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The Influence of Extrafloral Nectaries on Arboreal Ant Species Richness in Tree Communities

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Abstract

Studies investigating the role of resource availability in the species richness patterns can elucidate ecological processes and contribute to conservation strategies. In this study, we test two hypotheses: i) arboreal ant species richness increases with abundance of extrafloral nectaries-bearing trees; and ii) arboreal ant species richness increases with the diversity of extrafloral nectaries-bearing trees. We used data of ant sampling and tree inventories from 30 plots of Brazilian Cerrado. Arboreal ant species richness was positively influenced by the proportional abundance of extrafloral nectaries-bearing trees, total tree density and total tree diversity. There was no effect of species richness of extrafloral nectaries-bearing trees. Coefficient of determination of proportional abundance of extrafloral nectaries-bearing trees was larger when compared to coefficient obtained using tree density as explanatory variable. These results suggest that variation in arboreal ant species richness is better explained by extrafloral nectaries-bearing tree abundance than total tree density. Generalist foraging behavior of sampled ant species may explain their association with proportional abundance of extrafloral nectaries-bearing trees and their non-significant relation with proportional richness of extrafloral nectaries-bearing tree species. Extrafloral nectaries-bearing trees abundance may be a specific estimate of the amount of food resource available in plots. Thus, this is a more specific way to quantify which resources may explain variation of the arboreal ant species richness in tree communities. We hope these results will be helpful to understanding the local variation in ant species richness and as criteria to biodiversity conservation.

Introduction

The resource availability hypothesis presumes a bottom-up process in which species richness is limited by the amount of food resources in the next lower trophic level. In consequence, higher species richness is expected in areas with higher food resource availability (Ferger et al., 2014). Several studies have attempted to understand biodiversity patterns using resource availability as the main explanation to variation in species richness (Ferger et al., 2014; Hurlbert & Stegen, 2014; Rabosky & Hurlbert, 2015). In this sense, species richness is positively correlated to amount and resource variety although some studies have related absence and negative effect of resource availability (Dáttilo et al., 2014a, Staab et al., 2016).

An example of the role of resource availability in species diversity is the positive relationship between arboreal ant species richness with tree density and species richness in Cerrado habitats, as reported by Ribas et al. (2003). The authors considered the density and diversity of trees as surrogates of amount and variety of resources, respectively. Such correlations have been explained by changes in habitat conditions and by the increase in total resource availability, which allows a higher ant species coexistence, thus increasing ant species richness. In this sense, a greater amount of

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resources would allow the coexistence of more generalist species, increasing the ant diversity at a local scale. In contrast, competitively superior ant species can monopolize resources diminishing ant species richness as suggested by Dáttilo et al. (2014a). Additionally, sites with higher resource variety would support more ant species, because there would be greater coexistence of a higher number of specialist species. However, tree density and diversity as explanation to ant species richness are too general. Trees may provide several types of resources to ants, such as nesting sites (Yasuda & Koike, 2009; Fagundes et al., 2015), foraging area for prey and honeydew (Blüthgen et al., 2000; Oliveira & Del-Claro, 2005), fungal hyphae and other microorganisms (Davidson et al., 2003) and extrafloral nectaries (Blüthgen et al., 2000; Schoereder et al., 2010; Fagundes et al., 2015). Considering this, the study of relationships between species richness and specific resources may provide more informative explanations linked to ant species diversity.

Extrafloral nectaries (EFNs) are plant structures usually located on petioles and leaf blades, which produce a liquid substance rich in carbohydrates, amino acids and lipids (Gonzáles-Teuber & Heil, 2009) used as food by several animal groups (Beatie, 1985; Rosumek et al., 2009; Melo et al., 2010). Ants visit EFN-bearing plants for nectar consumption and some authors emphasize the possible role of EFNs in secondary defence against herbivory, because these ants frequently attack and/or drive away herbivore insects (Rico-Gray & Oliveira, 2007, and references therein). In these cases, the presence of ants is correlated to increases of the plant reproductive fitness (Nascimento & Del-Claro 2010; Lange & Del-Claro, 2014). In addition, ants regulate the abundance of associated insects in EFN-bearing plants in different ecosystems (Mody & Linsenmair 2004; Fernandes et al., 2005; Mathews et al., 2009; Rosumek et al., 2009). On the other hand, the presence of ants on EFN-bearing plants may not necessarily be beneficial to the plants (Cembrowski et al., 2014; Le Van et al., 2014; Alma et al., 2015). For ants, the consumption of extrafloral nectar enhances their aggressiveness, change predatory behaviour, increases survival rates and number of individuals per colony (Heil, 2015 and references therein).

