Is there a refuge for ants in litter accumulated at the base of *Attalea attaleoides* (Barb.Rodr.) Wess.Boer (Arecaceae)?

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Abstract

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The influence of the litter accumulated in the base of the acaulescent palm *Attalea attaleoides* (Barb. Rodr.) Wess. Boer on the composition of litter-dwelling ants in an upland rainforest in Central Amazon was investigated. The ant fauna was sampled from the litter of the base of 80 palms and in the open litter away from the palms. A list of 76 species identified and other 45 morphotypes is presented and their abundance is compared between microhabitats (litter trapped in the base of the palms and open litter). Our results suggests that the litter trapped in the palm base may be a refuge for non-dominant species, as the presence of aggressive ants in these microhabitats was relative rare. The litter trapped in the palm bases was occupied mostly by unaggressive predator and fungus-grower species, which probably find more prey or better conditions to cultivate their food there.

Additional key words: Arecaceae, Central Amazon, Formicidae, species richness, upland forest.

Resumen

Franken EP, Baccaro FB, Gasnier TR. 2013. Hay un refugio para las hormigas en la hojarasca acumulada en la base de *Attalea attaleoides* (Barb.Rodr.) Wess.Boer (Arecaceae)?.Entomotropica 28(1): 27-37.

La influencia de la hojarasca acumulada en la base de la palmera sin tallo *Attalea attaleoides* Barb. Rodr.) Wess. Boer en la composición de hormigas en una floresta de tierra firme de la Amazonia central fue investigada. La fauna de hormigas fue retirada de la hojarasca de la base de 80 palmeras y de la hojarasca en el suelo. Se presenta una lista de 76 espécies y otros 45 morfotipos y su abundancia es comparada entre los microhabitats (hojarasca retirada de la base de palmeras y hojarasca en el suelo). Los resultados sugieren que la hojarasca en la base de lãs palmeras pude servir de refugio para hormigas de especies no dominantes y la presencia de estas hormigas agresivas en este microhabitat fue relativamente rara. La hojarasca en la base de lãs palmeras estaba ocupada, en su mayoría, por depredadores no agresivos y especies cultivadoras de hongos, que probablemente encuentran más presas o mejores condiciones para el cultivo de su comida.

Palabras clave adicionales: Amazonia Central, Arecaceae, floresta de tierra firme, Formicidae, riqueza de especies.

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Introduction

The Amazon forest is physiognomically uniform, however, considerable local variations of vegetation and floristic composition are found (Pires and Prance 1985, Emilio et al. 2010). Variations in forest structural components produce forest microenvironmental heterogeneity (Cintra et al. 2005). This is important to the terrestrial fauna, because the litter produced by the vegetation has different quality and quantity in areas that are relatively close one to another, creating a microsites mosaic that varies in decomposition rates (Höfer et al. 1996, Kaspari 1996). Therefore, the heterogeneity of litter microhabitats may play a central role in structuring animal communities associated with ground litter in tropical forests.

Ants are an ecologically dominant group in the tropical rainforests (Fittkau and Klinge 1973) and frequently nest and forage on litter (Kaspari 1996). The most important factor for the success of an ant colony is where it is located (Bernstein and Gobbel 1979), and different species use different microhabitats to build their nests (Wilson 1959). Therefore, many factors can affect the distribution of ant nests on forest floor, such as litter distribution (Kaspari 1996), microclimate (Perfecto and Vandermeer 1996), and competition (Levings and Traniello 1981). Acaulescent palms are common in Amazon forests (Kahn et al. 1988, Henderson et al. 1995), and, because the size and arrangement of their leaves, they accumulate large amount of litter in different decomposition stages in their bases (Ribeiro et al. 1999). Apparently, the bases of these palms may be important elements structuring litter arthropods communities (Vasconcelos 1990). However, there are few studies comparing the arthropod fauna found in this microhabitat to the rest of ground or litter and there are no specific study on the ant fauna.

Our objective was to characterize the utilization by ants of the litter accumulated on the palm base of *A. attaleoides* and the litter on the ground, in an upland forest of Central Amazon, as well as to evaluate how the acaulescent palms affect the structure of ground ant communities.

Materials and Methods

The study site is located in an area of upland primary tropical rain forest (about 5 ha) in the Experimental Farm of the Federal University of Amazonas (UFAM), at 38 km north of Manaus, Central Amazon, Brazil (lat 2° 38'S; long 60° 03' W). The annual rainfall in this region is about 2,500 mm and there is a dry season between June and November (Salati 1985).

