

Foliage-dwelling ants in a neotropical savanna: effects of plant and insect exudates on ant communities

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Received: 10 June 2015 / Accepted: 22 February 2016 / Published online: 15 March 2016
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Abstract Ant dominance in tropical ecosystems can be explained by a capacity to exploit liquid foods such as extrafloral nectaries (EFNs) and secretions from honeydew-producing hemipterans (HPHs). Such nutritious exudates may determine ant distribution in space and shape specialization in ant–plant interactions. We provide a first assessment of how EFNs and HPHs mediate the structure of ant assemblages, ant visitation intensity, and characteristics of ant–plant interaction networks across space in Brazilian “cerrado” savanna. We used arboreal pitfall traps to sample visiting ants in four cerrado localities and recorded the presence of lepidopteran larvae to determine their possible response to ant visitation. Ant species composition and richness did not differ regardless of the presence of liquid rewards on plants, and most network patterns did not show consistent differences. However, in two of the four sites, ant densities were higher on plants with HPHs or EFNs due to increased activity by

Camponotus and *Pseudomyrmex* ants. At these two sites, plants with liquid food sources had a more specific ant assemblage (higher specialization d') than did plants without resources, and caterpillars were more frequently found on plants with fewer workers of *Camponotus* and *Pseudomyrmex*. Plants with HPHs had increased ant visitation and accumulated more ant species than did plants with EFNs or without liquid foods. Ant response to such food sources may thus depend on local conditions and identity of ant species, and may determine how ant assemblages are structured. Results highlight how different patterns of ant visitation to liquid resources can produce distinctive effects on herbivore infestation.

Keywords Extrafloral nectaries · Honeydew-producing insects · Multitrophic interactions · Cerrado · Lepidoptera · Interaction networks

Handling Editor: Stanislav Gorb.

Electronic supplementary material The online version of this article (doi:10.1007/s11829-016-9423-2) contains supplementary material, which is available to authorized users.

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Introduction

Ants comprise the most important component of the arthropod fauna on foliage in tropical ecosystems (Majer 1990). There is increasing evidence that most canopy-dwelling ants of tropical ecosystems feed on plant-derived liquid food sources, making them more similar to herbivores than to predators and explaining how they can reach such high abundances on foliage (Tobin et al. 1991; Davidson et al. 2003). One category of these food sources is exudates of extrafloral nectaries (EFNs) that may be visited by many ant species, including specialized predators (Rico-Gray and Oliveira 2007; Blüthgen and Feldhaar 2010). Many ant species also collect honeydew from sap-feeding hemipterans (HPHs = honeydew-producing hemipterans) or secretions from lepidopteran larvae (Stadler and Dixon 2005).

The foraging activities of ants can benefit plant fitness via herbivore deterrence on plants with EFNs (Heil and McKey 2003; Rico-Gray and Oliveira 2007) or indirectly via tending/patrolling activities at honeydew-secreting insects (Heil et al. 2001; Oliveira and Del-Claro 2005). From a plant's perspective, the positive effect of ant presence is conditioned by whether or not visiting ants have negative net effects on herbivores. This conditionality in turn depends on several factors, including the identity, aggressiveness and abundance of visiting ants (e.g., Mody and Linsenmair 2004; Sendoya et al. 2009). Although most studies have reported a general positive effect of ant presence on plants, the outcome of ant–plant interactions can be context-dependent and vary both spatially and temporally (see Chamberlain and Holland 2009 and included references).

The Brazilian cerrado is a savanna-like ecosystem especially rich in liquid food sources for foliage-foraging ants; in some areas, nearly 25 % of the plant species possess EFNs (Oliveira and Leitão-Filho 1987) and up to 30 % host HPHs (Lopes 1995). The frequent occurrence of EFNs promotes visitation to foliage by many ant species (Oliveira and Brandão 1991) and may decrease herbivore infestation and associated plant damage (Oliveira and Freitas 2004; Sendoya and Oliveira 2015). Available evidence suggests that insect honeydew is a more abundant, constant (renewable) and nutritious exudate than extrafloral nectar, and should thus be a more valuable resource for ants (Blüthgen et al. 2000; Blüthgen and Fiedler 2004). Indeed, honeydew as a predictable food source can alter ant behavior and increase ant aggressiveness toward other insects on foliage (Styrsky and Eubanks 2007; Campos and Camacho 2014). However, compared to tropical forest ant assemblages (Davidson et al. 2003), much less is known about the degree to which cerrado ant assemblages are dependent on plant and insect exudates.

Many studies have already looked at interactions between ants and EFN-bearing plants from a network perspective (Blüthgen et al. 2007; Guimarães et al. 2007; Díaz-Castelazo et al. 2010; Lange et al. 2013). Only recently, however, have these interactions been analyzed in the context of the surrounding plants lacking EFNs or HPHs, and differences in abundance and competitive ability of core dominant species have been suggested as key factors structuring ant–plant networks in a tropical forest (Dáttilo et al. 2014). Competition has indeed been pointed out as the determining factor mediating spatial patterns of ant species distribution (Blüthgen and Stork 2007). In Australian rain forests, for instance, a few dominant ant species possess a high capacity to repel subdominant ants from plants with abundant resources (especially HPHs) and to create spatial patterns of dominance on plants they visited (Blüthgen et al. 2004).

Competitive exclusion theory predicts increased levels of foraging specialization in the system following increased attractiveness of resources on plants, because some ants prefer rich food sources and monopolize resource-rich plants (Blüthgen et al. 2004). However, it is still unclear whether and how resource availability might influence coexistence of foliage-foraging ants in the cerrado, and thus the composition and structure of ant assemblages. It has been proposed that, if plant-derived food sources are not key resources for ants, then benefits of the mutualistic ant–plant interactions tend to be highly asymmetric (Schoereder et al. 2010).

Here, we investigate ant–plant interaction networks in cerrado savanna, taking into account the mosaic of plant and insect exudates available on foliage of diverse species. We compared patterns of ant visitation to plants possessing different liquid ant attractants (EFNs or HPHs) among other plants lacking liquid resources within the same community. We proposed three possible scenarios as alternative hypotheses for the effects of resource availability on visiting ant assemblages. First, if plant-derived resources are not primary resources of ants (i.e., neutral effect of ant attractants), assemblages on plants with plant- and insect-derived exudates should be representative of the foliage-foraging ant community as a whole, and thus, resource presence would not affect coexistence of foliage-foraging ants. Second, if at least certain ant groups respond strongly to ant attractants or compete for them, some ant species would be found more frequently foraging on plants with valuable food sources (HPHs), and assemblages on such plants should differ from those with less attractive resources (EFNs) or no ant attractants at all. These differences should in turn mediate how ants would affect herbivores. In this scenario, plants with attractants would interact with some species of ants more frequently than expected by the abundance of these taxa in the community of foliage-foraging ants and should present greater specialization in their interactions with ants. Third, because deterrence of herbivores by opportunistic exudate-feeding ants is known to vary across the cerrado landscape and local ant communities (Sendoya and Oliveira 2015), the effect of liquid foods on ant assemblages may also vary spatially in accordance with local patterns of ant communities.