Other extrafloral nectar consumers are distributed among several groups of arthropods such as spiders, wasps, beetles, bees, bugs and mites (Heil, 2015). As for ants, extrafloral nectar consumption enhanced the survivorship of spiders and wasps (Pfannenstiel & Patt, 2005; Géneau et al., 2013) and egg production in crab spiders (Wu et al. 2011). Despite many studies, the function of EFNs remains as open issue with four current hypotheses as following: 1) Protective: EFNs attracts predators which attack herbivores, 2) Exploitation: EFNs is secreted as excess of carbohydrates, 3) Flower- distraction: EFNs keep ants away from flowers optimizing pollination and 4) Ant- distracting: EFNs avoid ants from attending hemipterans reducing damages to the host plant (Del-Claro et al 2016 and included references).

Plants with EFNs are present in various habitats, and the Cerrado (Brazilian Savannah) harbours a large availability of this plant types (Rico-Gray & Oliveira, 2007). In this biome, EFN-bearing plants represent 15 to 25% of the plant diversity and comprise locally up to 31% of individuals (Oliveira & Freitas, 2004). Ants are the insects that most commonly exploit EFNs (Oliveira et al., 1987) and one plant species can harbour up to 34 species of visiting ants (Oliveira & Brandão, 1991). In the Cerrado, extrafloral nectar secretion by different plant species is influenced by their phenology and can occur along whole year attracting several ant species (Vilela et al., 2014). Thus, extrafloral nectar might be an important food resource for arboreal ants in these environments (Byk & Del Claro, 2011). Considering the wide availability of extrafloral nectar, ant dominance on the EFN-secreting plants, and dynamic network involving ants and EFN-bearing plants (Dáttilo et al., 2014a; Dáttilo et al., 2014b), EFNs availability can enhance arboreal ant species richness in Cerrado tree communities.

EFNs may affect the ant diversity by at least two different reasons. Firstly, ant diversity may be affected by the amount of EFN-bearing plants, due to the higher food resource availability. In this case, a higher abundance of EFN-bearing trees would allow the coexistence of more generalist ant species, *i.e*, those ant species visiting any EFN-bearing tree species (Dáttilo et al., 2013; Díaz-Castelazo et al., 2013; Dáttilo et al., 2014a). Secondly, ant diversity may respond to the diversity of EFN-bearing plants, because EFNs location, their density and chemical composition of nectar varies among plant species (Rios et al., 2008; Gonzáles-Teuber & Heil, 2009; Rosumek et al., 2009). Moreover, a same plant can vary its nectar quantity and quality along the day (Heil et al., 2000; Falcão et al., 2014) influencing the rate of ant foraging (Falcão et al., 2014). Then, there are reasons to expected different plants in a site attracting different ant species (Blüthgen et al., 2000), thus increasing local ant diversity.

Studies investigating the role of resource availability in the species richness patterns can elucidate ecological processes and contribute to conservation strategies, for example, providing criteria for selecting protected areas. Based on extrafloral nectaries as an important food resource to ants, the positive relationships between arboreal ant species richness and tree density and diversity found in Cerrado (Ribas et al., 2003) needs to be further analysed in order to understand the explanations of such correlations. In the present study, we addressed the following question: Why are there positive relationships between ant species richness and tree density and diversity? We tested here two hypotheses: i) arboreal ant species richness increases with the abundance of EFN-bearing plants; and ii) arboreal ant species richness increases with the diversity of EFN-bearing plants.

Methods

Study area and data collection

The study was carried out in the central portion of the Cerrado, in the Gama-Cabeça de Veado Reserve, Distrito

Federal (15°55’- 15°57’S; 47°55’- 47°57’W), Brazil, covering an area of approximately 10,000 ha, with an average altitude of 1,100 m a.s.l. The Cerrado is characterized by marked rainy (November-May) and dry seasons (June-October), with an average annual rainfall of 1,500 mm. The plant formations range from grasslands to forest areas, with trees that reach up to 12m height. There is no unified classification to Cerrado physiognomies and several criteria are used to this purpose (Ribeiro & Walter 1998; Oliveira-Filho & Ratter, 2002). Here, we choose a classification according to tree density because this criterion will be used as explanatory variable to ant species richness. In this sense, four vegetation physiognomies are recognized: “Campo sujo” (up to 1,000 trees / ha), “Campo Cerrado” (more than 1,400 trees / ha), “Cerrado *sensu stricto*” (more than 2,000 trees / ha) and “Cerradão” with more than 3,000 trees per hectare (Oliveira-Filho & Ratter, 2002).

