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Microhabitat Characteristics that Regulate Ant Richness Patterns: The Importance of Leaf Litter for Epigaeic Ants

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Abstract

We assessed the effect of conditions and resources on the species richness of epigaeic ants in a cloud forest of the Ibitipoca State Park, Brazil. We hypothesized that the characteristics that are best related with the epigaeic microhabitat affects ant richness more closely than other characteristics. At each sampling site (36 in total) we set up an epigaeic pitfall to capture ants and measured the following environmental variables (conditions and resources): tree density, tree height, circumference at breast height, density of the herbaceous and shrubby vegetation, weight and heterogeneity of the leaf litter, and canopy cover. We built general linear models and used a function that classifies alternative models according to the second-order Akaike information criterion (AICc), in order to assess which environmental variables affect ant species richness. We collected 37 ant species and the models that better explained the variations in ant richness were: (1) null model; (2) heterogeneity of the leaf litter; and (3) weight of the leaf litter. These two environmental variables are positively related to ant richness. It is possible that epigaeic ants are influenced by the high quantity and quality of food and nesting sites provided by a heterogeneous and abundant leaf litter. Relationships between species richness and environmental characteristics should consider different predictor variables related to the microhabitat, since each microhabitat may have a specific pattern and predictor variable. Thus, the understanding of the effects of the microhabitat variables on species richness could help predicting the consequences of anthropogenic impacts.

Introduction

Understanding the relationships between species diversity and environmental conditions is one major goal of community ecology, although some relationships are not clearly understood yet (Ricklefs, 2004). Higher structural complexity favors the diversity of ways to exploit resources and a higher number of niches, which in turn increases species richness (Bazzaz, 1975). However, the perception of structural complexity for some species can occur at different spatial scales. For example, both a higher density of patches in a landscape, or tree species richness in a forest may influence the community structure of different groups (Flick et al., 2012; Wenninger & Inouye, 2008; Wardhaugh et al., 2012).

Tropical forests harbor most of the Earth's biodiversity (Myers et al., 2000; Nageswara-Rao, 2012). A large part of this biodiversity in these ecosystems is attributed to soil arthropods, mainly social insects, which contribute with a large number of species as well as with a high abundance and biomass (Wilson, 1990). In these environments, ants are one of the dominant groups in terms of richness and abundance (Hölldobler & Wilson, 1990; Fisher, 2012) and therefore may influence the ecosystem as a whole, as they participate in several processes of the ecosystem such as seed dispersal, biological control, and nutrient cycling (Hölldobler & Wilson, 1990; Lach et al., 2010).

The distribution of ants can be attributed to biotic or abiotic factors, human impacts or habitat structure (Armbrecht et al., 2004; Philpott et al., 2010;Wittman et al., 2010). On a local scale, however, to have a better understanding of the relationship between ants and their environment is necessary to know about specific microhabitat features because ants have a great diversity of habits, diets and nesting sites (Blüthgen & Feldhaar, 2010). Thus, each microhabitat characteristic may

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affect differently ants of distinct strata. For example, the diversity of arboreal ants can be closely linked to the presence, quality and quantity of resources from the trees, as extrafloral nectaries or presence of trophobiont insects and other nitrogen-rich resources (Yanoviak & Kaspari, 2000; Schoereder et al., 2010). Therefore, it is possible to infer that this stratum will be the first to suffer with changes in vegetation structure. Epigaeic ants are closely related to the soil surface resources, especially in the litter, in tropical ecosystems (Yanoviak & Kaspari, 2000). The litter is a complex two-dimensional location covered by leaves, twigs and other components (Kaspari & Weiser, 1999). These more complex habitats can provide a greater number of resources, such as food resources (e.g. springtails, termites and other scavengers insects abundant in the litter) (Brühl et al., 1999), as well as sites for nesting, as trunks. On the other hand, subterranean ant species appear to be more related to physical characteristics of their microhabitat, such as soil density (Schmidt et al., 2013).

Studies on ant communities and their relationships with the environment are relatively common in tropical forests (e.g. Vasconcelos, 1999; Bihn et al., 2008; Neves et al., 2010; Teodoro et al., 2010). However, with the imminent threat to forests, further studies on ant communities may help predict the biota's responses to environmental changes. If we are able to understand the effects of these variables and the responses of ant communities to them, besides the particularities of each microhabitat, we can predict the consequences of the anthropogenic impacts on biota.