Specifically, we addressed the following questions regarding the hypotheses raised above with respect to the effect of the presence of liquid resources (EFNs or HPHs) on foliage-foraging dwelling ants: (1) Do exudates increase ant richness or ant visitation on plants? (2) Do they affect the composition of visiting ant assemblages? (3) Does the effect of these resources vary among localities? (4) Do these resources affect ant–plant interaction patterns through increased plant specialization in their interactions

with ants? Finally, (5) are the ant genera mostly attracted to liquid resources also the ones mostly affecting the presence of herbivores on plants?

Materials and methods

Fieldwork was carried out during the wet season (February–April 2009) at four cerrado localities in southeastern Brazil: Itirapina (22°15'S, 47°47'W), Mogi-Guaçu (22°15'S, 47°10'W), Assis (22°35'S, 50°21'55''W), and Uberlândia (18°59'S, 48°18'W). The vegetation physiognomy in all sampled sites consisted of a dense cover of trees and shrubs, corresponding to the cerrado *sensu stricto* (Oliveira-Filho and Ratter 2002). In each locality, we sampled plants (0.3–0.6 m tall) along a string line until we completed 50 individuals in each of 6 transects (2 m wide and ~30 m long). In each locality, transects were established in parallel toward the interior of the cerrado, at a distance of ~100 m from one another.

Insect sampling

We sampled visiting ants by using foliage-foraging pitfall traps during 24 h (modified from Ribas et al. 2003) so as to represent a complete survey of ant assemblages visiting plants during one entire day. We placed two pitfall traps per plant, one baited with sardine and one with honey. Patterns of visitation by foliage-foraging ant communities have previously been assessed by using attractive baits, even on plants possessing natural sources of liquid food (e.g. Blüthgen et al. 2000; Koptur et al. 2010; Sendoya and Oliveira 2015). For each plant, we also registered the presence of EFNs and HPHs (Fig. 1a, b). EFNs were detected by direct observation in the field of nectar-gathering ants as well as by comparison with available plant lists (e.g., Machado et al. 2008). In order to distinguish plant visitation by foraging ants from patrolling behavior near an arboreal nest, plants hosting ant colonies were not included in the surveys.

To evaluate the effects of visiting ants on herbivore presence, we also quantified the abundance of non-myrmecophilous, exophagous larvae of Lepidoptera. Twenty-four hours prior to ant sampling, each plant was visually inspected for 10 min for the occurrence of larvae. These insects are very important herbivores in tropical ecosystems, and their feeding behavior and low mobility make them likely to interact with ants on cerrado foliage (Freitas and Oliveira 1992; Freitas and Oliveira 1996). We categorized sampled plants into three groups: with EFNs, with HPHs, and without ant attractants. We investigated the structure of visiting ant assemblages by comparing

abundance, species richness, and composition between plant categories and among cerrado sites.

Plants and ants were counted and identified to the lowest possible taxonomic level (at least genera) and sorted to morphospecies when species identifications were not possible. Insect and plant voucher specimens were deposited, respectively, in the Museu de Zoologia (ZUEC) and in the Herbarium (UEC) of the Universidade Estadual de Campinas.

Ant visitation

To determine whether ant visitation varied among localities and among plants groups, we constructed a generalized linear mixed model (GLMMs; Zuur et al. 2009). To control for effects of plant size (stem diameter at 30 cm height) or plant phenological stage (reproductive or vegetative), both variables were included as fixed factors. A negative binomial distribution and a Laplace approximation were used to estimate model parameters (Sendoya and Oliveira 2015). To account for possible dependence among plants in the same transect, we included sampling transect (nested within locality) as a random factor in each model. The effects of the fixed variables and their interactions were evaluated by comparing concurrent models (constructed by sequentially deleting the effect of interest) using likelihood ratio tests.

To determine which ant groups exhibited differential visitation to plants in relation to the presence/absence of ant attractants, we split the analysis of visitation into two levels. First, we compared how many plants in each group were used by each ant genus (hereafter: ant presence on plants). To do this, we performed several GLMMs, modeling presence/absence of each genus as a binary variable (using a binomial distribution in the models), and using plant category and its interaction with sampling locality as predicting variables. Second, we compared the number of sampled workers from each genus on plants in each group (hereafter: intensity of ant visitation). In this case, GLMMs modeled the number of workers as a count variable (using a negative binomial distribution in the models) and included only plants where a particular ant genus was present. In both sets of analyses, we focused only on the predominant ant genera (those found on at least on 30 plants). These analyses were similar to those performed for the whole ant set. The models were constructed with the lme4 package for R environment V.2.15.2.2 (R Development Core Team 2012).

Ant species richness

Although sampling efforts were equivalent among sites, the frequency of occurrence of individuals differed among the

