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Do Leaf-Litter Attributes Affect the Richness of Leaf-Litter Ants?

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Abstract

The search for factors shaping leaf-litter ant communities has received particular attention due to the essential role of these insects in many ecological processes. Here, we aimed to investigate how the number of leaves and leaf morphotypes affect the litter-ant species density at forest edge and interior in an Atlantic Forest remnant in the state of Alagoas, Brazil. This study was developed based on 28 litter plots (1m^2 each), 14 in the forest interior and 14 in the forest edge. As we early expected, ant species density increased with increasing both the number of leaves and the number of leaf morphotypes, but this result was clearly influenced by plot location. Contrasting with the forest interior, ant species density did not increase as the number of leaves increased in the forest edge. Possibly, factors such as plant species richness, vegetation structure and environmental conditions affect ant species density as well as promote a patchy distribution of species in ant communities along the edge-to-interior gradient. Our findings suggest that edge-affected forests present more simplified ant communities, with different factors shaping its structure. We encourage future studies to include leaf litter heterogeneity as one of the explanatory variables investigated.

Introduction

Factors determining the diversity and distribution of ants have deserved attention of scientists for decades due to the essential role of these insects in many ecological processes such as nutrient cycling (Farji-Brener & Silva 1995), energy turnover (Basu 1997), herbivory (Wirth *et al* 2003), seed dispersal (Gorb & Gorb 2003) and seed predation (Brown & Davidson 1977). Environmental heterogeneity and resource availability, for example, have been pointed out as essential factors strongly affecting ant species richness (*e.g.*, Kaspari & Weiser 2000, Ribas *et al* 2003, Corrêa *et al* 2006, Ribas & Schoereder 2007). As a rough explanation, a community that occurs in a more heterogeneous and resource-rich habitat will clearly be faced with a higher niche diversification (*i.e.*, the division in the ecological roles and opportunities *sensu* Kimmins 2004), what generally allows the coexistence of more species (Hutchinson 1959, Pianka 1974, Ricklefs 1977). According to MacArthur & Levins (1967), the number of co-occurring competing species is (1) negatively affected by the unequal abundance of resources and (2) positively affected by increasing the dimensionality of the niche.

In the ground of tropical forests, the litter that covers the soil plays a key role in governing ant species diversity and colony survival (Kaspari 1996, Campos *et al* 2003, Theunis *et al* 2005). However, as emphasized by Kaspari (2000), little is known on how soil and litter heterogeneity influences ant species communities. Nonetheless, researches have already shown that the litter strongly affects the availability of nest sites, food resources, and microclimatic conditions, such as humidity and temperature, and, thus, the structure of ant communities (*e.g.*, Levings & Windsor 1984, Benson & Harada 1988, Kaspari 1996, Campos *et al* 2003). Because of its known correlation with ant community parameters, litter attributes such as depth or biomass are frequently measured in studies addressing richness and composition of litter ant fauna (see Carvalho & Vasconcelos 1999, Corrêa *et al* 2006, Vargas *et al* 2007). Besides these very rough measures, the composition of the leaf litter may also be important because many physical features, such as quantity of litter, leaf shape and size, toughness and chemical composition, are directly dependent on the plant species composition. However, no study has yet measured how the leaf-litter composition (*i.e.*, the different types and/or forms of leaves) affects litter ant assemblages. We expect that a site with a high diversity of leaf morphotypes will provide a more complex physical structure, therefore increasing the availability of resources to the ant species that live or forage there.

Furthermore, it is possible to consider that the heterogeneity of the leaf-litter may influence ant community in different ways depending on the habitat type, such as forest edge or interior, for instance. Near forest edges, drastic changes in moisture, temperature, light incidence and wind turbulence are observed (Kapos 1989, Laurance *et al* 2000). As a consequence, forest edges are known to differ from the forest interior in terms of plant species and functional group composition, presenting a decreased species richness of canopy and emergent trees (Laurance *et al* 2000), shade-tolerant plant species (Oliveira *et al* 2004, Laurance *et al* 2006, Almeida-Santos *et al* 2007), species pollinated by vertebrates (Lopes *et al* 2009), and large-seeded trees dispersed by medium to large-bodied frugivores (Melo *et al* 2006). Therefore, it is expected that the leaf litter composition (number of leaves and leaf morphotypes) reflects the differences on plant species composition found between forest edge and interior and consequently, that it promotes a dissimilar effect on the ant assemblages.

