). Subterranean pitfall traps: is it worth including them in your ant sampling protocol? Psyche: A Journal of Entomology, article ID 870794, 9 pages. doi: 10.1155/2012/870794.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar D. R (2019). nlme: Linear and Nonlinear Mixed Effects Models. Version 3.1-142.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabeling, C., Brown, J.M. & Verhaagh, M. (2008). Newly discovered sister lineage sheds light on early ant evolution. Proceedings of the National Academy of Science, 105 (39): 14913-14917. doi: 10.1073/pnas.0806187105.

Ranzani, G. (1980). Identificação e caracterização de alguns solos da Estação

Experimental de Silvicultura Tropical do Inpa. Acta Amazonica, 10(1): 7–41. doi: 10.1590/1809-43921980101007.

Ribeiro, J.E.L.S., Hopkins, M.J.G., Vicentini, A., Sothers, C.A., Costa, M.A.S., Brito, J.M., Souza, M.A.D., Martins, L.H.P., Lohmann, L.G., Assuncão, P.P.C.L., Pereira, E.C., Silva, C.F., Mesquita, M.R. & Procópio, L.C. (1999). Flora da reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central. Manaus: Instituto Nacional de Pesquisas da Amazônia - INPA and Department for International Development - DFID, 816 p.

Santorelli Jr, S., Magnusson, W.E. & Deus, C.P. (2018). Most species are not limited by an Amazonian river postulated to be a border between endemism areas Scientific Reports, 8: article ID 2294. doi:10.1038/s41598-018-20596-7.

Schmidt, F.A. & Solar, R.R.C. (2010). Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. Insectes Sociaux, 57: 261–266. doi: 10.1007/s00040-010-0078-1.

Schoener, T.W. (1974). Resource partitioning in ecological communities. Science, 174: 27–37.

Silva, R.R. & Silvestre, R. (2004). Riqueza da fauna de formigas (Hymenoptera: Formicidae) que habita as camadas superficiais do solo em Seara, Santa Catarina. Papéis Avulsos de Zoologia, 44(1): 1–11.

Silva, R.R. & Brandão, C.R.F. (2010). Morphological patterns and community organization in leaf-litter ant assemblages. Ecological Monographs, 80: 107–124. doi: 10.1890/08-1298.1

Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E. & Magnusson, W.E. (2012). Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages. Applied Soil Ecology, 56: 63–73. doi: 10.1016/j.apsoil.2012.01.004.

Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E., Magnusson, W.E., Pequeno, P.A.C.L. & Fernandes, I.O. (2016). Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. Diversity and Distributions, 22: 111–122. doi: 10.1111/ddi.12371.

Souza, J.L.P., Baccaro, F.B., Pequeno, P.A.C.L., Franklin, E. & Magnusson, W.E. (2018). Effectiveness of genera as a higher-taxon substitute for species in ant biodiversity analyses is not affected by sampling technique. Biodiversity and Conservation, 27: 3425 - 3445. doi: 10.1007/s10531-018-1607-x.

Stork, N.E. & Eggleton, P. (1992). Invertebrates as determinants and indicators of soil quality. American Journal of Alternative Agriculture, 7: 23–32. doi: 10.1017/S0889189300004446.

Underwood, E.C. & Fisher, B.L. (2006). The role of ants in conservation monitoring: if, when, and how. Biological Conservation, 132: 166–82. doi: 10.1016/j.biocon.2006.03.022

Vasconcelos, H. & Delabie, J.H.C. (2000). Ground ant communities from central Amazonia forest fragments. In: Agosti, D.; Majer, J.D.; Alonso, L. e Schultz, T. (Eds.), Sampling ground-dwelling ants: case studies from de world's rain forests (p. 59-70). Perth, Australia: Curtin University School of Environmental Biology.

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.

Vasconcelos, H.L. & Vilhena, J.M.S. (2006). Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. Biotropica, 38(1): 100–106. doi: 10.1111/j.1744-7429.2006.00113.x

Weiser, M.D. & Kaspari, M. (2006). Ecological morphospace of new world ants. Ecological Entomology, 31: 131–142. doi: 10.1111/j.0307-6946.2006.00759.x

Wilkie, K.T.R., Mertl, A.L. & Traniello, J.F.A. (2007). Subterranean Ant Probe: Instruction and advice. Naturwissenschaften, 94: 725–731. doi: 10.1007/s00114-007-0250-2

Wilkie, K.T.R., Mertl, A.L. & Traniello, J.F.A. (2010). Species diversity and distribution patterns of the ants of Amazonian Ecuador. PLoS One, 5(10): ID e13146. doi: 10.1371/journal.pone.0013146

Wong, M.K.L. & Guénard, B. (2017). Subterranean ants: summary and perspectives on field sampling methods, with notes on diversity and ecology (Hymenoptera: Formicidae). Myrmecological News, 25: 1–16.