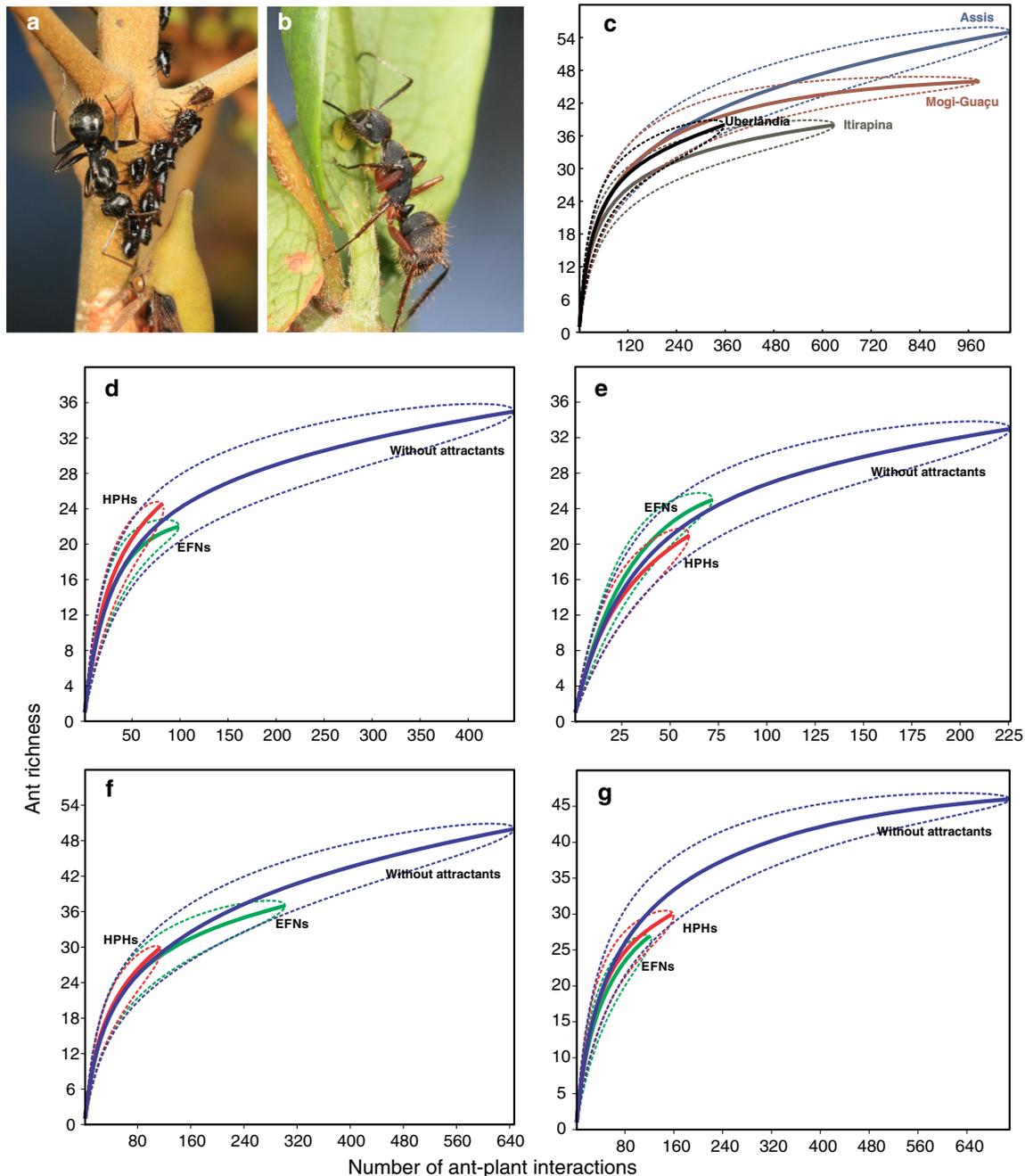


Fig. 1 **a** Worker of *Camponotus blandus* tending nymphs of the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae). **b** Worker of *Camponotus rufipes* collecting extrafloral nectar of *Banisteriopsis* sp. (Malpighiaceae). Rarefaction curves of richness of visiting ant assemblages for (c) all plant species per locality. **d**–

g Plants with extrafloral nectaries (EFNs; black lines), honeydew-producing hemipterans (HPHs; dark gray lines), and no ant attractants (light gray lines). Dotted lines represent 95% confidence intervals. Localities: **d** Itirapina, **e** Uberlândia, **f** Assis, **g** Mogi-Guaçu

three plant categories. Because ant diversity can be confounded by variation in number of individual records, data on ant species richness were compared across sites only following rarefaction (Krebs 1989), using the software PAST (Hammer et al. 2001). We rarefied ant species richness to the same number of occurrences of ant species

on individual plants. To test the effect of liquid sources of food as aggregators of ant species on individual plants, we conducted a GLMMs analysis (similar to ant abundance models) for comparing raw ant richness per plant among plant categories (see Table A5 for removal sequence based on likelihood ratio tests).

Composition of ant assemblages

To compare ant species composition among plant categories, we considered ant assemblages at the transect level. Thus, we had six replicates for each plant category at each locality (18 ant assemblages: 6 for plants with EFNs, 6 for plants with HPHs, and 6 for plants without ant attractants). We counted the number of individual plants per category where an ant species was found (irrespective of the number of workers). In order to address differences in sample size across plant categories, we developed a re-sampling approach. This method consisted of randomly re-sampling 1000 times (with replacement) every transect for each plant category, using the transect with the smallest sample size in each locality as reference for the sample size. Then, we calculated 1000 matrices of similarity between transects of each plant category (hence, 18 points for each locality) using the Morisita index (see Magurran 2004), and calculated a mean similarity matrix (for each pair inside the matrices). With this mean matrix, we performed an ordination analysis with Non-metric Multidimensional scaling (NMDS). To test whether the ant assemblages were actually forming groups with distinctive composition, we pooled all the data from the four localities together and used a two-way permutation MANOVA test, including both presence of ant attractants and locality as factors, and using a similarity matrix with the index of Morisita. All analyses were performed using the Vegan package for the software R 2.15.2 (R development Core Team 2012).

Network analyses

We studied how the specificity of ant–plant interactions was affected by the presence of ant attractants on plants by constructing bipartite ecological networks. In these networks, interacting species plant and ant species (or morphospecies) were represented by nodes, and plant visitations by ants (interactions) were represented by links. This approach has been used frequently to investigate how species in mutualistic systems interact, including ant–plant systems (Blüthgen et al. 2007; Lange et al. 2013; Dáttilo et al. 2014). We constructed three bipartite networks for each locality, each containing one category of plant species (with EFNs, with HPHs, or lacking ant attractant) versus the species of ant visitor. For each site, we then constructed a pooled network with all plants. In this network, individuals with and without HPHs of the same species plants were considered separately.

Considering the potential importance of liquid resources for cerrado ants, we compared levels of (complementary) specialization between plant categories by using the H_2' index (Blüthgen et al. 2006). In order to better describe each network, we calculated some commonly used metrics

for each network, such as connectance (realized proportion of possible links), generality (mean number of interacting plant species per ant species), and interaction diversity for both trophic levels (reflecting the connectivity between trophic groups and in therefore the complexity of interactions; see Blüthgen 2010). Despite limitations in the interpretation of the metric and sampling effects (see details in Blüthgen 2010), we also included nestedness (maximum differences in the number of links among the species measured by weighted NODF–WNODF; Almeida-Neto and Ulrich 2011), because it is a common metric used in other studies of ant–plant interactions and allows potential comparisons (see Dormann et al. 2009 for details on each metric). By comparing the values of those network indices in the networks with those expected for random networks (by constructing 1000 null models based on Patefield's algorithm), we established whether the values would depend on the dimension of the networks.