In this study we investigated the influence of the number of leaves and leaf morphotypes that compose the litter on the ant species richness at a 1m^2-scale at the forest edge and interior. We hypothesized that ant species richness increases as both number of leaves and leaf morphotypes increase. In addition, we expected that the ant fauna inhabiting the forest edge and the interior would respond differently to these two leaf-litter attributes.

Material and Methods

Study area

This study was conducted in a 3500 ha Atlantic forest remnant known as Coimbra, which is situated in the municipality of Ibateguara, state of Alagoas, Brazil (8º30'S, 35º50'W). This remnant belongs to a private sugarcane mill, the Usina Serra Grande. Annual rainfall is ca. 2000 mm, with a three-month-long dry season (< 60 mm/month) from November to January, and a mean annual temperature from 22-24°C (IBGE 1985, Oliveira *et al* 2004). The vegetation largely consists of well preserved old-growth forest and has been classified as lower montane rainforest (250-600 m; Veloso *et al* 1991), with Leguminosae, Lauraceae and Sapotaceae as the richest families in terms of tree species (Grillo *et al* 2006). The forest is surrounded by plantations of sugarcane and its edge zone has been shown to be largely dominated by pioneer species, which represent up to 90 percent of the adult trees (Grillo *et al* 2006). The forest has been strictly protected against disturbances such as wildfires and logging, which has guaranteed the stability of its forest borders (most forest edges in the area are at least 60 years old) (Almeida-Santos *et al* 2007).

Ant species and leaf-litter attributes

Leaf-litter ants were sampled in two months, December/2004 and March/2005. A total of 28 1-m^2 leaf-litter plots were collected, 14 in the forest interior (*i.e.*, > 100 m from edge *sensu* Laurance *et al* 1998) and 14 in the forest edge. Plots were unevenly placed in five distinct patches of each habitat (*i.e.*, four patches with three plots each and one patch with two plots), covering a larger area of the remnant Coimbra. Patches were more than 100 m apart from each other and plots in the same patch were at least 10 m distant from each other. In the laboratory, the ants were sorted and the number of leaves with more than 50% of leaf surface was counted. A random sample of 100 leaves per plot was selected and classified as to morphotypes. To reduce the bias associated with morphotype classification, only one person was responsible for doing this task. Ants were identified and voucher specimens were deposited in the laboratory of plant-animal interactions at the Departamento de Botânica, Universidade Federal de Pernambuco.

Statistical analysis

The effect of (1) number of leaves, (2) number of leaf morphotypes and (3) plot location (forest edge or interior) on ant species density was examined using multiple linear regressions. To choose the best subset among the above mentioned predictor variables, a forward stepwise regression was used; this procedure allows the selection of the "best model" from a number of possible models (Sokal & Rohlf 1995). The best model should present a minimum number of predictor variables with a significant *P* and the lowest Akaike information criterion (AIC) (see

Sokal & Rohlf 1995, Burnham & Anderson 2002). Three models were generated. In the first predictive model (Model 1), the three variables (number of leaves and leaf morphotypes, and plot location) and also the interaction between these variables were used. In the second predictive model (Model 2), only the number of leaves, plot location and their interaction were used. In Model 3, the number of leaf morphotypes, number of leaves and their interaction were used. The normality of samples was tested *a posteriori* via Lilliefors test. The analyses were based on Sokal & Rohlf (1995) and performed using the JMP software (SAS-Institute 2002).

Results

A total of 43 morphospecies of ants were found belonging to 19 genera and four subfamilies. Myrmicinae was the most speciose subfamily with 18 species (41.9%), followed by Ponerinae (13 species, 30.23%), Formicinae (11 species, 25.6%) and only one species of Dolichoderinae (2.3%). The genera with more species were *Pheidole* (eight species), *Hypoponera* and *Camponotus* (five species each). Only 18 species were sampled in the forest edge, while 32 species were captured in the interior plots (Fig 1). Both sampling curves do not approach an asymptote (Fig 1), indicating that the sampling design (14 plots per habitat), although appropriate for testing our hypothesis, was insufficient to capture all ant species in both habitats.

