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Research article

Spatial structure of litter-dwelling ant distribution in a subtropical dry forest

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Abstract. Understanding the spatial patterns of species distribution is essential to characterize the structure of communities, to optimize species inventories and to evaluate the impact of biotic and abiotic variables. Here we describe the spatial structure of the distribution of leaf litter ant species, and of biotic factors that could explain it, in a subtropical semi-deciduous forest of the Argentinian Chaco, characterized by a dense understorey of shrubs and terrestrial bromeliads. Environmental variables (leaf litter quantity and ground bromeliad density) were measured and ants were collected in 1 m^2 quadrats distributed along two 200 m transects at intervals of 1.25 m. Overall 87 species were collected. Sixteen positive associations and a single negative association were observed between the 11 most frequent species taken pair-wise. Our results suggest that the spatial distribution of leaf litter ants was determined at two different scales. At a small scale (period below 10 m) a periodic spatial structure, likely due to intraspecific competition, produced a succession of peaks of abundance separated by gaps. At a larger scale (period around 50 m), periodically distributed environmental factors induced aggregates of colonies of species responding positively to these factors. A high quantity of leaf litter and, to a lesser extent, a high density of ground bromeliads promoted a high density and a high species richness of ants. Numerically dominant ants being generally positively associated, interspecific competition was apparently weak. All ant species whose abundance was correlated with an environmental factor were not completely spatially structured by it. This suggests that some other factors, such as intraspecific competition, may have counter-effects.

Keywords: Spatial pattern, ant distribution, geostatistics, Chaco.

Introduction

Understanding the spatial patterns of species distribution is essential to characterize the structure of communities, to optimize species inventories (Leponce et al., 2004) and to evaluate the impact of biotic and abiotic variables. Little is known about the fine spatial scaling of the majority of species assemblages including leaf litter ants. Tropical ant assemblages show a high species richness and a patchy distribution of colonies (Wilson, 1958; Levings and Franks, 1982; Levings, 1983; Benson and Brandão, 1987; Kaspari, 1996a; Vasconcelos and Delabie, 2000) which depends on biotic and abiotic constraints. Leaf litter ants are not territorial and a considerable amount of evidence suggests that favourable resource availability, rather than competition, is a major force structuring tropical leaf litter ant assemblages (Franks, 1982; Byrne, 1994; Kaspari, 1996a,b; Soares and Schoereder, 2001) involving overlapping foraging areas (Jackson, 1984; Byrne, 1994). For ground-dwelling ants, causes of patchiness include predation by swarm-raiding army ants (Franks and Bossert, 1983; Kaspari, 1996b; Hirosawa et al., 2000), moisture content preferences (Levings, 1983; Levings and Windsor, 1984; Kaspari, 1996a), temperature preferences (Bestelmeyer, 2000), topography (Vasconcelos et al., 2003), nest-site and food availability (Herbers, 1989; Byrne, 1994; Kaspari, 1996b; Kaspari and Majer, 2000), leaf litter quantity and quality (Vasconcelos, 1990; Höfer et al., 1996; Kaspari, 1996a; Carvalho and Vasconcelos, 1999) and both vegetation structure and composition (Wilson, 1958; Gadagkar et al., 1993; Feener and Schupp, 1998; Moutinho, 1998; Retana and Cerdà, 2000; Bestelmeyer and Wiens, 2001).

In a previous study carried out at a high resolution and based on a nearly exhaustive sampling of a strip of 200 m^2 in a subtropical semi-deciduous forest of the Argentinean Chaco, we demonstrated the highly heterogeneous distribution of leaf litter ant species and evaluated its consequences on diversity estimates (Leponce et al., 2004). The present study aimed at extending this work by the spatial analysis of the ant species distribution and of the biotic factors that could explain it. To achieve this objective, we measured conspicuous environmental variables likely to affect ant distribution and measured the nature of interactions between numerically dominant ants.

Methods

Study site

The study site was located in Río Pilcomayo National Park, northern Argentina, in the wet Chaco region (25°04'06'' S, 58°05'36'' W). The habitat, called *"monte fuerte"* is a subtropical mesoxerophile oligarchic forest (Pujalte et al., 1995; habitat unit PHYSIS 48.2412 of Devillers and Devillers-Terschuren, 1996) dominated by *Schinopsis balansae* Engl., *Astronium balansae* Engl. and *Aspidosperma quebracho-blanco* Schlecht. and by a ground strata of bromeliads (*Aechmea distichantha* Lemaire and *Pseudananas sagenarius* (Arruda) Camargo) (Pujalte et al., 1995).

Sampling design

Ant sampling protocol

Two 200 m-long transects (A and B) located 400 m apart were sampled between July 23 and August 8, 2000 in a 16 ha forest fragment. Each transect consisted of 160 quadrats of 1 m^2 separated by 1.25 m intervals (transect A is extensively described in Leponce et al., 2004). At each sampling point, the leaf litter found inside the 1 m^2 quadrat was collected, sifted and put in a cotton bag. The sifted material was brought back to the field laboratory and its fauna was extracted with a mini-Winkler apparatus (Fisher, 1998) for 24 hours. Temperature, recorded every 10 minutes, ranged between 3.6 °C (at night) and 27.6 °C with an average of 14.1 ± 4.1 °C during the sampling session of transect A and between 10.6 and 30.2 °C (18.5 ± 4.2 °C) during the sampling of transect B. Average temperatures were lower (14.1 °C) during the sampling of transect A than during the sampling of transect B (18.5 °C) (t-test, $p < 0.001$). The weather was dry during the 17 days sampling campaign (only three short and light rains occurred).

Environmental measures

In order to interpret the pattern of species distribution, we measured three conspicuous environmental variables at each 1 m^2 quadrat: (1) the sifted litter weight (which integrates factors such as food, nest, temperature and moisture availability) (Levings, 1983) (2) the density of ground bromeliads (omnipresent in the habitat and affecting ant species density and composition (*unpublished results*)), (3) canopy openness (influencing the temperature and dryness at ground level). The percentage of canopy openness was estimated from hemispherical photographs, shot 1.5 m above ground level and quantified with the Gap Light Analyzer 2.0 program (Frazer et al., 1999).