We sampled ants at the base of *Attalea attaleoides* (Barb. Rodr.) Wess. Boer palms. These palms have a small and underground stem, and most of the leaves are positioned in an upward position, forming a funnel that accumulates the falling litter (Ribeiro et al. 1999). In the relatively drier areas, they are a dominant species of understory forest (Kahn and Castro 1985, Cintra et al. 2005).

A total of 80 points were sampled between June and December of 2004. Each sample unit consisted of the palm and its surrounding area, divided into 3 subsamples: the superficial litter accumulated on the palm base (LB), the partially decomposed litter (humus) below it (HB) and an area of 1 m² of litter (open litter) 1.5 m away from the palm (OL). The humus layer in the open litter rarely exceeded more than 2 cm depth, and therefore was not treated as a separated microhabitat. The ants (workers, reproductive castes and juveniles) were manually sorted. When reproductive castes (winged or wingless queens) and/or juveniles (eggs or larvae) were found, it was considered as a presence of a nest of that species. We established a maximum of 30 minutes to separate the ants from the substrate, because this seemed enough to capture all species and most individuals in a sample. The categorization of the species in relation to diet and behavior followed Carroll and Janzen (1973)

and Delabie et al. (2000). The specimens were deposited at the Entomological Collection of the National Institute for Amazonian Research (INPA) in Brazil.

Two indexes, IPP (index of preference by material accumulated in palm base) and IPH (index of preference by humus accumulated in the base of the palm), were created to analyze the species occurrence in each microhabitat. The indexes were calculated as:

IPP = OP/(OP + OOL) and IPH = OHB/(OHB + OLB)

were OP is the number of occurrences of a given species on the base of the palm (litter and humus); OOL is the number of occurrences of a given species on the open litter away from the palm; OHB is the number of occurrences of a given species on the humus accumulated on the base of the palm and *OLB* is the number of occurrences of a given species on the superficial litter layer accumulated on the base of the palm. The values between 0 and 0.49 were considered as low affinity for the analyzed microhabitat; values between 0.5 and 0.69 as medium affinity, and values between 0.7 and 1 as high affinity. Rare ant species that occurred less than ten times in each microhabitat were excluded from the analysis.

The total number of species found in each microhabitat was compared using incidence-based rarefaction curves (Gotelli and Colwell 2001). These taxon-sampling curves contain the basic information for valid richness comparisons when the sampling effort is different. Due to natural variation, the total litter volume sampled differed between microhabitats (LB, HB and OL). To remove the effect of sample order on the species accumulation curves, an average curve was plotted for randomly shuffled samples (100 runs). The program used in this analysis was EstimateS 9.1.0 (Colwell 2013).

We used Principal Coordinate Analysis (PCoA), to evaluate the ant-assemblage

composition changes between microhabitat types. PCoA analysis was done with presence/absence per sample and the Bray-Curtis index as dissimilarity measurement. Rare species (< 10 occurrences) were excluded from analysis. An inferential test on the effects of microhabitat type on species composition was made with multivariate analysis of variance (MANOVA), using the first two ordination axes as dependent variables and microhabitat type (open litter, humus layer and litter accumulated in the base of the palms) as grouping factors.

Results

We collected 121 species or morphospecies belonging to 36 genera (Table 1). The most species-rich genus was *Pheidole* (17 species), *Strumigenys* (9 species), *Camponotus* (8 species), *Crematogaster* (7 species), and *Pyramica* (7 species). The most frequent species was *Solenopsis* (*Diplorhoptrum*) sp.9 and *Crematogaster carinata* for the open litter and for the litter accumulated in the base of the palm, respectively. *Brachymyrmex heeri* and *Solenopsis* (*Diplorhoptrum*) sp.6 were the most common species in the humus accumulated on the base of the palm.

Species with nests or wingless queens were more abundant in the base of the palms (Table 1). In the open litter habitat (OL), nests of omnivorous species (including some arboreal species) were more common, compared with fungus-growers and generalist predators. A similar pattern was detected for the litter accumulated in base of the palms (LB). Most nests in this microhabitat were from omnivorous species, with few generalist predators. Conversely, in the humus layer (HB) predominated nests or wingless queens of generalist, specialist predators and fungus-growers species.