In Model 1 (which contained all variables), ant species density increased only in response to increasing leaf number (F = 3.498, P = 0.025; Table 1). Further, we did not observe any significant interaction between the tested variables (Table 1). In Model 2, ant species density also responded to the increase in the number of leaves (F = 3.747, P = 0.015; Table 1), but this was clearly influenced by plot location (the species richest samples all belonged to interior plots), which caused the significant pattern detected by regression analysis (F = 5.114, P = 0.033; Fig 2a). Finally, in Model 3, ant species density increased as both the number of leaves and leaf morphotypes increased (Overall F = 5.52, P = 0.005; Table 1, Fig 2b). This last model was the best model indicated by stepwise procedure, presenting the lowest AIC of all tested models (Table 1). Models 1, 2 and 3 explained 37.65%, 29.95% and 33.46% of ant species density variation, respectively.

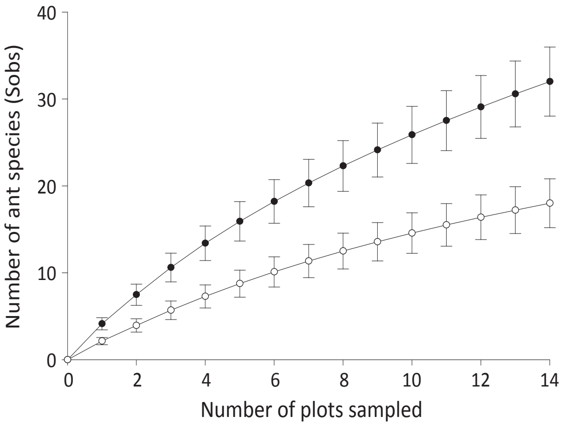

Fig 1 Accumulated number of ant species in the forest interior (●) and in the forest edge (○) (N = 14 1-m^2 plots in each habitat) sampled in an Atlantic forest remnant, state of Alagoas, Brazil. Bars indicate standard deviation.

Table 1 Multiple linear regressions using a stepwise regression *via* a forward selection process where three explanatory variables were examined (plot location - PL, *i.e.*, forest edge or interior; leaf morphotypes number - LMN; leaf number - LN), in an Atlantic forest remnant, state of Alagoas, Brazil.

Models Explanatory variables	F	P
Model 1 Overall F = 3.32, P = 0.0162, R^2 = 53.82%, R^2(Adj.) = 37.65%; AIC = 37.78		
PL	1.404	0.2688
LMN	1.741	0.1805
LN	3.498	**0.0254**
PL*LMN	1.065	0.3635
PL*LN	2.175	0.1398
LMN*LN	2.106	0.1479
PL* LMN*LN	2.028	0.1699
Model 2 Overall F = 4.848, P = 0.0089, R^2 = 37.73%, R^2(Adj.) = 29.95%; AIC = 38.15		
PL	4.544	**0.0212**
LN	3.747	**0.0383**
PL*LN	5.114	**0.0331**
Model 3 Overall F = 5.52, P = 0.005, R^2 = 40.85%, R^2(Adj.) = 33.46%; AIC = 36.71		
LMN	5.416	**0.0114**
LN	5.220	**0.0131**
LMN*LN	4.525	**0.0439**

Discussion

We expected the species richness of leaf-litter ants to be positively correlated with the number of leaves and leaf morphotypes, as many ground ant species not only nest in the soil and/or hollow twigs, but also between leaves on