Data analysis

All ants were determined to species or morphospecies level. In order to assess the impact of environmental variations on ant density and species composition, we pooled the data from the two transects. By contrast, the two transects were considered separately for the analysis of spatial structure. Numerically dominant ant species were defined as species found in at least 10 % of the samples, and will be hereafter referred as "frequent species".

Faunal similarity between transect A and B was estimated using Jaccard's index (Jaccard, 1912; Wilson and Schmida, 1984) calculated as follows:

$$S_j = \frac{c}{a + b - c}$$

(where a = total number of species in sample A, b = total number of species in sample B, c = number of common species to samples A and B).

Species associations and correlations between environmental factors and ant abundance were evaluated on the $\log_{10}(n+1)$-transformed abundance in order to limit the weight of samples collected around nests, trails and exploited resources. Standard parametric tests of significance could not be used here because of spatial autocorrelation (SA), which represents a bias to the assumption of independence among samples (Lennon, 2000; Legendre et al., 2002). Using simulation data, Legendre et al. (2002) showed that Dutilleul's modified t-test (Dutilleul, 1993) constitutes an efficient method to account for SA in estimating the significance of the correlation between two autocorrelated variables, and this method was used here to test the significance of all bivariate correlations. We re-adjusted the p-values for statistical acceptance with the Holm procedure (1979) (Legendre and Legendre, 1998) because the probability of a type I error becomes larger than the nominal value of α when several tests of significance are carried out simultaneously (i.e. in a correlation matrix).

Spatial analysis: autocorrelation and periodicity

Two methods were used to explore spatial patterns in environmental factors and ant species distributions. First, spatial correlograms were used to quantify the level of spatial dependence, i.e. the tendency of points close together to have more similar values than points farther apart. Spatial correlograms plot the values of the spatial correlations between observations separated by increasing distance classes, and allow describing the extent (distance over which no SA is measured), and intensity (when autocorrelation is strong, points separated by close distances have strongly correlated values) of SA (Rossi et al., 1992; Liebhold et al., 1993, Legendre et al., 2002; Liebhold and Gurevitch, 2002; Perry et al., 2002). Correlogram values range from –1 to +1 (Rho(h)) and can be interpreted as indicating negative or positive correlations in the same way as simple correlation coefficients. Second, periodograms were used to quantify the presence of periodic patterns in the transect data. Periodograms resulted from a Fourier-transformation decomposing the observed transect data into a sum of periodic terms, and plotting the intensity (as measured by the amplitude) as a function of the period of each term (Shumway, 1988; Legendre and Legendre, 1998). We ranked the level of periodicity in our transect data according to three arbitrary classes of amplitude: strong periodicity (highest peak >6), intermediate (highest peak is <6 and >1) and low (highest peak <1). Correlograms and periodograms were calculated using Statistica 6.0 software (StatSoft Inc, 2004).

Studies of spatial patterns along transects (representing a single dimension) allow obtaining fine SA coefficients and periodogram values (Legendre and Fortin, 1989).

Structuring effects

We aimed at exploring whether spatial periodicity observed in species distribution could be attributed to one or several environmental covariates. The periodograms and correlograms of the residuals from the linear regression between species abundance and a microhabitat factor were therefore estimated, and compared to those of the species abundance data. A strong structuring effect of a microhabitat factor on the species distribution would result in a substantial reduction in the amplitude of the highest peak in the periodogram of regression residuals once the variability related to microhabitat factor has been removed. This reduction was quantified and used as an estimate of the spatial structuring effect of the environmental variable: decreases over 50 %, between 50 % and 20 %, and lower than 20 % were considered as strong, intermediate or low structuring effects, respectively. A similar approach was used to explore the relationship between the environmental factors.

Results

Eighty-seven species corresponding to 1880 occurrences and 24114 individuals were found in the 320 quadrats of the two transects (species list in Appendix 1). Both transects had 11 frequent species in common which occupied similar ranks of occurrence (Spearman rank order correlation coefficient, $r = 0.691$, $p < 0.05$). Sixteen positive and a single negative associations were observed between these 11 frequent species (species found in at least 10% of the samples) (Table 1).

Relationships between ant density and environmental factors

Median leaf litter weight was 357 g (quartiles: 212–524), bromeliad density 2 plants/m^2 (0–4) and canopy openness 18.4% (16.9–19.9) (N = 320) along transects A and B. Because values of canopy openness varied very little (variation of ±5%) (Fig. 1), we did not undertake further investigations of its effects on ant distribution. Litter quantity varied considerably, up to 25 fold between contiguous quadrats. Species density (number of species/m^2) was positively correlated (Pearson's correlation) with leaf litter weight ($N = 320$, $r = 0.71$, $p < 0.05$) and with bromeliad density ($N = 320$, $r = 0.31$, $p < 0.05$). Leaf litter weight was also positively correlated with bromeliad density ($N = 320$, $r = 0.27$, $p < 0.05$). Quadrats devoid of bromeliads (N = 85 out of 320) had significantly less leaf litter (Mann-Whitney rank sum test $U = 5091$, $p < 0.001$), a lower ant species density (M-W rank sum test: $U = 5150$, $p < 0.001$) and a lower species richness (47 vs. 55 species for 314 occurrences) than quadrats with bromeliads (N = 235).