We then investigated the patterns of specialization within the pooled networks for each locality. We hypothesized that if the ants (or at least a group of ant species) prefer plants with liquid resources, this category of plants should present higher values of specialization. This should be true if plants with attractants interact with some groups of ants more frequently than expected by their frequency across all plants. The values of specialization were estimated using the standardized specialization index d' for each species (Blüthgen et al. 2006). The d' index is derived from the Kullback–Leibler distance and describes how strongly a species deviates from the distribution of all species together in the same guild across interaction partners (i.e., the species' exclusiveness). We compared the d' values of plant categories among localities by constructing GLMM models that considered the type of ant attractant as a fixed variable (EFNs or HPHs) and sampling locality as random variable. Similarly with ant visitation models (see above), we used a Laplace approximation to estimate model parameters and likelihood ratio tests to estimate factor effects. We compared between categories by using a posteriori Fisher's tests. All network analyses were performed using the package Bipartite (Dormann et al. 2008) for the software R 2.15.2 (R development Core Team 2012).

Effect of ants on lepidopteran larvae

The effect of ants on herbivore infestation was considered for each ant genus separately. We compared the number of workers of each genus visiting plants with and without caterpillars. Considering that ants may affect not only larval survival but also colonization decisions of ovipositing females (Sendoya et al. 2009), we compared ant visitation on the infested host plant (larva present) with that on

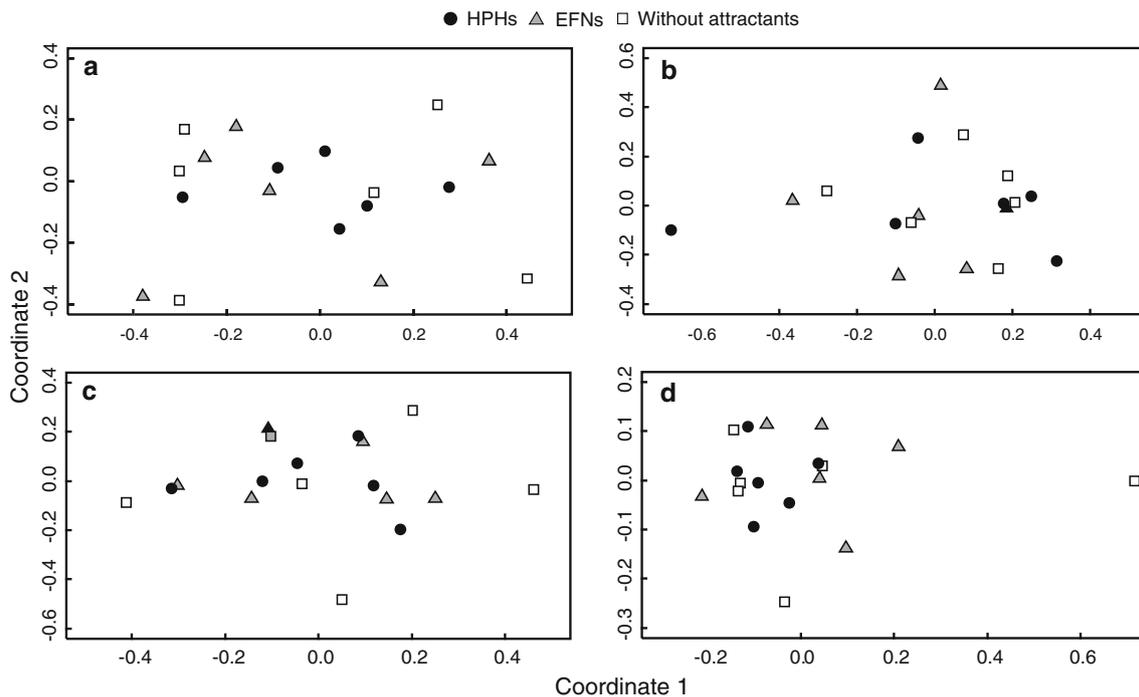


Fig. 2 NMDS ordination showing similarity of the composition of ant assemblages visiting plants with extrafloral nectaries (EFNs; gray triangles), honeydew-producing hemipterans (HPHs; black circles),

and no ant attractants (white boxes) in transects within localities. Localities: **a** Itirapina, **b** Uberlândia, **c** Assis, **d** Mogi-Guaçu

the nearest uninfested conspecific host plant (see Sendoya and Oliveira 2015 for additional details). We performed comparisons using Wilcoxon tests, considering only transects where each ant genus was found at least once. *P* values were corrected using false discovery rate (FDR) method (Benjamini and Hochberg 1995).

Results

The proportion of individual plants with EFNs ranged from 13.7 % in Itirapina to 27.6 % in Assis. The proportion of plants with HPHs ranged from 6.6 % in Uberlândia to 12.8 % in Mogi-Guaçu (Table A1). Only 1.01 % of plants presented both NEFs and HPHs (1.76 % in Itirapina, 0.72 % in Assis, 1.45 % in Uberlândia, and none in Mogi-Guaçu).

The number of ant species found was highest at Assis (52 species), followed by Mogi-Guaçu (47), Uberlândia (40), and Itirapina (37). Based on the rarefaction curves (Fig. 1c), Itirapina again presented the lowest richness, and Assis the highest (see complete lists of ant and plant species in Tables A1, A2, A3). At each locality, the total number of ant species on plants without liquid attractants exceeded that on plants with attractants (Table A4). However, this result was mainly attributable to inequality in the number of individuals per plant category, and

richness did not differ significantly between plants with and without ant attractants after rarefaction (Fig. 1d–g). Similarly, the MDS ordination showed no difference in species composition of ant assemblages by presence or type of liquid food sources on plants (Fig. 2). The two-way permutation MANOVA confirmed these results, indicating that ant assemblages are defined by locality, rather than the presence of ant attractants on plants (Table 1).

Locality and HPHs (but not EFNs) on plants had a positive effect on both the number of visiting workers and on the number of ant species per individual plant (Tables 2, 3, A5; Fig. 3). An interaction between both HPHs and EFNs and locality occurred for visitation intensity (Tables 2, A5; Fig. 3a), suggesting that ants are visiting plants with these liquid foods more intensively (in greater number of workers) only in certain localities. Plants with either EFNs or HPHs are visited more intensively by ants both in Itirapina and Uberlândia, but not in Assis or Mogi-Guaçu (Fig. 3a). Neither plant diameter nor phenological state influenced ant richness or abundance.

