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Research Article

Tree-Dwelling Ants: Contrasting Two Brazilian Cerrado Plant Species without Extrafloral Nectaries

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Ants dominate vegetation stratum, exploiting resources like extrafloral nectaries (EFNs) and insect honeydew. These interactions are frequent in Brazilian cerrado and are well known, but few studies compare ant fauna and explored resources between plant species. We surveyed two cerrado plants without EFNs, *Roupala montana* (found on preserved environments of our study area) and *Solanum lycocarpum* (disturbed ones). Ants were collected and identified, and resources on each plant noted. Ant frequency and richness were higher on *R. montana* (67%; 35 spp) than *S. lycocarpum* (52%; 26), the occurrence of the common ant species varied between them, and similarity was low. Resources were explored mainly by *Camponotus crassus* and consisted of scale insects, aphids, and floral nectaries on *R. montana* and two treehopper species on *S. lycocarpum*. Ants have a high diversity on cerrado plants, exploring liquid and prey-based resources that vary in time and space and affect their presence on plants.

1. Introduction

Foliage-dwelling ants are an important component in tropical environments [1–3], affecting locally the composition and abundance of other insect communities [4–6] and directly or indirectly driving mutualistic and trophic interactions in plant-herbivore-predator/parasite interactions [7–11]. High abundance and richness of ants on this stratum are due to a highly energetic liquid diet, mainly extrafloral nectaries (EFNs) and hemipteran honeydew [12–14]. Ants use a variety of resources from plants and their herbivores and these associations are facultative and vary temporally and spatially [1].

In the cerrado, a savanna-like vegetation in central Brazil, there is a high proportion of plants bearing EFNs, representing up to 31% of the plant individuals surveyed [15, 16] and a rich fauna of ants exploiting them [2, 17–19]. A vast literature about direct and indirect associations of ants and plants in this biome is available [20], but there are few studies comparing ant faunas and their resources between plant species, especially those without EFNs. Results

presented by Schoederer et al. [2] indicate that the presence of EFNs does not affect ant species richness within a given tree and there is no particular ant species composition typical of plants with EFNs.

To link the richness and seasonal variation of ants to attractive resources available on a particular plant species, we compared ant assemblages on two species that do not bear EFNs and are common of the cerrado region of central Brazil: *Roupala montana* Aubl. (Proteaceae) and *Solanum lycocarpum* St. Hill. (Solanaceae). In our sampling area, both plants have similar stature and structure, are consumed by myrmecophilous hemipterans [21, 22], and were found in different environments: *R. montana* occurring in native cerrado vegetation, where *S. lycocarpum* is rarely found, being common in altered areas at the borders of roads and agropastoral fields. The ability of *S. lycocarpum* to establish itself in a wider range of environments supposedly leads to bigger ant richness, in contrast to *R. montana*. On the other hand, impoverished areas, where *S. lycocarpum* occurs, can sustain weaker ant diversity, which can affect the ant fauna foraging on this species. We expect that differences

on the area of occurrence and resource availability between these plant species may lead to important differences in the composition of ant species.

2. Material and Methods

2.1. Study Area. This study was conducted in the Fazenda Agua Limpa (15°57'S, 47°54'W), Federal District, Brazil. This 4,500 ha farm belongs to the University of Brasilia and includes mainly undisturbed cerrado vegetation and agro-silvo-pastoral experimental areas. The region has altitudes around 1,050 m a.s.l., average annual temperature of 22°C, and average annual rainfall of 1,417 mm (series from 1980 to 2004, data from RECOR Meteorological Station, <http://www.recor.org.br/>), and a marked seasonality, with a lengthy dry season ranging from May to September and a wet season from October to April.

2.2. Plant Species. *Roupala montana* is widely distributed in the Brazilian cerrado [23] and is abundant in cerrado remnants of the Federal District. It is an evergreen shrub that simultaneously sheds leaves and produces new ones, reaching up to three meters height, blooms for a long period during the year, and is pollinated by moths [24–26]. It hosts ant-tended hemipterans like scale insects (Coccoidea), aphids (Aphidoidea), and, especially a leafhopper species, *Rotundicerus* sp. (Cicadellidae and Idiocerinae), which forms large aggregates of nymphs feeding on new leaves at the beginning of the rainy season [21]. A rich fauna of caterpillars, including *Hallonympha paucipuncta* (Spitz, 1930) (Riodinidae) and at least 10 species of Lycaenidae, consumes its leaves and inflorescences [27–29].

Solanum lycocarpum is an evergreen shrub with maximum height of about two meters, being extremely common in disturbed environments [30, 31]. New leaves and flowers grow throughout the year, but flowers do not reward nectar to insects, and pollen is the floral resource collected by bumblebees through buzz pollination behavior [30]. Leaf surfaces are covered with simple glandular and nonglandular trichomes and stellate trichomes [32]. The treehopper *Enchenopa brasiliensis* Strümpel, 2007 (Membracidae) is a common species feeding on apical meristems and inflorescences [22]. In the study area, two species of Membracidae, one of Aetalionidae and an indetermined number of species of scale insects were tended by ants on new leaves of this plant. One Cicadellidae species was very abundant too on the same plants, but it was not associated with ants. *Solanum lycocarpum* leaves are eaten by several microlepidoptera, especially *Symmetrischema chloroneura* (Meyrick, 1923) (Gelechiidae) [33], its stems are consumed by gall-forming weevil, *Collabismus clitellae* Boheman, 1837 (Curculionidae) [34] and its leaves and fruits are eaten by several species of mammals [31, 35–37]. Attini nests (Formicidae and Myrmicinae) favor the establishment of seedlings and enhance nutrient in the leaves of *S. lycocarpum* [38].

2.3. Samples and Data Analysis. