Leaf-litter ant communities (Hymenoptera: Formicidae) in a pristine Guianese rainforest: stable functional structure versus high species turnover

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Abstract

We compared the ant assemblages from four very heterogeneous habitats over a short-distance elevational gradient of vegetation (due to the presence of an inselberg) at the Nouragues Research Station, French Guiana. We focused on litter-dwelling ants, combining the use of pitfall traps and the Winkler method according to the Ants of the Leaf Litter Protocol. This permitted us to note (1) a high leaf-litter ant diversity overall and a decreasing diversity gradient from the lowland rainforest to the top of the inselberg, and (2) differences in species density, composition and functional structure. While the ant assemblages on the plateau and inselberg can be considered functionally similar and typical of an Amazonian rainforest, that of the transition forest, relatively homogenous, rather corresponded to an ant fauna typical of open areas. By contrast, the liana forest assemblage was unexpectedly richer and denser than the others, sheltering a litter-dwelling ant fauna dominated by numerous and abundant cryptic species. These taxonomical and functional dissimilarities may reflect the influence of the environmental heterogeneity, which, through variable abiotic conditions, can contribute to maintaining a notably rich ant biodiversity in these Neotropical habitats.

Key words: Litter-dwelling ant communities, taxonomic and functional structure, functional groups, local scale, habitat heterogeneity, diversity gradient, pristine Amazonian rainforest.

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Introduction

In the context of environmental studies, there is a growing consensus that species richness alone cannot appropriately describe the differences in community structure and the mechanisms involved in species coexistence and ecosystem processes (HOOPER & al. 2002, 2005). But biodiversity is a complex concept composed of multiple components, beyond the number of species (PURVIS & HECTOR 2000, DEVICTOR & al. 2010). Among them, one of the most currently popular is taxonomic diversity (TD) (HOOPER & al. 2005). Nonetheless, there is increasing interest in functional diversity (FD); i.e., the value, range, distribution and relative abundance of the functional characteristics of organisms in a community (HOOPER & al. 2005, DE BELLO & al. 2006, MAYFIELD & al. 2010). FD, along with functional richness and redundancy, is one of the components of the functional structure (i.e., the composition and diversity of functional traits; MOUILLOT & al. 2011) of communities.

FD can reveal why biodiversity changes in response to environmental change, as well as how biodiversity influ-

ences ecosystem functioning (DIAZ & CABIDO 2001). It also enables us to understand the link between the characteristics of communities and ecosystem functions and services (CORNELISSEN & al. 2003, LAVOREL & al. 2007). One of the classic FD approaches consists in measuring functional richness by estimating the functional group number in the community, a functional group being a subset of species sharing similar trait profiles in a given assemblage (PLA & al. 2012).

Of particular importance are the vast areas of biodiversity that involve small organisms, such as arthropods, which are important drivers of ecosystem processes. Among the terrestrial entomofauna in tropical rainforests worldwide, ants are highly diversified and represent one of the most dominant groups of insects both in terms of biomass and number of individuals (HÖLLDOBLER & WILSON 1990, DUNN & al. 2009). Moreover, they play a major ecological role and are sensitive to environmental changes (HÖLLDOBLER & WILSON 1990, HOFFMANN & ANDERSEN 2003), and so can be valuable indicators of changes in the integrity and biological functioning of ecosystems (LAVELLE & al. 2006). They have been widely studied in this context, but far more in Australia (for reviews, see HOFFMANN & ANDERSEN 2003, UNDERWOOD & FISHER 2006) than in either Central or South America, for example (BESTELMEYER & WIENS 1996, DELABIE & al. 2000a, SILVESTRE & al. 2003, HERNÁNDEZ-RUIZ & al. 2009, RYDER WILKIE & al. 2010, SILVA & BRANDÃO 2010, FERGNANI & al. 2013).

Recently, an increasing number of surveys has enabled us to considerably expand our understanding of the Amazonian ant fauna diversity (VASCONCELOS & VILHENA 2006, MERTL & al. 2009, RYDER WILKIE & al. 2009, VASCONCELOS & al. 2010, RYDER WILKIE & al. 2010, SOUZA & al. 2012); however, most of these studies only focused on species richness, diversity and / or composition. Moreover, only two studies to date have focused on French Guianese ground-dwelling ant assemblages (DELABIE & al. 2009, GROC & al. 2009). Thus, there is little current literature dealing with the functional structure of Neotropical ant communities and literature focusing on Amazonian ant communities is virtually nonexistent (RYDER WILKIE & al. 2009, 2010). In this context, the present study aims to investigate and compare the diversity and compositional and functional patterns of the leaf-litter ant communities in French Guianese forests. The ant communities were studied along a gradient of vegetation over a small geographic scale which enabled us to quantify the turnover of litter-dwelling ant communities based on the forest facies.

Material and methods
Study sites

The Nouragues Research Station (NRS) is located in the Balenfois Mountains, French Guiana. It is mainly dominated by hills covered by an expanse of dense forest that has remained uninhabited for over two centuries. This site is particularly interesting and remarkable for its granitic inselberg, a tabular rocky outcropping rising abruptly from the surrounding rainforest to 430 m above sea level (BREMER & SANDER 2000). As vegetal cover is influenced by variations in climate, geomorphology, soil fertility and topography over a small scale, one can find a variety of habitats and a succession of vegetal formations even within

relatively short distances of hundreds of meters from one another. Four different forested environments were sampled first in March 2006 and then in October 2009: a liana forest; a wide, forested plateau; a low transition forest and the inselberg's summit (hereafter FL, GP, FT, and IN, respectively). For a more detailed description of the study sites, see GROC & al. (2009).

Experimental protocol

The Winkler method (see BESTELMEYER & al. 2000) was used because it is highly recommended for invertebrate inventories in forested habitats where litter abounds (FISHER 1999, DELABIE & al. 2000b). We collected ant workers from a series of 1 m^2 leaf-litter samples that were then weighed. As it is essential to combine several sampling methods to come as near as possible to an exhaustive inventory of the litter-dwelling ant fauna (DELABIE & al. 2000b), we also used pitfall traps during the second field campaign (BESTELMEYER & al. 2000).

