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Research article

Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil

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Summary. Ant communities are generally extremely interactive, and competition between ant species seems to be widespread. This characteristic of ant communities tends to produce a uniform pattern of nest distribution. In this study, we aimed to test the nest distribution pattern, putting forward hypotheses to explain the pattern. Nest mapping was carried out by delimiting ten one-square-meter quadrats, randomly located in a remnant of tropical rainforest in Viçosa, Brazil. In each quadrat, the nests were surveyed in the litter and surface soil up to 3 cm deep. A total of 295 nests from 41 ant species were collected in the ten quadrats. The pattern of nest distribution in the whole forest was aggregated, while the species showed a random distribution. The pattern of nest distribution inside each quadrat was also aggregated. The presence of species, such as *Brachymyrmex* sp.$_1$ and *Hypoponera* sp.$_4$, with high nest densities suggests the occurrence of nest budding. This may be the reason for the aggregated nest distribution. Another explanation for this apparent aggregation is species specialization in a patchily distributed habitat. The results suggest that competition is not an important process in the regulation of soil and litter ants distribution and, consequently, in the regulation of species richness in the studied area.

Key words: Community assembly, competition, Formicidae, interactions.

Introduction

The success of an ant colony depends on where it is established (Bernstein and Gobbel, 1979). Suitable nesting sites and their distribution are controlled by several abiotic and biotic factors, namely, aspect, shade, moisture, altitude (Doncaster, 1981), availability of suitable food and nesting sites (Levings, 1983), and intra- and interspecific interactions (Levings and Traniello, 1981; Levings and Franks, 1982; Ryti and Case, 1984, 1986, 1988, 1992; Johnson et al., 1987; Cushman et al., 1988; Gordon and Kulig, 1996; Gordon and Wagner, 1997).

The most common pattern of ant-nest distribution is regular or overdispersed and is usually interpreted as the result of intra- or interspecific competition (Bernstein and Gobbel, 1979; Lewing and Traniello, 1981; Levings and Franks, 1982; Ryte and Case, 1984, 1986; Cushman et al., 1988; Deslippe and Savolainen, 1995; Wiernasz and Cole, 1995). However, processes such as predation and preference for regularly spaced microhabitats may also generate the regular pattern (Ryti and Case, 1986; Deslippe and Savolainen, 1995). Competition is often cited as the explanation of nest distribution, because this process is known to be important in structuring ant communities (Levings and Franks, 1982; Fellers, 1987; Savolainen and Vepsäläinen, 1988; Andersen and Patel, 1994). Litter-dwelling ant communities, however, have species with several different feeding habits and, therefore, can only compete for nesting sites.

Abiotic factors may influence ant communities over broad geographic scales (Kaspari et al., 2000). Biotic factors such as competition, predation, and other interactions between species are more prone to influence the communities on a local scale (Ricklefs and Schluter, 1993).

Although regular ant-nest spacing is common, other patterns have also been detected. Aggregated interspecific (Doncaster, 1981; Ryti and Case, 1984; Herbers, 1985, 1989, 1994) and intraspecific (Rissing et al., 1986; Henderson and Jeanne, 1992) nest distributions have been described for some ant communities. Aggregated nest distribution may result from (i) mutualistic interactions, (ii) specialization of several species for the same microhabitat, which in turn is patchily distributed, and (iii) colony fragmentation, through which

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several conspecific nests are formed near the original nest (Herbers, 1994).

Randomly distributed ant nests have also been documented (Bernstein and Gobbel, 1979; Herbers, 1985; Weseloh, 1994). According to Begon et al. (1996), this distribution occurs when environmental conditions are homogeneous throughout the habitat and the occurrence of one organism does not interfere with that of others. The detection of randomly distributed ant nests, therefore, is usually associated with weak interactions between species and between ants and their environment.