The ant genera *Camponotus* and *Pseudomyrmex* were the only ones whose presence on plants (i.e., number of plants where the genus was recorded) was significantly affected by the presence of liquid resources irrespective of sampling site (there were no effect of the interaction terms between resource and locality; Table A3). *Camponotus* occurred more frequently on plants with HPHs ($\chi^2 = 1.16$,

Table 1 Results of the permutation MANOVA test comparing the composition of ant assemblages visiting different categories of plants (considered as factors) on each transect

Factor	<i>df</i>	Sum of squares	<i>F</i>	<i>R</i> ²	<i>P</i>
Plant category	2	0.565	1.336	0.029	0.127
Sampling locality	3	5.457	8.596	0.279	<0.0001
Plant category × locality	6	0.833	0.656	0.043	0.989
Residuals	60	12.697	0.649		
Total	71	19.554			

Plants were categorized as having extrafloral nectaries (EFNs) present, exudate-producing hemipterans (HPHs) present, and ant attractants, as well as by sampling locality (Itirapina, Uberlândia, Assis, and Mogi-Guaçu)

Table 2 Results of the selected generalized linear mixed model (GLMM) investigating the effect of sampling locality, extrafloral nectaries (EFNs), and honeydew-producing hemipterans (HPHs) on foliage, on ant visitation intensity for plants across four cerrado localities

Fixed factor (factor level)	Estimate	SE	<i>P</i>
Intercept	3.042	0.203	–
Locality	–	–	0.006*
Itirapina	–0.926	0.286	–
Mogi-Guaçu	0.200	0.287	–
Uberlândia	–1.783	0.289	–
Presence of EFNs	–0.046	0.172	0.806
Presence of HPHs	0.691	0.267	0.009*
Phenological stage	–	–	0.383
Stem diameter	–	–	0.806
Locality × EFNs	–	–	<0.0001*
Itirapina	1.187	0.280	–
Mogi-Guaçu	–0.071	0.290	–
Uberlândia	1.110	0.273	–
Locality × HPHs	–	–	0.009*
Itirapina	0.981	0.350	–
Mogi-Guaçu	–0.357	0.362	–
Uberlândia	0.879	0.372	–

Sampling transects were included as random factors (variance in the model 0.225). The table shows the estimated coefficients for the linear model for each variable or category maintained in the final model (\pm standard error), and the results of likelihood ratio test for removal of that variable from the complete model. The estimated coefficients for the intercept of the model are the abundance of ants at the locality Assis on plants without attractants. Asterisks denote significant effect of factor at $P < 0.05$

$P = 0.008$), whereas *Pseudomyrmex* was found more frequently on plants with EFNs ($\chi^2 = 4.573$, $P = 0.003$; Table A3). In most localities, *Camponotus* ants exhibited higher visitation intensity on plants with one or the other type of liquid resource (Table A6; Fig. 4a). In contrast, *Pseudomyrmex* workers were more abundant on plants with EFNs, with visitation intensity affected by HPHs only in Itirapina and Uberlândia (Table A7; Fig. 4b). Visitation intensity by *Pheidole* ants was higher on plants with HPHs,

Table 3 Results of the selected generalized linear mixed model (GLMM) investigating the effect of EFNs and honeydew-producing insects (HPHs) on the raw number of ant species per plant across four cerrado localities

Fixed factor (factor level)	Estimate	SE	<i>P</i>
Intercept	1.254	0.109	–
Locality	–	–	<0.001*
Itirapina	–0.481	0.155	–
Mogi-Guaçu	0.023	0.154	–
Uberlândia	–1.034	0.160	–
Presence of EFNs	–	–	0.669
Presence of HPHs	0.194	0.053	<0.001*
Phenological stage	–	–	0.731
Stem Diameter	–	–	0.865
Locality × EFNs	–	–	0.349
Locality × HPHs	–	–	0.323

Sampling transects were included as random factors (variance in the model 0.225). The table shows the estimated coefficients for the linear model for each variable or category maintained in the final model (\pm standard error) and the results of likelihood ratio tests for removal of that variable from the complete model. The estimated coefficients for the intercept of the model are the richness of ants at the locality Assis on plants without attractants. Asterisks denote significant effect of factor; $P < 0.05$

being affected by EFNs only in Uberlândia (Table A7; Fig. 4c). Finally, *Ectatomma* workers were more abundant on plants with HPHs only in Assis (Table A7; Fig. 4d).

Network analyses

Networks had rather similar sizes across localities but were mostly asymmetric, with more ant species than plants. Because there were generally more plant species without liquid ant attractants, ant–plant interaction networks involving this category of plants were consistently larger than those with EFN-bearing plants (Table A4). All networks presented low values of specialization (low values of H2'–Table A4). In Assis and Mogi-Guaçu, some H2' values were even lower than expected by null models. Three of the networks constructed with plants with HPHs were also

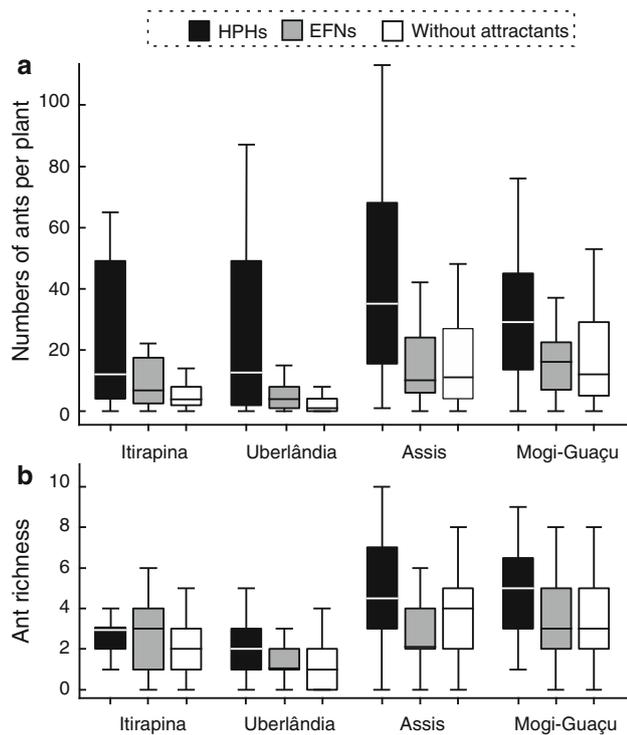


Fig. 3 At each of four localities, **a** raw number of individual ants and **b** number of ant species per sampled plant on plants with ant attractants [extrafloral nectaries (EFNs) or honeydew-producing hemipterans (HPHs)], or no ant attractants. Horizontal lines represent the median, boxes designate the second and third quartiles, and vertical bars indicate the range of data without outliers

less specialized than expected by null model. These results may suggest that both in Assis and Mogi-Guaçu, as well as on plants with HPHs, ants are visiting more plant species (i.e., are more generalized) than expected by their frequencies and those of their plants. Those networks also presented higher values of generality compared to the expected by null models. Connectance was in general low, but again networks of Assis and Mogi-Guaçu, as well as plants with HPHs, exhibited values higher than expected by null models. Irrespective of the presence of liquid resources on plants, the values of nestedness measured by WNODF were rather low (Table A4) and in most cases did not differ from null models. Values of interaction diversity and generality were always higher for plants without attractants, due to a higher richness and sample size in this category (Table A4).

