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Local and Temporal Effects on Ant Richness, Recruitment, and Resource Dominance in Two Cerrado Areas

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Abstract

Ecological interactions and environmental conditions are associated with community structuring, where the resource quality and availability, in addition to interspecific competition, determine potential local interactions. Using grounddwelling ant species as a methodological tool model, we evaluated how three different daily periods affected species richness, recruitment, and resource dominance (baits) within two Cerrado (Brazilian savanna) phytophysiognomies. We found a total of 34 ant species and significant differences in species composition between the cerrado areas. Camponotus and Pheidole genera were the most abundant in both studied areas in which several species shared baits. Ant richness did not vary between the cerrado areas, but ant recruitment was affected by observation periods: in both areas, the hottest period (afternoon) reflected the lowest recruitment, while the coolest period (morning) had the highest recruitment. We observed that the ant species that first found baits had a 29% chance of being the only species observed using the resource, while those that arrived after other species had only 7%. Both areas promote the coexistence of ant species by shaping their interactions. We suggest that environmental structuring promotes niche partitioning in both spatial and temporal scales, providing possibilities of microhabitats that allow species to explore the environment and forage.

Introduction

Competition is a major process related to community structuring, where the resource quality and the competitive ability of species determine the interaction outcomes (Traniello et al., 1989; Fonseca & Robinson, 1990; Dáttilo et al., 2013). It is known that competitively superior species can exclude their competitors, being able to dominate certain resources; however, it is not common to observe, in complex ecological systems, the total exclusion of a given population (Brose, 2008; Camarota et al., 2016). This occurs, partially, because of the great morphological and behavioral variation intrinsic to most species which grant them both competitive advantages and disadvantages. For instance, some animals are aggressive and large, but not so efficient when searching for food; others,

despite being fragile, may have keen senses, being able to detect resources from great distances (Bestelmeyer & Wiens, 2001; Parr & Gibb, 2010). This high interspecific variation observed in nature is mediated by trade-off mechanisms and allows the coexistence of countless species by reducing the intensity of competitive interactions (Fellers, 1987; Tillman, 2000; Miller & Chesson, 2009).

In addition to the competitive ability of species, it is known that the environmental conditions also interfere in the outcome of interspecific interactions, since they affect the resource distribution and microclimatic conditions (e.g., local temperature and moisture) (Traniello, 1989; Pol & Casenave, 2004; Dáttilo & Izzo, 2012; Mooney et al., 2016). Species are delimited by a heterogeneous distribution of resources and environmental conditions (Wang et al., 2001), which determine



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potential local interactions (Perfecto & Vandermeer, 1996; Camarota et al., 2016; Queiroga & Moura, 2017). For instance, some authors discuss how annual temperature and rainfall affect ants' survival and how warmer and wetter conditions can increase the diversity and frequency of ant-plant interactions (Costa et al., 2018; Anjos et al., 2019; Bujan et al., 2020).

While the competitive capacity of species has relative stability with time, the environmental conditions are more unstable, where certain physical conditions such as temperature and rainfall may have large variation within a single day. In this sense, the resource domination exhibited by some species may only occur on specific periods of the day where the abiotic quality is within their physiological tolerance, occurring, thus, a turnover of species with time (Pol & Casenave, 2004; Anjos et al., 2017). Bestelmeyer (2000), for example, showed that dominating ants are not as heat tolerant as subordinate ant species. He observed that subordinate ants dominated food baits in periods where the temperature reached extreme values, while dominating ants were not able to forage during periods of extreme temperatures.

The ants (Hymenoptera: Formicidae) are a good model for studying competition and dominance behaviors as they are omnipresent, with more than 15,000 species around the world (Bolton, 2014). They have great morphological and behavioral variation, with many species presenting strong territorial behavior and high recruitment capacity - allowing them to size critical food resources (Levings & Traniello, 1981).

The Cerrado (Brazilian savanna) biome has one the greatest numbers of endemic species (Myers et al., 2000). It is characterized by a well-delimited seasonality and a mosaic of plant phytophysiognomies with particular characteristics ranging from more open, heterogeneous, and dry areas such as the cerrado *stricto sensu* to dense and homogeneous forests such as the cerradão (Oliveira-Filho & Ratter, 2002). This biome represents an adequate landscape for the study of ants since the wide availability and distribution of resources and the vegetal mosaic (Klink & Machado, 2005) allow ants to be the most successful insects in terms of biomass, abundance, and ecological impact by acting as bioindicators, cycling soil nutrients, and providing plant defense against herbivores (Silva et al., 2004; Silva et al., 2011; Tibcherani et al., 2018; Swanson et al., 2019; Calixto et al., 2020).

In this study, our goal was to assess the species richness, recruitment, and resource dominance of ant species within two cerrado areas (phytophysiognomies) by offering food baits during three periods of the day. We hypothesized that (i) ant composition, species richness (hereafter ant richness), and recruitment capacity will be distinct between the two cerrado areas; (ii) that ant dominance, richness, and recruitment will change during the observation periods; (iii) the discovery moment of food baits will affect their dominance by the ant species; (iv) the ant recruitment capacity will also affect the food resource dominance. We predicted that (i) ant dominance and richness will be higher in cerrado stricto sensu, due to its high habitat heterogeneity, than in cerradão, a more homogeneous phytophysiognomy; (ii) ant dominance, richness, and recruitment will be lower during the hottest observation periods; (iii) ants that discovered food baits before other species will have a higher chance of dominating it and (iv) species with increased recruitment will dominate more food baits than species with low recruitment ability.

Material and Methods

Study area

The study was conducted in November 2015 at the Parque Estadual Serra de Caldas Novas (PESCAN) located in Goiás state, Brazil (17°46'28.88"S 48°40'46.07"W). The climate is seasonal with a dry (May to September) and a wet (October to April) season, with a mean temperature of 22.7 °C (Ferreira & Torezan-Silingardi, 2013). The region is characterized by a Cerrado biome with 123 km² of area and 1,043 m of altitude. The vegetation is a mosaic composed of fields, savanna, and forest formations (Lima et al., 2010). The area combines several cerrado types: cerrado *stricto sensu*, campo sujo, campo limpo, cerradão, and gallery forests (Lopes et al., 2009).

For this study, we selected two cerrado areas according to the landscape description developed by Ribeiro and Walter (1998). The first area represents a cerrado *stricto sensu* located within a plateau region characterized by the presence of xeromorphic shrubs and grasses, that do not form a continuous canopy, and a latosol with medium-low organic deposition. The second area is characterized by a cerradão (xeromorphic forest) located at the plateau's base, with latosol of medium



Fig 1. Characterization of the study areas. Cerrado stricto sensu (A) and cerradão (B) in PESCAN, Caldas Novas, Goiás, Brazil.

organic deposition, bearing both forest and cerrado *stricto sensu* tree species that form a continuous canopy (Fig 1).

Data sampling

In each cerrado area, we established 10 sampling plots 10 m away from the main trail border and 20 m away from each other. In the center at each site, we sampled ants by offering, on a napkin sheet, 20 g of a protein-based bait made of sardine. The distance between sampling sites and the time of observation (see below) was established accordingly to the ALL Protocol (Fisher et al., 2000).

We performed two trials at each cerrado area which were three kilometers apart from each other. In the first trial, we observed ant visitation on all 10 baits within two hours. We spent 12 minutes observing each bait until the arrival of the first ant, collecting it right away. For the second trial, we returned to the first bait to initiate a second round of observations, but we also collected at least two individuals of each ant species on each bait for identification and through a picture estimated the number of individuals (recruitment) (iPhone 7 camera with 16 megapixels, f/2.2 opening, 30 mm lens, field of vision of 73°). Furthermore, during the second trial, we classified the observed ant species as resource dominating and non-dominating, where we considered as dominating those species that did not share the bait with others (i.e., only one species per bait).

The method involving the first and second trials was repeated during three observation periods (period 1 = 8:00 to 10:00; period 2 = 12:00 to 14:00; period 3 = 16:00 to 18:00), at the same sampling sites so we could observe the arrival and dominance of ant species along the periods. All individuals collected were stored on microtubes with alcohol 70% and, afterward, they were identified with the aid of a taxonomic expert and deposited in the taxonomical collection of the Behavioral Ecology and Interactions Laboratory (LECI).

When performing bait trials during the three observation periods, we replaced each used sardine bait with a clean bait and removed all ants using the resource from the previous observation period. All new baits were positioned in the same place so we could observe potential changes of species over the three observation periods. All study was conducted during stable weather conditions (sunny days) to minimize data variability and avoid confounding effects caused by environmental factors such as rain.

Data analysis

We performed all statistical procedures using the R software, version 3.5.2 (R Development Team, 2018). To compare species composition between the two cerrado areas, we calculated the Jaccard similarity index (Magurran, 2013) by using the following formula: J = C / (A + B - C), where A is the number of ant species present at cerrado *stricto sensu*, B is the total number of species in cerradão, and C is the sum of ant species from both areas. This index varies from 0 to 1,

where numbers around 1 indicate high species similarity between compared areas. We performed an Analysis of Similarity (ANOSIM; see Clarke, 1993) to analyze differences in species composition between the cerrado areas, using the vegan package of R (Oksanen et al., 2013). We calculated the Bray-Curtis distance and performed 999 permutations using data on ant presence and recruitment (number of ants). After ANOSIM, we performed a non-metric multidimensional scaling (NMDS) in order to graphically expose the results. At last, we performed a similarity percentage breakdown (SIMPER) to identify what species most contributed to the observed patterns of dissimilarity between areas (Neves et al., 2013). Furthermore, to evaluate the most common ant species in each cerrado area, we observed the number of baits occupied by distinct species. Due to the high number of rare ant species, we selected only the species that occupied at least 10% of offered baits in each observation period.

To understand whether the ant richness varied according to the cerrado areas and observation periods, we modeled the total richness per offered bait by using a linear mixed model with Gaussian distribution. Since we repeated bait offers per sampling site in three observation periods, we included it as a random variable represented as 1|bait (Bates et al., 2015). We performed the same procedure to evaluate whether ant recruitment depended on the period of observation and cerrado area. We performed linear mixed models using the *lmer* function from the *lme4* package of R (Bates et al., 2015). We analyzed the effect of ant recruitment from each ant species on the number of dominated baits in each cerrado area by performing a generalized linear model (GLM) with Gaussian distribution. Also, we performed a chi-square test to verify whether the arrival order of ant species on the resource (first or second trial) influenced their capacity of dominating baits. We performed three tests, one for each studied cerrado area and one using the data from both cerrados, independently of the period of observation.

Results

We found 34 ant species, 24 from cerrado *stricto sensu*, 19 from cerradão, and 9 species shared by the two areas (Table 1). The total number of observed individuals (recruitment) was 2,739, and the most abundant species was *Solenopsis geminata* (849 individuals), found only in cerrado *stricto sensu* followed by *Camponotus* and *Pheidole* that were the most abundant genera in both studied areas.

The Jaccard similarity index revealed moderate similarity (J=0.47) in species composition between the two sampled cerrados. This result means that the cerrado areas share 47% of all sampled ant species. The differences among species composition between the two areas were significant (ANOSIM: R=0.53, p=0.001; Fig 2). Solenopsis geminata, Camponotus sp. 1, Camponotus sp. 2, C. novogranadensis, and C. senex strongly influenced the ant species composition, characterizing 32% of species dissimilarity between the two areas (SIMPER: p=0.001).

Table 1. The recruitment of ant species observed in each cerrado area and period of observation.

Species	Cerrado stricto sensu			Cerradão		
	Observation Periods					
	1	2	3	1	2	3
Atta laevigata	-	-	15	-	-	-
Atta sp.1	-	-	-	-	-	20
Camponotus atriceps	-	-	120	8	-	6
Camponotus blandus	180	23	-	1	-	-
Camponotus novogranadensis	19	16	-	-	-	-
Camponotus sp.1	2	-	-	76	50	97
Camponotus sp.2	8	9	6	-	-	-
Cephalotes depressus	-	1	-	-	-	-
Cephalotes pusillus	5	3	1	1	-	-
Crematogaster sp.1	131	5	117	10	80	-
Dinoponera australis	-	-	1	-	-	-
Ectatomma permagnum	-	-	-	7	-	-
Ectatomma brunneum	3	-	-	-	-	-
Ectatomma opaciventre	4	-	-	-	-	-
Gracilidris pombero	-	2	-	-	-	-
Forelius sp.1	5	-	-	-	-	-
Linepithema sp.1	-	-	-	2	-	6
Neoponera apicalis	-	-	-	7	-	-
Nylanderia sp.1	-	-	-	2	-	-
Odontomachus chelifer	-	1	-	-	-	-
Pheidole diligens	-	-	51	24	3	14
Pheidole gertrudae	60	-	-	-	-	-
Pheidole oxyops	1	-	-	80	51	240
Pheidole sp.1	-	3	-	58	23	-
Pheidole sp.2	-	4	-	-	-	-
Pheidole sp.3	-	-	40	20	-	-
Pheidole sp.4	-	-	-	44	30	-
Pheidole sp.5	-	-	-	1	-	-
Pheidole sp.6	-	-	-	-	-	7
Pheidole sp.7	-	-	-	-	33	32
Pheidole sp.8	-	-	-	-	32	-
Solenopsis geminata	197	37	615		-	
Total	613	104	966	341	302	422

We observed that the most frequent species, that is, those found on at least 10% of the offered baits (see Data analysis, for details), differed between both the cerrado areas and observation periods. Specifically, in cerrado *stricto sensu*, we found six abundant species during all three observation periods. In cerradão, we found four species, being *Camponotus* sp.1 recorded on more than 50% of baits during period 2 and more than 40% during period 3 (Fig 3).

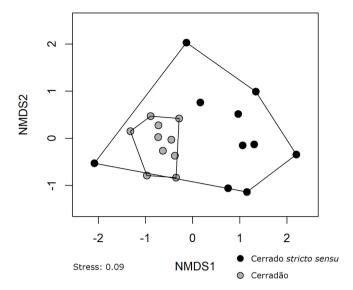


Fig 2. Ant species composition present in two adjacent cerrado areas. Each dot represents a sample spot (food bait). The ant species composition formed two distinct groups according to the cerrado area (ANOSIM: R = 0.53, p = 0.001).

In the cerrado *stricto sensu*, five species maintained resource dominance during the second observation period (Table 2). Furthermore, we observed that none of the species present in both cerrados were dominant in both areas. In cerrado *stricto sensu*, only *Camponotus* sp.2 found and dominated baits during periods 2 and 3. In contrast, in cerradão, *Pheidole oxyops* dominated baits during periods 1 and 3, while *Camponotus* sp.1 was observed dominating baits during all periods.

Several species shared resources during the second trial with up to three other species. In cerrado *stricto sensu*, the *Camponotus* genus was observed 34 times on the offered baits and shared them on six occasions: three times with *Camponotus* sp.2 and three times with different species of *Pheidole*. *Pheidole* ants were observed 10 times on the offered baits and shared them three times with other species. In cerradão, the *Camponotus* genus was observed 41 times, where *Camponotus* sp.1 shared the resource 19 times with other species, while *Pheidole* ants were observed on baits 35 times and shared them with other 23 species, *Pheidole diligens* specifically, was observed sharing baits on 6 occasions.

According to the linear mixed models, there was no effect of the cerrado area on ant recruitment (F = 0.17, p = 0.68), but there was a difference regarding the observation periods (F = 6.95, p = 0.002). In period 3, we observed higher recruitment on both cerrado areas, while in period 2 we noticed low recruitment in cerrado *stricto sensu* (Tukey post-hoc: p < 0.05). We also verified an interaction effect between the observation periods and the cerrado areas, where ant recruitment was very low in cerrado *stricto sensu* (F = 4.12, p = 0.022; Fig 4a). There were no differences regarding ant richness per bait between the cerrado areas (F = 2.53, p = 0.12), among the observation periods (F = 0.94, p = 0.37) and neither interaction effects between these two variables (F = 1.43, p = 0.25; Fig 4b).

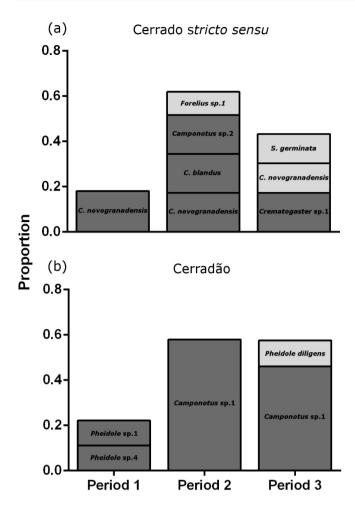


Fig 3. The proportion of ant species found on food baits according to the cerrado area and observation period (period 1 = 8:00 to 10:00; period 2 = 12:00 to 14:00; period 3 = 16:00 to 18:00). Only the most frequent ant species – those that occupied at least 10% of all baits – were considered (see Material and Methods for details). In (a), Camponotus novogranadensis was found during all three periods of observation, being predominant during period 1. In (b), there was a smaller number of ant species, with the predominant ant, Camponotus sp. 1, being observed on more than 50% of baits during period 2 and 40% during period 3. Species in light gray boxes have a lower proportion when compared to the species below (dark gray). Species matching colors within the same bar have equal proportions.

We found a significant, positive relationship between ant recruitment and the number of dominated baits for both cerrado *stricto sensu* ($F_{1,22} = 51.75$, $R^2 = 0.70$, p < 0.001) and cerradão ($F_{1,18} = 11.24$, $R^2 = 0.38$, p = 0.004). In cerradão, the chi-square tests revealed an association between the ant arrival moment (observation trials) and resource dominance ($\chi^2 = 8.40$, p = 0.004); species that arrived during the first trial had a 29.73% chance of dominating the resource, while those arriving during the second trial had only a 7.14% chance of dominating it. We did not observe significant differences regarding the ant arrival moment and resource domination in the cerrado *stricto sensu* ($\chi^2 = 1.81$, p = 0.18).

Table 2. The number of food baits in which ant species shared the resource (A) and the number of baits in which they did not share it (dominating ants) (B) in each cerrado area. Asterisks represent species found in both studied areas.

Species in cerrado stricto sensu	A	В
Atta laevigata	1	0
*Camponotus atriceps	2	2
*Camponotus blandus	8	4
Camponotus novogranadensis	12	2
Camponotus senex	2	0
*Camponotus sp.1	2	0
Camponotus sp.2	8	2
Cephalotes depressus	2	0
*Cephalotes pusillus	3	1
*Crematogaster sp.1	3	4
Dinoponera australis	1	0
Dorymyrmex sp.1	1	0
Ectatomma brunneum	1	0
Ectatomma opaciventre	1	0
Forelius sp. l	1	1
Gracilidres pombero	1	0
Odontomachus chelifer	1	0
*Pheidole diligens	3	1
Pheidole gertrudae	1	0
*Pheidole oxyops	1	0
*Pheidole sp.1	3	0
Pheidole sp.2	1	0
*Pheidole sp.3	1	0
Solenopsis geminata	7	4
Species in cerradão	A	В
Atta sp.1	1	0
*Camponotus atriceps	2	1
*Camponotus blandus	1	0
*Camponotus sp.1	18	3
*Cephalotes pusillus	1	0
*Crematogaster sp.1	2	0
Ectatomma permagnum	3	1
Linepithema sp.1	2	0
Neoponera apicalis	2	0
Nylanderia sp.1	1	0
*Pheidole diligens	5	0
*Pheidole oxyops	8	2
*Pheidole sp. l	6	1
*Pheidole sp.3	1	0
Pheidole sp.4	7	0
Pheidole sp.5	1	0
Pheidole sp.6	2	0
Pheidole sp.7	4	1
Pheidole sp.8	2	0

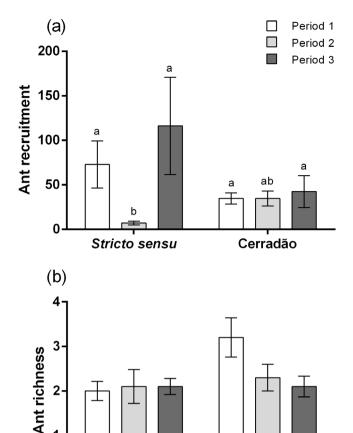


Fig 4. The effects of cerrado area (*stricto sensu* and cerradão) and observation period (period 1 = 8:00 to 10:00; period 2 = 12:00 to 14:00; period 3 = 16:00 to 18:00) on ant recruitment (a) and richness (b). In (a), the linear mixed models revealed differences in ant recruitment considering the observation period, where recruitment was particularly low during period 2 of cerrado *stricto sensu*. Ant richness has not varied significantly in any treatment (b). Bars represent means, and all variability measures represent the standard error of the mean.

Cerradão

Stricto sensu

Discussion

0

In this study, we evaluated how ground-dwelling ants varied in richness, recruitment, and resource dominance between two cerrado areas and distinct day periods (observation periods). We observed differences in species composition between the two areas, where ant richness and recruitment were greater in cerrado *stricto sensu* than in cerradão, as predicted by our first hypothesis. The *Camponotus* and *Pheidole* genera were highlighted in this study not only by their increased abundance but for being found in both cerrados. For both areas, there were no differences in richness among the observation periods, but cerrado *stricto sensu* had the lowest recruitment during the highest temperature period (period 2), while the highest

recruitment occurred at the end of the day (period 3), partially corroborating our second hypothesis. For both areas, the recruitment capacity determined bait domination, where ants with increased recruitment were frequently observed seizing baits, which corroborates our fourth hypothesis. In cerradão, but not in cerrado *stricto sensu*, ant species that arrived early had increased chances of dominating the resource, partially corroborating our third hypothesis.

The differences in ant richness and recruitment found between the cerrados are influenced by competitive interactions and environmental structuring and conditions (Neves et al., 2013). We observed fewer ant species in cerradão than in cerrado stricto sensu possibly due to their distinct habitat heterogeneity. The environmental structuring in savannas is positively related to species richness, increasing in open habitats such as cerrado stricto sensu, and decreasing in shaded forests such as cerradão (Andersen, 1992; Oliveira Filho & Ratter, 2002; Fisher, 2010). In addition to the environmental structuring, temperature is another abiotic factor able to shape the ant community throughout the day (Dáttilo & Izzo, 2012). Ants often forage during daylight, but their activity levels drop during the hottest periods and increase during the coolest ones (Wittman et al., 2010). We observed this pattern since the most intense ant activity (recruitment) occurred during the cooler period in both cerrado areas. In addition, we have to consider the effects of biotic factors such as interspecific competition as these interactions interfere and determine the coexistence, richness, and abundance of species (Cavender-Bares et al., 2009; Gibb & Parr, 2010). In fact, some of the main dominant ant species found in this study (e.g., Camponotus genus) are usually very aggressive and tend to monopolize food resources (Fagundes et al., 2017)

The species dissimilarity found between the sampled areas reflects their structural differences, determining the distribution and coexistence of species (Gibb & Parr, 2010). The general composition of species was not very similar between the cerrado areas, showing species with distinct evolutionary histories and different capacities to find and explore resources. Pheidole and Camponotus genera are usually found in great abundance not only within the Cerrado (Andrade et al., 2007) but also within the Atlantic Forest (Gomes et al., 2014) and crop areas of Cerrado and Caatinga (Neves et al., 2013). In our study, these genera were not only the most abundant but also those that most often found and dominated the offered resources in both areas. Pheidole and Camponotus are highly abundant, aggressive, and generalist groups able to actively patrol the substrate in search of food (Silvestre & Silva, 2001; Fonseca & Dihel, 2004, Queiroga & Moura, 2017). Given this, their outstanding capacity in finding and dominating food baits relies not only on their recruitment capacity but their high aggressiveness should play a major role in order to subdue weaker competitive species (Andersen, 1992; Parr et al., 2005).

In cerradão, we observed that species that found food baits in the first trial had higher chances of dominating it until the second trial. This challenges the idea that species with good abilities in finding resources are not effective in maintaining the resource; in other words, it does not indicate trade-off effects concerning the resource encounter and domination abilities (Fellers, 1987; Lebrun et al., 2007; Wiescher et al., 2011). Similar results were observed with invasive/alien species since their superior competitive capacity prevents or reduces the possibility of turnover with native species (Holway, 1999; Lessard et al., 2009; Bestelsmeier & Courchamp, 2014; Bertelsmeier et al., 2015). According to Parr and Gibb (2012), trade-offs between encounter and dominance of resources represents an exception and not a requisite to the structuring and coexistence of ant species, meaning that the observed interactions here might be explained by other mechanisms such as the ant nest distance from resources (resource accessibility) and distribution (Wagner, 1997; Fagundes et al., 2015).

Our study demonstrated that the cerrado phytophysiognomy is an important factor that shapes the diversity and interactions of ants. Environmental structuring is reflected by niche partitioning in both spatial and temporal scales (Albercht & Gotelli, 2001), providing several possibilities of microhabitats that allow species to explore the environment and forage (Gibb, 2005; Fagundes et al., 2005; Neves, 2013). We emphasize the importance of studies comparing the richness, abundance, and behavior of ant species between different phytophysiognomies and biomes. Such studies may allow us to understand the ecological role of many species, a fundamental knowledge useful for conservation practices involving not only ants but all kinds of organisms.

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Author's Contribution

LRS: conceptualization, investigation, methodology, writing RFM: conceptualization, methodology, formal analysis, writing.

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