We applied the "Ants of the Leaf Litter" (ALL) Protocol (AGOSTI & ALONSO 2000) which suggests using a minimum of 20 sampling points separated by 10 m intervals to collect at least 70% of the ant fauna at a given site. We selected 50 sampling points in all of the habitats, except for the inselberg forest (only 20 sampling points) given its relatively small size. Thus, during the two field campaigns, two sets of 170 Winkler samples were collected and 170 pitfall traps were set, resulting in 510 ant samples.

All of the ant samples were preserved in 70% ethanol. For each sample, at least one individual per species or morphospecies was pinned and mounted in order to constitute a reference collection resulting in a total of 3,414 individuals (or 1,270, 957, 782 and 405 morphospecies per liana, plateau, transition, and inselberg forest sampled, respectively). We focused our analysis on the worker caste since alates are difficult to identify. The ants were sorted to species or morphospecies and the genera identified based on the method developed by BOLTON (1994). Voucher specimens were deposited in the Laboratório de Mirmecologia, Cocoa Research Centre CEPEC / CEPLAC (Ilhéus, Bahia, Brazil) and in the Royal Belgian Institute of Natural Sciences (RBINS; Brussels, Belgium).

Data analysis

Richness, diversity and species composition. Four species × sample presence / absence matrices (one per habitat) were analyzed and compared between the four forests. Because ants are social insects, incidence data are preferred over abundance to avoid bias due to sampling near nests and trails (LONGINO 2000). Thus, only species occurrences (i.e., the number of times that a given species was collected at a sampled site) were taken into account, and the percentages of the relative number of species occurrences per sample (i.e., for a given species: total number of occurrences in a given habitat / sample number × 100) were used as a proxy for ant abundance (LONGINO 2000, LEPONCE & al. 2004).

EstimateS 7.5 software (COLWELL 2005) was used to produce sample- and individual-based rarefaction curves with the Coleman method (sensu GOTELLI & COLWELL 2001), representing the cumulated rarefied number of species according to the number of samples and species occurrences, respectively (LEPONCE & al. 2004). The curves

and their standard deviations (SD) were plotted for the real number of samples (N = 150 for the liana, plateau, and transition forests, and N = 60 for the inselberg forest) and for N = 60 samples for each habitat to (1) estimate and standardize the comparison of ant sampling efficiency for each habitat and (2) compare the patterns of species density (i.e., the number of species per unit area – in this case, 1 m^2) and richness between habitats (GOTELLI & COLWELL 2001). The estimated number of species was also calculated using the Chao2 estimator. Because the order in which each sample is added influences the shape of these curves, the matrices of species occurrences were treated with 100 randomizations of the sampling order without replacement (COLWELL & al. 2004). All of the rarefaction curves were plotted with Sigmaplot software (BRANNAN & al. 2002).

We used Simpson's diversity index ($1 - D$) with a 95% confidence interval (CI) to analyze the α-diversity and evenness ($E_{1/D}$) of the ant species in the four habitats, and all possible inter-habitat comparisons were statistically tested using a bootstrapping procedure with 1000 randomizations. The overdependence of the various published diversity indices on sampling effort is stated as one of the fundamental difficulties in all fields of biodiversity assessment (WARWICK & CLARKE 2001). Simpson's index is a notable exception making it one of the most meaningful and robust indices currently available (MAGURRAN 2004). Its evenness measurement is not sensitive to species richness and is particularly useful when symmetry between rare and abundant species is required (SMITH & WILSON 1996). Moreover, the difference between the average species density per sample was tested using a Kruskall-Wallis test.

The similarity in the taxonomic composition of each sampled ant community from the four forests was then assessed and represented by agglomerative dendrograms produced by an UPGMA cluster analysis. These dendrograms were based on the Sørensen and Bray-Curtis distances for presence / absence and relative abundance data, respectively. Past software (HAMMER & al. 2001) was used to compute the diversity indices and to build all of the dendrograms. In addition, the relationship between the number of species and the number of forested habitats occupied was plotted.

Functional structure of ant assemblages. Information regarding diet, foraging and nesting habits was used to create one functional group matrix. Species were placed into functional groups based on recent classifications for Neotropical ants (SILVESTRE & al. 2003, BRANDÃO & al. 2009, SILVA & BRANDÃO 2010) and on personal field observations. Species belonging to the same genus and for which detailed dietary and nesting information are known were distributed widely within the functional group matrix; species belonging to rare, cryptic genera for which no biological or ecological information is available were placed into one functional group. The *Acropyga* genus, represented by few species because of its specialized ecology (i.e., they are obligate coccidophile ants), were not considered. The matrix was composed of nine groups comprising two groups of fungus-growers (i.e., leaf-cutter ants and cryptobiotic attines), three groups of omnivores (i.e., ground-nesting, generalist-nesting, and arboreal omnivorous ants) and four groups of predators (i.e., ground-dwelling generalist, ground-dwelling specialist, raid-hunting, and arboreal predators) (for details on the species in each functional group, see Appendix S1, as digital supplementary material to this article at the journal's web pages). Then, the values for the relative species richness and abundance per functional group (%) were used to produce agglomerative dendrograms (UPGMA; the Bray-Curtis distance) in order to compare the functional composition of each ant fauna from each forest sampled.

Results

A total of 284 ant species belonging to 54 genera from nine subfamilies was collected (for a list of species collected in each forest type, see Appendix S2 as digital supplementary material to this article at the journal's web pages). The most diversified subfamilies were the Myrmicinae, Ponerinae, and Formicinae. The most speciose and abundant genus overall was *Pheidole* and the most abundant species was *Pyramica denticulata* (MAYR, 1887) (Appendix S2). In all of the forests sampled, only a small fraction of the most frequent species was responsible for the greatest part of the overall ant abundance (i.e., species for which the occurrence number was greater than 50 such as *Basiceros betschi* (PERRAULT, 1988), *Crematogaster carinata* MAYR, 1862, *Crematogaster limata* SMITH, 1858, and *P. denticulata*), all ubiquitous in our study sites (Appendix S2).