Studying the pattern of nest distribution is an important step in understanding biological interactions in ant communities. It is expected that different patterns of distribution result from different biological processes, acting through various mechanisms. In this study, we aimed to test the hypothesis that litter and soil ant nests are uniformly distributed. We also put forward some hypotheses to explain the detected pattern.

Methods

We carried out fieldwork in a secondary forest remnant (ca. 60.5 hectares) in Viçosa, Minas Gerais, Southeastern Brazil (20°45′S, 42°50′W). The vegetation in this area is classified as seasonal semi-deciduous forest (Veloso et al., 1991). Trees of the genus *Araucaria* were planted inside the remnant and they have survived.

From April to June 1997 (at the end of the rainy season), we randomly distributed ten one-square-meter quadrats in the remnant. In each quadrat, we surveyed the ants in the litter and the soil surface down to a depth of 3 cm. To accurately record the nest positions, the wooden frame quadrat was gridded at centimeter intervals. We also recorded the specific nesting site (branch, leaves, seeds, fruits, etc.) and collected samples of ants from each nest for subsequent identification. We identified the ants to genus level using Hölldobler and Wilson (1990) and Bolton (1994) and to species level on the basis of their external morphology and the advice of a local taxonomist (J.H.C. Delabie). Voucher specimens have been deposited in the collection of the Ecology Section of the General Biology Department at the Federal University of Viçosa.

Considering that litter ant nests are very small, we expected that the area under the influence of each nest would also be very restricted. The one-square-meter scale was chosen to guarantee that all species within the quadrat were part of a local community and, therefore, that the species potentially interacted with each other. According to Srivastava (1999), species interaction is the criterion to be used in fixing the limits of local communities.

A map of nest distribution was then compiled for each quadrat. We evaluated the distribution pattern on two different scales: inside each quadrat and between quadrats. The latter was a surrogate for the remnant as a whole. We tested both ant species distribution and nest distribution, the latter disregarding the species distribution. Since there were few species within each quadrat, we tested only the distribution pattern of the nests on this scale. On the larger scale, the forest remnant, the pattern of distribution was analyzed using the standardized Morisita index (Krebs, 1989).

We evaluated the nest distribution pattern inside each quadrat using the nearest neighbor index, according to Clark and Evans (1954). The statistical significance of R was tested by z transformation (Krebs, 1989). It is not possible to establish the exact distance to the nearest neighbor of the nests close to the quadrat border, because the nearest neighbor may be situated outside the surveyed area. Therefore, all nests located nearer the quadrat border than the closest nest were excluded from the analyses.

We compared the average distance from conspecific nearest neighbors to the average from interspecific nearest neighbors using a Kruskal-Wallis test. We confined this comparison to the five most frequent species, since only these species were frequent enough to allow this statistical test.

Forest litter contains food resources and nesting sites used by litter ants, and there is a direct possible relation between litter weight and resource (food and nesting sites). To evaluate the influence of resource availability on species richness and on the number of individuals inside each quadrat, we selected 10 more one-square-meter quadrats in the same forest remnant. All of the litter in the quadrat was collected and sieved. The sieved portion was transferred to Winkler sacs (Olson, 1991; Majer and Delabie, 1999) for one week to extract the ants. The ants were then counted and identified at the species level. Both litter portions were then oven-dried and weighed. Dry litter weight was used as an indirect estimate of resource availability for the litter-dwelling ants. We carried out linear regression analyses between litter weight (explanatory variable) and the number of ant species and the number of ant individuals (response variables).

Results

We collected a total of 295 nests from 41 ant species in the 10 quadrats. The majority of the nests (73%) were from five species: *Brachymyrmex* sp.$_1$ (14%), *Hypoponera* sp.$_4$ (18%), *Pheidole* sp.$_1$ (13%), *Solenopsis* sp.$_1$ (24%), and *Pheidole* sp.$_2$ (4%).

