

Ant species distribution along a topographic gradient in a "terra-firme" forest reserve in Central Amazonia

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Abstract – In Amazonia, topographical variations in soil and forest structure within “terra-firme” ecosystems are important factors correlated with terrestrial invertebrates’ distribution. The objective of this work was to assess the effects of soil clay content and slope on ant species distribution over a 25 km² grid covering the natural topographic continuum. Using three complementary sampling methods (sardine baits, pitfall traps and litter samples extracted in Winkler sacks), 300 subsamples of each method were taken in 30 plots distributed over a wet tropical forest in the Ducke Reserve (Manaus, AM, Brazil). An amount of 26,814 individuals from 11 subfamilies, 54 genera, 85 species and 152 morphospecies was recorded (*Pheidole* represented 37% of all morphospecies). The genus *Eurhopalothrix* was registered for the first time for the reserve. Species number was not correlated with slope or clay content, except for the species sampled from litter. However, the Principal Coordinate Analysis indicated that the main pattern of species composition from pitfall and litter samples was related to clay content. Almost half of the species were found only in valleys or only on plateaus, which suggests that most of them are habitat specialists. In Central Amazonia, soil texture is usually correlated with vegetation structure and moisture content, creating different microhabitats, which probably account for the observed differences in ant community structure.

Index terms: beta diversity, environmental gradient, Formicidae, soil texture, tropical forest.

Distribuição de espécies de formigas ao longo de um gradiente topográfico em uma reserva florestal de terra firme na Amazônia Central

Resumo – Na Amazônia, variações topográficas em ecossistemas de terra-firme são variáveis comuns que afetam a distribuição de invertebrados terrestres. O objetivo deste trabalho foi avaliar os efeitos do conteúdo de argila no solo e da inclinação do terreno na distribuição de espécies de formigas em uma área de 25 km² que cobre a variação topográfica natural. Usando três métodos de coleta complementares (iscas de sardinha, armadilhas de fosso e amostras de serapilheira extraídas de sacos de Winkler), foram coletadas 300 subamostras de cada método em 30 parcelas distribuídas em uma floresta tropical úmida na Reserva Ducke (Manaus, AM). Foram registrados 26.814 indivíduos em 11 subfamílias, 54 gêneros, 85 espécies e 152 morfoespécies (*Pheidole* representou 37% das morfoespécies). O gênero *Eurhopalothrix* foi registrado pela primeira vez nesta reserva. O número de espécies não foi correlacionado com a inclinação do terreno ou o conteúdo de argila, exceto para espécies na serapilheira. No entanto, a Análise das Coordenadas Principais indicou que a composição de espécies das armadilhas e da serapilheira esteve correlacionada com o conteúdo de argila. Aproximadamente metade das espécies foi encontrada somente nos baixios ou nos platôs, sugerindo que a maioria é especialista do habitat. Na Amazônia Central, a textura do solo está geralmente correlacionada com a estrutura da vegetação e o teor de umidade, criando micro-habitats heterogêneos que provavelmente contribuíram para as diferenças observadas na estrutura da comunidade de formigas.

Termos para indexação: diversidade beta, gradiente ambiental, Formicidae, textura do solo, floresta tropical.

Introduction

Approximately one third of the animal biomass in Amazonian “terra-firme” forests is composed by ants and termites (Fittkau & Klinge, 1973), and one hectare could contain more than eight million ant individuals

and one million termite individuals (Hölldobler & Wilson, 1990). Besides the high abundance, ants are a diverse group, with more than 12,500 described species (Antbase.org, 2009). Ants have also been widely used as bioindicators in land management (Andersen et al., 2002), because of their roles as seed dispersers (Hughes

& Westoby, 1990), herbivory controllers (Dyer & Letourneau, 1999), and ecosystems engineers (Folgarait, 1998). The use of ants or other organisms as bioindicators is more useful when supported by relationships with environment changes at spatial scales relevant to the management of biological reserves. For example, studies using ants or other terrestrial invertebrates at the Ducke Reserve, a 10,000-ha “terra-firme” forest reserve close to Manaus which has been intensively studied in the last 40 years, were normally targeted on small-scale distributions (Beck, 1968; Penny & Arias, 1982), and basic management questions about how these animals respond to environmental gradients remain unanswered.

In Central Amazonia, the topographic gradient is correlated with soil characteristics, creating a gradient with sandy soils in the valleys and clay soils on the plateaus (Chauvel et al., 1987). Soil traits, such as soil clay content, are correlated with moisture content, with poorly drained areas concentrated on valleys and relatively dry areas concentrated on plateaus (Ranzani, 1980). Humidity can influence the composition and activity of terrestrial ant species even in tropical ecosystems, with an increase in ant activity in more humid seasons and habitats (Levings, 1983; Kaspari & Weiser, 2000). Patterns of litter deposition and decomposition are also associated with topography. Litter production is lower in valleys than in plateaus. Therefore, the amount of litter on the ground is usually lower in valleys and slope areas (Luizão et al., 2004). Litter is an important resource for nesting sites and food, and, in conjunction with moisture availability, it can generate microhabitat variability, which may affect demographic patterns in ground-dwelling ant assemblages (Vasconcelos et al., 2003).

Most previous studies normally targeted small scale or used coarse differences or habitat type (i.e. forests compartments – valleys and plateaus) assuming that microhabitats are relatively homogeneous and discrete. The objective of this work was to assess the effects of soil clay content and slope on ant species distribution along a topographic gradient in a mesospatial scale (25 km²) at the Ducke Reserve, Manaus, AM, Brazil.

Materials and Methods

The fieldwork was conducted between June and August 2006 at Reserva Florestal Adolpho Ducke (hereafter Ducke Reserve), located at Km 26 on the Manaus-Itacoatiara highway (3°00'S, 59°55'W), close to Manaus, AM, Brazil

(Figure 1). Most of the reserve ecosystems are “terra firme” (upland) forest, covering topographic and edaphic variation typical for many areas in Central Amazonia (Ribeiro et al., 1999). The reserve terrain is rugged with an altitudinal gradient (30–140 m a.s.l.), covering 10,000 hectares. The nutrient-poor soils located on the plateaus are classified as Latossolo Amarelo (Xanthic Hapludox), which grade to sandy soils – Espodossolo Cárstico (Typic Epiaquods) (Santos, 2006); Espodossolo Ferrocárstico (Typic Endoaquods) in the valleys (Chauvel et al., 1987). The vegetation is “terra-firme” non-flooded rain forest with closed canopy. The understory is relatively open and characterized by the abundance of sessile palms, such as *Astrocaryum* spp. and *Attalea* spp. The canopy height is of 30–37 m with some emergent trees reaching up to 40–45 m. The mean temperature is 26°C and the mean annual rainfall between 1965 and 1980 was of 1,362±400 mm, with a short dry season between July and September (Marques-Filho et al., 1981).

