ECOLOGY, BEHAVIOR AND BIONOMICS

Environment Heterogeneity and Seasonal Effects in Ground-Dwelling Ant (Hymenoptera: Formicidae) Assemblages in the Parque Estadual do Rio Doce, MG, Brazil

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Efeitos da Heterogeneidade Ambiental e da Sazonalidade em Assembléias de Formigas (Hymenoptera: Formicidae) no Parque Estadual do Rio Doce, MG

RESUMO - Este trabalho objetivou explorar os padrões de distribuição das assembléias de formigas em resposta aos tipos estruturais de florestas no Parque Estadual do Rio Doce, MG. Foram comparadas bordas antropomórficas do parque e ecótones naturais, tais como orlas de lagoas com florestas, e florestas em bom estado de preservação. Investigou-se se a riqueza, a abundância de formigas e a composição de espécies modificam-se de acordo com os tipos estruturais de vegetação. Esperava-se maior riqueza de espécies no interior de mata alta, comparada com mata baixa ou ecótones. Além disso, testaram-se os efeitos da sazonalidade sobre as assembléias de formigas encontradas em cada vegetação estudada. Cada tipo vegetacional foi amostrado com no mínimo um transecto de 150 m de comprimento, somando-se 30 armadilhas *pit-fall* por transecto. Duas amostragens foram feitas, uma na estação seca (setembro de 2001) e outra na estação úmida (janeiro de 2002). Para ambas as estações, a mata alta apresentou a menor média de riqueza e abundância de formigas, fato que corrobora a predição de que ecótones podem apresentar maior diversidade alfa. A riqueza e abundância média de formigas não foram diferentes entre mata baixa e orla de lagoa, ou entre esses habitats e borda de floresta. Os resultados obtidos sugerem que a perda de espécies devido ao desflorestamento provavelmente é maior do que se pensava anteriormente, e que para se compreender os padrões de diversidade e distribuição de espécies de insetos em ecossistemas tropicais deve-se levar em conta um desenho amostral mais compreensivo.

PALAVRAS-CHAVE: Diversidade alfa, diversidade beta, efeito de borda, grupo funcional, Mata Atlântica

ABSTRACT - This work aimed to explore the response of ant species assemblage to contrasting types of forests in a semideciduous stationary rainforest, in the Parque Estadual do Rio Doce, South Eastern Brazil. We compared antropomorphic borders of this park and natural ecotones, such as lake margins continuous with forests, as well as preserved forests far from ecotones. We investigated whether ground-dwelling ant species richness, abundance and composition would change according to forest types and ecotones. We expected greater species richness in interior tall forest, compared with low forest or ecotone habitats. In addition, we tested the effect of climate seasonality on ant assemblages found in each studied vegetation type. Each forest type was surveyed based on a minimum transect sampling unit of 150 m long summing up 30 pit-falls per unit. Two sampling events, one in dry season(September of 2001) and another in the rainy season (January of 2002) were performed. For both seasons, tall forest presented greater total number of ant species, however lower mean ant species and abundance per trap than other forest types, thus corroborating the prediction that ecotones might present high alpha diversity. Mean species richness and abundance did not differ between interior low forest and lake edge, or between these habitats and reserve border. In general, species composition were not clearly defined by forest types. Results here found suggest that species loss or community dominance by generalist species, eventually due to deforestation, is probably a much greater problem than previously thought. However, to understand patterns of insect species diversity and distribution in tropical ecosystem should be taken in account much more comprehensive, spatially explicit sampling designs.

KEY WORDS: Alpha diversity, beta diversity, edge effect, functional groups, Atlantic rainforest

Tropical ecology is a discipline divided between description of unknown patterns of species distribution in barely studied ecosystems, and the study of consistent ecological explanations beyond such trends. Factors such as humidity, altitudinal variation and soil are good predictors of the occurrence of particular species or structural types (Dangerfield *et al.* 2003). In this sense, abiotic environment may define local composition of organisms, as predicted in the "habitat templets" theories (Southwood 1977, Greenslade 1983). However, disruptive species distribution and complex pattern of species composition found along abiotic gradients which are hardly understood, makes very difficult to apply these theories in tropical ecological communities. Indeed, habitat templets as well as phytosociological methods, are clearly applicable to temperate communities, or particular tropical insect communities, such as benthic organisms (Marques 2004). Nevertheless, the difficulties in defining habitat edges in tropical rainforest makes the investigation of heterogeneity and diversity rather more difficult.

Considering complex and unknown community patterns, the best approach might be to study clear environmental contrasts. Changes in slope, soil or drainage may produce very distinct vegetation patterns with sharp edges (Farnsworth & Ellison 1996). Van der Maarel (1990) discuss that these edges might be distinguished from zones with a more diffuse vegetation change. Mosaic-type of vegetation transitions are sometimes defined as ecotones, but the term can be also applied to sharp changes, for instance, from gallery forest to grassland. Studies of heterogeneity and habitat fragmentation resulted in an increasing emphasis to species richness patterns in edged habitats and to vegetation transition next to these edges (Leopold 1933, Odum 1971, Kunin 1998). On the other hand, studies comparing patterns of species distribution between artificial and natural edges are rare.

Ants are dominant insects in almost all environments of the world. Ants have numerous attributes that make them ideal for biodiversity studies, such as high diversity, numerical and biomass dominance in almost all continental habitats throughout the world, a fairly good taxonomic knowledge, easy collecting and stationary nesting habits that allow them to be re-sampled over time. In addition, ants are sensible to environmental changes and play important roles in ecosystem functions monitoring, including interactions with other organisms at every trophic level (Andersen 1991, Alonso & Agosti 2000).

There are few studies that emphasize the influences of temperature and moisture oscillations throughout the year on ant assemblages. In certain tropical regions, the amount rain precipitation changes sharply through the year, defining dry and rainy seasons, what certainly can interfere in distribution and foraging activity of ants. In general, the effects of seasonality versus broader variations on abundance and species richness are still open question in ecology, mainly in tropical rainforest ecology (Wolda 1998, Kaspari 2000). Andersen (1995) considered low temperature to be the primary stress factor that controls patterns of ant productivity and community structure.

On the other hand, nest sites vary with the structural complexity of the habitat. Structurally complex habitats, such as lowland tropical rainforest, offer nest sites which are less frequent or abundant in simpler habitats, and therefore may support ant species that are often uncommon or absent elsewhere (Wilson 1987, Benson & Harada 1988, Byrne 1994).