The ants were nesting in hollow or perforated tree branches, leaves, inside legumes, litter, seeds (from *Araucaria* species), and soil (Table 1). Most of the nests (65%) were found inside branches, although soil nests were also frequent (24%).

The nest distribution in each quadrat is presented in Fig. 1. The distribution pattern of the nests in the entire remnant, disregarding ant species, was aggregated ($I_p = 0.52$), while the species were randomly distributed ($I_p = 0.26$). The nest distribution inside each quadrat was also aggregated (Table 2).

The average distance to the nearest conpecific and interspecific neighbors are shown in Fig. 2. There were no significant differences between the average distance from conspecific neighbors, and interspecific neighbors ($p = 0.32$) for each of the five most common species.

Sixty-four species were collected in the ten quadrats used to test the influence of litter weight on ant species richness. Litter weight influenced neither the number of litter ant species ($n = 10$, $p = 0.996$) nor the number of litter ant individuals ($n = 10$, $p = 0.994$). (Fig. 3).

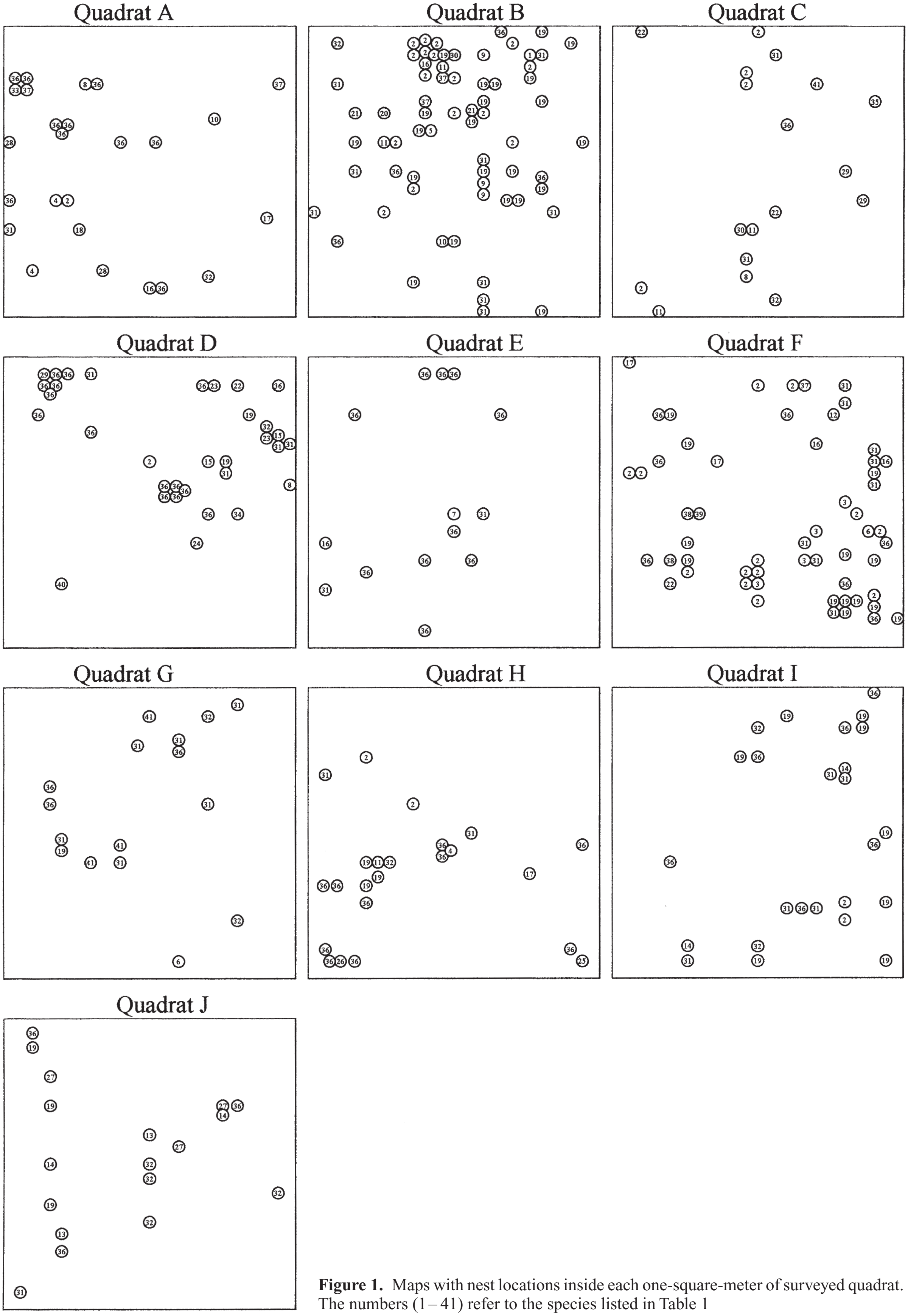

Figure 1. Maps with nest locations inside each one-square-meter of surveyed quadrat. The numbers (1 – 41) refer to the species listed in Table 1

Table 1. Nesting sites of ant species surveyed in the litter and surface soil in the forest remnant

	Specis	Rolled leaves	Litter	Fruits (legume)	Branch	Seed (*Araucaria*)	Soil	Total
1-	*Amblyopone lurilabes*	–	1	–	–	–	–	1
2-	*Brachymyrmex* sp.$_1$	2	–	–	12	–	26	40