The frequency of ant species per microhabitat also changed in function of their diet (Table 2). The most common species (10 or more

Table 1. Occurrence of ant species (OC), number of nests (N) and nesting queens (Q) in subsamples of the acaulescent palm A. attaleoides (LB – litter accumulated in base of the palm; HB – humus accumulated in base of the palm; OL – open litter away from the palm).

Ant species	LB		НВ		OL	
	OC	N – Q	OC	N – Q	OC	N – Q
Acropyga sp.1	2	0	2	1N	0	0
Anochetus bispinosus (Smith)	0	0	10	1N+1Q	1	0
Anochetus emarginatus (Fabricius)	0	0	0	0	1	0
Anochetus horridus Kempf	3	0	11	3N	4	0
Apterostigma (Pilosum gr.) sp.1	0	0	1	1N	1	0
Apterostigma (Pilosum gr.) sp.2	0	0	0	0	1	0
Apterostigma pilosum Mayr	5	0	8	1N	3	0
Apterostigma urichii Forel	0	0	2	1N	1	0
Azteca sp.1	2	0	0	0	1	0
Blepharidatta brasiliensis Wheeler	8	1N	5	1N	9	1N
Brachymyrmex heeri Forel	20	1N	44	9N+2Q	4	0
Camponotus coptobregma Kempf	1	1N	1	0	0	0
Camponotus crassus Mayr	0	0	1	0	0	0
Camponotus femoratus (Fabricius)	10	0	6	0	8	0
Camponotus godmani Forel	2	0	1	0	0	0
Camponotus rapax (Fabricius)	2	0	0	0	0	0
Camponotus sp.1	1	0	0	0	0	0
Camponotus sp.2	0	0	0	0	1	0
Camponotus tenuiscapus Roger	0	0	0	0	1	0
Cephalotes sp.1	1	0	0	0	0	0
Crematogaster brasiliensis Mayr	16	2N	8	0	21	3N
Crematogaster carinata Mayr	28	4N	16	0	22	2N
Crematogaster limata Smith	0	0	0	0	1	0
Crematogaster minutissima Mayr	11	5N	7	1N+1Q	16	1N
Crematogaster nigropilosa Mayr	3	1N	1	0	10	0
Crematogaster sp.1	0	0	0	0	1	0
Crematogaster tenuicula Forel	1	0	0	0	0	0
Cyphomyrmex laevigatus Weber	1	0	0	0	2	0
Cyphomyrmex hamulatus Weber	5	0	9	1N+1Q	5	2N+1Q
Cyphomyrmex peltatus Kempf	1	0	4	0	2	0
Cyphomyrmex rimosus (Spinola)	5	0	9	4N	1	1N
Cyphomyrmex strigatus Mayr	0	0	1	1Q	0	0
Discothyrea sexarticulata Borgmeier	0	0	3	0	1	0
Dolichoderus imitator Emery	15	8N	19	6N+1Q	1	0
Ectatomma edentatum Roger	0	0	0	0	1	0
Gnamptogenys continua (Mayr)	0	0	0	0	1	0
Gnamptogenys horni (Santschi)	1	0	3	0	3	0
Gnamptogenys minuta (Emery)	0	0	1	0	0	0

Continue....

Table 1. (continuation). Occurrence of ant species (OC), number of nests (N) and nesting queens (Q) in subsamples of the acaulescent palm *A. attaleoides* (LB – litter accumulated in base of the palm; HB – humus accumulated in base of the palm; OL – open litter away from the palm).