The GLMM models of plant specialization at the species level (d') detected effects of both locality [χ^2 ($df = 3$) = 13.756; $P = 0.003$] and type of liquid resource on plants [χ^2 ($df = 2$) = 10.928; $P = 0.004$], but also for the interaction between them [χ^2 ($df = 6$) = 14.721; $P = 0.023$]. Plants with both types of liquid resource had higher levels of specialization than plants lacking ant

attractants only in Itirapina and Uberlândia (Fisher's HSD, Fig. 5).

Effect of ants on lepidopteran larvae

The number of ants was in general lower on plants hosting caterpillars than on neighboring plants of the same species (i.e., potential host plants) without larvae. Specifically, plants with larvae had significantly lower visitation levels by ants in the genera *Camponotus* and *Pseudomyrmex* (Fig. 6; Wilcoxon test: $Z = 2.58$; $P = 0.044$).

Discussion

Our results show that ant assemblages feeding on plant-derived liquid resources are similar to those visiting plants lacking such attractants. Indeed, our results show that most ant genera visit all groups of plants equally (Table A6) and in proportion to their local availability. In contrast to what has been found in other habitats (Blüthgen and Fiedler 2004; Dáttilo et al. 2014), our data suggest that neither dominance interactions nor interspecific competitive exclusion from liquid resources affects the distribution and structure of foliage-foraging ant communities in the cerrado. Contrary to the expectation of competitive exclusion in ant mosaics (Leston 1973), liquid food sources did not produce spatial segregation patterns among ant species. However, ant foraging preferences are known to be affected by the quality of liquid resources (Styrsky and Eubanks 2007), and our results confirm that the two types of resources affected ant assemblages in different ways. EFNs and HPHs differ in their nutritional value for ants and vary in quantity and quality among plant species (Blüthgen and Fiedler 2004). This variation in exudate richness translates into differences in attractiveness to ants (González-Teuber and Heil 2009) that may produce patterns of aggressive resource monopolization of HPHs plants in tropical forests (Blüthgen et al. 2004). In our study, valuable liquid resources, especially honeydew, had a stronger effect on intensity of ant visitation and attracted a broader spectrum of ant genera, but several ant species nevertheless foraged on the same plant without evidence of competitive exclusion.

The high diversity of cerrado ants has been related to variation in plant diversity, density (Ribas et al. 2003), and size (Powell et al. 2011), but Schoereder et al. (2010) found that neither ant species richness nor composition were affected by the presence of EFNs on plants. The findings of Schoereder et al. (2010) suggest that ant-plant interactions in this biome are highly facultative and that seasonality of EFN production may account for the lack of specialization. Our results confirm the generalized nature of ant-plant

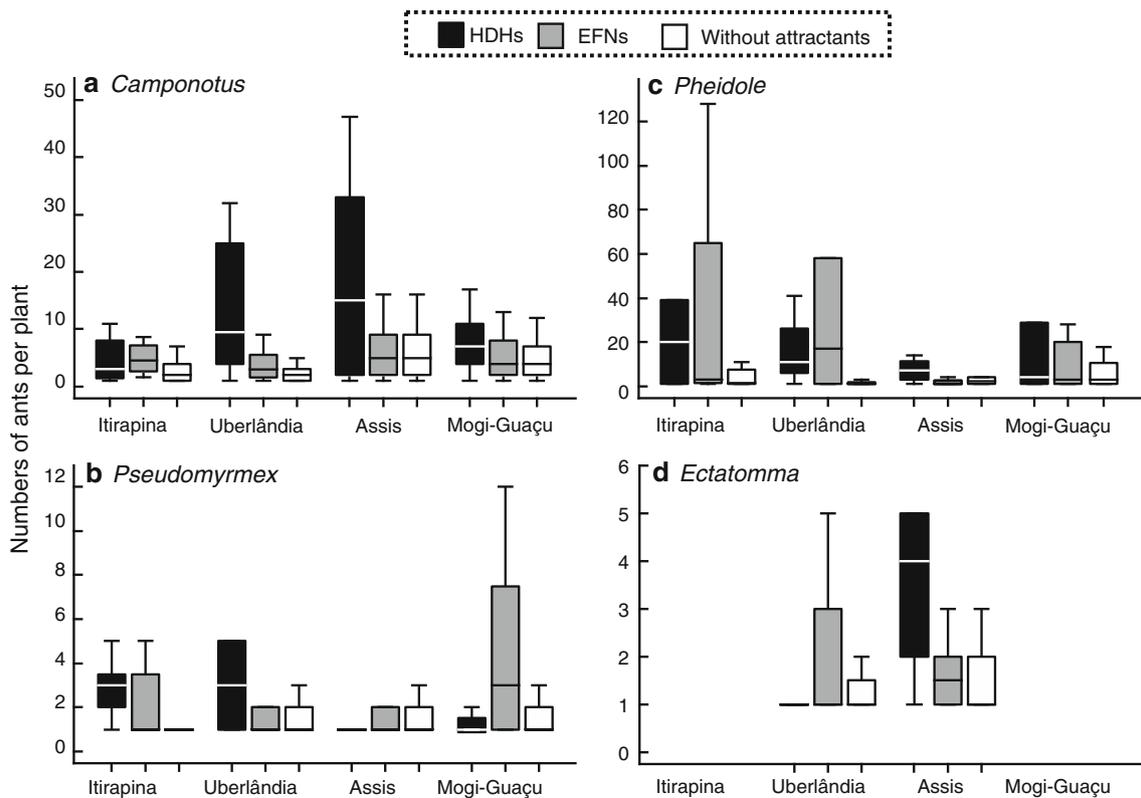


Fig. 4 Intensity of ant visitation (number of ants per plant) for **a** *Camponotus*, **b** *Pseudomyrmex*, **c** *Pheidole*, and **d** *Ectatomma*, for plants with ant attractants [extrafloral nectaries (EFNs) or honeydew-producing hemipterans (HPHs)], and no ant attractants at each

sampling locality. *Horizontal lines* represent the median, *boxes* designate the second and third quartiles, and *vertical bars* indicate the range of data without outliers