Ducke Reserve has 144 km of trails (a grid formed by 8-km long trails) systematically distributed along the forest and covering the topographical gradient. A regular system of 72 permanent plots was distributed over 64 km² of trails, and each plot was at least 1 km distant from any other. Plots were 250-m long and positioned to follow altitudinal contour lines, and thus minimize altitudinal and soil variation within each plot (Magnusson et al., 2005). All plots were at least 1 km distant from the edge of the reserve (Figure 1).

Data were collected in 30 of those permanent plots, covering an area of 25 km² (Figure 1). Ants were collected using pitfall traps, sardine baits, and litter samples extracted in Winkler sacks. These methods tend to complement each other and thus their combined use can better characterize diverse ant assemblages (Olson, 1991; Bestelmeyer et al., 2000). In each plot, at 25-m intervals following the center line, litter was sampled in 1-m² delimited areas. In the same places, one pitfall trap and half a spoon of canned sardine (used as bait) were placed, totalizing 10 subsamples for each method per plot (total of 900 subsamples).

The ants were extracted from the 1-m² sifted litter in Winkler sacks, through a sieve of 1-cm² mesh size. The sieved litter was placed into a mesh bag suspended inside a cotton bag for 48 hours. Before the set was suspended, the litter material was mixed to improve chances of the ants falling into the collecting pot. The ants and other invertebrates migrate from the suspended litter sample as a

behavioral response to disturbance of their habitat (response to drying), and fall into the pot partially filled with alcohol at the bottom of the bag (Bestelmeyer et al., 2000). The pitfall traps (6.5 cm diameter; 8 cm depth; 200 mL volume), partially filled with water and detergent, were installed and left for 48 hours. The sardine baits were placed on a piece of paper (10x10 cm) on the forest floor and removed after 40 minutes. The invertebrates were preserved in a 75% alcohol solution. The ant species were identified using

taxonomic keys and specific papers. Voucher specimens were deposited in the invertebrates collection of Instituto Nacional de Pesquisas da Amazônia (INPA).

Soil characteristics (clay content) were measured in a previous study by collecting six samples to a depth of 5 cm in each plot. Samples were combined for each plot and analyzed at the soil laboratory of the Departamento de Agronomia at INPA. Methodology for textural analyses is described in Claessen (1997). Slope measures were