Ant species	LB		НВ		OL	
	OC	N – Q	OC	N – Q	OC	N – Q
Gnamptogenys relicta (Mann)	3	1N	4	1N	0	0
Gnamptogenys striatula Mayr	0	0	0	0	1	0
Hylomyrma reginae Kutter	1	0	0	0	1	1N
Hylomyrma sp.1	0	0	1	0	0	0
Hylomyrma sp.7	0	0	0	0	1	1N
Hypoponera opaciceps (Mayr)	0	0	3	1N	0	0
Hypoponera sp.1	4	1N+1Q	19	4N+3Q	3	1Q
Hypoponera sp.2	11	3N+1Q	13	3N+2Q	8	1N+1Q
Hypoponera sp.3	7	1Q_	34	5N+6Q	5	0
Hypoponera sp.4	0	0	5	0	1	0
Labidus praedator (Smith)	1	0	1	0	2	0
Lachnomyrmex amazonicus Feitosa & Brandão	3	1N	7	1N	0	0
Megalomyrmex cuatiara Brandão	0	0	0	0	2	0
Megalomyrmex drifti Kempf	0	0	1	1N	0	0
Megalomyrmex goeldii Forel	0	0	0	0	2	1N
Nylanderia sp.2	3	0	0	0	1	0
Nylanderia sp.3	12	1N	9	1N	17	1N
Nylanderia sp.5	17	5N+1Q	11	1N+1Q	13	1N
Nylanderia sp.6	4	2N	5	0	4	2N
Nylanderia sp.7	3	0	0	0	1	0
Pheidole embolopyx Brown	1	0	0	0	1	0
Pheidole exigua Mayr	4	0	2	0	17	1N
Pheidole mamore Mann	1	1N	3	0	1	0
Pheidole meinerti Forel	3	1N	5	0	5	0
Pheidole sp.1	6	0	3	0	4	0
Pheidole sp.2	0	0	0	0	4	0
Pheidole sp.3	0	0	0	0	2	0
Pheidole sp.4	5	0	10	3N	8	0
Pheidole sp.5	0	0	1	0	2	0
Pheidole sp.6	7	0	3	0	6	1N
Pheidole sp.8	1	0	2	0	4	0
Pheidole sp.9	0	0	1	0	3	0
Pheidole sp.10	1	0	1	0	2	1N
Pheidole sp.11	8	0	4	0	4	0
Pheidole sp.12	8	0	3	0	15	3N
Pheidole sp.13	17	5N	17	1N	8	0
Pheidole sp.15	0	0	0	0	1	0
Prionopelta modesta Forel	5	0	15	1N	7	0

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Table 1. (continuation).Occurrence of ant species (OC), number of nests (N) and nesting queens (Q) in subsamples of the acaulescent palm *A. attaleoides* (LB – litter accumulated in base of the palm; HB – humus accumulated in base of the palm; OL – open litter away from the palm).

Ant species	LB		НВ		OL	
	OC	N – Q	OC	N – Q	OC	N – Q
Pseudomyrmex flavidulus (Smith)	0	0	0	0	1	0
Pyramica alberti (Forel)	1	1Q_	1	0	1	0
Pyrmica denticulata (Mayr)	7	1Q_	1	0	14	1N
Pyramica sp.2	1	1Q_	0	0	0	0
Pyramica sp.4	0	0	0	0	1	0
Pyramica subedentata (Mayr)	0	0	0	0	1	0
Pyramica wheeleri (Smith)	0	0	0	0	2	0
Pyramica zeteki (Brown)	0	0	0	0	1	0
Rogeria alzatei Kugler	1	0	11	1Q_	1	0
Rogeria innotabilis Kugler	0	0	1	0	0	0
Rogeria sp.1	1	0	0	0	0	0
Rogeria sp.2	0	0	3	1Q_	0	0
Sericomyrmex bondari Borgmeier	1	0	1	0	2	0
Solenopsis geminata (Fabricius)	0	0	2	0	1	0
Solenopsis globularia (Smith)	1	0	0	0	0	0
Solenopsis sp.	1	0	1	0	2	1N
Solenopsis (Diplorhoptrum) sp.6	24	3N	40	3N	20	0
Solenopsis (Diplorhoptrum) sp.9	28	2N	27	2N	40	2N
Strumigenys consanii Brown	3	0	1	0	1	0
Strumigenys cordovensis Mayr	5	0	4	1Q_	1	0
Strumigenys elongata Roger	2	0	11	1N	1	0
Strumigenys precava Brown	1	0	1	0	0	0
Strumigenys sp.4	1	0	4	1Q_	0	0
Strumigenys sp.5	0	0	0	0	1	0
Strumigenys sp.6	0	0	0	0	1	0
Strumigenys trinidadensis Wheeler	3	0	5	0	0	0
Strumigenys trudifera Kempf & Brown	4	1Q_	5	1Q_	5	0
Tetramorium simillimum (Smith)	22	0	23	0	19	0
Trachymyrmex bugnioni (Forel)	3	0	1	1N	2	0
Trachymyrmex cornetzi (Forel)	1	0	10	5N	1	0
Trachymyrmex sp.1	0	0	0	0	1	0
Wasmannia auropunctata (Roger)	4	1N	6	1N	8	0
Wasmannia scrobifera Kempf	0	0	0	0	1	0
TOTAL		52N+8Q		73N+27Q		28N+3Q

Table 2. Diet and indexes of preference (see text) of ant species by the material accumulated (IPP) and by the humus accumulated (IPH) on the base of the acaulescent palm *A. attaleoides*.