3-	*Brachymyrmex* sp.$_2$	–	4	–	–	–	–	4
4-	*Camponotus* sp.$_1$	–	–	–	3	–	–	3
5-	*Camponotus* sp.$_2$	–	–	–	1	–	–	1
6-	*Camponotus* sp.$_3$	–	–	–	2	–	–	2
7-	*Camponotus trapezoideus*	–	–	–	1	–	–	1
8-	*Crematogaster* sp.$_1$	–	–	–	3	–	–	3
9-	*Crematogaster* sp.$_2$	–	–	–	3	–	–	3
10-	*Cyphomyrmex salvini*	–	–	–	–	–	2	2
11-	*Gnamptogenys* sp.$_1$	–	–	–	3	–	2	5
12-	*Gnamptogenys menozzii*	–	–	–	1	–	–	1
13-	*Gnamptogenys striatula*	–	–	–	2	–	–	2
14-	*Hylomyrma* sp.	–	–	–	3	–	1	4
15-	*Hypoponera foreli*	–	–	–	2	–	1	3
16-	*Hypoponera* sp.$_1$	–	1	–	3	–	1	5
17-	*Hypoponera* sp.$_2$	–	–	–	–	–	4	4
18-	*Hypoponera* sp.$_3$	–	–	–	–	–	1	1
19-	*Hypoponera* sp.$_4$	–	10	1	29	–	12	52
20-	*Hypoponera* sp.$_5$	–	–	–	1	–	–	1
21-	*Hypoponera* sp.$_6$	–	–	–	–	–	1	1
22-	*Hypoponera* sp.$_7$	–	1	–	2	–	1	4
23-	*Hypoponera* sp.$_8$	–	–	–	2	–	–	2
24-	*Hypoponera* sp.$_9$	–	–	–	–	–	1	1
25-	*Hypoponera* sp.$_{10}$	–	–	–	–	–	1	1
26-	*Hypoponera* sp.$_{11}$	–	–	–	–	–	1	1
27-	*Hypoponera* sp.$_{12}$	–	–	–	1	–	2	3
28-	*Labidus* sp.	–	–	–	–	–	2	2
29-	*Megalomyrmex goeldii*	1	–	–	1	–	1	3
30-	*Octostruma rugifera*	–	–	–	1	–	1	2
31-	*Pheidole* sp.$_1$	–	2	2	32	–	2	38
32-	*Pheidole* sp.$_2$	–	–	2	10	–	1	13
33-	*Pheidole* sp.$_3$	–	–	–	1	–	–	1
34-	*Pheidole* sp.$_4$	–	–	–	–	–	1	1
35-	*Procryptocerus convergens*	–	–	–	1	–	–	1
36-	*Solenopsis* sp.$_1$	–	2	1	63	1	3	70
37-	*Solenopsis* sp.$_2$	–	–	–	2	–	3	5
38-	*Solenopsis* sp.$_3$	–	–	–	2	–	–	2
39-	*Solenopsis* sp.$_4$	–	–	–	1	–	–	1
40-	*Strumigenys louisianae*	–	–	–	1	–	–	1
41-	*Tapinoma melanocephalum*	–	–	–	4	–	–	4
	Total	3	21	6	193	1	71	295