Since ants are important biological indicators, and studies in preserved habitats are needed to uncover richness patterns and help in conservation strategies (Hölldobler & Wilson, 1990; Gardner et al., 2009; Leal et al., 2010; Ribas et al., 2012), in the present study, we assessed the influence of environmental characteristics, which represent conditions and resources for ants, on ant richness in a cloud forest. We hypothesized that the characteristics that are best related with the epigaeic microhabitat affects ant richness more closely than other characteristics.

Material and Methods

Study area

We carried out the present study in October 2011 in Mata Grande, a cloud forest in Ibitipoca State Park, Zona da Mata, state of Minas Gerais, southeastern Brazil (21º40'–21-º44'S and 43º52'–43º54'W). The altitude in the park varies from 1,000 to 1,700 meters. The local climate is characterized by dry winters, from April to September, and rainy summers, from October to March, with an annual average temperature of 14.8 ºC and annual rainfall of 1,544 mm. The cloud forest is a type of Atlantic Forest with trees that reach from 15 to 25 m in height (Aragona & Seitz, 2001). In the park, the cloud forest covers 90 ha, is surrounded by campos rupestres (rupestrian grasslands), and harbors several epiphytes and lichens. Some characteristics, such as frequent mist, wind, and sunlight incidence exert a strong influence on this forest (Carvalho et al., 2000). The most common plant families in this environment are Myrtaceae, Melastomataceae, Lauraceae, Rubiaceae, and Fabaceae (Oliveira-Filho & Fontes, 2000).

We can define cloud forests as a tropical forest that occurs at high altitudes. This vegetation type has great conservation importance because it is naturally distributed in patches and harbors several endemic species (Merlin & Juvik, 1993). Its well-defined boundaries and dissimilarity to surrounding environments can result in peculiar communities (Ricklefs, 2004). Furthermore, this forest is considered one of the most threatened vegetation types due to environmental changes and human disturbance through changes in the habitat and conversion of these forests to different land use regimes (Loope & Giambelluca, 1998; Schonberg et al., 2004).

Sampling

We delimited 36 sampling sites with a minimum distance of 20 m between them. For sampling ants we set up epigaeic pitfalls without bait at each site, and left them opened for 48 h. Then we identified the ant genera with taxonomic keys (Bolton, 1994; Palacio & Fernández, 2003), and calculated the species richness in each trap based on morphospecies. Specimens of each morphospecies were deposited in the collection of the Laboratory of Ant Ecology, Universidade Federal de Lavras.

To measure environmental variables, we delimited a 6 x 6 m plot around each trap and measured the following variables: tree density (of trees with circumference at breast height above 15 cm) (Dtree), tree height (Htree), tree circumference at breast height (Cbhtree), density of herbs and shrubs (Dhs), weight (Wll) and heterogeneity of the leaf litter (Hll), and canopy cover (Ccan). These variables (related to habitat structure, habitat heterogeneity, resource availability, and microclimatic variation) represent conditions and resources for ants. We counted all trees within the plot in order to calculate tree density, and we estimated their height and measured their circumference at breast height. To measure the density of herbs and shrubs we took standardized photographs at the four directions of the trap in each sampling site. The photographs were taken with a 100 x 100 cm white background, 3 m away from the background and at 1 m above the ground (Nobis, 2005). We calculated the density of herbs and shrubs using the option Global Analysis in the software SideLook (Nobis, 2005). To calculate density, we used the following formula: vegetation density = background area* (black pixels / white pixels) background length.

We collected leaf litter inside a 25 x 25 cm square, counted the items present in it, and calculated leaf litter heterogeneity with the Shannon index, a new approach suggested by Lucas Paolucci (personal communication, October 28, 2011). After this procedure, we dried out the leaf litter in an oven for 96 h to measure its dry weight, and weighted it on a precision balance.

To estimate canopy cover, we made a digital hemispherical photograph of the canopy using a camera equipped with a 0.20 x fisheye objective lens. The camera was positioned at 1.5 m above the ground and adjacent to the pitfall. With these photographs it was possible to indirectly calculate canopy cover (Engelbrecht & Herz, 2001). We analyzed photographs in the software Gap Light Analyzer 2.0 (GLA), which calculates canopy cover (Frazer et al., 1999).

Data analysis

We used general linear models (GLM) to test which environmental variables affect ant species richness within a theoretical approach based on the second-order Akaike information criterion (AICc - Burnham & Anderson, 2002). We tested the data normality with a Shapiro-Wilk test (W = 0.9635, p = 0.2758) and ran the model (based on the normal distribution) with R software 2.14 (R Development Core Team 2011) using the AICcmodavg package (Mazerolle, 2013).