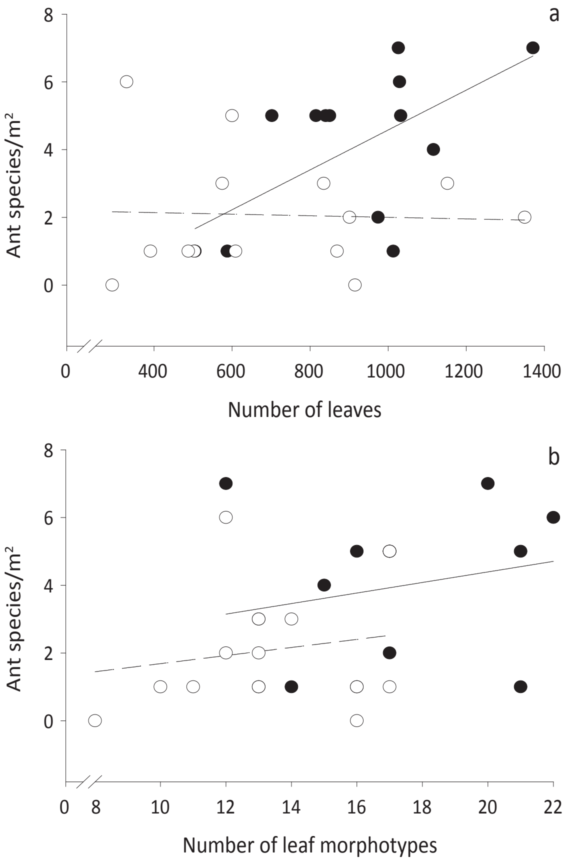

Fig 2 (a) Relationship between ant species density and leaf number in (●—) the interior (y = 0.0059x - 1.3073; R^2 = 0.38) and (○– –) the edge of plots (y = -0.0002x + 2.2333; R^2 = 0.002). (b) Relationship between ant species density and leaf morphotypes number in (●—) the interior (y = 0.1557x + 1.281; R^2 = 0.04) and (○– –) the edge of plots (y = 0.1194x + 0.4941; R^2 = 0.03). Samples (N = 14 1-m^2 plots in each habitat) were made in an Atlantic forest remnant, state of Alagoas, Brazil. Some points are superposed, thus the figures do not show the 28 sampling points.

the ground (*e.g.*, Wilson 1959, Longino & Nadkarni 1990, Kaspari 1996). Likewise, ants also use the leaf-litter as a foraging site (e.g., Majer *et al* 1997, Yanoviak & Kaspari 2000). In fact, our results strongly indicate that both the number of leaves and leaf morphotypes synergistically influence the ant species richness density at the ground level (Model 3). However, we are not able to point out exactly in which way(s) leaf-litter heterogeneity affects ant species co-occurrence at this point.

The accumulation of leaves and leaf morphotypes may not only promote an increase in structural heterogeneity, but also may create favorable physical conditions for nesting and/or foraging activities (*e.g.*, milder temperatures and higher humidity), reducing the desiccation risk for ants and increasing resource availability (*e.g.*, number of preys). For example, the numbers of ant species in four Neotropical litter ant assemblages were found to increase with nest density, which was positively affected by the increase of litter depth (Kaspari 1996). Besides, gradients of desiccation risk, caused by high temperature and low humidity, together with food availability are the two most likely factors shaping ant foraging activity (Lighton & Feener 1989, Kaspari & Weiser 2000).

Moreover, our data showed that there are inherent differences between edge and interior plots in the way ants respond to the increase in the amount of leaves present in the litter. While leaf number positively influences ant species density in the interior forest, there is no such trend when analyzing edge samples (see Fig 2). Most of the edge plots presented three or less species (only two out of the 14 plots presented more than three species) and the cumulative curve of species observed in the edge is significantly smaller than that of the interior forest. It seems that the forest edge harbors a simplified myrmecofauna and that something other than litter heterogeneity (as measured here) is preventing the number of ant species to increase at the 1m^2- scale. Factors such as diversity of other organisms (*e.g.*, plant species), vegetation structure and environmental conditions may affect the ant species density and promote a patchy distribution of species in ant communities along the edge-to-interior gradient.

In this context, ant species richness has been shown to correlate positively to tree species richness and density in the Brazilian Cerrado (Ribas *et al* 2003), and the number of ant species per sampling plot in the savanna is lower than in the forest sites far distant from the edge (Majer *et al* 1997). Moreover, it was already demonstrated that changes in microclimatic conditions (*e.g.*, environment temperature) are followed by a rearrangement of dominance/competitive hierarchies, enabling some ant species to dominate the area and to eliminate less competitive species (Perfecto & Vandermeer 1996, Cerdá *et al* 1997, 1998, Lessard *et al* 2009). Besides, because edge-affected forests present harsher abiotic conditions, especially in recent edges created by forest fragmentation, probably there is a relatively limited number of specialists able to explore all available nest sites and food items compared to the interior forests (see Hölldobler & Wilson 1990).

In synthesis, as we predicted, there is a positive and synergistic effect of number of leaves and leaf morphotypes on ant species density sampled at the 1m^2-scale. However, as we also expected, ants of forest edge and interior respond in different ways to these explanatory variables. We believe that physical changes and resource availability at the ground level are shaping the dominance hierarchies in the ant communities. Our outcomes and also other studies (e.g., Majer *et al* 1997, Ribas *et al* 2003) suggest that edge-affected forests present simplified ant communities, with different factors determining its structure in terms of number of species, species composition and distribution. Based on our results, we encourage future studies to include leaf litter heterogeneity as one of the explanatory variables investigated. Furthermore, we suggest that future studies should evaluate how changes in the number of leaves and leaf morphotypes can affect the number of preys (*i.e.*, resource availability) and micro-environmental conditions, such as temperature and humidity.

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