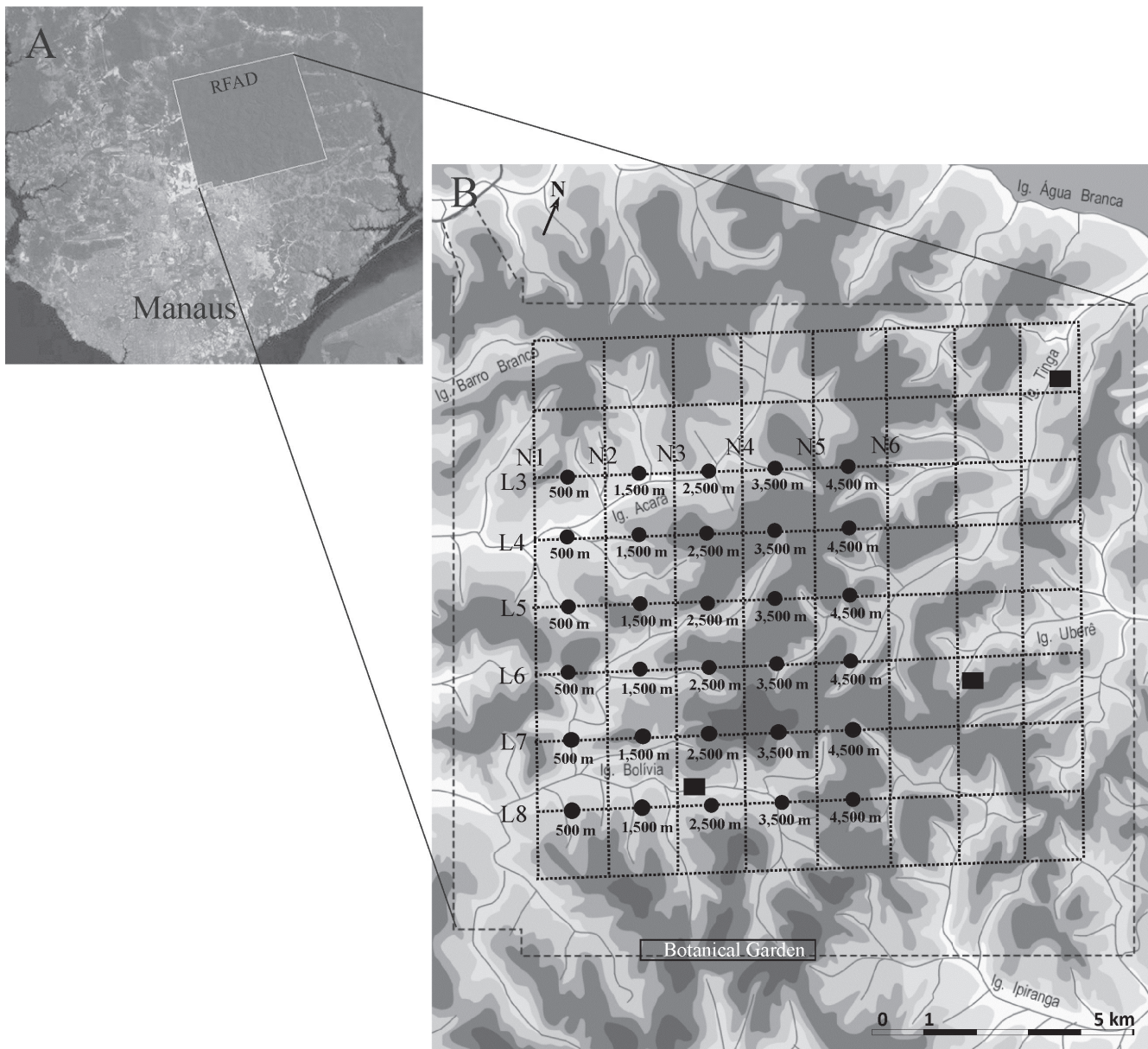


Figure 1. Map of the Ducke Reserve RFAD (A). Distribution of the system of trails (fine dotted lines), the position of the 30 plots (black spots) and the field camps (black squares) (B). Shadings indicate altitudinal gradients from the lowest areas (lightest color, <40 m.a.s.l.) to the highest areas (darkest shading, >120 m.a.s.l.). The reserve limit is shown by the dashed line.

taken every 50 m perpendicularly to the main axis of the plot with clinometers, and summarized as plot average.

In order to avoid problems of site identification, caused during the transportation of the samples to the laboratory, 50 subsamples of litter sorting (Winkler sacks) of five plots at trail L-7 (Figure 1) were excluded from the analyses. All subsequent analyses were based on the results of 30 plots sampled by sardine baits and pitfall traps and of 25 plots sampled with Winkler method.

We used multiple regression analyses to explore the factor or factors accounting for the observed variability in ant species richness per plot. The predictor variables included in the model were the soil clay content and slope. Principal coordinate analysis (PCoA) was used to ordinate plots by their similarity in ant species composition. The Bray-Curtis distance measurement on site-standardized frequency (percentage of occurrence of each species in each site) was used. The soil clay content and slope were used as surrogates for the topographic gradient. An inferential test on the effects of topography on species composition (expressed as ordination scores of the first two PCoA axes) was made by multivariate analyses of covariance (MANCOVA). The predictor variables included in the model were the soil clay content and slope. All analyses were performed using the R software (R Development Core Team, 2008).

Results and Discussion

A total of 26,814 ant specimens belonging to 11 subfamilies, 54 genera, 85 species and 152 morphospecies were sampled. Fifty-eight species of *Pheidole* (56 of them classified as morphospecies), 14 of *Crematogaster*, 13 of *Trachymyrmex*, 11 for both *Solenopsis* and *Camponotus* and 8 for *Hypoponera* genera were identified. *Crematogaster tenuicula* was the most abundant species collected (10,907 specimens, approximately 40% of the total) and the most widespread, present in all sampled plots (30), followed by *Pyramica* sp. 1 and *Paratrechina* sp. 1, sampled in 26 plots, and *Blepharidatta brasiliensis*, sampled in 25 plots. As in other tropical ant communities, the number of “rare” species was high, with 72 singletons and 28 doubletons, representing 30 and 12% of the total number of species (Table 1). The

genus *Eurhopalothrix* was registered for the first time in the Ducke Reserve.

Table 1. Frequency (%) of ant taxa sampled with pitfall traps, sardine baits in 30 plots and from litter sorting (Winkler sacks) in 25 plots, at Ducke Reserve. The values obtained for frequency represent the number of observed presences divided by the number of subsamples (n = 850).

Genus	Taxa	Frequency (%)
Subfamily Amblyoponinae		
<i>Prionopelta</i>	<i>punctulata</i>	2.47
Subfamily Cerapachyinae		
<i>Acanthostichus</i>	sp. 1	0.24
Subfamily Dolichoderinae		
<i>Azteca</i>	sp. 1	0.71
<i>Dolichoderus</i>	<i>bispinosus</i>	0.12
<i>Dolichoderus</i>	sp. 1	0.12
<i>Dolichoderus</i>	sp. 2	0.12
<i>Dolichoderus</i>	sp. 3	0.12
<i>Dolichoderus</i>	sp. 5	0.24
<i>Tapinoma</i>	sp. 1	0.12
Subfamily Ecitoninae		
<i>Eciton</i>	<i>dulcium</i>	0.12
<i>Eciton</i>	<i>rapax</i>	0.35
<i>Labidus</i>	<i>coecus</i>	1.18
<i>Labidus</i>	<i>mars</i>	0.12
<i>Labidus</i>	<i>praedator</i>	2.35
<i>Labidus</i>	<i>spininodis</i>	0.12
<i>Neivamyrmex</i>	<i>gibbatus</i>	0.94
<i>Neivamyrmex</i>	sp. 1	0.24
<i>Neivamyrmex</i>	sp. 2	0.12
<i>Neivamyrmex</i>	sp. 3	0.12
<i>Neivamyrmex</i>	sp. 4	0.12
<i>Nomamyrmex</i>	<i>esenbeckii</i>	0.47
<i>Nomamyrmex</i>	<i>hartigi</i>	0.12
Subfamily Ectatomminae		
<i>Ectatomma</i>	<i>edentatum</i>	5.06
<i>Ectatomma</i>	<i>lugens</i>	5.41
<i>Ectatomma</i>	<i>tuberculatum</i>	0.35
<i>Gnamptogenys</i>	<i>moelleri</i>	0.24
<i>Gnamptogenys</i>	sp. 1	2.00
<i>Gnamptogenys</i>	sp. 2	0.24
<i>Gnamptogenys</i>	sp. 3	1.18
<i>Gnamptogenys</i>	sp. 4	0.12
<i>Gnamptogenys</i>	sp. 5	0.24
<i>Gnamptogenys</i>	<i>tortuolosa</i>	0.94
Subfamily Formicinae		
<i>Acropyga</i>	sp. 1	0.94
<i>Acropyga</i>	sp. 2	0.12
<i>Brachymyrmex</i>	<i>heeri</i>	0.35
<i>Camponotus</i>	<i>novogranadensis</i>	0.47
<i>Camponotus</i>	<i>rapax</i>	2.59
<i>Camponotus</i>	sp. 2	0.71
<i>Camponotus</i>	sp. 4	2.59
<i>Camponotus</i>	sp. 5	2.47
<i>Camponotus</i>	sp. 6	0.24
<i>Camponotus</i>	sp. 7	0.12
<i>Camponotus</i>	sp. 8	0.24
<i>Camponotus</i>	sp. 9	0.35
<i>Camponotus</i>	sp. 10	0.12
<i>Camponotus</i>	sp. 11	0.12
<i>Gigantiops</i>	<i>destructor</i>	0.47
<i>Paratrechina</i>	sp. 1	9.06

Continue...