To test the premises and hypotheses (see below), we used data available in Ribas et al. (2003) and Schoereder et al. (2010), in which full details of ant and tree sampling may be obtained. The ant sampling was conducted from January to March 2000. We used ant relative abundance, *i.e*. percentage of arboreal pitfall traps in which each species was caught (Lindsey & Skinner, 2001), ant species richness, tree species richness and abundance, species richness and abundance of EFN-bearing trees from 30 20x50 m plots, 15 located in campo sujo areas and 15 in campo Cerrado areas. We arbitrarily chose these physiognomies to increase the likelihood of achieving greater variation in the values of tree abundance and diversity.

Statistical Analyses

Our hypotheses assume that plots with greater tree abundance and species richness offer more resources to arboreal ants, represented here by EFNs. Therefore, before testing the hypotheses of this study, we tested two premises related to this assumption: i) EFN-bearing tree abundance is positively related to total abundance of trees; and ii) Species richness of EFN-bearing trees is positively related to total tree species richness. Although these may look like obvious probabilistic relationships, we tested these two premises to avoid a potential paralogism (Renon, 2010), once diversity and abundance of trees with EFNs are used as estimates of resource availability.

In order to test the premises, we performed two regression analyses. In the first, the abundance of EFN-bearing trees was our response variable and the explanatory variable was the total abundance of trees from each plot. In the second, we used species richness of EFN-bearing trees and total number of tree species from each plot as response and explanatory variable, respectively.

We used proportional abundance and richness of EFN-bearing trees in relation to the total of trees in each sampled plot as estimates of quantity and variety of resources, respectively. Since trees represent a broad spectrum of resource to ants, we used the proportion of EFN-bearing tree individuals and species richness because these parameters estimate how much extrafloral nectaries represent of the total tree resource available in each plot. We obtained the proportional abundance of EFN-bearing trees by dividing the number of EFN-bearing trees by the total tree individuals per plot. Likewise, we calculated the proportional species richness of EFN-bearing trees by dividing the number of EFN-bearing tree species by the total tree species per plot.

To test the hypotheses that abundance and diversity of EFN-bearing trees increase arboreal ant species richness, we carried out a multiple regression analysis in which the response variable was the number of ant species within plots. Our explanatory variables were proportional abundance and richness of EFN-bearing trees and the interaction between these variables.

We expect positive correlations between arboreal ant species richness and proportional abundance and diversity of EFN-bearing trees. However, the number of ant species may be correlated to total trees as well as EFN-bearing trees. Then, it is needed to distinguish the relationship of ant species richness with EFN-bearing trees from ant species richness with overall trees. For this purpose, we used the coefficients of determination (R^2) to quantify the goodness-of-fit of fixed models as a measure of variance explained. Coefficients of determination were obtained from regression analyses using arboreal ant species richness as response variable. Tree density and tree species richness were used as explanatory variables likewise Ribas et al. (2003). Then, we compared the coefficients of determination to evaluate what variables are better associated to arboreal ant species richness: tree density versus proportional abundance of EFN-bearing trees, and total tree species richness versus proportional species richness of EFN-bearing trees.

Our models followed Poisson distribution corrected for over dispersion (Crawley, 2007). We adjusted the complete model and the minimal adequate model was obtained by removing non-significant explanatory variables. Coefficients of determination were calculated using maximum likelihood of the full and null models for generalized linear models (Nagelkerke, 1991; Menard, 2000). We carried out all analyses under R environment (R Development Core Team 2017). The analyses were followed by residual analyses to check for the suitability of model and distribution employed.

Results

EFN-bearing trees represented 25% of total plant species richness (Table S1 in the Supplementary) and their proportional abundance varied from 50 to 90% in sampled plots. The most representative EFN-bearing plant species were *Ouratea hexasperma* (St. Hil.) Baill. (468 individuals), *Qualea grandiflora* (Mart.) (165), *Qualea parviflora* (Mart.) (124), and *Cariocar brasilisensis* (Camb.) (113). Both premises postulated were corroborated. There was a positive correlation between EFN-bearing tree abundance and total tree abundance ($F_{1, 28}$=158.5; p=0.0001). Equally, EFN-bearing tree richness and total tree richness were positively correlated ($F_{1, 28}$ =18.9; p=0.001).