Species	IPP	IPH	Diet	
Cyphomyrmex hamulatus	0.72	0.64	Fungivorous	
Apterostigma pilosum	0.79	0.62	Fungivorous	
Trachymyrmex cornetzi	0.91	0.91	Fungivorous	
Cyphomyrmex rimosus	0.93	0.64	Fungivorous	
Hypoponera sp.2	0.71	0.54	Generalist Predator	
Anochetus horridus	0.76	0.79	Generalist Predator	
Odontomachus meinerti	0.79	0.69	Generalist Predator	
Hypoponera sp.1	0.86	0.83	Generalist Predator	
Hypoponera sp.3	0.87	0.83	Generalist Predator	
Anochetus bispinosus	0.91	1	Generalist Predator	
Pheidole exigua	0.26	-	Omnivorous	
Crematogaster nigropilosa	0.29	-	Omnivorous	
Pheidole sp.12	0.38	0.27	Omnivorous	
Nylanderia sp.3	0.48	0.43	Omnivorous	
Blepharidatta brasiliensis	0.5	0.38	Omnivorous	
Crematogaster brasiliensis	0.5	0.33	Omnivorous	
Solenopsis (Dipl.) sp.9	0.51	0.49	Omnivorous	
Crematogaster minutissima	0.52	0.39	Omnivorous	
Pheidole meinerti	0.55	-	Omnivorous	
Pheidole sp.6	0.57	0.3	Omnivorous	
Nylanderia sp.5	0.59	0.39	Omnivorous	
Tetramorium simillimum	0.6	0.51	Omnivorous	
Crematogaster carinata	0.6	0.36	Omnivorous	
Camponotus femoratus	0.62	0.38	Omnivorous	
Pheidole sp.4	0.62	0.67	Omnivorous	
Nylanderia sp.6	0.64	-	Omnivorous	
Pheidole sp.1	0.64	-	Omnivorous	
Dolichoderus imitator	-	0.56	Omnivorous	
Solenopsis (Diplorhoptrum) sp.6	0.7	0.63	Omnivorous	
Pheidole sp.11	0.71	0.33	Omnivorous	
Pheidole sp.13	0.78	0.5	Omnivorous	
Brachymyrmex heeri	0.92	0.69	Omnivorous	
Wasmannia auropunctata	0.47	0.6	Omnivorous	
Pyramica denticulata	0.36	-	Specialist Predator	
Strumigenys trudifera	0.64	-	Specialist Predator	
Prionopelta modesta	0.68	0.75	Specialist Predator	
Strumigenys elongata	0.92	0.85	Specialist Predator	
Lachnomyrmex amazonicus	-	0.7		
Rogeria alzatei	0.92	0.92	Ę	

occurrences) collected in the open litter (OL) had an omnivorous diet. Fungivorous, generalists and specialist predators were also present in OL, but in lower frequency. Predator and fungus-grower species were more common in the material accumulated in the base of the palm (LB+HB).

Higher ant diversity was observed in OL and in LB, compared with the humus in the base of the palm (HB). In the open litter away from the palms, we found an average of 5.3 species/ m²; a total of 92 ant species (25 were exclusive sampled in this microhabitat). In the litter trapped in the base of the palms, we found an average of 5.11 in LB and 6.73 species in HB. Considering that normally each sample of LB+HB had less than 1m², the species density was higher in these microhabitats. However, the species richness was higher in open litter (Figure 1). The accumulation curve for HB reached an asymptote of about 20 species, while the accumulation curve of open litter and the litter accumulated in base of palms seems to be far from an asymptote with 92 and 71 species, respectively (Figure 1).

Despite general differences in diet, the species composition was similar between microhabitats at assemblage level (MANOVA; Pillai = 1.973; P = 0.181). The same pattern holds using all species (MANOVA; Pillai = 2.669; P = 0.071), suggesting that both rare and common species share these microhabitats at local scale (Figure 2). The variance explained in the first two PCoA axes was 20 %. This result probably reflects the low number of species occurrence per sample.