Table 1. Continuation...

Genus	Taxa	Frequency (%)
<i>Paratrechina</i>	sp. 2	6.35
<i>Paratrechina</i>	sp. 3	0.94
Subfamily Myrmicinae		
<i>Acanthognathus</i>	sp. 1	0.35
<i>Acromyrmex</i>	sp. 1	0.24
<i>Apterostigma</i>	sp. 1	0.12
<i>Apterostigma</i>	sp. 2	0.59
<i>Apterostigma</i>	sp. 3	0.24
<i>Apterostigma</i>	sp. 4	0.35
<i>Atta</i>	<i>sexdens</i>	0.35
<i>Atta</i>	sp. 2	0.12
<i>Blepharidatta</i>	<i>brasiliensis</i>	8.71
<i>Carebara</i>	sp. 1	0.47
<i>Carebara</i>	sp. 2	1.41
<i>Carebara</i>	sp. 3	0.59
<i>Carebara</i>	sp. 4	0.12
<i>Cephalotes</i>	sp. 3	0.47
<i>Cephalotes</i>	sp. 4	0.12
<i>Cephalotes</i>	sp. 5	0.12
<i>Crematogaster</i>	<i>brasiliensis</i>	9.53
<i>Crematogaster</i>	<i>curvispinosa</i>	0.12
<i>Crematogaster</i>	<i>erecta</i>	0.47
<i>Crematogaster</i>	<i>flavomicrops</i>	0.12
<i>Crematogaster</i>	<i>flavosensitiva</i>	0.71
<i>Crematogaster</i>	<i>limata</i>	5.88
<i>Crematogaster</i>	<i>sotobosque</i>	3.76
<i>Crematogaster</i>	sp. 1	0.24
<i>Crematogaster</i>	sp. 2	0.12
<i>Crematogaster</i>	sp. 3	0.12
<i>Crematogaster</i>	sp. 4	0.12
<i>Crematogaster</i>	sp. 5	0.12
<i>Crematogaster</i>	<i>stollii</i>	0.12
<i>Crematogaster</i>	<i>tenuicula</i>	33.76
<i>Cyphomyrmex</i>	cf. <i>lectus</i>	0.12
<i>Cyphomyrmex</i>	cf. <i>peltatus</i>	4.35
<i>Cyphomyrmex</i>	<i>laevigatus</i>	1.06
<i>Cyphomyrmex</i>	sp. 1	0.12
<i>Eurhopalothrix</i>	sp. 1	0.12
<i>Hylomyrma</i>	sp. 1	0.12
<i>Lachnomyrmex</i>	<i>amazonicus</i>	0.12
<i>Megalomyrmex</i>	<i>balzani</i>	0.59
<i>Megalomyrmex</i>	sp. 2	0.59
<i>Megalomyrmex</i>	sp. 4	0.35
<i>Megalomyrmex</i>	sp. 5	0.12
<i>Monomorium</i>	<i>pharaonis</i>	0.24
<i>Mycocepurus</i>	<i>smithi</i>	0.12
<i>Mycocepurus</i>	sp. 1	0.12
<i>Myrmicocrypta</i>	sp. 1	0.71
<i>Myrmicocrypta</i>	sp. 2	0.12
<i>Ochetomyrmex</i>	<i>semipolitus</i>	2.47
<i>Octostruma</i>	<i>iheringi</i>	0.12
<i>Octostruma</i>	sp. 1	3.06
<i>Pheidole</i>	<i>cephalica</i>	0.71
<i>Pheidole</i>	<i>fracticeps</i>	8.47
<i>Pheidole</i>	JL	0.24
<i>Pheidole</i>	<i>meinerti</i>	4.82
<i>Pheidole</i>	sp. 1	4.12
<i>Pheidole</i>	sp. 2	6.71
<i>Pheidole</i>	sp. 4	0.47
<i>Pheidole</i>	sp. 5	0.24
<i>Pheidole</i>	sp. 6	6.24
<i>Pheidole</i>	sp. 7	0.12
<i>Pheidole</i>	sp. 8	3.88
<i>Pheidole</i>	sp. 9	1.41
<i>Pheidole</i>	sp. 11	5.06
<i>Pheidole</i>	sp. 12	0.59
<i>Pheidole</i>	sp. 13	2.47
<i>Pheidole</i>	sp. 14	0.35
<i>Pheidole</i>	sp. 15	3.76

Continue...

Table 1. Continuation...