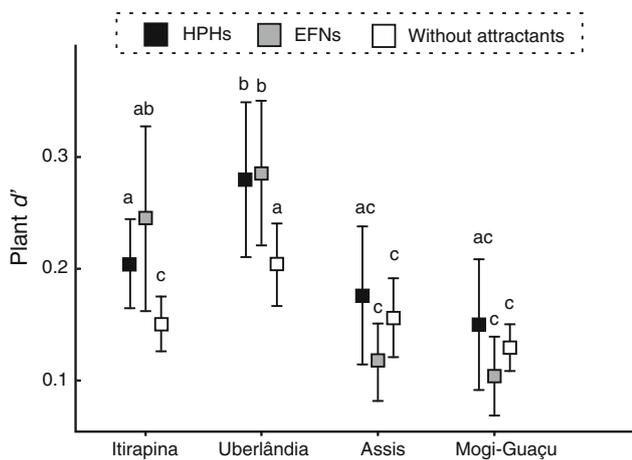


Fig. 5 Values of standardized specialization index (d') for plants with ant attractants [extrafloral nectaries (EFNs) or honeydew-producing hemipterans (HPHs)], or without ant attractants at each sampling locality. *Bars* indicate confidence intervals (95 %) around the mean. *Different letters* above symbols designate significant difference between plant categories within localities (post hoc Fisher's LSD tests; $P < 0.05$)

interactions in cerrado. We showed that distribution of EFNs does not affect ant spatial distribution (i.e., which plants the visited) but only how intensively they visit the

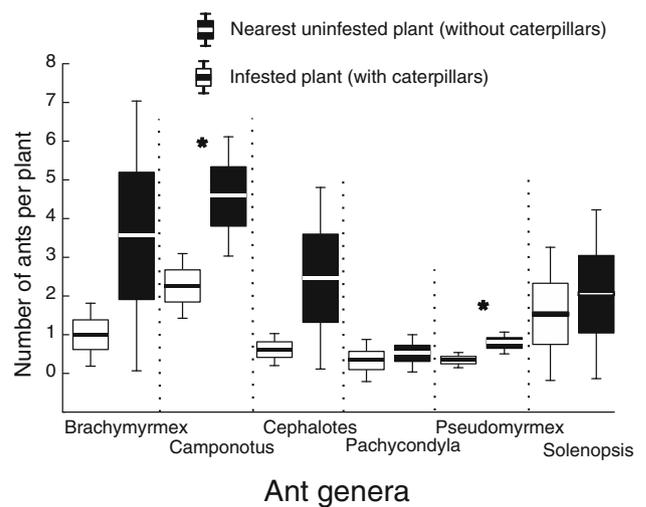


Fig. 6 Ant visitation intensity on plants with and without lepidopteran caterpillars of the most common ant genus. The plants without caterpillars refer to uninfested neighboring potential hosts in the same transect. Workers of other ant genera (*Crematogaster*, *Paratrechina*, *Pheidole*, and *Wasmannia*) were equally abundant on plants with and without caterpillars. *Horizontal lines* are means, *boxes* are *standard errors*, and *whiskers* are 95 % confidence intervals. *Asterisks* indicate $P < 0.05$ after Wilcoxon paired test (using FRD correction)

plants. Highly rich sources of food such as HPHs affected ant foraging patterns (as in forestry systems; Blüthgen and Stork 2007; Campos and Camacho 2014), but only of certain foliage-foraging groups such as *Camponotus*.

The lack of differentiation of ant assemblages in the presence versus absence of EFNs and HPHs, and the apparent species accumulation at these food sources found here may be due to various factors. The presence of resources, their nutritional quality, or even their spatiotemporal stability may all affect ant visitation (Blüthgen and Fiedler 2004; Diaz-Castelazo et al. 2004). Exudate-feeding ants in the cerrado may be segregated along the day rather than between plants (Oliveira and Brandão 1991; Del-Claro and Oliveira 1999). The highly rich resource of HPHs attracts many ant species that share individual plants (hence, no evidence of competitive exclusion) but that may be using the honeydew in different ways and times (suggesting a possible niche differentiation of foraging strategies). For instance, some ants in the genus *Camponotus* (as well as other formicines) are specialized to forage on liquid sources and present digestive adaptations to deal efficiently with sugars and amino acids from honeydew, and a proventriculus especially adapted to process large amounts of liquid (Davidson 1997; Blüthgen and Fiedler 2004). These ants forage continuously along their activity period on plants with liquid resources (Del-Claro and Oliveira 1999). Other ants lacking those adaptations may opportunistically forage on plants with HPHs (even when *Camponotus* are present), due to their bigger body size and the ability to hold exudate droplets in open mandibles (e.g., *Ectatomma*), their ability to show a high numerical response to resource presence (e.g., *Pheidole*), or by visiting HPHs during periods of the day when specialized foragers are not present (Del-Claro and Oliveira 1999). On the other hand, EFN plants are highly visited by many foliage-foraging ants but the resource may not be abundant and predictable enough to aggregate as many species on the same plant individual. Although *Camponotus* ants are also very common on EFN-bearing plants, the intensity of visitation is lower than on that plants with HPHs. Fast and opportunistic ants (e.g., *Pseudomyrmex*) may visit EFNs on plants without *Camponotus* (or at intervals in their absence), and several smaller (e.g., *Brachymyrmex*, *Pheidole*, *Crematogaster*) or timid ants (e.g., *Cephalotes*) may be the main visitors to plants with fewer or less productive EFNs. Furthermore, canopy connectivity among plants with and without resources, or their spatial distribution relative to ant nests, can also mediate ant visitation to cerrado foliage (Powell et al. 2011). Considering the differences in foraging strategies and local ant abundances, it may not be advantageous or productive for *Camponotus* to actively and continuously exclude other ant taxa. Competitive exclusion of ants may still have a role in

structuring the foliage-foraging ant assemblages, but this effect may be detectable only at a very small spatial and temporal scale, where certain ants may monopolize a particularly rich liquid source on an individual plant.

The low levels of specialization found in all networks of our study match those observed for other ant–plant interaction systems mediated by EFNs, as well as other facultative mutualist systems (e.g., seed dispersal, Blüthgen et al. 2007). We also did not detect higher levels of nestedness associated with EFNs or HPHs in the cerrado. Evidence from ant–HPHs interaction studies also suggests low levels of specialization (but with marked resource monopolization by dominant ant species; see Blüthgen et al. 2004; Staab et al. 2014). This pattern may be explained by the highly opportunistic feeding behavior of most ants and also by the relatively low structural or chemical constraints in the accessibility of liquid food sources to ants (Blüthgen and Fiedler 2004).

Whereas ants are mostly generalist visitors and their presence on plants is not dependent on the presence of liquid resources, our results suggest that there is some spatial variation in specialization of interactions. In Itirapina and Uberlândia (but not in Assis and Mogi-Guaçu), species-level specialization (d') was higher for plants with either type types of liquid resource. In these two localities, ants co-occurred less frequently on plants (compared with Assis and Mogi-Guaçu), and plants were visited by some ants in higher proportions than expected by the relative abundances of plant categories (with and without ant attractants). This variation in specialization levels is consistent with geographic differences in ant responses to plant-derived liquid resources noted in previous studies (Sendoya and Oliveira 2015). It is possible that bottom-up effects, driven by local plant diversity, and corresponding effects on trophobiont diversity and population size, contribute for the spatial variation on ant–plant interactions (Staab et al. 2014).

Although foliage-foraging ant assemblages in the cerrado lack behaviorally dominant species (Ribas and Schoereder 2004), there is evidence suggesting the existence of a group of ant species constant over time and space in most plants (i.e., core species), which shapes the structure of ant–plant interactions (Dáttilo et al. 2013; Lange et al. 2013). The response of the ant community to resource presence varied among localities (Fig. 3a), and key foliage-foraging genera such as *Camponotus* and *Pseudomyrmex* (together with *Ectatomma* and *Pheidole*) largely accounted for the spatial variation of visitation intensity to plants with liquid resources (Fig. 4a, c; Table A7). The numerical dominance of *Camponotus* ants in arboreal habitats and their frequent consumption of plant and insect exudates is widespread globally (e.g., Davidson et al. 2003), and well documented in the cerrado (Oliveira and Brandão 1991;

Del-Claro and Oliveira 1999; Schoederer et al. 2010). The great dependence of *Camponotus* species on liquid food sources (Davidson et al. 2003) likely explains their numerical response to the presence of exudates on foliage in all localities. *Pseudomyrmex* ants are less frequently found on cerrado foliage and forage in minor intensity, but are very opportunistic and actively use liquid food sources from plants (Oliveira and Brandão 1991; Schoederer et al. 2010). Comparatively, liquid resources may be only a nutritional complement for ants less specialized to forage on plants (e.g., *Pheidole*, *Ectatomma*). The numerical response of these ants to liquid resources may depend on the local availability of alternative food sources, on the local abundance or quality of the exudate (i.e., number of functional EFNs on plants), or on the proximity of the liquid source to their nests.

The protection that visiting ants can provide to plants may vary spatially and temporally, and depend on the characteristics of the ant assemblage or on the efficiency of particular ants as bodyguards (Mody and Linsenmair 2004; Koptur 2005; Sendoya et al. 2009). Although ant abundance on plants can negatively affect the presence of herbivores, this effect has been shown to vary geographically in the cerrado landscape and is mediated by how local ants respond to the presence of ant attractants on foliage (Sendoya and Oliveira 2015). Here, we presented evidence that ants in the genera *Camponotus* and *Pseudomyrmex* are most likely responsible for a negative effect on caterpillar infestation (Fig. 6a). Indeed, *Camponotus* ants are known as efficient bodyguards in cerrado (Del-Claro and Oliveira 2000; Oliveira and Freitas 2004). These ants not only behave aggressively toward caterpillars on foliage, but their presence also discourages oviposition by butterfly females (Sendoya et al. 2009). Cerrado species of *Pseudomyrmex* tend to be less aggressive against herbivores than those inhabiting myrmecophytes (see Oliveira and Brandão 1991; Janzen 1966), but may consume eggs opportunistically (S.F. Sendoya, personal observation). However, aggressive *Camponotus* and timid *Pseudomyrmex* frequently share plants bearing liquid resources in cerrado, which likely explains their combined negative effect on caterpillars.

In summary, we have shown that even if the general structure of visiting ant assemblages is rather homogeneous among plants with different resources, there are still small differences in ant visitation and patterns of specialization that may vary geographically. Some ant groups (*Camponotus* and *Pseudomyrmex*) typically respond to the availability of liquid food sources by increasing visitation levels, although this may depend on local conditions. There are potential implications of this pattern for the evolution of ant–plant facultative mutualisms mediated by liquid resources. The benefits for plants may depend on the specific composition of local ant

assemblages and on the actual level of dependence of ant species on plant-derived resources across the cerrado landscape. Thus, the variability in the strength of ant–plant interactions among ant taxa and cerrado sites has to be considered when addressing the conditions under which possession of ant-attracting sugar glands (EFNs), or even ant-tended trophobionts, can render fitness benefits to cerrado plants. Although networks of mutualistic interactions are highly heterogeneous not all interactions (links) are equivalent (Vazquez et al. 2009, 2015), and the role of some “core” groups (Dáttilo et al. 2013) can be relevant for the stability and evolution of the interactions as a whole. The links generated by key or core species are stronger, not only in terms of their frequency but also in terms of their net benefits generated for the mutualists (see Vazquez et al. 2015). Moreover, as we show here, it is necessary to consider that the response of core groups of species to local conditions and resources associated with the mutualistic interactions may change spatially on a large spatial scale. As consequence, the variable response of key species groups should be a strong factor driving the evolution of mutualism-related traits to be considered in other highly generalized systems such as some pollination and seed dispersal networks.

Acknowledgments We thank B. Dalsgaard, L. Jorge, M. Pareja, P. I. Prado, and S. Ribeiro for comments on the manuscript. G. Bieber, M. Vidal, A. Moreira, H. Soares, L. Sendoya, M. Pareja, and L. Kaminski helped in the field. A. V. Freitas provided valuable logistic support. We thank the Instituto Florestal do Estado de São Paulo, the Clube Caça e Pesca Itororó, and K. Del-Claro for support during fieldwork in Uberlândia. S.F.S. was sponsored by fellowships from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 07/59881-5, 12/23399-3). P.S.O. was supported by grants from FAPESP (11/18580-8, 12/23671-5, 14/23141-1), the Brazilian Research Council (CNPq, 306115/2013-1), and the Universidade Estadual de Campinas through Faepex.

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