As important as climate seasonality, disturbance regimes affecting a community in ecological and evolutionary time, may define patterns of ant species distribution. An environment subjected to severe stress and disturbance is occupied by a combination of highly specialized stress-tolerant species and generalist ruderal species. Conversely, according to Andersen (2000), at very low levels of stress and disturbance, competition becomes the primary factor regulating community structure, and highly competitive species predominate. Species composition responses to disturbance could be very useful in studying human impacts in preserved forest large fragments. Highly fragmented forests, even if large reserves, can be affected by border effects. An important issue in conservation biology is to understand species diversity variation between preserved forest types, and how much these forests can be affected by habitat borders. In this sense, to study both artificial as natural borders might be essential to define species patterns in contrasting natural habitats, in comparison to disturbed equivalent communities.

This work aims to explore ant assemblage patterns found in response to contrasting forest types within a same reserve of semideciduous stationary rainforest, in South Eastern Brazil. Part of the Brazilian interior Atlantic rainforest, this physiognomy is largely fragmented, with only10 % of its original area preserved. However, large forest patches are still present. At the Doce river mid basin, a 36,000 ha forest is preserved as the Parque Estadual do Rio Doce, in a region rich in natural lakes. In this study, we are comparing antropomorphic borders of the park and natural ecotones, namely, lake margins continuous with forests, and equivalent well preserved forests far from ecotones.

We investigate whether ground-dwelling ant species richness, abundance and composition would change according to forest types and ecotones. We expect greater species richness in interior tall forest, compared with low forest or ecotone habitats. On the other hand, more generalist ant species are expected to be found in the border of the reserve with agroecosystems around. In addition, we tested the effect of climate seasonality on ant assemblages across vegetation type. Ant functional groups concepts ought to be utilize to analyse the effects of environmental heterogeneity and seasonal effects on richness and abundance of ants.

Material and Methods

Study site. This study was carried out in the Parque Estadual do Rio Doce, hereafter PERD, Minas Gerais State, Brazil. This park has, with approximately 36,000 ha, the largest preserved semidecidous Atlantic rainforest of interior still found in Minas Gerais State, between parallels 19º 48' 18" - 19º 29' 24" S and meridians 42º 38' 30" - 42º 28' 18" W. The park is located in the middle of the third largest lake system of South America, which resulted from tectonic moves that blocked many affluent streams of the ancient

Doce river along it's geological history. Thus, the park has nine percent of its area occupied by over 42 lakes (out of 150 in the region), most of them in the south part of the park (IEF 1994).

The park is characterized by low altitude that varies from 230 meters to 515 meters (SOCT 1981), presenting a transition of mesothermic humid tropical climate and mesothermic rainy tropical climate (Antunes 1986) with rainy season (October to March) and dry season (April to September) well defined (Gilhuis 1986). Its vegetation can be considered as the submontane semidecidual stationary forest kind (Lopes 1988) being characterized between 20% and 50% by a percentage of caducifolious trees (Veloso *et al*. 1991). Nevertheless, at least 10 vegetation categories can be identified in the PERD (Gilhuis 1986), varying from tall dense forest to dense savanna type vegetation. Although well preserved, and free of fire incidents since 1967 (except for a very small event in 1991), only 8.4% of the area is considered primary tall forest (Gilhuis 1986). However, it is worthwhile noticing that a certain part of this reserve has a very specific floristic composition, apparently related to soil quality, which is normally low trees (10-15 m), with high canopy roughness, and therefore naturally more likely to suffer fire events, but more resilient to its effects (Ribeiro 2003, Goulart *et al.* 2004).

The selected areas for this study were: Trilha da Tereza (TT, primary tall forest), Trilha do Gambá (TG, low and open forest), Salão Dourado (SD, secondary forest edge with open pasture area in dried out wetland) and two forest ecotones with lake ashores: Orla da Lagoa Bonita (OLB) e Orla da Lagoa do Bispo Dom Helvécio (OLH) (Fig. 1). TG site were divided in two points, one next to the Lagoa do Bispo (we called TGA) and the other point inside the forest (we called TGB). Vegetal transition in lake borders consisted