We tested if there is a correlation between tree height and tree circumference at breast height because both represent the tree size (Spearman, p = 0.0003, R^2 = 0.56). Because there is a positive correlation between the variables, we chose the tree circumference because it was the more accurate measure, since tree height was visually estimated.

We build models with four combinations of variables (Hll+Wll, Dtree+Dhs, Dtree+Ccan, Cbhtree+Ccan), and the null model. Since we do not have enough sampling points to run all possible models, we use the above combinations of variables, believing they could be related between themselves, as litter variables or vegetation structure variables, and as being the better predictors of ant richness.

Posteriorly, we used the function "aictab" to test which variables affect ant species richness the most. This function classifies the models according to the AICc (Burnham & Anderson, 2002). We considered as acceptable the models with the smallest AICc-values and with a delta value (difference between AICc-values) smaller than two (Burnham & Andersen, 2002). After this, we used the function "importance" for the considered models (delta < 2) to calculate the importance values (w+).

Results

Ant fauna and environmental variables

We collected 37 epigeic ant species of four subfamilies (Table 1). The most frequent species was *Acromyrmex* sp.1, the most common genera were *Pheidole* and *Hypoponera*, and the most frequent subfamilies were Myrmicinae and Ponerinae. The average (± Standart Deviation, SD) ant richness was 4.11 ± 2.05 species per pitfall.

The average tree density was 0.22 ± 0.07 trees/m^2 and the average CBH was 38.85 ± 10.63 cm. The average herb-shrub density was 31.7 ± 38.56. The average diversity of the leaf litter was 2.39 ± 0.19 and its average dry weight was 46.54 ± 22.50 g. The average canopy cover was 82.45 ± 3.24%.

Model selection

The null model had the smallest AICc-value, i.e., with no environmental variables affecting ant richness (Table 2).

Table 1. Species of epigeic ants sampled in the cloud forest of Ibitipoca State Park.

Subfamilies	Genus	Species
Ectatomminae	*Gnamptogenys*	1
Formicinae	*Brachymyrmex*	2
	Camponotus	2
Myrmicinae	*Acromyrmex*	1
	Basiceros	2
	Eurhopalotrix	2
	Hylomyrma	2
	Pheidole	9
	Sericomyrmex	2
	Solenopsis	2
	Strumigenys	1
	Trachymyrmex	2
	X sp.	1
Ponerinae	*Hypoponera*	4
	Leptogenys	2
	Pachycondyla	2
	Total	37

Table 2. Model selection based on the second-order Akaike information criterion (AICc) for richness of epigeic ants in the cloud forest of Ibitipoca State Park. The general linear model was built with the following explanatory variables: tree density (Dtree), weight (Wll) and heterogeneity of the leaf litter (Hll), and canopy cover (Ccan). We considered only the models with delta-values equal or larger than 2. Number of predictor variables (K), differences in AICc-values (Δ), and Akaike weight (ω).

Ranking	Model	K	AICc	Δ	ω	ω Accumulated	Log Likelihood
1	Intercept	2	157.3	0.00	0.25	0.25	-76.47
2	Hll	3	158.3	0.97	0.16	0.41	-75.76
3	Wll	3	158.8	1.53	0.12	0.52	-76.05
4	Dtree	3	159.3	2.01	0.09	0.62	-76.29
5	Ccan	3	159.7	2.34	0.08	0.69	-76.45

However, two other models also showed small AICc-values, and could also explain the variation in species richness. These models pointed to leaf litter heterogeneity (w+ = 0.39) and weight of leaf litter (w+ = 0.32) as the most important correlates of ant richness. Leaf litter heterogeneity and weight positively affected ant species richness.

Only the models with up to 70% of the accumulated value of Akaike weights (ω accumulated) are presented.

Discussion

The environmental characteristics that best explained the variation in species richness of epigeic ants were leaf litter heterogeneity and weight. These variables represent the availability of space, food and nesting resources, as well as microhabitat complexity.

Ant fauna

The number of species observed in our samples was similar to other studies on leaf litter ants in cloud forests (Longino & Nadkarni, 1990; Patrick et al., 2012). Likewise, the most common subfamilies in our study, Myrmicinae, Ponerinae, and Formicinae, are the most frequent in cloud forests (Longino & Nadkarni, 1990). Furthermore, as in Longino and Nadkarni (1990), the subfamily Dolichoderinae, which is common in the Neotropics, was not found in the present study.

The number of ant species in the present study was smaller than in other Atlantic Forest areas in Brazil (61 species in Leal et al., 1993; 146 species in Gomes et al., 2010), but the most representative families were the same. The small number of species in cloud forests may be explained by long-term isolation, which makes it more difficult for ants to colonize this environment and thus reduces its species richness. Ecological isolation may also make local species more vulnerable to extinction (Gillespie & Roderick, 2002).