Relationships between ant species composition and environmental factors

The abundance of eight frequent species was positively correlated with leaf litter weight and that of two species with bromeliad density (Table 2). *Solenopsis* sp.01 and

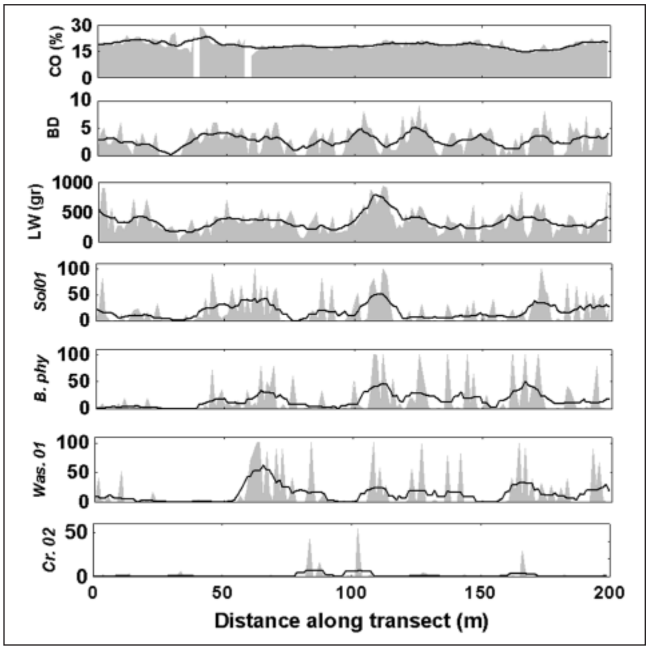

Fig. 1. Spatial distribution of canopy openness (CO), bromeliad density (BD), leaf litter weight (LW) and distribution of abundance of the four most frequent species (*Solenopsis* sp.01, *Brachymyrmex physogaster, Wasmannia* sp. prox. *auropunctata* and *Crematogaster* sp.02) along transect A. Black line corresponds to smoothed curves calculating mobile mean of data.

Table 1. Square matrix with Pearson's correlation coefficients between abundance of individuals ($\log_{10}$(ur1)-transformed) of the eleven species taken by pair (transects pooled, N = 320). Statistically significant positive or negative associations between species are greyed or blackened respectively. Levels of significance were adjusted first using Dutilleul's modified t-test and then using Holm's procedures. Infrequent species were discarded because too little data was available to draw conclusions.

Occurrence Rank	Species	1	2	3	4	5	6	7	8	9	10	11
1	*Solenopsis* sp.01	1										
2	*Brachymyrmex physogaster*	0.49	1									
3	*Wasmannia* sp. prox. *auropunctata*	0.37	0.32	1								
4	*Crematogaster* sp.02	0.07	0.07	0.06	1							
5	*Octostruma rugifera*	0.35	0.29	0.15	0.09	1						
6	*Hypoponera* sp. prox. *trigona*	0.32	0.33	0.26	0.08	0.26	1					
7	*Paratrechina* sp.02	0.26	0.08	0.16	0.02	0.16	0.06	1				
8	*Pyramica denticulata*	0.21	0.16	0.16	0.25	0.29	0.37	0.15	1			
9	*Solenopsis* sp. 17	–0.30	0.12	–0.01	0.03	0.10	0.16	0.04	0.10	1		
10	*Pheidole flavens*	0.07	–0.01	0.07	0.17	0.07	–0.01	0.02	0.01	0.04	1	
11	*Pheidole nubila*	0.07	0.15	–0.01	0.08	0.24	0.31	0.02	0.22	0.24	0	1

Table 2. Effect of environmental factors on the distribution of frequent ant species (LW = litter weight and BD = bromeliad density). Pearson's correlation coefficients between the abundance of frequent species ($\log_{10}$(ur1)-transformed) and environmental factors (raw data) are indicated for pooled quadrats from the 2 transects (N = 320). Levels of significance were adjusted using Dutilleul's modified t-test and Holm's procedures. Species were sorted by decreasing rank of occurrence in the two pooled transects. Periodicity in species spatial distribution were measured on periodograms and were categorized as either none (highest peak < 1), intermediate (highest peak 1–6) or strong (highest peak > 6). Between brackets, the periodicity of highest peak was noted. The structuring effect of leaf litter weight and bromeliad density on species spatial distribution corresponded to the percentage of decrease of the 50 m (LW) and 66.7 m and 100 m (BD) periodical peak and was categorized as either none (decrease < 20 %), intermediate (decrease 20–50 %) or strong (decrease > 50 %) and were analysed for each transect separately (N = 160).

Frequent species	Environmental factors		Transect A			Transect B		
	LW	BD	Periodicity	Structuring effect		Periodicity	Structuring effect	
				LW (50 m)	BD (66.7 m)		LW (50 m)	BD (100 m)
Solenopsis sp.01	**0.49** ***	**0.31** ***	**strong (50 m)**	strong	**strong**	**strong (66 m)**	**strong**	**intermediate**
Brachymyrmex physogaster	**0.51** ***	0.16	**strong (50 m)**	**strong**	**intermediate**	**strong (50 m)**	**strong**	none
Wasmannia sp. prox. *auropunctata*	**0.33** ***	0.06	**strong (50 m)**	**intermediate**	none	**strong (18 m)**	**strong**	none
Crematogaster sp.02	0.17	0.06	none			**intermediate (5.25 m)**	**strong**	none
Octostruma rugifera	**0.47** ***	0.11	**intermediate (12.5 m)**	none	none	**intermediate (50 m)**	**strong**	none
Hypoponera sp. prox. *trigona*	**0.47** ***	0.09	none	none	none	**strong (100 m)**	**strong**	none
Paratrechina sp.02	**0.27** ***	**0.28** ***	**intermediate (13.3 m)**	none	none	**intermediate (10 m)**	none	none
Pyramica denticulata	**0.33** **	–0.02	none			**intermediate (50 m)**	**strong**	none
Solenopsis sp. 17	0.23	0.07	**intermediate (22 m)**	none	none	**intermediate (66 m)**	none	none
Pheidole flavens	0.10	0.07	none			none		
Pheidole nubila	**0.34** ***	0.00	none			**intermediate (33 m)**	none	none

Paratrechina sp.02 were positively correlated with both leaf litter weight and bromeliad density. *Crematogaster* sp.02, *Solenopsis* sp.17 and *Pheidole flavens* did not show any significative correlation with either litter weight or bromeliad density.