An examination of the sample-based rarefaction curves (Fig. 1a) and the Chao2 values (Tab. 1) indicated that a representative part (ca. 77%) of the leaf-litter ant fauna present at the NRS was actually sampled. The sample-based rarefaction curves also indicated that the liana forest presented the greatest density of species, followed by the forested plateau, the transition forest and the inselberg forest. However, an analysis of the individual-based rarefaction curves (Fig. 1b) showed that, with the exception of the inselberg forest, all of the forests presented a similar species richness. Despite presenting a lower species richness, the inselberg forest had a greater evenness of ant species (eveness ($E_{(1 - D)}$) and the 95% confidence interval (IC): $E_{(1 - D) \text{ Liana forest}}$ = 0.47 (0.47 - 0.52); $E_{(1 - D) \text{ Forested plateau}}$ = 0.50 (0.50 - 0.56); $E_{(1 - D) \text{ Transition forest}}$ = 0.51 (0.51 - 0.58); $E_{(1 - D) \text{ Inselberg}}$ = 0.61 (0.59 - 0.68)).

Consequently, the Simpson's diversity index was quite similar between the four forest types (diversity ($1 - D$) and the 95% confidence interval (IC): $(1 - D)_{\text{Liana forest; Forested plateau}}$ = 0.98 (0.97 - 0984); $(1 - D)_{\text{Transition forest; Inselberg plateau}}$ = 0.97 (0.97 - 098)).

In terms of the average number of species recorded per sample (1 m^2 of leaf-litter), there were significantly more species in the liana forest than in the other forests and more species in the forested plateau and the inselberg forest than in the transition forest (Tab. 1; Kruskall-Wallis: $H = 47.85$, $P < 0.001$; for details of the Mann-Whitney test U values for pairwise habitat comparisons, see Appendix S3 as digital supplementary material to this article at the journal's web pages).

In terms of taxonomic composition, the inselberg forest sheltered the most distinct ant fauna, whereas that of the plateau and liana forests were the most similar to each other. This pattern was observed both for the analysis using presence / absence data as well as for that using data on species abundances (Fig. 2a, b). However, even between
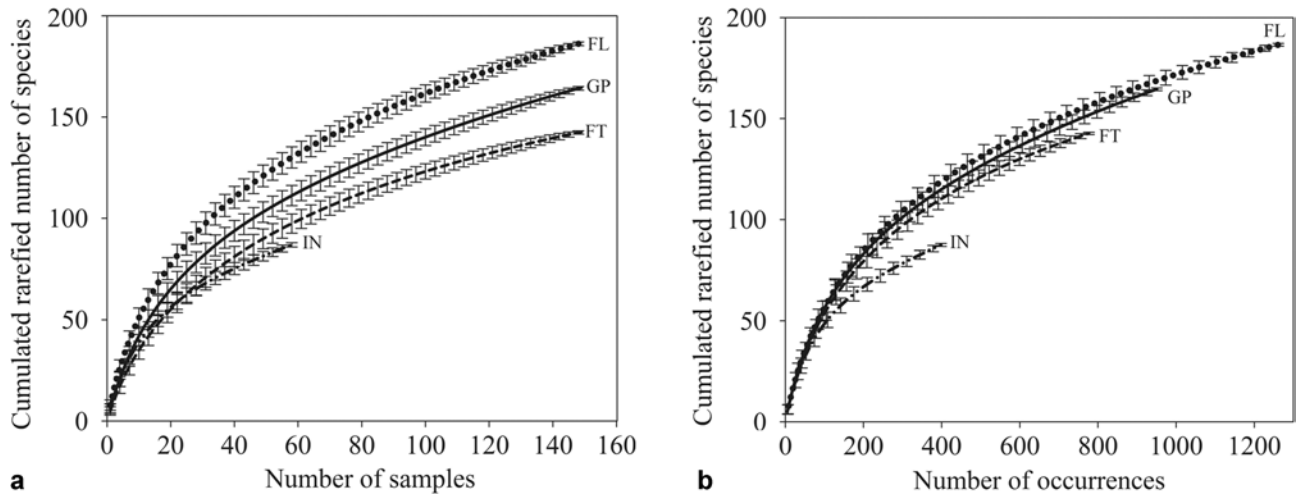
Fig. 1: Sampled- and individual-based species rarefaction curves representing the cumulated number of rarefied species (Coleman) depending on (a) the number of samples (± SD) and (b) the number of occurrences (± SD) for each forest sampled (GP, FL, FT and IN refer to grand plateau, liana, transition and inselberg forest, respectively).

Tab. 1: Number of samples, taxonomic characteristics for an observed and a rarefied number of species (for N = 60 samples), Chao2 estimations and average species density by sample for the ant faunas at the Nouragues Research Station and for each forest sampled.