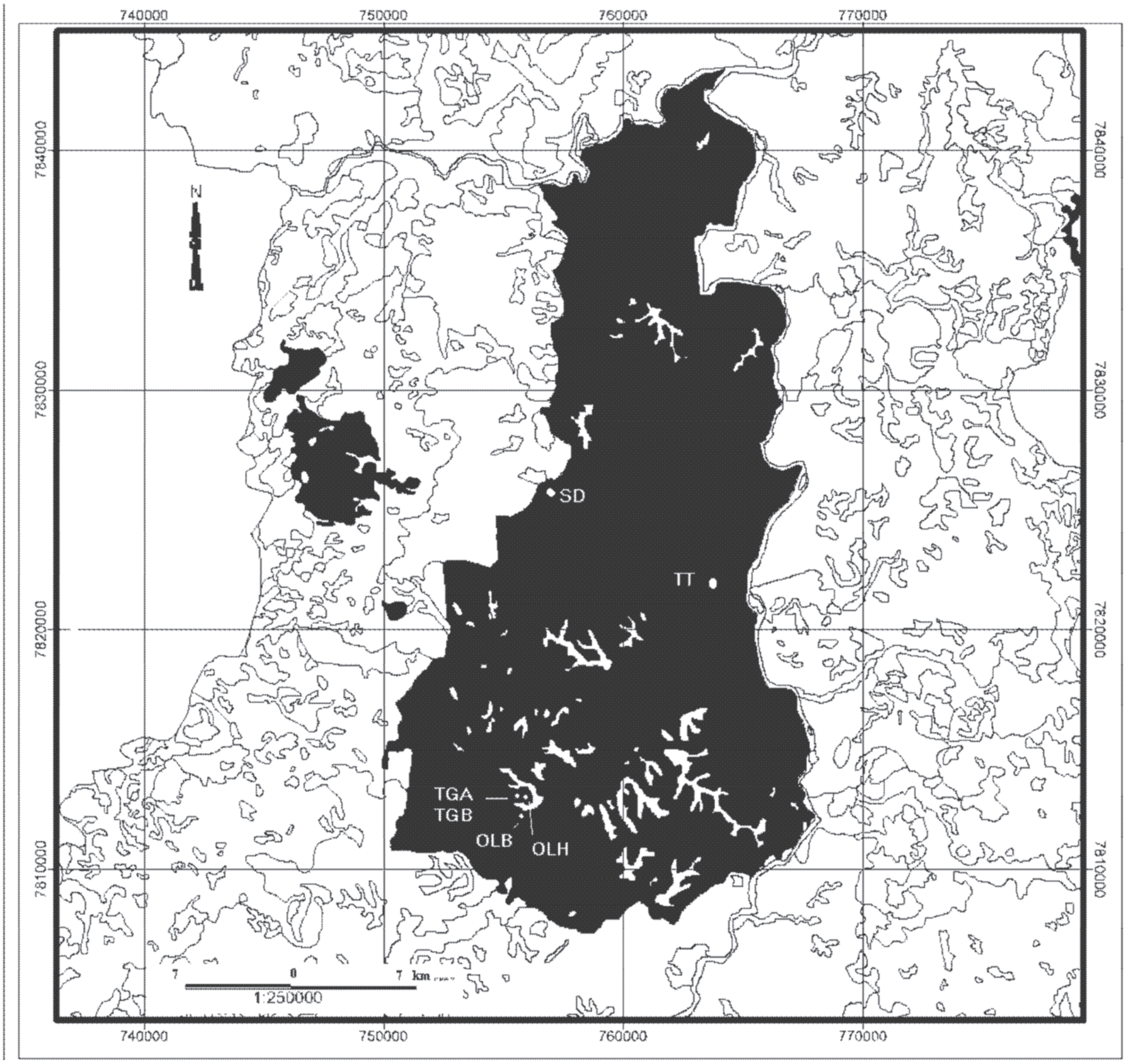


Figure 1. Map of the Parque Estadual do Rio Doce showing the sampling sites. TT - Trilha da Tereza; SD - Salão Dourado; TGA, TGB - Trilha do Gambá A/B; OLB - Orla da Lagoa Bonita and OLH - Orla da Lagoa Dom Helvécio.

of an arboreal-shrub vegetation adjacent to a macrophyte fields. Forest edges with agroecosystems were characterized by a secondary vegetation that suffers constant impacts due to opening and maintenance of pathways, and dominated by *Mabea fistulifera* (Euphorbiaceae) tree.

Sampling protocol. Each forest type was surveyed based on a minimum transect sampling unit, of 150 m long and with one pit-fall trap at each 5 m, thus summing up 30 pit-falls per unit. Each 150 m long transect was considered to build up mean and variance estimates for studies of ant species richness and abundance. In addition, at least two specific locations were sampled from each vegetation type, aiming to include heterogeneity effects in the study. Moreover, the species composition should increase proportionally to the area of a certain forest type, being beta diversity expected to increase with sample size within a certain habitat. Considering the prediction that a habitat type may influence the species composition, and in accordance to current ecological theory, it is expected that species accumulation would step up higher in larger forest types. Base on such assumption, the tall forest type (TT), which is one of the largest vegetation types in the PERD reserve, was sampled in twice more locations than other forest types aiming to approach such effects. Borges *et al.* (2005) has used similar scaling up sampling protocol to study herbivores and soil coleopteran in oceanic forest reserves. Hence, two sampling events, one in dry season (September of 2001) and another in the rainy season (January of 2002) were performed. In each season, the same transects were sampled: two in the SD border, two in the TG low forest (TGA and TGB), two in ashore/forest edge of independent lakes (LDH and OLB), and four in the tall forest (TT), along a same geomorphologic formation (Table 1).

In order to characterise the whole border effect rather than only the vegetation transition line, in the SD disturbed ecotone, the transect was split in three equal parts, and set perpendicular to the forest edge, at 50 m to each other. Therefore, each line had 10 pit-falls distributed from the edge into the forest, along 50 m. Conversely, in the lake ashore, transects were placed along the edge, under the first line of shrubs and trees, as that is a particular vegetation type, with a clear cut change towards both sides. On the lake side there is herbaceous temporarily flooded plants, and on the forest side all understorey foliage and sampling trees disappeared due to the lack of light, and were substituted by a low upper canopy mixed with trees and bamboos. None of these changes compromise the statistical analysis, as the assumption of independent and random sample was respected between each pit-fall.

In summary, the same 10 transects were sampled in each season, being each placed in considerable distances from the rest (more than 500 m), in order to characterize distinct sample units, apart the increasing distances from each forest type. For instance, the most distant transects are 13 km apart to each other, but separated by untouched well preserved forest. Such sampling effort resulted in one of the most comprehensive protocols affording heterogeneity of an only one large forest patch in the tropical world. On the other hand, to produce such comprehensive protocol, some aspects need to be more descriptive than exactly designed for comparison. One unavoidable confounding factor behind the sampling design, is the fact that low forest types surround most of the accessible lakes of the reserve, which are concentrated in the south part of the reserve, while the better accessible (and safe for sampling) borders are in the north, where tall forest dominates. Therefore, the studied lake ecotones are natural edges of the low forest studied (TG), and SD is an artificial border of a tall forest, with some similarities with TT tall forest. Unbalanced design ought to be for a proper characterization of the system. The present sampling design is an initial study within a Long Term Ecological Research. PERD reserve is one permanent study site of the International Long Term Ecological Research network (ILTER). Statistical models used and hypothesis tested have taken in consideration the limitations of such design (see below).

Pit-fall traps consisted of open plastic pots in the soil containing alcohol 70% and glycerin in 3% filling up to 1/3 of the cup. Dimensions of cups were 8.5 cm in depth and 6.5 in diameter. Active animals on surface fell down inside these traps and then were killed. Pitfall traps were placed for a period of seven days and, then, cups were closed and packed in plastic bags to return in laboratory, where samples were hand sorted and preserved. Ants were counted, identified at genera (Bolton 1994) and morphospecies level

Table 1. Distribution of transects and pitfalls per sample site. This sample design was performed in both seasons.