Spatial pattern of environmental factors and ant distribution

The spatial distribution of the environmental factors and of the 4 most frequent species (present in at least 1/3 of samples) along transect A is presented in Fig. 1. All variables except canopy openness varied significantly along the transect, with a succession of peaks and gaps. Similar results were obtained for transect B, except around a depressed zone of 15 m long that was temporarily flooded and devoid of both bromeliads and leaf-litter.

Leaf litter weight and bromeliad density showed a strong spatial structure in their distribution along transects A and B (Fig. 2). Leaf litter quantity correlogram indicated evidence of a periodic spatial distribution along both transects (Fig. 2A, B). Positive autocorrelations (peaks) were observed at distances below 20 m, between 45 and 65 m and over 90 m. At other lag distances, samples were negatively autocorrelated (troughs). The distance between successive peaks (period) was thus $T = 50$ m as indicated by the highest peak in corresponding periodograms (Fig. 2C, D). In transect B, a second large peak was observed at $T = 100$ m. Bromeliad density periodograms showed a different periodicity in transects A and B (Fig. 2G, H). In transect A, we observed four large peaks corresponding to periods of 66.6 m, 22.2 m, 16.6 m and 11.8 m. In transect B, we observed a single peak corresponding to a period of 100 m. The shape of bromeliad density correlogram of transect B corresponded to a gradient spatial structure, i.e. autocorrelation values decreased with increasing intervals.

Periodic spatial structures were observed in the distribution of 10 out of 11 frequent ant species (all but *Pheidole flavens,* Fig. 3) (Table 2). A strong (example of *B. physogaster*;

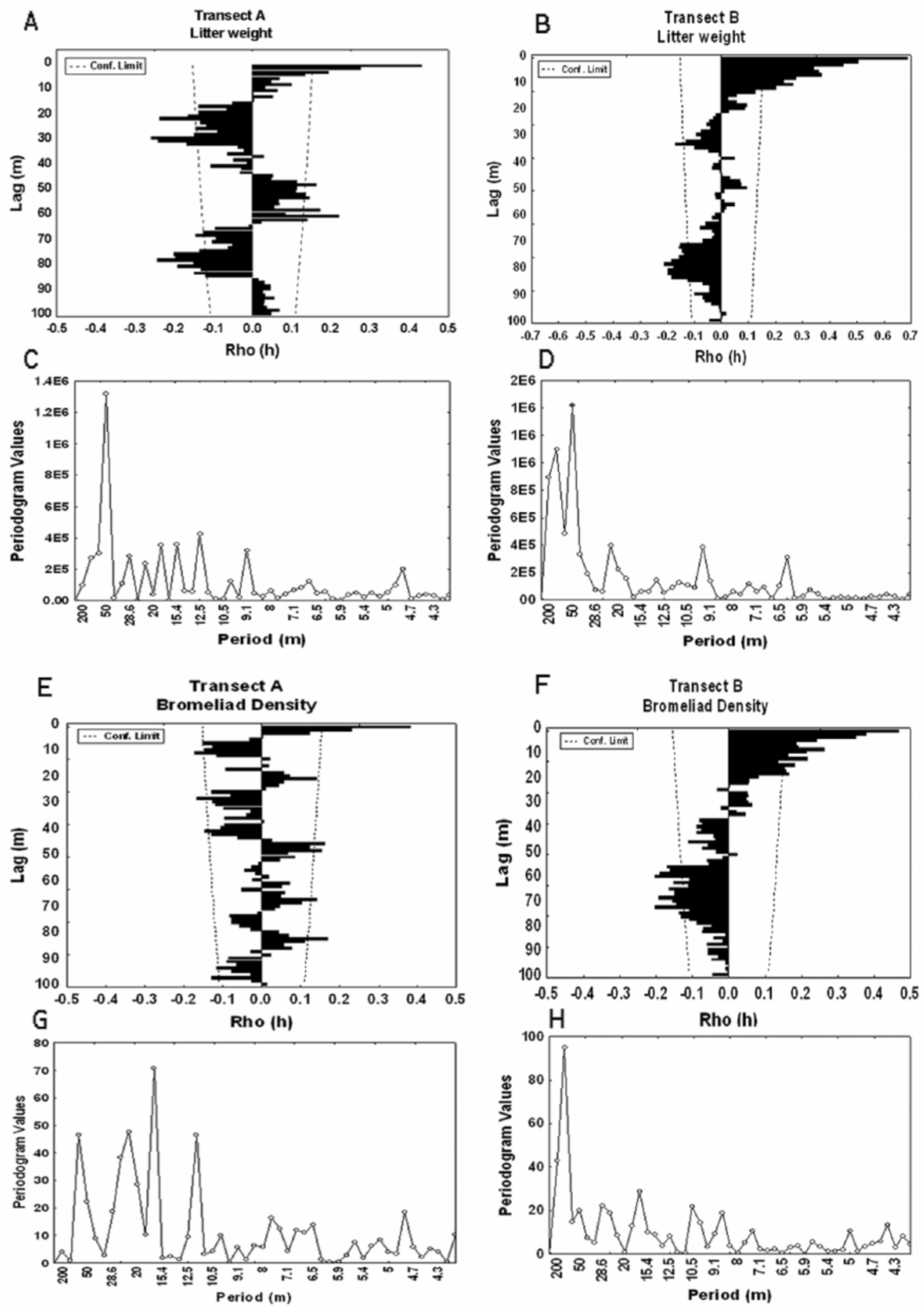

Fig. 2. Spatial analysis (correlograms and periodograms) of litter weight (above: A, B, C, D) and bromeliad density (below: E, F, G, H) for transects A (A, C, E, G) and B (B, D, F, H). Highest peaks in periodograms indicate a periodicity of environmental variables. Litter weight was distributed with a 50 m period in each transect. Bromeliad density showed different periodicity in his spatial distribution between transects (see text for more details). Rho (h) is the coefficient of autocorrelation varying between –1 and +1.