Genus	Taxa	Frequency (%)
<i>Pheidole</i>	sp. 22	1.53
<i>Pheidole</i>	sp. 23	0.71
<i>Pheidole</i>	sp. 24	2.47
<i>Pheidole</i>	sp. 25	1.41
<i>Pheidole</i>	sp. 26	1.41
<i>Pheidole</i>	sp. 27	0.71
<i>Pheidole</i>	sp. 28	0.59
<i>Pheidole</i>	sp. 29	1.65
<i>Pheidole</i>	sp. 30	0.24
<i>Pheidole</i>	sp. 31	1.88
<i>Pheidole</i>	sp. 32	4.94
<i>Pheidole</i>	sp. 33	0.47
<i>Pheidole</i>	sp. 34	0.71
<i>Pheidole</i>	sp. 35	1.76
<i>Pheidole</i>	sp. 36	1.41
<i>Pheidole</i>	sp. 37	1.53
<i>Pheidole</i>	sp. 38	1.41
<i>Pheidole</i>	sp. 39	2.12
<i>Pheidole</i>	sp. 40	0.12
<i>Pheidole</i>	sp. 41	0.12
<i>Pheidole</i>	sp. 42	2.24
<i>Pheidole</i>	sp. 43	0.24
<i>Pheidole</i>	sp. 44	0.71
<i>Pheidole</i>	sp. 45	0.71
<i>Pheidole</i>	sp. 46	0.35
<i>Pheidole</i>	sp. 47	1.06
<i>Pheidole</i>	sp. 48	0.12
<i>Pheidole</i>	sp. 49	0.47
<i>Pheidole</i>	sp. 50	0.82
<i>Pheidole</i>	sp. 51	0.59
<i>Pheidole</i>	sp. 52	0.24
<i>Pheidole</i>	sp. 53	0.12
<i>Pheidole</i>	sp. 54	0.82
<i>Pheidole</i>	sp. 55	2.12
<i>Pheidole</i>	sp. 56	0.12
<i>Pheidole</i>	sp. 58	0.12
<i>Proccryptocerus</i>	sp. 1	0.12
<i>Pyramica</i>	sp. 1	12.12
<i>Pyramica</i>	sp. 2	1.88
<i>Pyramica</i>	sp. 3	0.82
<i>Pyramica</i>	sp. 4	0.35
<i>Pyramica</i>	sp. 5	0.12
<i>Rhopalothrix</i>	sp. 1	0.12
<i>Rogeria</i>	sp. 1	0.47
<i>Sericomyrmex</i>	sp. 1	1.06
<i>Sericomyrmex</i>	sp. 2	0.12
<i>Solenopsis</i>	<i>geminata</i>	2.00
<i>Solenopsis</i>	sp. 1	3.76
<i>Solenopsis</i>	sp. 2	3.41
<i>Solenopsis</i>	sp. 3	2.94
<i>Solenopsis</i>	sp. 4	1.65
<i>Solenopsis</i>	sp. 5	6.00
<i>Solenopsis</i>	sp. 6	3.65
<i>Solenopsis</i>	sp. 7	1.41
<i>Solenopsis</i>	sp. 8	0.12
<i>Solenopsis</i>	sp. 9	0.59
<i>Solenopsis</i>	sp. 10	0.35
<i>Strumigenys</i>	sp. 1	2.00
<i>Strumigenys</i>	sp. 2	0.35
<i>Strumigenys</i>	sp. 3	0.12
<i>Strumigenys</i>	sp. 4	0.12
<i>Strumigenys</i>	sp. 5	0.59
<i>Strumigenys</i>	sp. 6	0.12
<i>Strumigenys</i>	sp. 7	0.24
<i>Trachymyrmex</i>	<i>bugnioni</i>	0.12
<i>Trachymyrmex</i>	<i>opulentus</i>	0.82
<i>Trachymyrmex</i>	sp. 1	0.94
<i>Trachymyrmex</i>	sp. 2	1.06
<i>Trachymyrmex</i>	sp. 3	0.47

Continue...

Table 1. Continuation...

Genus	Taxa	Frequency (%)
<i>Trachymyrmex</i>	sp. 9	0.24
<i>Trachymyrmex</i>	sp. 10	0.24
<i>Trachymyrmex</i>	sp. 11	0.12
<i>Wasmannia</i>	<i>auropunctata</i>	11.88
<i>Wasmannia</i>	<i>iheringi</i>	0.12
<i>Wasmannia</i>	<i>scrobifera</i>	0.24
<i>Xenomyrmex</i>	<i>stolli</i>	0.12
Subfamily Paraponerinae		
<i>Paraponera</i>	<i>clavata</i>	0.12
Subfamily Ponerinae		
<i>Anochetus</i>	<i>diegensis</i>	0.94
<i>Anochetus</i>	<i>emarginatus</i>	0.12
<i>Anochetus</i>	<i>horridus</i>	0.71
<i>Centromyrmex</i>	<i>gigas</i>	0.12
<i>Hypoponera</i>	sp. 9	0.12
<i>Hypoponera</i>	sp. 1	1.06
<i>Hypoponera</i>	sp. 2	0.35
<i>Hypoponera</i>	sp. 3	0.35
<i>Hypoponera</i>	sp. 4	1.53
<i>Hypoponera</i>	sp. 5	0.35
<i>Hypoponera</i>	sp. 6	2.35
<i>Hypoponera</i>	sp. 7	0.24
<i>Hypoponera</i>	sp. 8	0.24
<i>Leptogenys</i>	sp. 1	0.12
<i>Leptogenys</i>	sp. 2	0.47
<i>Leptogenys</i>	<i>wheeleri</i>	0.24
<i>Odontomachus</i>	<i>brunneus</i>	0.12
<i>Odontomachus</i>	<i>caelatus</i>	0.94
<i>Odontomachus</i>	<i>haematodus</i>	0.47
<i>Odontomachus</i>	<i>laticeps</i>	0.24
<i>Odontomachus</i>	<i>meinerti</i>	0.12
<i>Odontomachus</i>	<i>opaciventris</i>	0.94
<i>Odontomachus</i>	<i>scalptus</i>	0.24
<i>Pachycondyla</i>	<i>apicalis</i>	0.24
<i>Pachycondyla</i>	cf. <i>arhuraca</i>	0.12
<i>Pachycondyla</i>	<i>commutata</i>	0.12
<i>Pachycondyla</i>	<i>constricta</i>	3.76
<i>Pachycondyla</i>	<i>crassinoda</i>	4.12
<i>Pachycondyla</i>	<i>harpax</i>	2.24
<i>Pachycondyla</i>	sp. 2	0.12
<i>Pachycondyla</i>	sp. 1	0.24
Subfamily Proceratiinae		
<i>Discothyrea</i>	sp. 1	0.12
Subfamily Pseudomyrmicinae		
<i>Pseudomyrmex</i>	sp. 1	0.12
<i>Pseudomyrmex</i>	sp. 2	0.12
<i>Pseudomyrmex</i>	sp. 3	0.12

The soil clay content varied from 1.6% near streams to 87.2% on plateaus, and the slope varied from 0.6 to 26.4 degrees. As the slope was not correlated with soil clay content (Pearson $r = 0.184$, $p = 0.329$), both variables were used on multiple regressions and MANCOVA analyses to explore the factors accounting for the observed variability in ant species richness and composition.

The ant assemblage richness and composition sampled with canned sardine baits were not correlated with the environmental gradients (Tables 2 and 3). Baits are widely used to investigate the activity of ground and litter-dwelling ants in response to microclimate changes (Hölldobler & Wilson, 1990; Davidson, 1998). However, this is a selective

method that attracts mainly omnivorous species that are recruited to rich food sources. This sampling method provides a momentary estimative of species richness, but is normally sensitive due to the daily variation in ant activity (Bestelmeyer et al., 2000), which may add confounding effects to sampling.

There were no significant relationships between the soil clay content or slope and the ant species richness sampled with baits ($R^2 = 0.013$; $F_{2,27} = 0.812$; $p = 0.454$) and pitfall traps ($R^2 = 0.046$; $F_{2,27} = 1.713$; $p = 0.199$). However, the number of species sampled with Winkler sacks was significantly and negatively related to the slope (Table 2), with the overall regression model accounting for 23% of the observed variance ($R^2 = 0.228$; $F_{2,22} = 4.559$; $p = 0.022$). This method samples cryptic and litter-specialist species that generally have relatively small colonies, much of them occupying short-lived nest sites (Byrne, 1994). Litter-dwelling ants move more frequently than ground-dwelling species, and are probably more sensitive to soil and litter changes. However, as moisture is correlated with soil clay content, the negative relationship between number of species sampled by litter sorting and clay content may be a response to the moisture gradient.

The number of species – or, for some authors, species richness – is probably the most simple and used measurement for diversity. However, this metric gives the same weight to rare and abundant species, and it is not surprising that the results using community composition and species richness were not congruent. Although the percentage of variance captured by the two PCoA ordination axes varied between 20 and 35%, a significant relationship between clay content and ant community composition was observed for pitfall and litter sorting samples, and between slope and pitfall traps (Table 3). Previous studies conducted in Central Amazonia showed patterns similar to those described here.

Table 2. Multiple regression models for the effects of clay content and slope on number of ant species sampled with sardine baits, pitfall traps and litter sorting (Winkler sacks), at the Ducke Reserve. Standardized partial regression coefficients (b) represent the relative degree of influence of a predictor variable in the model.

Sampling method	Predictor variable	Coefficient	b	p
Bait	Clay content	-0.011	-0.192	0.321
	Slope	0.037	0.110	0.569
Pitfall	Clay content	-0.012	-0.077	0.680
	Slope	0.291	0.313	0.102
Winkler	Clay content	-0.146	-0.538	0.150
	Slope	-0.390	-0.243	0.003

At the Ducke Reserve, Fagundes (2003) detected correlation of the Ponerinae ants, particularly of the *Hypoponera* genus, with the variation on soil texture. The influence of clay percentage (between valleys and plateaus) on ant community composition was also detected in the Biological Dynamics of Forest Fragments Project at Reserve 1501, located about 80 km north of Manaus (Vasconcelos et al., 2003). However, this pattern also seems to occur in other parts of the Amazon forest. For instance, Souza et al. (2007) detected correlation between clay content and the ant community structure in a relatively flat terrain forest located in Estação Ecológica de Caxiuana, in eastern Amazonia.

Figures 2 and 3 show the relative frequency of species of ten subfamilies sampled along the environmental gradients.

The Myrmicinae subfamily is too numerous to build such graphical representation. As the percentage of clay content changed, the ant assemblage sampled with pitfall traps and litter sorting also changed. Almost half of the total of species sampled (105) were rare (singletons and doubletons) and occurred mostly in only one end of the clay texture gradient. Half of the singletons and doubletons (48%) was concentrated on plots with less than 5% of clay content (valleys).

As previous studies point out (Vasconcelos et al., 2003; Costa et al., 2005), it is not clear if these results originated from a direct effect of soil texture, of water drainage or from a combination of these variables. Variation in soil texture is closely related to the topography in the region of Manaus

Table 3. Results of multivariate analyses of covariance (MANCOVA) models for the effects of clay content and slope on the first two ordination Principal Coordinate Analysis' axes of ant community composition, sampled with sardine baits, pitfall traps and litter sorting (Winkler sacks), at the Ducke Reserve.

Sampling method	Variance captured by each ordination axes (%)	Predictor variables	MANCOVA		
			Pillai	F	p
Bait	20.51	Clay content	0.042	0.575	0.569
	15.49	Slope	0.005	0.075	0.927
Pitfall	12.61	Clay content	0.329	6.375	0.006
	9.15	Slope	0.224	3.761	0.037
Winkler	16.66	Clay content	0.302	4.552	0.023
	11.22	Slope	0.018	0.201	0.819

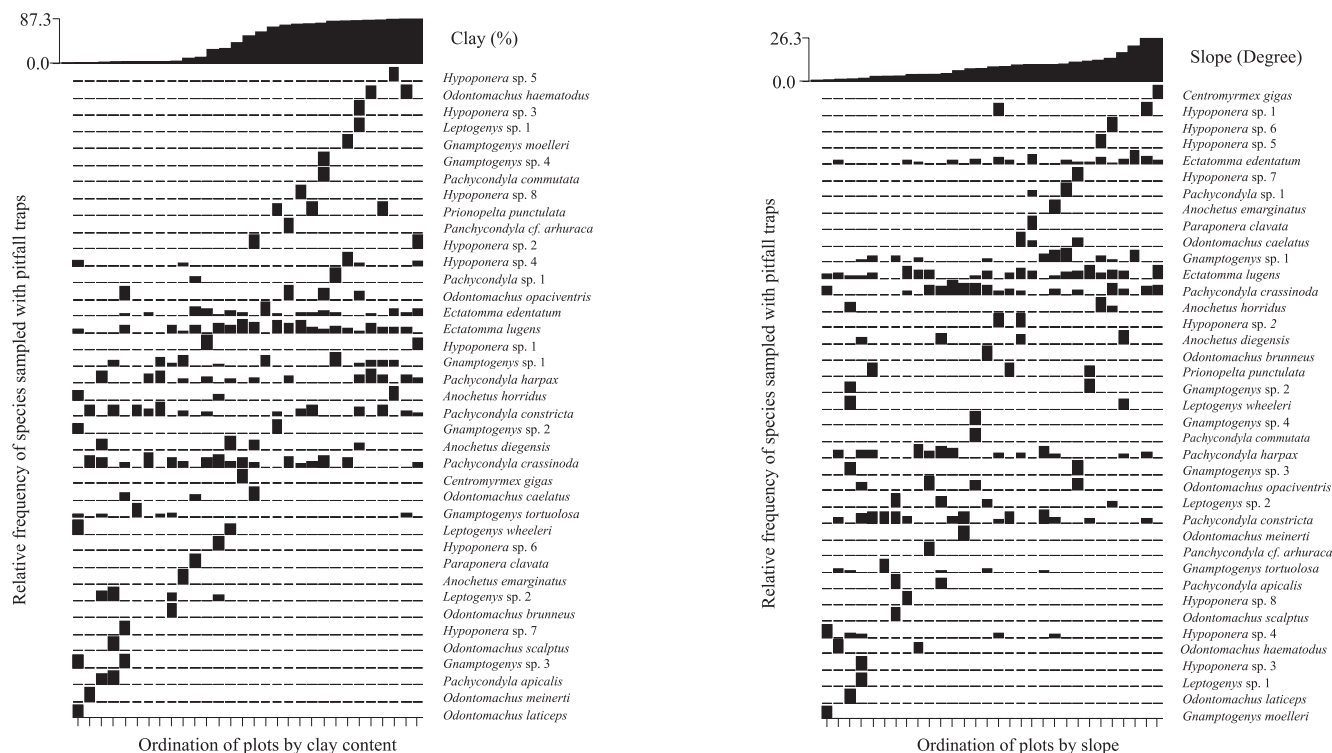


Figure 2. Distribution of poneromorph species along clay content gradient and slope in the 30 plots at the Ducke Reserve.

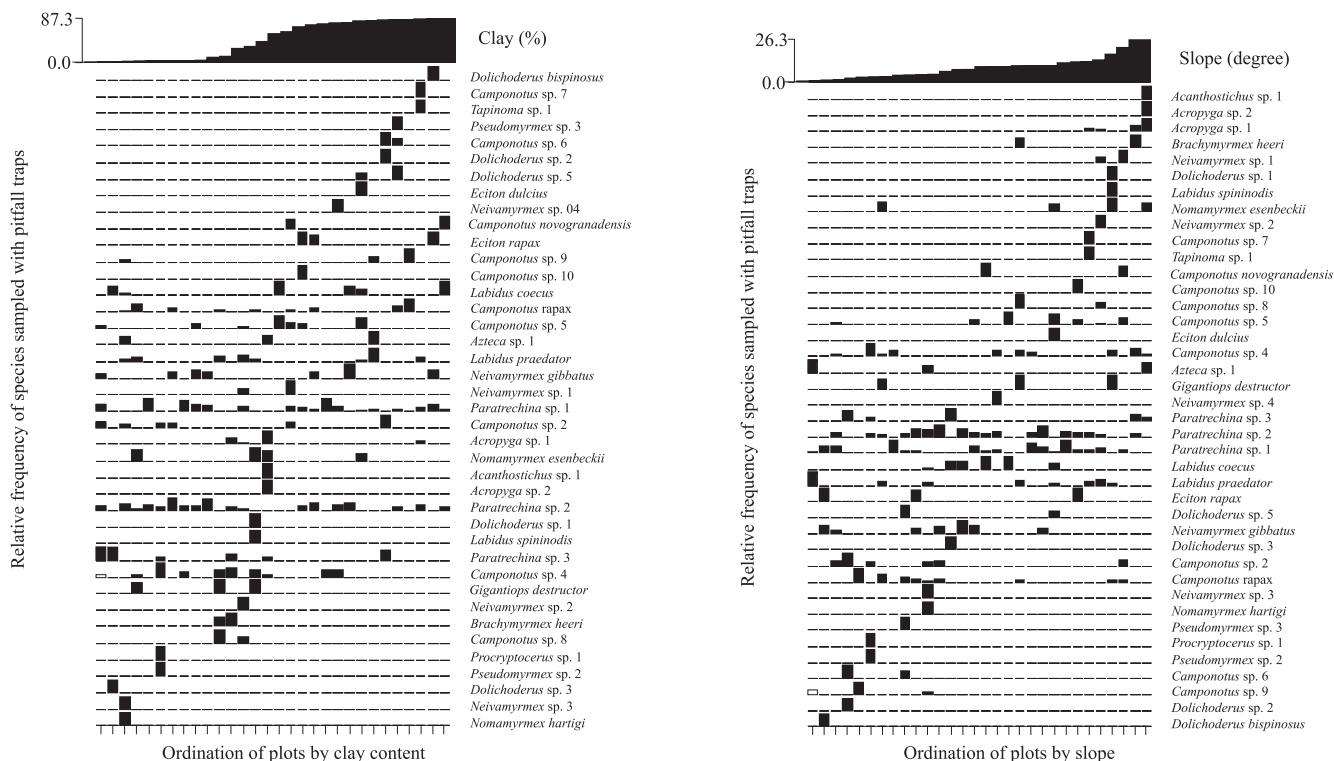


Figure 3. Distribution of Formicinae, Ecitoninae, Dolichoderinae, and Pseudomyrmecinae species along clay content gradient and slope in the 30 plots at the Ducke Reserve.

(Chauvel et al., 1987). At the Ducke Reserve, the highest clay percentage is concentrated on the plateaus, and the soils along stream valleys are normally hydromorphic and particularly poorly drained (Ranzani, 1980). The temporary accumulation or lateral percolation of water near small streams (Chauvel et al., 1987) probably limits the establishment and growth of some ground-nesting species (Vasconcelos et al., 2003). Disturbance probably accounts for the distribution pattern detected, with more singletons in valleys than on plateaus. In addition, other environmental variables are correlated or interact with the topography and, therefore, with the soil texture. Tree density and litter production tends to be lower in valleys than in plateaus (Luizão et al., 2004; Castilho et al., 2006), and moisture content is normally higher in valleys than in plateaus (Kaspari & Weiser, 2000). The interaction of those variables may promote a high environmental heterogeneity along the landscape, creating different microhabitats that maintain such diverse ant communities. Field experiments involving the ant community and these environmental variables are necessary to answer the relationship between the causes and effects of those variables on the reserve's ant community structure.

Conclusions

1. A distinct pattern of ant species diversity and composition is found along the gradient of soil texture and slope at the Ducke Reserve.
2. The distribution of ant species along the topographic gradient indicates that there is no environmental and biotic homogeneity within the Ducke Reserve.