Sample site	Characteristics	N. of transects	N. of pit-falls
Orla da Lagoa Dom Helvécio (LDH)	Forest ecotones with lake ashores	1	30
Orla da Lagoa Bonita (OLB)	Forest ecotones with lake ashores	1	30
Salão Dourado (SD)	Secondary forest edge	2	60
Trilha do Gambá A (TGA)	Low and open forest	1	30
Trilha do Gambé B (TGB)	Low and open forest	1	30
Trilha da Tereza (TT)	Tall Forest	4	120
Total		10	300

and, when possible, at species level. Five individuals of each species (workers, soldiers, males or females) were mounted in entomological pins, using card triangles. After, they were inserted in the Invertebrate Zoology main collection at the Departmento de Ciências Biológicas of the Universidade Federal de Ouro Preto.

Statistical analysis. To test the effects of habitat heterogeneity and seasonality, it was developed a bi-factorial analyses of variance (ANOVA) with transect as random nested factor. Type III sum of squares were used to deal with unbalanced replicates at the nested level, using a mixed linear model procedure in SPSS 11.5. Ant abundance was log transformed to match homoscedastic assumptions of normal distribution. In addition, we used a cluster of faunal similarity with Bray-Curtis distance to examine if there is species overlapping among transects in different habitats and seasons. We considered alpha diversity (local richness) as the average number of species per pitfall taken from sample unity. Gamma diversity was taken from the cumulative number of species in all samples at a site. A simple species accumulation curves (generate with the software Species Diversity & Richness 3.0 – Pisces Conservation ltd, 2002) were produced to describe patterns of the increasing Beta diversity within and between forest types.

Results

Ant species diversity and species composition. In total, we collected 9291 individuals distributed in six subfamilies, 35 genera and 110 morphospecies (hereafter called only species). The most abundant subfamily was Ecitoninae with almost 49% of total individuals showing 6 different species. In second, Myrmicinae composed 42.9% of total abundance. The other subfamilies such as Ponerinae, Formicinae, Pseudomyrmecinae and Dolychoderinae had low abundance varying from 0.3% to 6.6%. Otherwise, Myrmicinae was the family with the biggest number of species, followed by Ponerinae, Formicinae, Dolychoderinae and Ecitoninae (with the same species number) and Pseudomyrmecinae.

Otherwise, the most abundant genera were *Nomamyrmex*, with 46.7% of total individuals and only two species, *Pheidole* (17.13% - 9 species) and *Solenopsis* (12.63% - four species). However, many genera with lower densities showed considerable number of species, such as *Camponotus* (1% - 12 species) and *Hypoponera* (0.54% - seven species). Climate specialists were the most representative group in both seasons, including 51 species.

In dry season, we found 3075 individuals, six subfamilies, 24 genera and 65 species. The most abundant genera were *Solenopsis* (31.1%), *Pheidole* (24.7%) and *Nomamyrmex* (11.3%), but the genera with more species were *Camponotus* (eight species), *Acromyrmex*, *Pheidole*, *Crematogaster* and *Sericomyrmex* with five species each.

In the rainy season, we found 6216 individuals, six subfamilies, 30 genera and 78 species. Also, the most representative genera were *Nomamyrmex* (64.2% of total individuals) and *Pheidole* (13.4%). Genera with biggest number of species were *Camponotus* (seven species), *Pheidole* (eight species), *Hypoponera* (five species), *Ectatomma*, *Sericomyrmex*, *Acromyrmex*, *Solenopsis* and *Leptothorax* with four species.

Few species occurred in all habitats and all seasons, such as *Pheidole* sp.4, *Pheidole* sp.9, *Sericomyrmex* sp.1 and *Solenopsis* sp.2 that belong to generalist genera; *Ectatomma* sp.1, probably a ruderal and opportunist species; and *Ponera* sp.1, a cryptic species that nest in litter. On the other hand, many species with lower densities showed a restrict distribution to a determined habitat and season (Fig. 2).

The tall forest (TT) had a cumulative value of 69 ant species, quite above the reserve border (SD – 54), and much more than the low forest (TG – 53) or lake edges (OLB – 35; OLH – 36). This shows that these habitats differ from each other, contributing for increasing Beta diversity in the forest. Still, ecotones (lake borders particularly) accumulate less species than interior of forests, differing from what was expected. However, this result contrasted strongly with alpha diversity data (next section). In conclusion, increasing species number was found both within as well as between vegetation types. The species-sample curve does not stabilise by increasing sampling effort within any forest type, not even for TT, which had the double sample size than the other forests (Fig. 3). Even though sample size has not been exhaustive, most importantly it does show a high Beta diversity within reserve, which may reflect a strong heterogeneity between north-south and border-interior of these large preserved forest.

Habitat heterogeneity and seasonality effects. Consistently for both seasons, the tall forest presented the lower mean ant species and abundance (NESTED ANOVA: richness $F_{3;\,15} = 8.22$; $P < 0.002$; abundance (log transformed $F_{3;\,15} = 4.4$; $P < 0.02$), and corroborates with the prediction that ecotones might present high alpha diversity. Least significant differences (LSD) showed that mean species richness and abundance did not differ between low forest interior and lake edge, or between these habitats and reserve border (Table 2 and 3). Interestingly, the habitats amongst those with the highest number of species per pit-fall (lake edges:

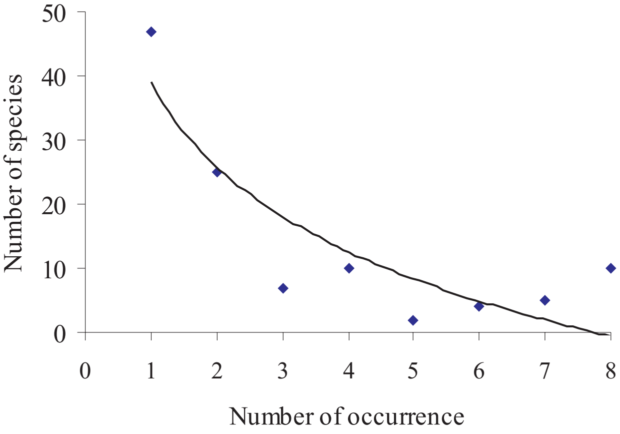
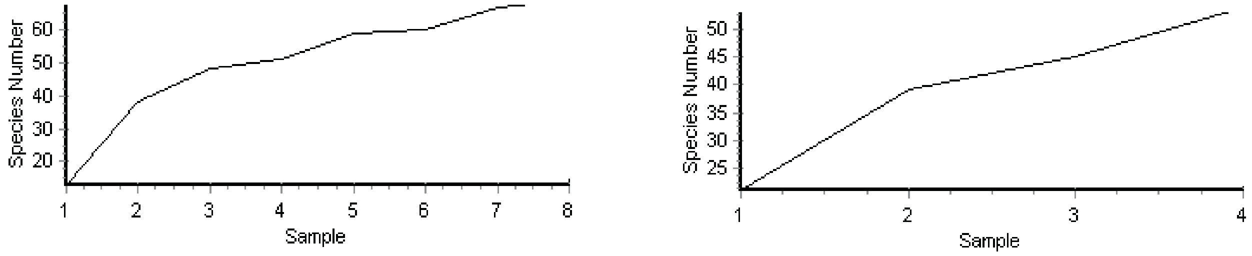
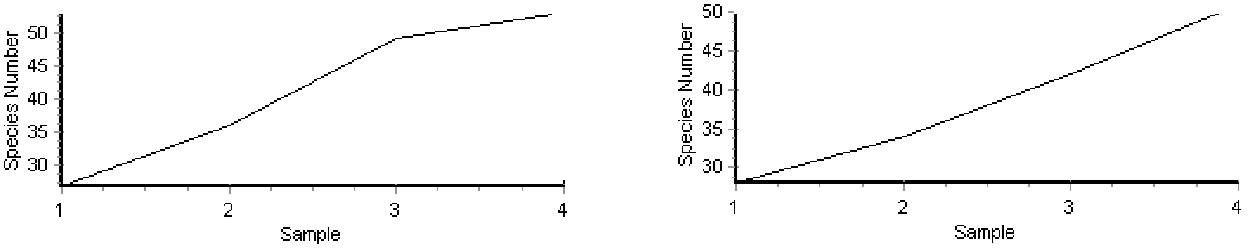


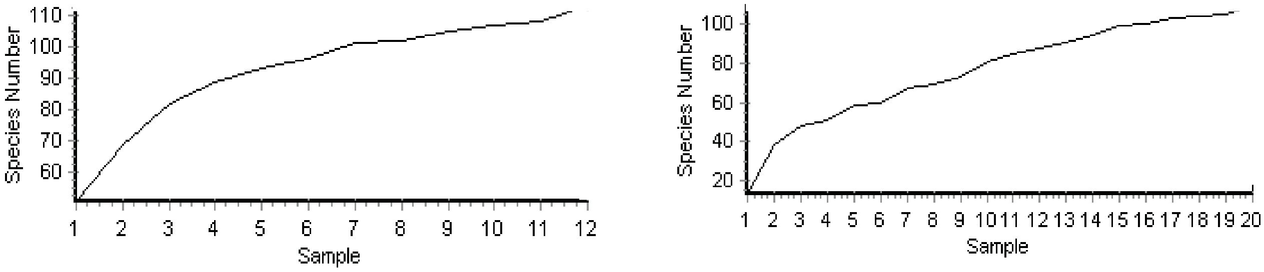
Figure 2. Number of occurrence of ant species ($F_{1,8} = 6.523$; $P = 0.043$; $n = 8$).


a) TT

b) SD


c) TGA/TGB

d) OLB/OLH


e) Summary per habitat

f) Summary per transect

Figure 3. Curves of species accumulation per sampled habitat. 3a: TT – Trilha da Tereza (tall Forest); 3b: SD – Salão Dourado (secondary forest edge); 3c: TGA/TGB – Trilha do Gambá A/B (low and open forest); 3d: OLB/OLH – Orla da Lagoa Bonita e Orla da Lagoa do Helvécio (Forest ecotones with lake ashores); 3e: summary per habitat and 3f: summary per transect.

4.3 species, against 2.5 in the tall forest) had the smallest cumulative number of species.

Consistently amongst all forest types, more species richness was found in the rainy season than in the dry season. Although variance calculation in the overall model makes this difference only marginal (NESTED ANOVA, $F_{2;28} = 3.1$; $P < 0.06$), post-hoc contrasts calculated on marginal means, showed more clearly this difference, when values were overtaken above forest types (LSD = 0.751; $P < 0.03$). No differences were found in abundance of ants between the seasons (NESTED ANOVA, $F_{2;28} = 1.5$; $P < 0.3$). Five genera and 32 species were exclusive to dry season and 11 genera and 45 species were exclusive to rainy season.

A slightly diffuse species composition was observed, with little consistence of species similarity between locations (Fig. 4). Three distinct cluster groups were found, but only one joined predominantly close transect, namely six out of eight TT transects (regardless season) plus two SD transects, one from rainy and other from dry season. A second group was formed by five transects from different vegetation types, but mostly joining samples taken during the rainy season. Finally, a third group was observed which could not group any particular site or season. Hence, 35% of samples are not distinguished by species composition, not even by vegetation structure or season. About 20% of samples presented some faunal similarity during rainy season. The present pattern indicate the presence of some dominant species that occur in high frequency in all habitats during this season. Even though, a certain level of differentiation was found between TT and the other vegetations, which corroborates the previous analyses.

Discussion

Recent studies demonstrate that ant assemblages can represent a certain habitat type to which most of these ant species

Table 2. Pairwise comparisons of mean species richness amongst habitats.

(I) Habitat	(J) Habitat	Mean difference (I-J)	Std. error	df	Sig.[1]	95% Confidence interval for difference[1]	
						Lower bound	Upper bound
Forest edge	Tall forest	1.222*	0.434	15.029	0.013	0.297	2.148
	Low forest	-0.504	0.502	15.079	0.331	-1.573	0.565
	Lake ashores	-0.517	0.502	15.049	0.319	-1.585	0.552
Tall forest	Forest edge	-1.222*	0.434	15.029	0.013	-2.148	-0.297
	Low forest	-1.726*	0.435	15.070	0.001	-2.652	-0.800
	Lake ashores	-1.739*	0.434	15.029	0.001	-2.664	-0.814
Low forest	Forest edge	0.504	0.502	15.079	0.331	-0.565	1.573
	Tall forest	1.726*	0.435	15.070	0.001	0.800	2.652
	Lake ashores	-0.013	0.502	15.079	0.980	-1.082	1.056
Lake ashores	Forest edge	0.517	0.502	15.049	0.319	-0.552	1.585
	Tall forest	1.739*	0.434	15.029	0.001	0.814	2.664
	Low forest	0.013	0.502	15.079	0.980	-1.056	1.082

Based on estimated marginal means
[1]Adjustment for multiple comparisons: Least significant difference (equivalent to no adjustments)
*The mean difference is significant at the 0.05 level.

have some level of adaptation (Estrada & Fernández 1999, Vasconcelos 1999, Fisher & Robertson 2002). We could identify a differentiated composition of species at tall forest (TT), mainly in dry season. This habitat showed more rare or exclusive species, standing out those with specialized diet such as specialist predators. It is interesting to emphasize that, in forest environments, the number of species with behaviour typically dominant is very small (Vasconcelos & Davidson 2000).

Table 3. Pairwise comparisons of mean ant abundance amongst habitats.

(I) Habitat	(J) Habitat	Mean difference (I-J)	Std. error	df	Sig.[1]	95% confidence interval for difference [1]	
						Lower bound	Upper bound
Forest edge	Tall forest	0.241	0.150	14.990	0.128	-0.078	0.560
	Low forest	-0.132	0.173	15.015	0.456	-0.501	0.236
	Lake ashores	-0.257	0.173	14.999	0.157	-0.626	0.111
Tall forest	Forest edge	-0.241	0.150	14.990	0.128	-0.560	0.078
	Low forest	-0.373*	0.150	15.011	0.025	-0.692	-0.054
	Lake ashores	-0.498*	0.150	14.990	0.005	-0.817	-0.180
Low forest	Forest edge	0.132	0.173	15.015	0.456	-0.236	0.501
	Tall forest	0.373*	0.150	15.011	0.025	0.054	0.692
	Lake ashores	-0.125	0.173	15.015	0.481	-0.493	0.243
Lake ashores	Forest edge	0.257	0.173	14.999	0.157	-0.111	0.626
	Tall forest	0.498*	0.150	14.990	0.005	0.180	0.817
	Low forest	0.125	0.173	15.015	0.481	-0.243	0.493

Based on estimated marginal means
[1]Adjustment for multiple comparisons: Least significant difference (equivalent to no adjustments)
*The mean difference is significant at the 0.05 level.

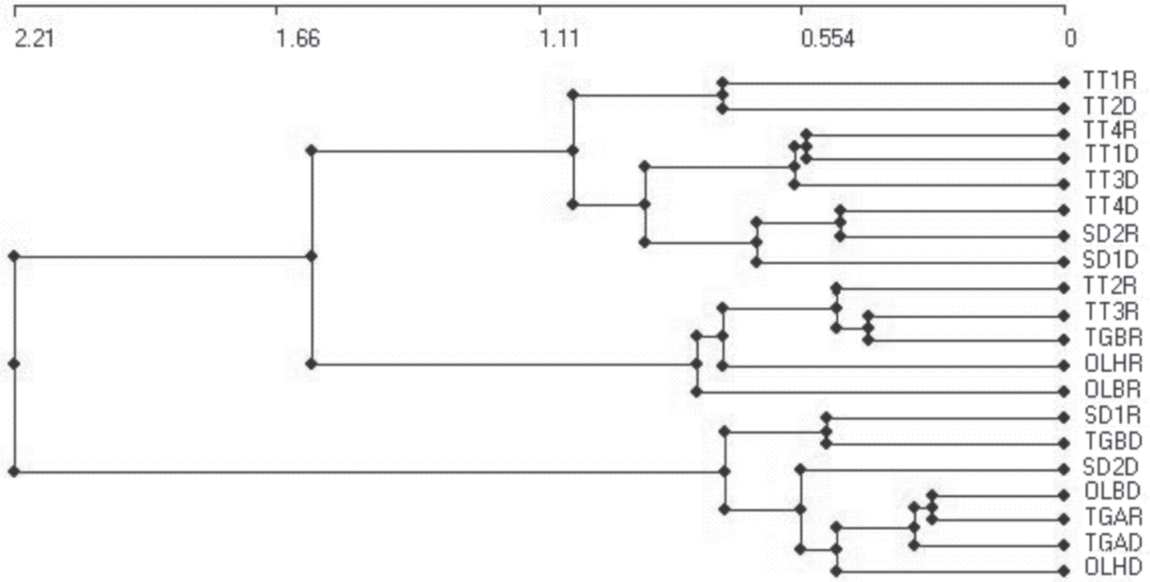


Figure 4. Cluster of faunal similarity with Bray-Curtis distance amongst transects. TT – Trilha da Tereza; SD – Salão Dourado; TGA/TGB – Trilha do Gambá A/B; OLB – Orla da Lagoa Bonita and OLH – Orla da Lagoa Dom Helvécio. R – Rainy season; D – Dry season.

However, present result showed TT gamma diversity higher than all other habitats, even though lake borders showed great alpha diversity per sample. Bell *et al.* (2000) showed that interior of forests, particularly if a more complex habitat, with heterogeneous vegetal coverage, may support more species. This hypothesis is based on the idea that complex habitats offer more potential niches than simple habitats (Heck & Wetstone 1977). Ant abundance also tends to increase as plant species composition changes from the edge into interior of forest (Vasconcelos *et al.* 2001). Species richness is undoubtedly a complex variable modified by a number of factors, including the history of a determined area (Kaspari 2000).

In other hand, Torres (1984) found a different pattern and support that greater structural diversity in a forest may act reducing the number of climatic microhabitats, then reducing the number of ant species in this kind of habitat. Moreover, the author argued that vegetal ecotones could present a great diversity of insects associated with the vegetal transitions, producing more accessibility to prey and increasing diversity of ants. The fact that our transition type of forests, in natural and artificial ecotones, did not show a great total number of species, but the largest values of species per trap, is suggestive that a few aggressive, and dominant species, may share a considerable amount of resources, so that co-occurrence become trivial. Moreover, analyzing abiotic effects on ant composition, field experiments shows that intensity of light reaching the ground has an important role in distribution of ant species (Torres 1984, Estrada & Fernández 1999). Therefore, temperature can determine foraging activity, nesting and be an essential factor to the development of larvae and pupae (Wilson 1971). Edged habitats seem to be significantly warmer and less humid than forested habitats, even in the lake ashore. Regardless water saturation in the ground, the atmosphere must be extremely dry due to high desiccation due to sun reflection in the water during the hottest hours of the day.