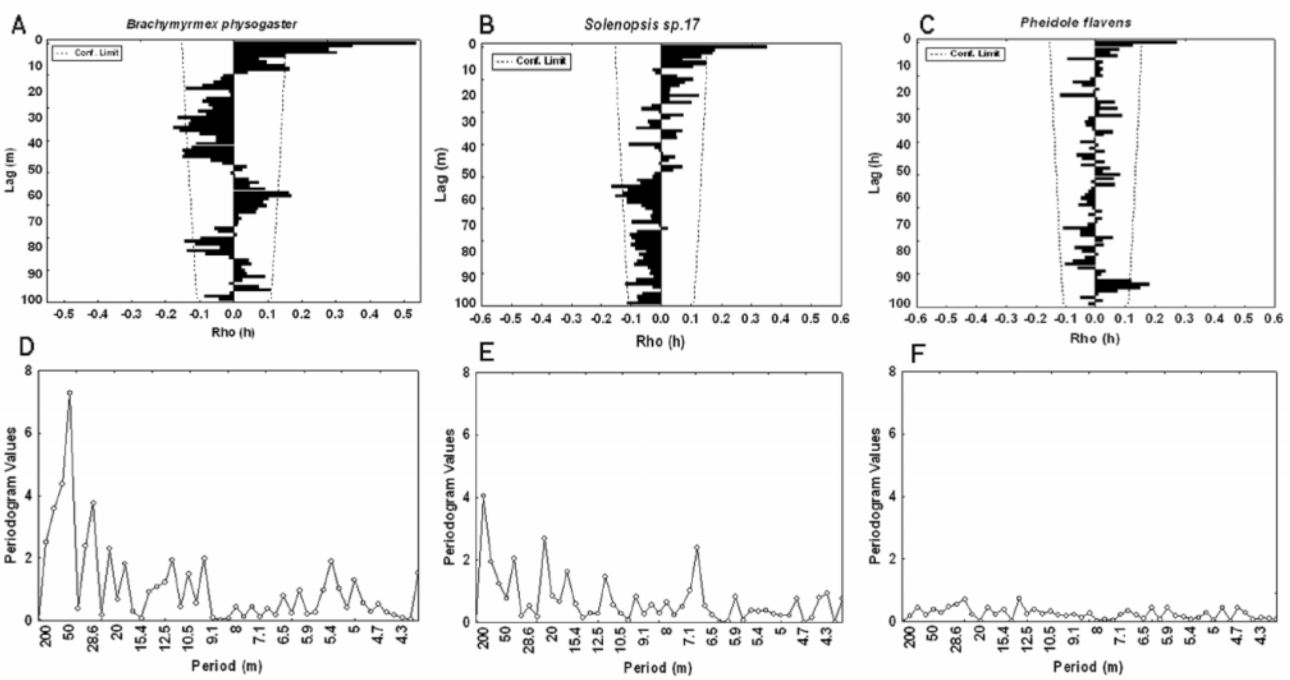

Fig. 3. Periodicity categories of spatial distribution of frequent ant species. Example of correlograms (above A, B, C) and periodograms (below F, G, H) of species showing a strong (A, D), an intermediate (B, E) and a lack of periodicity (C, F) in their spatial distribution along the transect B. The degree of periodicity was estimated according to the amplitude of the highest principal peak of the periodogram and was categorized as either strong (highest peak >6), intermediate (highest peak >1) or none (highest peak <1). Rho (h) is the coefficient of autocorrelation varying between –1 and +1.

Fig. 3A, D) and an intermediate periodicity (example of *Solenopsis* sp. 17; Fig. 3B, E) were observed in the spatial distribution of four and six species respectively. *Solenopsis* sp.01, *Brachymyrmex physogaster*, *Wasmannia* sp. prox. *auropunctata, Octostruma rugifera* and *Pyramica denticulata* showed the same periodicity (example of *B. physogaster* on Fig. 3D) as litter weight (Fig. 2C, D) with the highest peak at a period of 50 m. All frequent species but *Crematogaster* sp.02 and *Paratrechina* sp. 02 showed a positive autocorrelation for distance lags below 10 m (Fig. 3, example for 3 species).

Environmental variation and spatial structure of ant species distribution

First, we verified whether the periodicity of leaf litter weight distribution could be related to bromeliad density and vice versa, since the two environmental factors were correlated. Correlograms and periodograms of standardised residuals from the regression between these two factors showed the same highest peak(s) as the initial ones (as in Fig. 2C, D, G, H) although weak variations in periodogram values could be observed. Indeed, we observed no effect of litter weight on the periodicity of bromeliad density. In contrast, bromeliad density influenced periodogram values of litter weight at $T = 66.7$ m (transect A) and at $T = 100$ m (transect B) but had no effect on the highest peak of periodicity at $T = 50$ m (for both transects).

In a second step, we evaluated the structuring effect of litter weight and bromeliad density on frequent species distribution with correlograms and periodograms of residuals (e.g. Fig. 4A, B) obtained from the regression between species abundance and the environmental factor considered. Correlograms allowed a visualisation of the decrease of periodicity and periodograms allowed us to quantify it. The percentage of decrease of periodogram values were measured relative to periods where environmental variables showed the highest peak of periodicity, i.e. for litter weight at 50 m (transect A and B, Fig. 2C, D) and for bromeliad density at 66.7 m (transect A, Fig. 2G) and 100 m (transect B, Fig. 2H).

The litter weight was a structuring factor for seven frequent ant species as well as the bromeliad density for two of them (Table 2).