Sixty-three ant species were collected in 300 arboreal pitfall traps. The ten most frequent species were *Camponotus genatus* (Santschi) (54.5%), *Camponotus punctulatus* (Mayr) (34.1%), *Camponotus crassus* (Mayr) (31.1%), *Camponotus atriceps* (Smith) (27.1%), *Camponotus melanoticus* (Emery) (25.8%), *Cephalotes minutus* (Fabricius) (25.4%), *Cephalotes betoi* (Andrade) (22.1%), *Solenopsis* sp1 (19.1%), *Azteca instabilis* (Smith) (17.4%) and *Cephalotes grandinosus* (Smith) (12%). The complete list of ant species sampled by Ribas et. al. (2003) is available in Table S2 as supplementary material.

Arboreal ant species richness and proportional abundance of EFN-bearing trees were positively related ($F_{3,26}$=5.54; p=0.027; Fig 1) but the relation with the proportional richness of EFN-bearing trees ($F_{3,26}$=0.43; p=0.51) and the interaction term were not significant ($F_{3,26}$=0.27; p=0.60). As expected, coefficient of determination of proportional abundance of EFN-bearing trees was greater (0.156) when compared to tree density (0.014). As the relationship between ant species richness and proportional EFN-bearing tree species richness was not significant, we did not compare the R^2 values of the total plant species richness and proportional EFN-bearing tree species richness (Table 1).

Discussion

Proportional abundance of EFN-bearing trees may be a more specific estimate of the amount of resources relative to tree density. Thus, we argue that ant species richness may be better associated to proportional abundance of EFN-bearing trees because this one shows a higher coefficient of determination (Table 1). Our results differ from Dáttilo et al. (2014a) in which ant species richness was not correlated to number of EFNs from three plant species analyzed separately. These authors explain their results based on dominance of EFNs by competitively superior ants, resulting in the coexistence of only a few other ant species (Blüthgen & Fiedler, 2004a; Blüthgen & Fiedler, 2004b). In contrast, we estimated the availability of EFNs at a larger scale, i.e., in each sampled plot. In this way, a higher proportion of EFN-bearing trees could reduce the interspecific competition allowing a higher coexistence of ant species in the sampled plots. Taken together, these findings suggest that extrafloral nectar availability do not affect ant species richness on tree individuals, in spite of this, the positive correlation between proportional abundance of EFNs-bearing trees and arboreal ant species richness may indicate the role of extrafloral nectar at a larger scale. In other words, in tree communities the ant species richness may be associated to the amount of EFN-bearing trees but not necessarily explained by EFNs number on tree individuals.

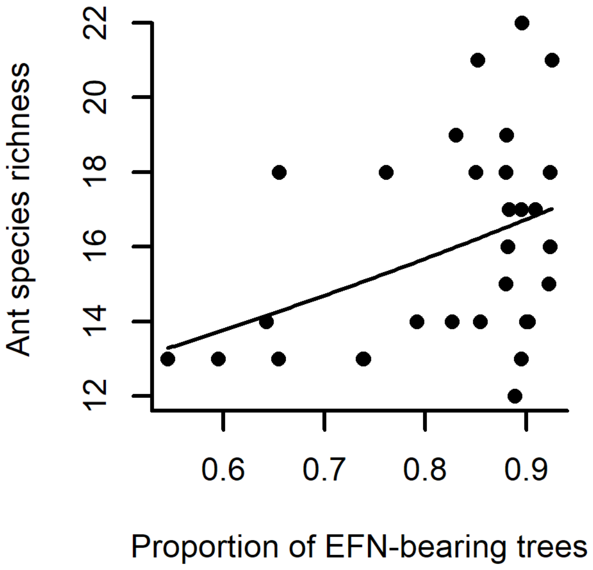

Fig 1. Influence of the proportional abundance of EFN-bearing trees on arboreal ant species richness ($F_{3,26}$=5.54; p=0.027).

Table 1. Coefficients of determination and p-values of explanatory variables used in linear regression analyses. Highlighted (*) p-values are according to Ribas et al. (2003). As the relationship between ant species richness and proportional EFN-bearing tree species richness was not significant, we did not compare the R^2 values of the total plant species richness and proportional EFN-bearing tree species richness.

Explanatory variable	R^2	p-value
Proportional abundance of EFN-bearing trees	0.156	0.027
Total density of trees	0.014	0.046*
Proportional species richness of EFN-bearing trees	----	0.421
Total species richness of trees	----	0.007*

Plant phenology is an important trait related to EFN activity (Lange et al., 2013). For plant species in Cerrado the highest extrafloral nectar production occurs simultaneously to flowering period resulting in an associated ant and herbivore insects fauna (Vilela et al., 2014; Muniz et al., 2012). In addition, several plant species have a sequential phenological development in which individuals of different species bloom in sequence (Torenzan-Silingardi 2007; Mendes et al. 2011) followed by highest extrafloral nectar production and ants moving from plant species to plant species along whole year (Del-Claro et al., 2016; Vilela et al., 2014). Based on this, one cannot exclude the possibility that proportion of EFN-bearing trees explains arboreal ant species richness because some abundant tree species sampled were in their flowering period, for example *Qualea grandiflora* and *Q. parviflora* which bloom from January to February (Silvério & Lenza, 2010). In contrast, two abundant tree species sampled (*Ouratea hexasperma* and *Caryocar brasiliense*) bloom from August to November (Muniz et al., 2012). In spite of this, even though not all plants were flowering and producing extrafloral nectar, the positive relationship between arboreal ant species richness and proportional abundance of EFN-bearing trees highlights the importance of extrafloral nectar as food resource to ant communities in Cerrado.

As there was a positive correlation between the species richness of EFN-bearing trees and total number of the tree species, with arboreal ant species richness not being associated with proportional richness of EFN-bearing trees, we suppose that generalist foraging on extrafloral nectaries may have caused such result. Hereafter, we present two arguments to generalist foraging of the ants: variation of extrafloral nectaries phenology and foraging on myrmecophylic plants.

Sugar and amino acids are known as components of extrafloral nectar that are attractive to ants (Lanza et al., 1993; Blüthgen et al., 2004) and their different concentrations and compositions have previously explained the different ant faunas on EFN-bearing plants (Rios et al., 2008). However, if there is a high generalist ant species richness foraging on several different nectar compositions, the expected effect of the proportional richness of EFN-bearing trees on ant species richness would disappear. Ants can explore different EFN-bearing plant species generating complex ecological networks and recent studies have found groups of generalist ants visiting extrafloral nectaries (Dáttilo et al., 2013; Díaz-Castelazo et al., 2013; Dáttilo et al., 2014a; Lange & Del-Claro, 2014). This pattern is stable over time and exhibits more significant level of generalisation at rainy season when extrafloral nectar is more abundant (Lange et al., 2013). In our study, the ants were sampled at the rainy season (January to March 2000). In this sense, despite the variation in proportional richness of EFN-bearing trees between plots, the high availability of extrafloral nectar could attract equal groups of ants feeding on different EFN-bearing tree species, nullifying the expected effect of nectar heterogeneity on the ant fauna. Also, ants that forage on myrmecophylic plants (without domatia) are usually more generalist than ants that forage on myrmecophytic plants (Blüthgen et al., 2000; Gonzales-Teuber & Heil, 2009). Because trees sampled in our study did not have domatia, we expected a higher number of generalist ant species, which in turn may be influenced by extrafloral nectar availability. Thus, the generalist foraging of ant species may explain their association with proportional abundance of trees and their non-significant relation with proportional richness of EFN-bearing tree species.

Studies analysing the ant community on EFN-bearing plants in Cerrado have reported a core of generalist species being these ones the most abundant (Lange et al., 2013; Dáttilo et al., 2014a; Lange & Del-Claro, 2014). For example, *Azteca* genus, *Camponotus crassus*, *Campontus melanoticus* and *Cephalotes* sp. are pointed as generalist and the most frequent in three ecological network studies (Lange et al., 2013; Dáttilo et al., 2014a, Lange & Del-Claro, 2014). In our data, these ant groups are among the most abundant sampled species (e.g., *C. crassus*, *C. melanoticus*). In this sense, we have an additional evidence to explain the positive relationship between ant species richness and proportional abundance of EFN-bearing trees. These results highlight the importance of the resource availability (EFNs) and its association with generalist species as explanation to arboreal ant species richness in Cerrado.

Our results support the idea that abundance of EFN-bearing trees may be more important than its diversity to explain variation in ant species richness. Several studies have reported the role of EFNs as defence structures for plants (Rosumek et al., 2009 and included references). Other studies have reported how extrafloral nectaries affect ant species richness on plant individuals, by comparing ant fauna on sampled trees (Blüthgen et al., 2000; Goítia & Jaffé, 2009). Here, we reported how the proportion of EFN-bearing trees influences the arboreal ant species richness in tree communities, reinforcing the idea linked to the resource availability hypothesis in which areas with higher food resource amount have higher species richness. We hope these results will be helpful to understanding the local variation in ant species richness and as criterion to biodiversity conservation. For example, since extrafloral nectar is an important food to several arthropod species, plant communities harbouring high abundance of EFN-bearing plants would be selected as protected areas to conserving biodiversity in Cerrado.

Supplementary material

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