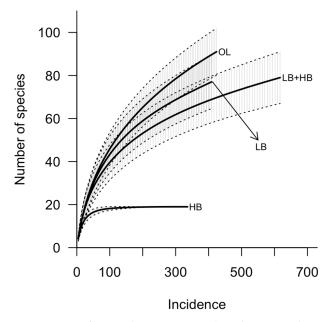
Discussion

The number and species composition of the litter-dwelling ants collected in this work was similar to previous studies in Central Amazon (Vasconcelos 1999, Souza et al. 2012). Most of the collected species are inhabitants of leaf litter, however, a few species were characteristic

of other microhabitats. Considering the microhabitat use, as proposed by Carroll and Janzen (1973) and Delabie and Fowler (1995), we have also found some arboreal species (*Pseudomyrmex flavidus, Azteca* sp.1, *Cephalotes* sp.1, *Pachycondyla constricta*) and hypogaeic species (*Acropyga* sp.1, *Gnamptogenys minuta*, *G. horni*, *Rogeria* and *Hypoponera*).

The litter accumulated in the base of A. attaleoides palms (superficial litter and humus below it) showed high ant species richness, considering that the area represented by this microhabitat is smaller than the open litter area. The results, however, support the hypothesis that the number of species is not just a consequence of the refuges that result from the structural complexity of this microhabitat. The litter accumulated in the base of A. attaleoides, may also represent a more stable environment, comparable with the unpredictable litter fall away from the palm (Facelli and Pickett 1991). As a consequence, the occurrence of fungusgrowers and predators species was higher in the litter accumulated at A. attaleoides palms.

Fungus-grower species can have benefits from the larger nutrients concentration and humidity in the litter accumulated in the base of A. attaleoides to cultivate their fungi (Bernal and Balslev 1996). Predator species probably encounter a larger concentration of smaller invertebrates in this microhabitat (Santos et al. 2003). According to Andersen (1995), fungus cultivators and predators species tend to have a cryptic behavior, and would have little competitive interaction with other ant species because they have a specialized diet and typically a low population density. However, if the litter in the base of the palms was attractive for all ant species, proportionally more omnivorous ants should be found in this microhabitat. Omnivorous species, such as Wasmannia auropunctata or Crematogaster brasiliensis are generally more aggressive, and could exclude the other ants in the dispute to use this resources



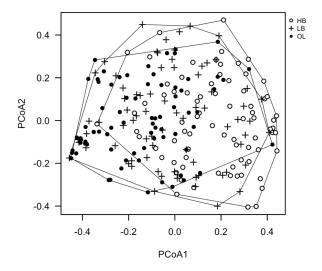


Figure 1. Accumulation curves based in incidence (occurrence) of ant species in litter trapped in the base of *A. attaleoides* (LB); humus accumulated in base of *A. attaleoides* (HB); open litter away from *A. attaleoides* (OP); and all litter accumulated in the base of the palm (LB+HB). Dotted lines represent the 95 % confidence intervals around the mean.

Figure 2. Principal Coordinate Analysis (PCoA) of ant species in three microhabitats (HB – humus accumulated in base of *A. attaleoides*; LB – litter accumulated in base of *A. attaleoides*; OL – open litter away from *A. attaleoides*). Only species with 10 occurrences were used. The lines delimitate the species composition of each microhabitat.

(Baccaro et al. 2010, Vonshak et al. 2009). Therefore, our results corroborate the suggestion of Fowler et al. (1991), that the distribution of ant species in a community is strongly influenced by the distribution of food resources. This suggests that the litter accumulated in the base of *A. attaleoides* (specially the humus layer) is a different microhabitat, which may be important for species co-occurrence at local scales.

Although protection seems not to be the primary factor to determinate the species composition in the base of the palm compared with the open litter, it is probably important for the species with established nests. Most of the founding queens and nests were in the base of the palms humus (HB), which is more protected and has a more stable microclimate. Palm base humus is more similar to underground environment compared with open litter, and may explain the occurrence of typical hypogaeic species in

this microhabitat. In general, hypogaeic fauna composition is different and has more specialist species than epigaeic species (Schmidt and Solar 2010, Andersen and Brault 2010, Delabie and Fowler 1995). Relative high number of specialists species, suggests that the same probably applies for the ant fauna sampled in the base of the palm humus.

Our results suggest that the palm bases may be structural elements, which affect the litter-dwelling ants assemblages at this Amazon forest. There are certainly other elements, however, that may also act as key element and should be considered for a more complete understanding of the ecology of the ant community in this forest. For example, future studies should investigate the humus layer located in forests on sandy soils regionally called *campinaranas*, abandoned termite nests, and the decaying wood under fallen trunks.

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