Litter quantity and bromeliad density as strong structuring factors of ant spatial distribution

The structuring effect of environmental variable on each species spatial distribution was explored by inspecting the periodograms of standardised residuals between the abundance of a species and the value of the variable. A strong structuring effect was evident when a peak of abundance of

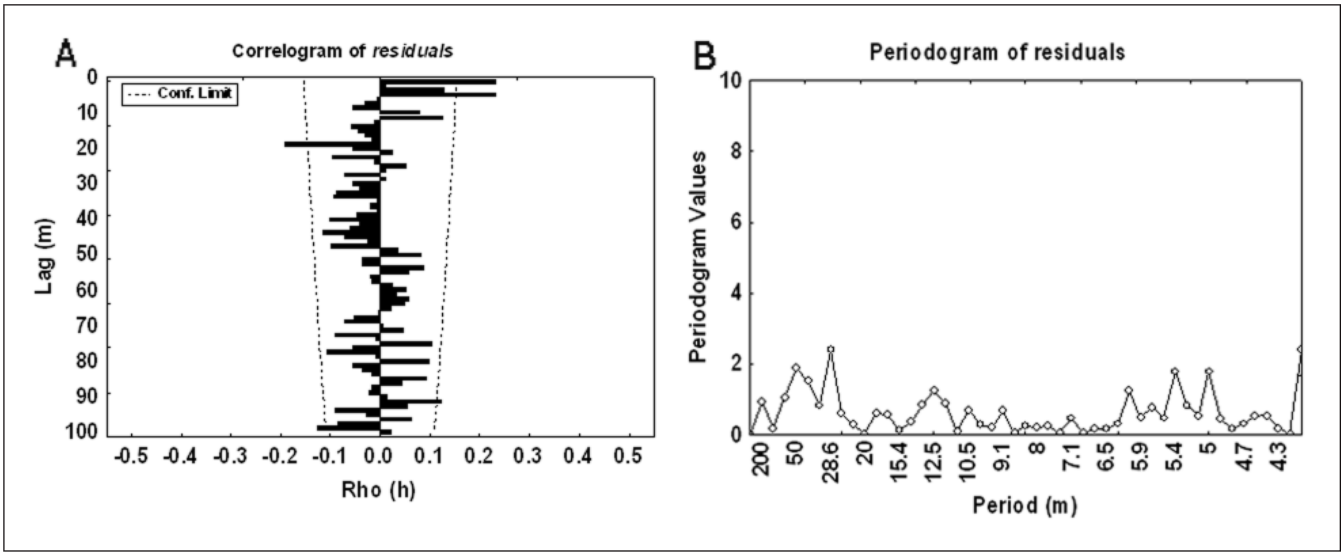

Fig. 4. Measure of structuring effect intensity of environmental factors (leaf litter quantity and bromeliad density) on frequent ant species distribution. Correlogram (A) and periodogram (B) of residuals from the linear regression between *Brachymyrmex physogaster* abundance ($\log_{10}$ (n+1)-transformed) and leaf litter weight in transect B. Periodic spatial structure of species distribution disappeared after removing (by regression) leaf litter effects. Rho (h) is the coefficient of autocorrelation varying between –1 and +1.

a species experienced a decrease in amplitude over 50%. For example, the peak at a period of 50m in the periodogram of *Brachymyrmex physogaster* abundance decreased from 7.28 (Fig. 3 D) to 1.89 in the periodogram of residuals (74% decrease) (Fig. 4B) indicating that leaf litter quantity had a strong structuring effect on *Brachymyrmex physogaster* distribution.

The comparison between the correlogram of a species and of the residuals allowed assessing the structuring effect of an environmental variable (e.g. Fig. 3A and Fig. 4A).

The structuring effect of litter weight on the distribution of the two most frequent ant species was strong in both transects (Table 2). In contrast, a strong structuring effect of litter weight was only observed in transect B for *Wasmannia* sp. prox. *auropunctata, Crematogaster* sp. 02, *Octostruma rugifera, Hypoponera* sp. prox. *trigona* and *Pyramica denticulata.* The structuring effect of bromeliad density on the distribution of *Solenopsis* sp. 01 was only strong in transect A.

Litter quantity and/or bromeliad density as intermediate structuring factors of ant spatial pattern

The analysis of correlograms and periodograms of residuals showed that litter weight had an intermediate spatial structuring effect (20–50% decrease of peaks) on the distribution of *Wasmannia* sp. prox. *auropunctata* in transect A. Bromeliad density had an intermediate spatial structuring effect on the spatial distribution of *Solenopsis* sp.01 (transect B) and *Brachymyrmex physogaster* (transect A), although the latter was not significantly correlated to bromeliad density (Table 2).

In addition, a positive autocorrelation remains at short distance (below 10m) in the correlograms of residuals demonstrating a strong or intermediate structuring effect of leaf litter weight or bromeliad density on species distribution (Fig. 4).

Species not structured by litter quantity or bromeliad density

Two frequent species (*Pa.* sp. 02 and *Ph. nubila*) were not structured by the leaf litter weight as determined by a residual analysis although they were correlated to this factor. In the same way, *Pa.* sp.02 abundance was correlated to, although not spatially structured by, bromeliad density.

Discussion

Effects of environmental factors vs. interspecific interaction on ant species density and composition

Our results suggest that most of the frequent ant species coexist in leaf litter. Indeed, numerous species foraged in the same quadrat (up to 16 species m^{-2}) and 16 positive vs. a single negative associations between frequent species suggested low interspecific competition in our assemblage where foraging ranges may overlap considerably. These results are in agreement with those of previous works (Levings, 1983; Levings and Windsor, 1984; Byrne, 1994; Kaspari, 1996a, b). Moreover, the only negative association was found between two *Solenopsis* species, which probably occupied very close ecological niches. Weak interspecific competition could be explained by sufficiency of nesting sites and food (Herbers, 1989; Kaspari, 1996b; Soares and Shoereder, 2001) or by avoidance behaviours between heterospecific individuals allowing a high overlap in food utilisation (Byrne, 1994). On the ground, as opposed to the canopy, numerically dominant ants (mostly generalist in our study) do not form a mosaic of non-overlapping territories.