	Liana forest	Forested plateau	Transition forest	Inselberg forest	Nouragues Research Station
Abbreviation	FL	GP	FT	IN	NRS
Number of samples	150	150	150	60	510
Winklers / Pitfall traps	100 / 50	100 / 50	100 / 50	40 / 20	340 / 170
Number of:					
1) genera	47	39	36	32	54
2) observed species	186	164	142	88	284
3) species for N = 60	131.93	112.84	98.92	–	–
samples ± SD	± 5.22	± 4.99	± 4.71		
Chao2 estimations:					
1) number of species	255.9	241.5	186.0	143.2	369.8
2) % of species collected	73	68	76	62	77
Average species density (sp / m²)	8.5	6.4	5.2	6.8	6.7

Tab. 2: Relative number (a) and abundance (b) of ant species per functional group for each habitat sampled (GP, FL, FT and IN refer to the plateau, liana, transition and inselberg forests, respectively).

|		Relative species number per functional group (%)				Relative species abundance per functional group (%)			
		FL	GP	FT	IN	FL	GP	FT	IN
Fungus-growers	Leaf-cutters	3.2	4.3	3.6	2.3	1.0	1.2	1.3	0.6
	Cryptobiotic attines	7.5	6.1	4.3	5.8	5.2	2.9	1.4	6.1
Omnivorous ants	Ground-dwelling omnivores	15.1	11.7	14.2	15.1	11.3	14.2	14.7	19.2
	Generalist omnivores	24.2	27.0	31.2	24.4	25.0	28.7	37.3	40.1
	Arboreal omnivores	7.5	6.1	10.6	7.0	12.5	12.3	13.7	4.3
Predatory ants	Ground-dwelling generalist predators	22.6	25.2	21.3	23.3	17.3	18.7	14.3	2.4
	Ground-dwelling specialist predators	15.1	14.1	9.9	14.0	26.1	18.5	14.6	21.9
	Raid-hunting predators	3.2	3.1	2.8	4.7	1.3	3.1	0.6	3.0
	Arboreal predators	1.6	2.5	2.1	3.5	0.2	0.5	2.1	2.4
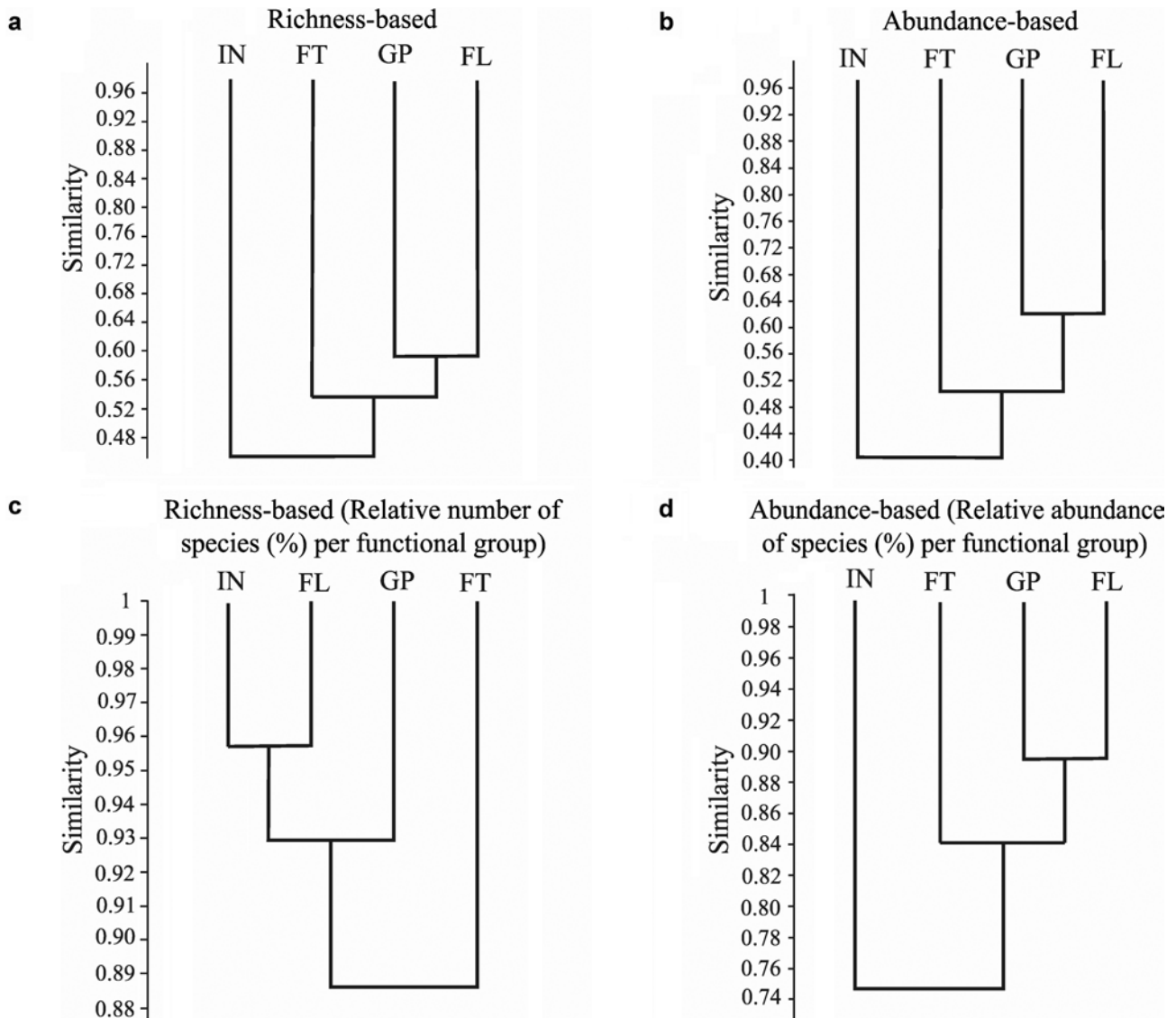
Fig. 2: Presence / absence and abundance data-based dendrograms representing the taxonomic (Sorensen (a) and Bray-Curtis (b) distances) and the functional (Bray-Curtis distance: c and d) similarity of the leaf-litter ant faunas sampled in the four forest types (GP, FL, FT and IN refer to grand plateau, liana, transition and inselberg forest, respectively).

the liana and the plateau forests, species turnover was relatively high (pairwise similarity < 0.65; Fig. 2a - d) given the high proportion of habitat-specific species composing these communities. In fact, nearly 45% of all of the species we collected at the NRS were found in just one forest type, whereas only 17% were found in all four forests (Fig. 3).