Table 2. Patterns of distribution of ant nests in the 10 sampling sites. R is the Clark and Evans' (1954) dispersion index and *z* is the value of the significance test

Quadrats	R	*z*	Distribution pattern
A	0.37	– 5.13	aggregated
B	0.56	– 6.36	aggregated
C	0.58	– 2.69	aggregated
D	0.38	– 6.15	aggregated
E	0.54	– 2.64	aggregated
F	0.62	– 5.26	aggregated
G	0.43	– 3.80	aggregated
H	0.50	– 4.08	aggregated
I	0.42	– 4.82	aggregated
J	0.59	– 3.18	aggregated

Discussion

Nest aggregation may be associated with three factors: (i) the aggregated distribution of adequate microhabitats; (ii) colony budding; and (iii) mutualistic interactions. When several species have the same environmental needs and optimal microhabitats are patchily distributed, the nests of species adapted to that microhabitat will also be aggregated (Herbers, 1989). This explanation seems to apply to many species in this study, since the majority of nests were found in tree branches, suggesting species specialization. The distribution of branches inside tropical forests, however, is not regular (Luizão, 1989), with some regions having more nesting resourccs than others. Therefore, ant-nest aggregation may simply reflect an aggregation of fallen branches and the

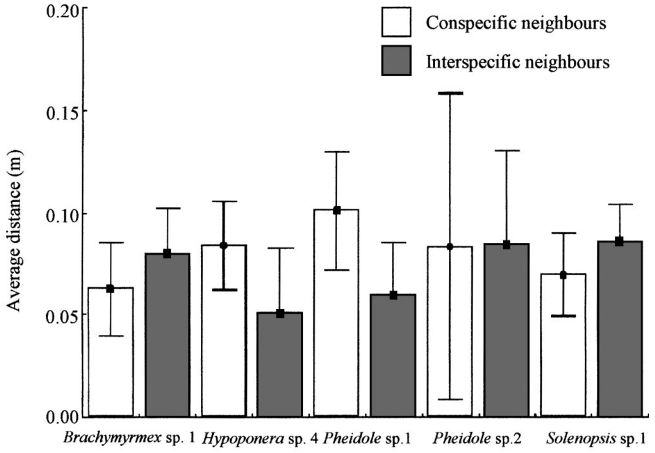

Figure 2. Average distance (± 1.96 standard error) of nearest conspecific and interspecific neighbors to the five most frequent species

existence of so many branch-nesting species in the remnant would explain some of the interspecific aggregations that were observed. An example of this interspecific aggregation was seen in Quadrat D (Fig. 1), where the species *Hypoponera* sp.$_4$, *Pheidole* sp.$_2$, *Hypoponera* sp.$_8$, *Hypoponera foreli*, and *Pheidole* sp.$_1$ occurred in an aggregation (see Table 1 for species codes).