Model selection

The first selected model did not explain the variation in richness of epigaeic ants, as in other studies, in which relationships between habitat heterogeneity and ant richness were not found (Corrêa et al., 2006; Ribas & Schoereder, 2007; Muscardi et al., 2008). This shows that the ant species richness can also be linked to unmeasured characteristics of the environment or be distributed randomly. Although other studies present similar variation in some of these predictors (Ribas et al., 2003; Neves et al., 2013) the variation of these variables in this study may not have been sufficient to detect stronger relationships with species richness.

However, other models, which comprised variables that represent environmental conditions and resources for ants, pointed to positive relationships between leaf litter heterogeneity, leaf litter weight and richness of epigaeic ants. This is probably due to a higher availability of space, heterogeneity, food and nesting resources leading to a larger number of ant species. Leaf litter parameters regulate the species richness of soil and leaf litter ants (Mezger & Pfeiffer, 2011). The richness of soil arthropods is related to factors that operate at small spatial scales, such as differences in nutrient concentrations among layers of organic matter, which suggests that habitat quality is one of the most important correlates of species diversity (Sayer et al., 2010). Leaf litter heterogeneity may indirectly indicate higher environmental quality, explaining the higher richness of epigaeic ants in our study. The natural dynamics of the leaf litter may also alter the heterogeneity of this stratum, creating new sites for colonization and a higher variety of food resources and thereby increasing the richness of this group (Campos et al., 2007).

The relationship between leaf litter weight and ant richness shows that resource availability may be a limiting factor for epigaeic ants in cloud forests (Soares & Schoereder, 2001). The richness of epigeic ants is higher in microhabitats with a large number of nesting sites and a high availability of food (Paolucci et al., 2010). These arthropods may be more abundant in sites with large amounts of leaf litter, as space is also an important predictor of the species abundance of soil arthropods (Sayer et al., 2010). Other factors that operate at different spatial scales and may affect the structure of epigeic ant communities, such as topographic variation (Gunawardene et al., 2012) and soil humidity (Lassau & Hochuli, 2004), were not considered in the present study and should be assessed in future studies.

Probably, characteristics that are directly related to the vegetation (e. g. habitat structure) or to a large temporal scale (e.g. area size) may strongly affect arboreal ants and other groups of epigaeic ants, which are sensitive to variations in environmental heterogeneity and resource availability (Ribas et al., 2003; Campos et al., 2006; Costa et al., 2011). This has also been found in cloud forests (Schonberg et al., 2004). It is known that the combination of fragment area and habitat structure is an important predictor of species and functional group richness, and that habitat structure affects some functional groups such as arboreal ants in fragments of Atlantic Forest (Leal et al., 2012). Together with our results these findings corroborate our hypothesis that ants are strongly related to microhabitat characteristics (e.g., heterogeneity and weight of leaf litter for epigaeic ants, and richness and density of trees for arboreal ants). Alternatively, characteristics of habitat structure have been also considered important predictors of species richness in studies that assessed environmental impacts on ant communities.

Other common factors in the montane forest of Ibitipoca that could indirectly affect ant richness, are tree fall and, consequently, clearing opening (Carvalho et al., 2000; Patrick et al., 2012). This kind of disturbance is the main factor responsible for increasing sunlight incidence and improved establishment success of some plant species. The canopy cover variation can negatively affect the ant richness, because it alters microclimatic conditions, quality and quantity of resources (Neves et al., 2013). Nevertheless, our results do not support that canopy cover may affect the community of epigaeic ants in the studied cloud forest, since this model was not selected in the results. In our case, we found a small variation in the studied area that could be not enough to influence ant species richness.

Leaf litter heterogeneity and weight of litter were the best predictors of the species richness of epigaeic ants. As we hypothesized, ant richness can be better explained by the specific characteristics of the microhabitat in which ants live or forage. Relationships between species richness and environmental characteristics should consider different predictor variables related to the microhabitat, since each microhabitat may have a specific pattern and predictor variable. In this study we detect a relationship between ant species and its microhabitat, and the modification of habitat by anthropogenic impacts can cause a loss of this relationship and affect the biological communities negatively. Thus, the conservation of habitats and their species richness patterns are essential to the ecosystem functioning. Bioindicators studies that evaluate the effects of anthropogenic impacts should focus on the specific characterization of the microhabitats to better detect community changes since the understanding of the effects of the microhabitats variables on species richness could help predicting the consequences of anthropogenic impacts.

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