The distribution of frequent species of our assemblage was principally associated to leaf litter quantity, rather than competition. Several studies have highlighted the dominant influence of such environmental factors on tropical litter ant assemblages (Franks, 1982; Byrne, 1994; Kaspari, 1996a, b; Soares and Shoereder, 2001). Leaf litter provides nesting sites (Vasconcelos, 1990; Didham, 1998), favorable moisture content (Levings, 1983; Vasconcelos, 1990; Bestelmeyer, 1997), and food resources (Andersen, 1983) for ants and other arthropods (Bestelmeyer and Schooley, 1999a). We observed, as in other studies, a positive correlation between the litter quantity and ant density (Vasconcelos, 1990; Kaspari, 1996b) and composition (Kaspari, 1996b; Carvalho and Vasconcelos, 1999). However several studies did not find an effect of the leaf litter quantity on ant species density and species abundance (Soares and Shoereder, 2001; Delabie and Fowler, 1995). Litter quantity was found to be positively related to litter structural complexity, because of vertical layering (Vasconcelos, 1990). Litter samples displayed variable vertical stratification, some being mainly composed of intact leaves, others of leaves at more advanced stages of decomposition. Vertical litter stratification may allow an increase in the number of coexisting species of ground-dwelling arthropods through habitat partitioning (Anderson, 1978; Vasconcelos, 1990) and by limiting competition (Yanoviak and Kaspari, 2000).

Seventy percent (8 out of 11) of frequent species were positively correlated with litter weight. These species could occupy sub-layer(s) of litter composed of decayed leaves and might be specialized to exploit a thick cover of leaf litter. Among species not correlated with litter quantity, we found *Crematogaster* sp.02 which is arboreal, *Pheidole flavens* which has the ability to use different microhabitats as nesting sites with some preference for pieces of wood (Wilson, 2003) and *Solenopsis* sp.17 whose biology is unknown.

Bromeliad density was also related to species density and abundance of several ant species but on the whole the impact of bromeliads on the ant assemblage was more limited than the effect of leaf litter quantity (Table 2). Bromeliad leaves form a rosette accumulating rain and litter, and contribute to favorable moisture and temperature conditions for most arthropods (Benzing 1980). Moreover, their spiny leaves provide protection against predators such as opossums, giant anteaters, tamanduas or armadillos (Pujalte et al., 1995; Eisenberg and Redford, 1999). In the same habitat, soil termite diversity is also positively correlated to bromeliad density (Roisin and Leponce, 2004).

Spatial pattern of environmental variables

We observed variation in litter quantity between contiguous quadrats up to 25 fold, which is consistent with the results obtained elsewhere in the tropics (Kaspari, 1996b). The present study suggests a periodic distribution of the leaf litter. A possible explanation for this phenomenon would be related to topographic differences (microrelief). In another Chacoan *Schinopsis balansae* forest, Barberis et al. (1998) have demonstrated that most woody species and bromeliads grow preferentially on well-drained convex zones of the soil. The clumped distribution of trees would induce an accumulation of leaf litter on the slightly higher zones whereas the leaf litter would tend to be carried away by temporary inundations in the depressed zones of the forest. Bromeliads, preferring convex zones, tend to increase the quantity of litter possibly because they affect the litter composition, adding their own dead material, and accumulation, due to their root network (Benzing, 1980). This might explain why we observed that some peaks of periodicity of litter quantity could be attributed to bromeliad density. Unfortunately, the periodicity of convex zones remains to be demonstrated. Nevertheless it seems a reasonable hypothesis since periodic patterns of vegetation are sometimes observed (e.g. tiger bush in semi-arid African landscapes, Couteron and Lejeune, 2001).

The bromeliad density was also spatially structured but differently so in each transect. We observed a periodic structure in transect A with a period ($T = 66.6$ m) close to that of litter quantity. A gradient was observed in transect B ($T = 100$ m). Gradient structure (Legendre and Fortin, 1989; Legendre and Legendre, 1998) was probably an artefact (false gradient) caused by the presence of a gap, deprived of bromeliads, inside transect B. This trend was also weakly expressed in the leaf litter correlogram (Fig. 2B). Bromeliads showed strong SA below 5 m in both transects. This could be a consequence of the asexual reproduction by rhizomes (Benzing, 1980).

Structuring effect of environmental variables on the spatial distribution of ants

Among the eight species whose abundance was correlated to leaf litter weight, six were strongly spatially structured (period around 50 m) by this environmental factor in at least one transect. Structuring effects were generally more apparent in transect B because the ant activity was increased by more favourable temperature conditions. *Solenopsis* sp. 01 was correlated to and structured by bromeliad density in both transects.

The correlation between species abundance and a factor is not necessarily spatial, and may be observed at the quadrat scale without implying a structuring spatial effect of the factor at a larger scale. Conversely, the presence of a structuring effect does not necessarily imply a strong local correlation: species abundance and a factor can fluctuate together at large scale (when the whole transect is considered), but still show a loose association when observed for each quadrat. Two examples illustrate this observation. First, *Crematogaster* sp.02 (in transect B) was not correlated to litter weight and was found to be distributed with a period of 50 m. Its highest peaks of abundance occurred in zones of high litter quantity so that a structuring effect of this factor was detected. Second, *Ph. nubila* was locally correlated to leaf litter quantity, but not structured by this factor along the whole transect: this species was concentrated mostly at the end of the transects and thus could not be spatially structured by the leaf litter quantity with a 50 m period.

After removing the structuring effect of the environmental factors (with residual analysis), some peaks of periodicity (at periods different from those that corresponded to our environmental factor effects) persisted indicating that other factors structured the species distribution. These factors could be predation by army ants (Franks and Bossert, 1983; Kaspari, 1996b), other biotic factors (e.g. competition, prey availability), abiotic factors (e.g. soil characteristics, nest-site availability), or stochastic events.