Colony budding may also produce nest aggregation. Some ant species fragment their colonies when queens and workers leave the original colony to form new ones. The number of new colonies is variable, but they usually remain near each other and close to the mother colony (Franks and Hölldobler, 1987). Nest budding frequently generates polydomy or colonies formed by several nests, which exchange workers and brood (Bourke and Franks, 1995). The presence of ant species exhibiting high densities in the surveyed quadrats, such as *Brachymyrmex* sp.$_1$, *Solenopsis* sp.$_1$, and *Hypoponera* sp.$_4$ (Table 1; Figure 1), may be evidence of the occurrence of colony budding in these species. If so, then colony budding may be one of the mechanisms responsible for conspecific nest aggregation in the forest remnant. However, it does not explain the occurrence of the interspecific aggregations.

Individuals involved in mutualistic interaction are usually located close to each other, resulting in aggregated patterns of distribution. Consequently, the observed ant-nest aggregation may result from the occurrence of mutualistic interactions between ant colonies. However, although social parasitism is commonly described in the literature (Hölldobler and Wilson, 1990 and references therein), and Herbers (1994) cites this trait as one possible explanation of aggregated nest distribution, we are not aware of descriptions of actual mutualisms. Some forms of social parasitism may resemble mutualisms, such as xenobiosis and parabiosis (Wheeler, 1986; Hölldobler and Wilson, 1990). Hence, the hypothesis of mutualisms generating nest aggregation needs formal testing.

Nest aggregation and random species distribution indicate that negative interactions between ants may be weak or that they affect only a small fraction of the community. This suggests that competition between ant species that nest in shallow soil and litter was not an important factor for determining spatial distribution in the studied remnant.

If some species tolerate more conspecific than interspecific nests, we expect that the average distance to the nearest conspecific neighbor would be smaller than the average distance to the nearest interspecific neighbor. The data, however, did not confirm this expectation. We concluded, therefore, that the aggregation was both intra- and interspecific, indicating weak competition within and between ant species.

Several studies have detected a regular pattern of ant-nest distribution, with the most frequent explanation being resource competition (Bernstein and Gobbel, 1979; Levings and Traniello, 1981; Levings and Franks, 1982; Ryti and Case, 1984; 1986; Cushman et al., 1988, Deslippe and Savolainen, 1995; Wiernasz and Cole, 1995). The usual limiting resources for ants are food and nesting sites (Fowler et al., 1991). It is possible, however, that these resources are not limited in soil and litter ant communities, so that intra- and interspecific competition might not be strong. Although litter constitutes an ephemeral resource, due to its fast decomposition in tropical soils (Louzada et al., 1997), a constant litterfall accompanies the constant litter decomposition, thus maintaining a high abundance of food resources and nesting sites.

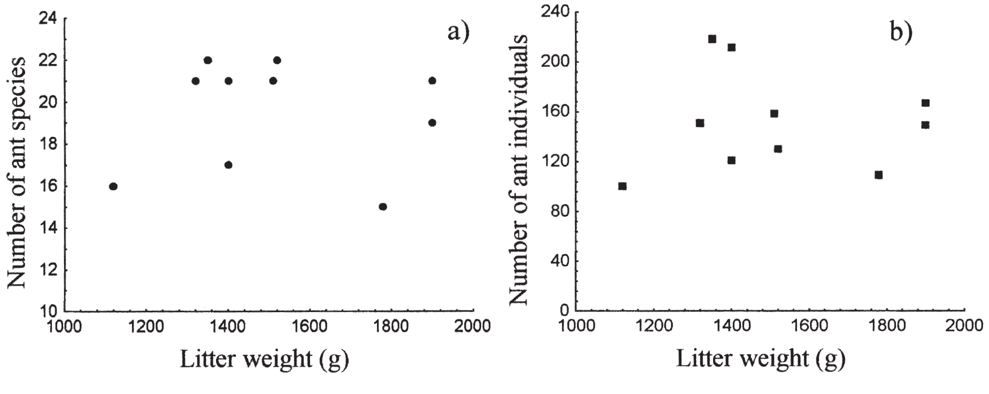

Figure 3. Relationship between litter weight and (a) number of ant species and (b) number of ant individuals sampled in 10 quadrats of litter

This resource abundance, therefore, may prevent intra- and interspecific competition from being an important structuring factor in soil and litter ant communitics. Alternatively, if competition exists in these communities, it may affect only a small fraction of the community, making its effect upon the whole community undetectable.