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References

- ANDERSEN, A.N.; HOFFMANN, B.D.; MÜLLER, W.J.; GRIFFITHS, A.D. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology*, v.39, p.8-17, 2002.

- ANTBASE.ORG. **How many ants (Formicidae) are there?** 2005. Available at: <http://osuc.biosci.ohio-state.edu/hymenoptera/tsa.sppcount?the_taxon=Formicidae>. Accessed on: 25 June 2009.
- BECK, L. Sobre a biologia de alguns aracnídeos na floresta tropical da Reserva Ducke (Inpa, Manaus/Brasil). *Amazoniana*, v.1, p.247-250, 1968.
- BESTELMEYER, B.T.; AGOSTI, D.; ALONSO, L.E. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: AGOSTI, D.; MAJER, J.D.; ALONSO, L.E.; SCHULTZ, T.R. (Ed.) *Ants: standard methods for measuring and monitoring biodiversity*. Washington: Smithsonian Institution Press, 2000. p.122-144.
- BYRNE, M.M. Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica*, v.26, p.61-72, 1994.
- CASTILHO, C.V. de; MAGNUSSON, W.E.; ARAÚJO, R.N.O. de; LUIZÃO, R.C.C.; LUIZÃO, F.J.; LIMA, A.P.; HIGUCHI, N. Variation in aboveground tree life biomass in a central Amazonian forest: effects of soil and topography. *Forest Ecology and Management*, v.234, p.85-96, 2006.
- CHAUVEL, A.; LUCAS, Y.; BOULET, R. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia*, v.43, p.234-241, 1987.
- CLAESSEN, M.E.C. (Org.). **Manual de métodos de análise de solo**. 2. ed. Rio de Janeiro: Embrapa-CNPq, 1997. 221p. (Embrapa-CNPq. Documentos, 1).
- COSTA, F.R.C.; MAGNUSSON, W.E.; LUIZÃO, R.C. Mesoscale distribution patterns of Amazonian understory herbs in relation to topography, soil and watersheds. *Journal of Ecology*, v.93, p.863-878, 2005.
- DAVIDSON, D.W. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology*, v.23, p.484-490, 1998.
- DYER, L.A.; LETOURNEAU, D.K. Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia*, v.119, p.265-274, 1999.
- FAGUNDES, E.P. **Efeitos de fatores do solo, altitude e inclinação do terreno sobre os invertebrados da serapilheira, com ênfase em Formicidae (Insecta, Hymenoptera) da Reserva Ducke, Manaus, Amazonas, Brasil**. 2003. 70p. Dissertação (Mestrado) - Universidade Federal do Amazonas, Manaus.
- FITTKAU, E.J.; KLINGE, H. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica*, v.5, p.2-14, 1973.
- FOLGARAIT, P.J. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, v.7, p.1221-1244, 1998.
- HÖLDOBLER, B.; WILSON, E.O. **The ants**. Cambridge: Harvard University Press, 1990. 733p.
- HUGHES, L.; WESTOBY, M. Removal rates of seeds adapted for dispersal by ants. *Ecology*, v.71, p.138-148, 1990.
- KASPARI, M.; WEISER, M.D. Ant activity along moisture gradients in a Neotropical forest. *Biotropica*, v.32, p.703-711, 2000.
- LEVINGS, S.C. Seasonal, annual and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecological Monographs*, v.53, p.435-455, 1983.
- LUIZÃO, R.C.C.; LUIZÃO, F.J.; PAIVA, R.Q.; MONTEIRO, T.F.; SOUSA, L.S.; KRUIJ, B. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Global Change Biology*, v.10, p.592-600, 2004.
- MAGNUSSON, W.E.; LIMA, A.P.; LUIZÃO, R.; LUIZÃO, F.; COSTA, F.R.C.; CASTILHO, C.V. de; KINUPP, V.F. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica*, v.5, p.1-6, 2005.
- MARQUES-FILHO, A.O.; RIBEIRO, M.N.G.; SANTOS, J.M. Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. IV – Precipitação. *Acta Amazonica*, v.11, p.759-768, 1981.
- OLSON, D.M. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. *Biotropica*, v.23, p.166-172, 1991.
- PENNY, N.D.; ARIAS, J.R. **Insects of an Amazon forest**. New York: Columbia University Press, 1982. 269p.
- R DEVELOPMENT CORE TEAM. **R: a language and environment for statistical computing**. Vienna: R Foundation for Statistical Computing, 2008. Available at: <<http://www.R-project.org>>. Accessed on: 5 Feb. 2008.
- RANZANI, G. Identificação e caracterização de alguns solos da Estação Experimental de Silvicultura Tropical do Inpa. *Acta Amazonica*, v.24, p.19-30, 1980.
- RIBEIRO, J.E.L. da S.; HOPKINS, M.J.G.; VICENTINI, A.; SOTHERS, C.A.; COSTA, M.A. da S.; BRITO, J.M.D.; SOUZA, M.A.D. de; MARTINS, L.H.P.; LOHMANN, L.G.; ASSUNÇÃO, P.A.C.L.; PEREIRA, E. da C.; SILVA, C.F. da; MESQUITA, M.R.; PROCÓPIO, L.C. **Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central**. Manaus: INPA/DFID, 1999. 816p.
- SANTOS, H.G. dos; JACOMINE, P.K.T.; ANJOS, L.H.C. dos; OLIVEIRA, V.A. de; OLIVEIRA, J.B. de; COELHO, M.R.; LUMBRERAS, J.F.; CUNHA, T.J.F. (Ed.). **Sistema brasileiro de classificação de solos**. 2.ed. Rio de Janeiro: Embrapa Solos, 2006. 306p.
- SOUZA, J.L.P.; MOURA, C.A.R.; HARADA, A.Y.; FRANKLIN, E. Diversidade de espécies dos gêneros de *Crematogaster*, *Gnamptogenys* e *Pachycondyla* (Hymenoptera: Formicidae) e complementaridade dos métodos de coleta durante a estação seca numa estação ecológica no Estado do Pará, Brasil. *Acta Amazonica*, v.37, p.649-656, 2007.
- VASCONCELOS, H.L.; MACEDO, A.C.C.; VILHENA, J.M.S. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. *Studies on Neotropical Fauna and Environment*, v.38, p.115-124, 2003.

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