With regard to the functional composition of the ant faunas in the different forest types, contrasting patterns were observed depending on whether the analysis was based on the relative abundance of ant occurrences per functional group or on the relative number of species per functional group (Fig. 2c, d). When relative abundance data was used, the similarity pattern observed was the same as that observed in the analysis of taxonomic composition (i.e., the inselberg forest presented the most distinct ant fauna, whereas that of the plateau and liana forests were the most similar to each other; Fig. 2d). In this case, the greater dissimilarity of the inselberg forest is largely explained by the relative paucity of arboreal omnivores and the compara-
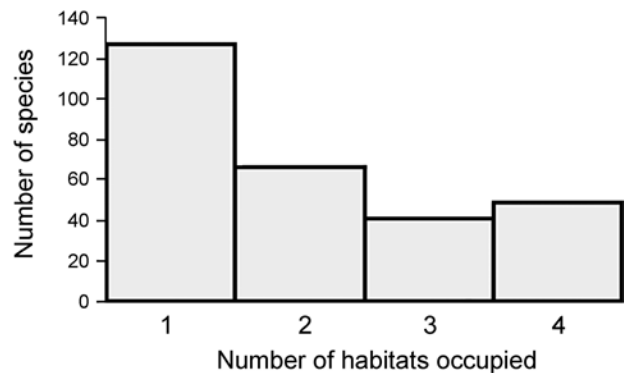

Fig. 3: Relationship between the number of species and the number of forested habitats occupied.

tively greater abundance of generalist and ground-dwelling omnivores (Tab. 2). By contrast, when data on the relative number of species per functional group was used, the transitional forest was the most dissimilar and this was be-

47

cause, compared to the other forest types, it presented more generalist and arboreal omnivorous species and fewer ground-dwelling specialist predators (Tab. 2). However, these are variations of low amplitude because all of the forests were characterized by a high global functional similarity (0.74 - 0.9; Fig. 2c, d), which was notably higher than that of the taxonomic composition (similarity: 0.50 - 0.7; Fig. 2a, b).

Discussion

Several practical reasons account for the limited number of replicates in our study. Although invertebrate sampling is relatively fast, sorting and identifying specimens, particularly when the Winkler extraction is used, is highly time-consuming and labor intensive (SOUZA & al. 2009, PARR & CHOWN 2001). In addition, especially in Amazonia, financial costs limit the amplitude of biodiversity studies (COSTA & MAGNUSSON 2010). In spite of that, our survey recorded a representative part of the rich litter-dwelling ant fauna at the NRS.

In our study, all of the species making up the sampled ant communities, regardless of the habitat type, were rather heterogeneously distributed. These variations in assemblage composition might be explained by the features thought to shape ant communities, such as litter biomass, soil moisture and the heterogeneous distribution of nutrients and nesting sites (e.g., small twigs and seeds) on the forest floor (BYRNE 1994; MCGLYNN & al. 2009, BACCARO & al. 2010). They might also be caused by the slight clumping in the spatial distribution of uncommon, Neotropical species associated with the generally clumped distribution of the most frequent species (LEPONCE & al. 2004).

Contrary to our expectations and to other studies reporting that species diversity is often positively correlated with habitat diversity and heterogeneity (ROSENZWEIG 1992, PACHECO & VASCONCELOS 2012), of all the ant faunas sampled only the inselberg forest had a significantly different level of species richness. However, our results corroborate those of other ecological surveys reporting major differences in species composition in spite of no significant differences in species richness over a local scale (RIBAS & SCHOEREDER 2007). Indeed, we show a notable species turnover between the ant faunas sampled that can be explained by the relatively high fraction of habitat-specific species and low fraction of numerically-dominant species, as previously demonstrated for Neotropical leaf-litter ant faunas (LONGINO & al. 2002, LEPONCE & al. 2004). However, although ant species richness at a given Amazonian site can be high, over a larger scale, beta diversity appears to be low for Amazonian ants and not significantly enhanced by differences between habitats (WILSON 1987, MAJER & DELABIE 1994, VASCONCELOS & VILHENA 2006). This is mainly related to the fact that many Amazonian ants appear to be habitat generalists (WILSON 1987, MAJER & DELABIE 1994, VASCONCELOS & al. 2010). This potentially explains why a relatively large number of the species collected in our study are characterized by a broad distribution, not only at the local scale, but also in the Neotropical region (BOLTON & al. 2007).

Our results show that there was a low level of taxonomic diversity (TD) in a naturally disturbed and less structurally complex habitat (based on the gradient of vegetation) contrasting with the high stability of the functional diversity (FD), suggesting that FD might not be tied to TD (CARMONA & al. 2012). Despite a high turnover rate between even the most taxonomically similar ant faunas (that of the liana and plateau forest), the functional similarity between all of them remained very high and stable, reflecting a high functional redundancy (sensu LAWTON & BROWN 1993). The pool of species at the NRS showed a significant decrease in diversity and density from the liana to the inselberg forest, and the TD and FD followed the same pattern (except in one case). Taxonomically and functionally, the ant fauna of the forested plateau represented the referential assemblage for a mature, preserved forest while those of the liana and the inselberg forests were at the opposite extreme in terms of diversity, density and functional structure (except in one case). Contrary to what might be expected, these differences were not the result of an undersampling artifact. According to GOTELLI & COLWELL (2001), because ecological disturbances reduce abundance, we expected changes in the vegetation gradient from the liana to the inselberg forest to decrease species density simply because there are fewer individuals present to be sampled after a disturbance (i.e., the habitat has a lower structural complexity and resource abundance and the abiotic and microclimatic conditions are more stressful for terrestrial entomofauna). Thus, the ant fauna of the inselberg forest was represented by a subset of species from the plateau forest characterized by fewer species with special ecological requirements that were replaced by generalist and ground-dwelling omnivores more adapted to highly variable abiotic conditions.