We did not detect an effect of litter abundance on species richness or on the number of ants inside each quadrat. Delabie and Fowler (1995) obtained a similar result. Considering that we used litter abundance as an indirect estimate of resource abundance, this result supports the hypothesis that resource limitation is absent in litter ant communities. If there was a resource limitation, then we should have found a positive relationship between litter abundance and species richness and/or the number of individuals in each quadrat.

It is also possible that litter weight cannot be used as a parameter to evaluate resource availability, because some litter components are more important for nesting than others (see Table 1). Further studies, therefore, must be carried out to test this hypothesis; for example, testing the relationship between the abundance of species/individuals and the abundance of the most used component, in this case tree branches. Experimental studies, such as resource introduction or removal, could also be carried out. Adding artificial nesting sites and analyzing the outcome on ant communities may also help understand the effects of resource availability on individual and species abundance.

Another factor that may explain the absence of competition in litter and soil ant communities is the presence of disturbance. Although the concept of disturbance itself can cause polemic (see, for example, Begon et al., 1996) and it may be argued that a natural process, such as litterfall, cannot be a source of disturbance, it seems clear that falling branches can cause a considerable disturbance to litter ants (Byrne, 1994). In any case, litter ants relocate their nests every 34–140 days (Herbers, 1986; Byrne, 1994), and the unstable environmental conditions of litter prevents nests from growing in a way that causes saturation of the community (Kaspari, 1996). This factor also delays the process of competitive exclusion by dominant species, thus avoiding the exclusion of nondominant species by interspecific competition (Connell, 1978). When a site is disturbed, colonies may move to other sites or have their populations reduced. Thus, the disturbance may remove or reduce the populations of competitive dominant species, enhancing resource availability for other species and allowing the persistence of poor competitors in the community (Connell, 1978). Litter is an environment that suffers constant disturbances due to litterfall and fast decomposition. These alterations in litter quality may also lead to the constant moving of a colony, which may cause a reduction in population abundance or even an exclusion of some species from a given site.

Army ants of the subfamilies Ecitoninae (Neotropics), Dorylinae (Africa), and Aenictinae (Southeast Asia) can also cause frequent disturbance among forest floor ant communities (Hirosawa et al., 2000). These predatory ants make large foraging trails, that have great impact on the fauna (Sudd and Franks, 1987). We noted the occurrence of one species of the subfamily Ecitoninae (*Labidus* sp.) in our survey, although other species, such as *Neivamyrmex planidorsus* (Emery, 1906) and *Nomamyrmex* sp.$_2$, have been recorded in the same remnant during other studies (personal observation). While passing through an area, army ants remove or reduce some ant colonies nesting on the forest floor (Sudd and Franks, 1987), thus preventing the process of competitive exclusion by dominant ants.

Furthermore, colony movements produce a constant modification in neighboring species composition, so that the identity of the neighbor is highly unpredictable. In this case, any strategy used in the defense of resources would rarely be efficient, and the use of territory defense would not be very frequent compared to ants occupying more stable environments, such as in arboreal ants (Byrne, 1994).

Although competition has been frequently reported in ant communities, we found no evidence of its role as a structuring factor in litter and soil ant communities. Species richness and composition in these communities does not seem to be influenced by either intra- or interspecific competition. They are probably regulated by factors acting on larger scales. Factors other than competition act on the local scale, although studies emphasizing the influence of local and regional processes on litter and soil ant species richness are needed to clarify which factors are responsible for community structure.

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