Another factor also responsible for changing in ant fauna is the frequency and intensity of disturbance produced in a determined area (Vasconcelos 1999). Therefore, area where disturbance are frequently generated, for example, forest edges at SD, is expected a differentiated ant fauna where more generalists species, with great potential of colonization, would be present (Greenslade & Greenslade 1977, Molano 1994, Roth *et al.* 1994, Vasconcelos *et al.* 2000).

Another important question to be broached is the difference found in ant abundance in rainy season. It is essential to consider that higher value found during this season is due exclusively to only one genera. Two species of *Nomamyrmex* presented great densities, mainly species of *Nomamyrmex* sp.2, which represented more than 50% of all individuals. Therefore, statistical analysis may be overestimating this discrepancy and any affirmation could be wrong. Davidson (1997a, 1997b), studying deserted habitats in North America, found a similar pattern between diversity of ants and amount of precipitation. Humid environments present higher diversity of ants although, during dry season, in neotropical semidecidual forests, many species can be sampled in function of more foraging activity and seed/fruit production by trees.

Functional group composition respond predictably to disturbance of habitats in temperate and semiarid regions (Andersen 1990, Bestelmeyer & Wiens 1996), but actual effects of disturbance on functional groups of ants in tropical forests are rarely studied. According to Andersen (1995), in any functional group analysis there is a trade-off between being generalist and specialist. It means that ant species, which explore open and sunny environments, have to be territorial and competitive; while to avoid these interactive effects they have to be highly tolerant to shaded environments and to low temperatures.

We found all seven functional groups according to Andersen (1995). Functional groups with higher number of species and individuals were Tropical climate specialists, with 51 species, and generalized Myrmicinae presenting 16 species. All habitats showed great number of species represented by Tropical climate specialists. However, groups such as Cryptic species and subordinated Camponotini, although they had very small densities (in terms of abundance), they had reasonable number of species, 15 and 13, respectively. The other functional groups as specialist predators, dominant Dolychoderinae and opportunists also showed very small densities varying from 0.2 to 2.9% of total individuals and six, five e five species, respectively.

In dry season, tropical climate specialists represented 61.7% of total individuals and 32 species, being *Solenopsis* sp.2 and *Atta* sp.1 the most abundant. Generalized Myrmicinae species represented 28.9% of individuals and only 10 species, including *Pheidole* sp.4 and *Pheidole fallax* (Mayr) (Fig. 5). In the same way, in rainy season, Tropical climate specialists had greater abundance, showing 78.5% and also 32 species, being *Nomamyrmex* sp.2 the most abundant, with 51% of total individuals. Generalized Myrmicinae represented only 13.9% and 12 species, being *Pheidole* sp.4 the most representative in terms of abundance (Fig. 5).

The present study brought a new approach comparing edge effects with disturbed areas and natural ecotones, as well as a novelty by exploring an extremely vast area of only one natural reserve, including unexplored habitats, such as well preserved natural ecotones between forests and lake ashores. Considering that the present work is part of a Long Term Ecological programme, such approach showed to be extremely useful in terms of subsidising political decisions aiming conservation, as well as scientific decisions about how and where to invest years of sampling effort. Clearly, although the fact that 36,000 ha is not an enormous area, this is the last great continuous natural vegetation patch within the Piracicaba/Doce River Basin, one of the most important river basin in the domain of Atlantic rainforest at the South-Eastern Brazil. Results here found suggest that the lost of species in the soil due to deforestation probably was much greater than previously thought, and that understanding patterns of insect species diversity and distribution in tropical ecosystem should be taken in account much more comprehensive, spatially explicit sampling designs.

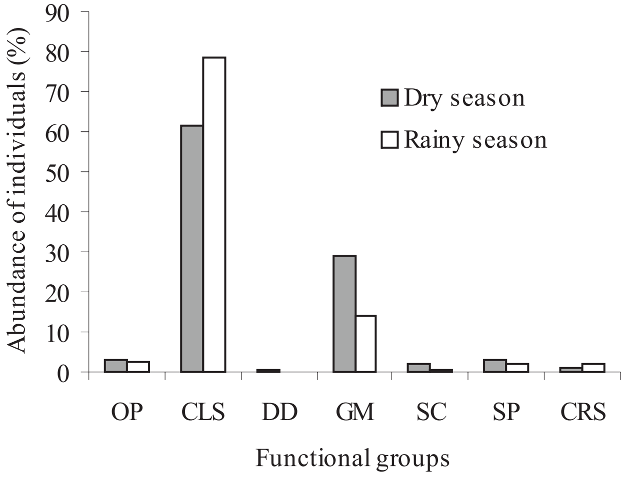


Figure 5. Composition of ant functional group in dry and rainy seasons. OP – opportunists; CLS – climate specialists; DD – dominant Dolychoderinae; GM – generalized Myrmicinae; SC – subordinated Camponotini; SP – specialist predators and CRS – cryptic species.

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References

Alonso, L.E. & D. Agosti. 2000. Biodiversity studies, monitoring, and ants. An overwiew, p.1-8. In D. Agosti, J.D. Majer, L.E. Alonso & T.R. Schultz (eds.), Ants standard methods for measuring and monitoring biodiversity. Smithsonian Inst. Press, Washington and London, 280p.

Andersen, A.N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: A review and a recipe. Proc. Ecol. Soc. Aust.16: 347-357.

Andersen, A.N. 1991. Parallels between ants and plants: Implications for community ecology, p.539-558. In C.R. Huxley & D.F. Cutler (eds.), Ant plant interactions. Oxford University Press, Oxford, 601p.

Andersen, A.N. 1995. A classification of Australia ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. J. Biogeogr. 20: 15-29.

Andersen, A.N. 2000. Global ecology of rainforest ants. Functional groups in relation to environment stress and disturbance, p.25-34. In D. Agosti, J.D. Majer, L.E. Alonso & T.R. Schultz (eds.), Ants standard methods for measuring and monitoring biodiversity. Smithsonian Inst. Press, Washington and London, 280p.

Antunes, F.Z. 1986. Caracterização climática do estado de Minas Gerais. Inf. Agro. 12: 1-13.

Bell, G., M.J. Lechowicz & M.J. Waterway. 2000. Environmental heterogeneity and diversity of sedges. J. Ecol. 88: 67-87.

Benson, W.W. & A.Y. Harada. 1988. Local diversity of tropical and temperate ant faunas. Acta Amazonica 18: 275-289.

Bestelmeyer, B.T. & J.A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine chaco. Ecol. Appl. 6: 1225-1240.

Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, 224p.

Borges, P.A.V., C. Aguiar, J. Amaral, I.R. Amorim, G. André, A. Arraiol, A. Baz, F. Dinis, H. Enghoff, C. Gaspar, F. Ilharco, V. Mahnert, C. Melo, F. Pereira, J.A. Quartau, S.P. Ribeiro, J. Ribes, A.R.M. Serrano, A.B. Sousa, R.Z. Strassen, L. Vieira, V. Vieira, A. Vitorino & J. Wunderlich. 2005. Ranking protected areas in the Azores using standardized sampling of soil. Biod. Conserv. 14: 2029-2060.

Byrne, M.M. 1994. Ecology of twig-dwelling ants in a wet lowland tropical forest. Biotropica 26: 61-72.

Davidson, D.W. 1997a. Species diversity and comunity organization in deserts seed-eating ants. Ecology 58: 711-724.

Davidson, D.W. 1997b. Foraging ecology and community in deserts seed-eating ants. Ecology 58: 725-737.

Dangerfield, J.M., A.J. Pik, D. Britton, A. Holmes, M. Gillings, I. Oliver, D. Briscoe & A.J. Beattie. 2003. Patterns of invetebrate biodiversity across a natural edge. Aust. Ecol. 28: 227-236.

Estrada, C.M. & F.C. Fernández. 1999. Diversidad de hormigas (Hymenoptera: Formicidae) em un gradiente sucesional del bosque nublado (Nariño, Colombia). Rev. Biol. Trop. 47: 189-201.

Farnsworth, E.J. & A.M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecol. Monogr. 66: 45-66.

Fisher, B.L. & H.G. Robertson. 2002. Comparison and origin of forest and grassland ant assemblages in high plateau of Madagascar (Hymenoptera: Formicidade). Biotropica 34: 155-167.

Gilhuis, J.P. 1986. Vegetation survey of the Parque Florestal Estadual do Rio Doce, MG, Brasil. Msc. Thesis, Agricultural University Wagaeningen, 112p.

Goulart, M.F., S.P. Ribeiro, M.B. Lovato. 2005. Genetic, morphological and spatial characterization of two populations of *Mabea fistulifera* Mart. (Euphorbiaceae), in different successional stages. Braz. Arch. Biol. Tech. 48: 275-284

Greenslade, P.J.M. 1983. Adversity selection and the habitat templet. Am. Nat. 122: 352-65.

Greenslade, P.J.M. & P. Greenslade. 1977. Some effects of vegetation cover and disturbance on a tropical ant fauna. Insect. Soc. 24: 163-182.

Heck, K.L. & G.S. Wetstone. 1997. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeogr. 4: 135-142.

IEF – Instituto Estadual de Florestas. 1994. Pesquisas prioritárias para o Parque Estadual do Rio Doce, Brasil. Belo Horizonte. 35p.

Kaspari, M. 2000. A primer of ant ecology, p. 9-24. In D. Agosti, J.D. Majer, L.E. Alonso & T.R. Schultz (eds.), Ants standard methods for measuring and monitoring biodiversity. Smithsonian Inst. Press, Washington and London, 280p.

Kunin, W.E. 1998. Biodiversity at the edge: A test of the importance of spatial "mass effects" in the Rothamsted Park grass experiments. Proc. Nat. Acad. Sc. USA 95: 207-212.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York, 481p.

Lopes, W.P. 1988. Florística e fitosociologia de um trecho de vegetação arbórea no Parque Estadual do Rio Doce, Minas Gerais. Dissertação de mestrado, Universidade Federal de Viçosa, 72p.

Marques, M.M. 2004. Aplicação da teoria de habitat-templets à avaliação de qualidade de água: Proposta de protocolo de biomonitoramento no trecho médio da bacia do rio Doce, MG. Tese de doutorado. Instituto de Ciências Biológicas, UFMG. Belo Horizonte, 118p.

Molano, A. 1994. Hormigas (Hymenoptera: Formicidae) del bosque seco tropical y de agrosistemas de la región de Zambrano, Bolivar. Tesis de Pregrado, Universidad Nacional de Colombia, Santafé de Bogotá, 227p.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. Saunders, Philadelphia, 574p.

Ribeiro, S.P. 2003. Insect herbivores in the canopies of savannas and rainforests, p.348-359. In Y. Basset, V. Novotny, S. Miller & R.Kitching (eds.), Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. 1 ed. Cambridge, Cambridge University Press, 2003, v.1, 490p.

Roth, D.S., I. Perfecto & B. Rathcke. 1994. The effects of management systems on ground foraging ant diversity in Costa Rica. Ecol. Appl. 4: 423-436.

SOCT – Sistema Operacional de Ciências e Tecnologia. 1981. Fundação Centro Tecnológico de Minas Gerais – CETEC. Programa de pesquisas ecológicas do Parque Estadual do Rio Doce. Belo Horizonte v.2., 285p.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46: 337 - 365.

Torres, J.A. 1984. Diversity and distribution of ant communities in Puerto Rico. Biotropica 16: 296-303.

Maarel, E. van der. 1990. Ecotones and ecoclines are different. J. Veg. Sci. 1: 135-138.

Vasconcelos, H.L. 1999. Effects of forest disturbance on the struture of ground-foraging ant communities in central Amazonia. Biodiv. Conserv. 8: 409-420.

Vasconcelos, H.L. & D.W. Davidson. 2000. Relationship between plant size and ant associate in two Amazonian ant-plants. Biotropica 51: 21-41.

Vasconcelos, H.L., K.S. Carvalho & J.H.C. Delabie. 2001. Landscape modifications and ant communities, p.199-207. In R.O. Bierregard, C. Gascom Jr., T.E. Lovejoy & R. Mesquita (eds.), Lessons from Amazonia: The ecology and conservation of a fragmented forest. v.1., New Haven, Edit., 478p.

Veloso, H.P., A.L.R. Rangel Filho & J.C.A. Lima. 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. Rio de Janeiro, IBGE, 124p.

Wilson, E.O. 1971. The insect societies. Belknap Press, Cambridge, Massachusetts, 548p.

Wilson, E.O. 1987. The arboreal ant fauna of Peruvian Amazon forests: A first assessment. Biotropica 19: 245-251.

Wolda, H. 1998. Insect seasonality: Why? Annu. Rev. Ecol. Syst. 19: 1-18.

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