In the transition forest, the ant assemblage was poorer than that of the plateau forest, thus corroborating numerous studies showing that vegetal formations that are characterized by scattered small trees (i.e., a low, non-continuous canopy and little accumulation of leaf-litter) may lead to lower ant diversity (BESTELMEYER & WIENS 1996, PACHECO & VASCONCELOS 2012). The functional structure of this ant fauna, conversely to that of the other ant faunas, surprisingly reflected a rather "typical" trophic pyramid for tropical ant communities (TOBIN 1994) where omnivores specifically and numerically dominated specialized predator species. In addition, due to the presence of small trees, the proportion of arboreal ant species was higher than in the three other assemblages, making this ant fauna perhaps closer to that of open environments (e.g., savannas). This naturally-disturbed habitat, where microclimatic conditions (i.e., a dry, thin and sparse litter layer; high temperatures and vast sun exposure during the daytime) (GROC & al. 2009) are stressful for litter-dwelling arthropods, favors ecologically generalist species adapted to open areas (HÖLLDOBLER & WILSON 1990, PACHECO & VASCONCELOS 2012), including Formicines. Moreover, recurrent and intense rainfall during the rainy season associated with the sloping rocky ground may prevent the establishment of ant nests on the scarce woody vegetation, and ground-dwelling species may only survive in places where this disturbance is minimal (MAJER & DELABIE 1994, MERTL & al. 2009).

The case of the liana forest is particularly interesting due to its unexpectedly high global ant diversity (GROC & al. 2009) and significantly high average density of (1) species per sample and (2) habitat-specific species. This habitat, likely disturbed and altered a long time ago by both substantial paleofires and Amerindian tribes (TARDY 1998),

is still subject to continual, intermittent disturbances of varying intensities (BALÉE & CAMPBELL 1990). Indeed, lianas can cause treefall gaps and vegetal material to fall onto the ground (PHILLIPS 2005). There may thus be a constant level of disturbance to the habitat and, as a consequence, greater niche diversification and specialization. This consequently favors more nest and foraging sites for ground-dwelling, specialized cryptic and strictly predaceous species (ARMBRECHT & al. 2004, BLÜTHGEN & FELDHAAR 2009). Indeed, high ant species density, in particular that of Ponerinae species, has already been linked to greater leaf-litter depths (DELABIE & FOWLER 1995, BASTOS & HARADA 2011). The leaf-litter is a habitat sheltering a high diversity of arthropod taxa that are potential prey items for ants (BENSON & HARADA 1988), in particular for rare cryptic species; e.g., those belonging to the Amblyoponinae, Ectatomminae, or the *Thaumatomyrmex* genus characterized by specific diets and predatory habits.

Conclusion

To conclude, the NRS shelters ground-dwelling ant faunas characterized by a high species richness, density and diversity whose species compose heterogeneous taxonomic but homogeneous functional communities. These peculiarities may reflect the influence of species habitat specialization and environmental heterogeneity through variable abiotic conditions in the Neotropical rainforest which can contribute to the structure and maintaining of such ant diversity. This survey may also provide some basis for future studies focusing on the link between TD and FD in a current context in which relatively few studies have related the response of FD to changes in habitat structure and even fewer have assessed how the functional turnover is affected by environmental conditions. Finally, our survey represents a baseline study for future research on the abundance and functional role of ant diversity in ecosystems and possibly other terrestrial invertebrates in the Guianese Amazon, a region that has high global conservation significance.

Acknowledgements

References

AGOSTI, D. & ALONSO, L.E. 2000: The ALL protocol: a standard protocol for the collection of ground-dwelling ants. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants: standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington and London, pp. 204-206.

ARMBRECHT, I., PERFECTO, I. & VANDERMEER, J. 2004: Enigmatic biodiversity correlations: ant diversity responds to diverse resources. – Science 304: 284.

BACCARO, F.B., KETELHUT, S.M. & DE MORAIS, J.W. 2010: Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian forest. – Austral Ecology 35: 274-281.

BALÉE, W. & CAMPBELL, D.G. 1990: Evidence for the successional status of liana forest (Xingu river basin, Amazonian Brazil). – Biotropica 22: 36-47.

BASTOS, A.H.S. & HARADA, A.Y. 2011: Leaf-litter amount as a factor in the structure of a ponerine ant community (Hymenoptera: Formicidae, Ponerinae) in an eastern Amazonian rainforest, Brazil. – Revista Brasileira de Entomologia 55: 589-596.

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

BESTELMEYER, B.T., AGOSTI, D., ALONSO, L.E., BRANDÃO, C.R.F., BROWN Jr., W.R., DELABIE, J.H.C. & SILVESTRE, R. 2000: 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. (Eds.): Ants: standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington and London, pp. 122-144.

BESTELMEYER, B.T. & WIENS, J.A. 1996: The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. – Ecological Applications 6: 1225-1240.

BLÜTHGEN, N. & FELDHAAR, H. 2009 [2010]: Food and shelter: How resources influence ant ecology. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): Ant ecology. – Oxford University Press, New York, NY, pp. 115-136.

BOLTON, B. 1994: Identification guide to the ant genera of the world. – Harvard University Press, Cambridge, MA, 222 pp.

BOLTON, B., ALPERT, G., WARD, P.S. & NASKRECKI, P. 2007: Bolton's catalogue of ants of the World: 1758 - 2005. – Harvard University Press, Cambridge, MA, CD-ROM edition.

BRANDÃO, C.R.F., SILVA, R.R. & DELABIE, J.H.C. 2009: Formigas (Hymenoptera). In: PANIZZI, A.R. & PARRA, J.R.R. (Eds.): Bioecologia e nutrição de insetos. Base para o manejo integrado de pragas. – Embrapa Informação Tecnológica, Brasília, pp. 321-369.

BRANNAN, T., ALTHOFF, B., CABASA, F., DIXON, F., JACOBS, L.J., NEKORYSTNOVA, I., NORBY, J. & RUBENSTEIN, S. 2002: SigmaPlot. Exact graphics for exact science. – SPPS. INC.