Nine out of the 11 frequent species showed a strong spatial structure in their distribution below 10 metres (as shown in Figs. 3 and 4). In other words, species displayed a clumped distribution. The correlogram of residuals (Fig. 4A), indicated that leaf litter quantity was not the cause of this pattern, even for species strongly structured by litter quantity. It is likely that this pattern would be related to the size of the foraging area of individual colonies (Brühl et al., 2003; Delabie et al., 2000b; Kaspari, 1993, 1996b) or to nest aggregation in suitable zones (Herbers, 1989; Soares and Shoereder, 2001). Peaks of species abundance represented in Fig. 1 may indicate the location of nests and gaps between them could reflect intraspecific competition. This would be in agreement with several studies showing that intraspecific interactions affect nest spacing (Levings and Franks, 1982; Ryti and Case, 1984, 1986, 1988, 1992). Dispersal or other environmental factors may also be partly responsible of this pattern.

Species showing no spatial structure could be either randomly distributed (Leponce et al., 2004) or could be submitted to several structuring factors with opposing forces.

Conclusions

Our results suggest that in the subtropical forest studied, the spatial distribution of leaf litter ants is determined at two different scales. At a small scale (period below 10 m) a periodic spatial structure is likely to be related to intraspecific competition since we observed, for the most frequent species, a succession of peaks of abundance separated by gaps reducing aggression between allocolonial individuals. At a larger scale (period around 50 m), environmental factors, also periodically distributed, may induce aggregates of colonies of species responding positively to these factors. A high quantity of leaf litter and, to a lesser extent, a high density of bromeliads promoted a high density and a high species richness of ants. Interspecific competition, even between numerically dominant ants, was weak. All ant species correlated to an environmental factor were not obligatorily spatially structured by it, suggesting that some other factors, such as intraspecific competition, dipersal and/or environmental factors not measured may have counter-effects.

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Appendix 1. List of species found in transect A and B. Numbers represent their occurrences in the 160 samples collected in each transect.

Subfamily	***Species***	**Transect A**	**Transect B**
DOLICHODERINAE	*Linepithema* group *humile* sp.2	0	9
ECITONINAE	*Eciton vagans*	0	3
	Labidus coecus	0	3
FORMICINAE	*Brachymyrmex physogaster*	**89**	**95**
	Brachymyrmex sp.05	2	**20**
	Camponotus (Myrmothrix) renggeri	5	0
	Camponotus arboreus	2	0
	Camponotus crassus	15	**23**
	Camponotus sp. 19	0	1
	Camponotus sp.11 *(Myrmosphincta)*	3	1
	Camponotus sp.13 *(?Myrmaphaenus)*	0	1
	Camponotus sp.14	0	2
	Camponotus sp.17 *(Pseudocolobopsis)*	1	0
	Myrmelachista sp.02	1	7

Subfamily	***Species***	**Transect A**	**Transect B**
FORMICINAE	*Paratrechina pubens*	4	5
	Paratrechina sp.02	**48**	**47**
MYRMICINAE	*Acromyrmex hispidus fallax*	2	13
	Apterostigma sp.complex *pilosum*	3	10
	Carebarella bicolor	3	3
	Cephalotes minutus	6	13
	Crematogaster corticicola	5	2
	Crematogaster euterpe	0	6
	Crematogaster montezumia	2	0
	Crematogaster sp.02	**28**	**78**
	Crematogaster sp.07	1	1
	Crematogaster sp.11	1	6
	Crematogaster sp.14	2	0
	Crematogaster sp.16	0	2
	Cyphomyrmex rimosus	10	13
	Leptothorax sp.01	0	8
	Leptothorax sp.02	0	2
	Megalomyrmex drifti	1	5
	Mycocepurus goeldii	0	2
	Myrmicocrypta foreli	0	2
	Octostruma rugifera	**39**	**66**
	Oxyepoecus reticulatus	1	1
	Pheidole aberrans	11	2
	Pheidole nubila	**17**	**37**
	Pheidole sp.01	**23**	**34**
	Pheidole sp.04	9	0
	Pheidole sp.21	0	2
	Pheidole sp.22	12	**47**
	Pheidole sp.30	7	**40**
	Pyramica crassicornis	2	1
	Pyramica denticulata	**21**	**81**
	Pyramica gr. *appretiata* sp.01	2	0
	Pyramica gr. *appretiata* sp.02	0	2
	Pyramica sp.02	8	4
	Rogeria scobinata	10	**24**
	Solenopsis clytemnestra bruchi	0	1
	Solenopsis sp. 17	**20**	**46**
	Solenopsis sp. 18	5	6
	Solenopsis sp.01	**101**	**98**
	Solenopsis sp.02	11	15
	Solenopsis sp.10	0	6
	Solenopsis sp.13	5	1
	Solenopsis sp.15	3	5
	Strumigenys louisianae	0	2
	Strumigenys ogloblini	1	0
	Strumigenys sp. prox. *elongata* 1	1	4
	Trachymyrmex sp.01	0	7
	Wasmannia sp. prox. *auropunctata*	**66**	**102**
	Wasmannia sp.03	4	4
PONERINAE	*Amblyopone* sp.01	1	0
	Anochetus diegensis	4	2
	Discothyrea neotropica	8	0
	Ectatomma edentatum	13	**19**
	Ectatomma permagnum	0	1
	Gnamptogenys striatula	4	6
	Heteroponera sp.01	3	0
	Hypoponera clavatula	1	0

Subfamily	***Species***	**Transect A**	**Transect B**
PONERINAE	*Hypoponera opaciceps*	4	12
	Hypoponera opacior	6	18
	Hypoponera sp. 09	0	2
	Hypoponera sp. prox. *opaciceps* 1	1	5
	Hypoponera sp. prox. *trigona*	**29**	**66**
	Hypoponera sp.04	**29**	3
	Hypoponera sp.05	1	1
	Hypoponera sp.07	0	1
	Leptogenys consanguinea	2	1
	Odontomachus chelifer	4	5
	Odontomachus meinerti	1	0
	Pachycondyla ferruginea	1	1
	Pachycondyla harpax	4	9
	Pachycondyla obscuricornis	0	5
	Pachycondyla villosa	1	0
	Prionopelta punctulata	1	2
	Typhlomyrmex pusillus	1	1
PSEUDOMYRMECINAE	*Pseudomyrmex gracilis*	3	0

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