BREMER, H. & SANDER, H. 2000: Inselbergs: geomorphology and geoecology. In: POREMBSKI, S. & BARTHLOTT, W. (Eds.): Inselbergs: biotic diversity of isolated rock outcrops in tropical and temperate regions. – Springer, Berlin, pp. 7-35.

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

CARMONA, C.P., AZCÁRATE, F.M., DE BELLO, F., OLLERO, H.S., LEPŠ, J. & PECO, B. 2012: Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. – Journal of Applied Ecology 49: 1084-1093.

COLWELL, R.K. 2005: EstimateS: Statistical estimation of species richness and shared species from samples. Version user's guide & application. – <http: //purl.oclc.org/estimates>, retrieved in December 2011.

COLWELL, R.K., MAO, C.X. & CHANG, J. 2004: Interpolating, extrapolating, and comparing incidence-based species accumulation curves. – Ecology 85: 2717-2727.

CORNELISSEN, J.H.C., LAVOREL, S., GARNIER, E., DÍAZ, S., BUCHMANN, N., GURVICH, D.E., REICH, P.B., TER STEEGE, H., MOR-

GAN, H.D., HEIJDEN, M.G.A., VAN DER PAUSAS, J.G. & POORTER, H. 2003: A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. – Australian Journal of Botany 51: 335-380.

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 & Conservacao 8: 3-12.

DE BELLO, F., LEPS, J. & SEBASTIA, M.T. 2006: Variations in species and functional plant diversity along climatic and grazing gradients. – Ecography 29: 801-810.

DELABIE, J.H.C., AGOSTI, D. & NASCIMENTO, I.C. 2000a: Litter ant communities of the Brazilian Atlantic rain forest region. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Sampling ground-dwelling ants: case studies from the world's rainforests. – Curtin University School of Environmental Biology Bulletin n°18, Perth, pp. 1-17.

DELABIE, J.H.C., CÉRÉGHINO, R., GROC, S., DEJEAN, A., GIBERNAU, M., CORBARA, B. & DEJEAN, A. 2009: Ants as biological indicators of Wayana Amerindian land use in French Guiana. – Comptes Rendus Biologies 332: 673-684.

DELABIE, J.H.C., FISHER, B.L., MAJER, J.D. & WRIGHT, I.W. 2000b: Sampling effort and choice of methods. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants: standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington and London, pp. 145-154.

DELABIE, J.H.C. & FOWLER, H.G. 1995: Soil and litter cryptic ant assemblages of Bahian cocoa plantations. – Pedobiologia 39: 423-433.

DEVICTOR, V., MOUILLOT, D., MEYNARD, C., JIGUET, F., THUILLER, W. & MOUQUET, N. 2010: Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. – Ecology Letters 13: 1030-1040.

DIAZ, S. & CABIDO, M. 2001: Vive la différence: plant functional diversity matters to ecosystem processes. – Trends in Ecology & Evolution 16: 646-655.

DUNN, R.R., AGOSTI, D., ANDERSEN, A.N., ARNAN, X., BRUHL, C., CERDA, X., ELLISON, A.M., FISHER, B.L., FITZPATRICK, M.C., GIBB, H., GOTELLI, N.J., GOVE, A.D., GUENARD, B., JANDA, M., KASPARI, M., LAURENT, E.J., LESSARD, J.P., LONGINO, J.T., MAJER, J.D., MENKE, S.B., MCGLYNN, T.P., PARR, C.L., PHILPOTT, S.M., PFEIFFER, M., RETANA, J., SUAREZ, A.V., VASCONCELOS, H.L., WEISER, M.D. & SANDERS, N.J. 2009: Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. – Ecology Letters 12: 324-333.

FERGNANI, P.N., SACKMANN, P. & RUGGIERO, A. 2013: The spatial variation in ant species composition and functional groups across the Subantarctic-Patagonian transition zone. – Journal of Insect Conservation 17: 295-305.

FISHER, B.L. 1999: Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. – Ecological Applications 9: 714-731.

GOTELLI, N.J. & COLWELL, R.K. 2001: Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – Ecology Letters 4: 379-391.

GROC, S., ORIVEL, J., DEJEAN, A., MARTIN, J.M., ETIENNE, M.P., CORBARA, B. & DELABIE, J.H.C. 2009: Baseline study of the leaf-litter ant fauna in a French Guianese forest. – Insect Conservation and Diversity 2: 183-193.

HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2001: Past: Paleontological statistics software package for education and data analysis. – Palaeontologia Electronica 4: 9.

HERNÁNDEZ-RUIZ, P., CASTAÑO-MENESES, G. & CANO-SANTANA, Z. 2009: Composition and functional groups of epidaphic ants (Hymenoptera: Formicidae) in irrigated agroecosystem and in nonagricultural areas. – Pesquisa Agropecuaria Brasileira 44: 904-910.

HOFFMANN, B.D. & ANDERSEN, A.N. 2003: Responses of ants to disturbance in Australia, with particular reference to functional groups. – Austral Ecology 28: 444-464.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 732 pp.

HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. 2005: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecological Monographs 75: 3-35.

HOOPER, D.U., SOLAN, M., SYMSTAD, A.J., DIAZ, S., GESSNER, M.O., BUCHMANN, N., DEGRANGE, V., GRIME, P., HULOT, F., MERMILLOD-BLONDIN, F., ROY, J., SPHEN, E. & VAN PEER, L. 2002: Species diversity, functional diversity, and ecosystem functioning. In: INCHAUSTI, P., LOREAU, M. & NAEEM, S. (Eds.): Biodiversity and ecosystem functioning: Synthesis and perspectives. – Oxford University Press, New York, NY, pp. 195-208.

LAVELLE, P., DECAENS, T., AUBERT, M., BAROT, S., BLOUIN, M., BUREAU, F., MARGERIE, P., MORA, P. & ROSSI, J.P. 2006: Soil invertebrates and ecosystem services. – European Journal of Soil Biology 42: S3-S15.

LAVOREL, S., DÍAZ, S., CORNELISSEN, J.H., GARNIER, E., HARRISON, S.P., MCINTYRE, S., PAUSAS, J., PÉREZ, N., ROUMET, C. & URCELAY, C. 2007: Plant functional types: are we getting any closer to the Holy Grail? In: CANADELL, J.G., PATAKI, D. & PITELKA, L. (Eds.): Terrestrial ecosystems in a changing world. – Springer, New York, NY, pp. 149-164.

LAWTON, J.H. & BROWN, V.K. 1993: Redundancy in ecosystems. In: SCHULZE, E.D. & MOONEY, H.A. (Eds.): Biodiversity and ecosystem function. – Springer, New York, NY, pp. 255-270.

LEPONCE, M., THEUNIS, L., DELABIE, J.H.C. & ROISIN, Y. 2004: Scale dependence of diversity measures in a leaf-litter ant assemblage. – Ecography 27: 253-267.

LONGINO, J.T. 2000: What to do with the data. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants: standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington and London, pp. 186-203.

LONGINO, J.T., CODDINGTON, J. & COLWELL, R.K. 2002: The ant fauna of a tropical rain forest: estimating species richness three different ways. – Ecology 83: 689-702.

MAGURRAN, A.E. 2004: Measuring biological diversity. – Blackwell Science, Oxford, 192 pp.

MAJER, J.D. & DELABIE, J.H.C. 1994: Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon. – Insectes Sociaux 41: 343-359.

MAYFIELD, M.M., BONSER, S.P., MORGAN, J.W., AUBIN, I., MCNAMARA, S. & VESK, P.A. 2010: What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. – Global Ecology and Biogeography 19: 423-431.

MCGLYNN, T.P., FAWCETT, R.M. & CLARK, D.A. 2009: Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. – Biotropica 41: 234-240.

MERTL, A.L., RYDER WILKIE, K.T.R. & TRANIELLO, J.F.A. 2009: Impact of flooding on the species richness, density and composition of amazonian litter-nesting ants. – Biotropica 41: 633-641.

MOUILLOT, D., VILLÉGER, S., SCHERER-LORENZEN, M. & MASON, N.W.H. 2011: Functional structure of biological communities predicts ecosystem multifunctionality. – Public Library of Science ONE 6: e17476.

PACHECO, R. & VASCONCELOS, H.L. 2012: Habitat diversity enhances ant diversity in a naturally heterogeneous Brazilian landscape. – Biodiversity and Conservation 21: 797-809.

PARR, C.L. & CHOWN, S.L. 2001: Inventory and bioindicator sampling: testing pitfall and Winkler methods with ants in a South African savanna. – Journal of Insect Conservation 5: 27-36.

PHILLIPS, O.L.R. 2005: Large lianas as hyperdynamic elements of the tropical forest canopy. – Ecology 86: 1250-1258.

PLA, L., CASANOVES, F. & DI RIENZO, J. 2012: Quantifying functional biodiversity. – Springer, Berlin, 98 pp.

PURVIS, A. & HECTOR, A. 2000: Getting the measure of biodiversity. – Nature 405: 212-219.

RIBAS, C.R. & SCHOEREDER, J.H. 2007: Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. – Biodiversity and Conservation 16: 1511-1520.

ROSENZWEIG, M.L. 1992: Species diversity gradients: we know more and less than we thought. – Journal of Mammalogy 73: 715-730.

RYDER WILKIE, K.T., MERTL, A.L. & TRANIELLO, J.F.A. 2009: Diversity of ground-dwelling ants (Hymenoptera: Formicidae) in primary and secondary forests in Amazonian Ecuador. – Myrmecological News 12: 139-147.

RYDER WILKIE, K.T., MERTL, A.L. & TRANIELLO, J.F.A. 2010: Species diversity and distribution patterns of the ants of Amazonian Ecuador. – Public Library of Science ONE 5: e13146.

SILVA, R.R. & BRANDÃO, C.R.F. 2010: Morphological patterns and community organization in leaf-litter ant assemblages. – Ecological Monographs 80: 107-124.

SILVESTRE, R., BRANDÃO, C.R.F. & SILVA, R.R. 2003: Grupos funcionales de hormigas: el caso de los gremios del Cerrado. In: FERNÁNDEZ, F. (Ed.): Introducción a las hormigas de la región Neotropical. – Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, pp. 113-148.

SMITH, B. & WILSON, J.B. 1996: A consumer's guide to evenness indices. – Oikos 76: 70-82.

SOUZA, J.L.P., MOURA, C.A.R. & FRANKLIN, E. 2009: Efficiency in inventories of ants in a forest reserve in Central Amazonia. – Pesquisa Agropecuaria Brasileira 44: 940-948.

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.

TARDY, C. 1998: Paléoincendies naturels, feux anthropiques et environnements forestiers de Guyane française du Tardiglaciaire à l'Holocène récent (approche chronologique et anthracologique). – PhD thesis, University of Montpellier II, Montpellier, 493 pp.

TOBIN, J.E. 1994: Ants as primary consumers: diet and abundance in the Formicidae. In: HUNT, J.H. & NALEPA, C.A. (Eds.): Nourishment and evolution in insect societies. – Westview Press, Boulder, CO, pp. 279-308.

UNDERWOOD, E.C. & FISHER, B.L. 2006: The role of ants in conservation monitoring: If, when, and how. – Biological Conservation 132: 166-182.

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: 100-106.

VASCONCELOS, H.L., VILHENA, J.M.S., FACURE, K.G. & ALBERNAZ, A.L.K.M. 2010: Patterns of ant species diversity and turnover across 2000 km of Amazonian floodplain forest. – Journal of Biogeography 37: 432-440.

WARWICK, R.M. & CLARKE, K.R. 2001: Practical measures of marine biodiversity based on relatedness of species. – Oceanography and Marine Biology: an Annual Review 39: 207-231.

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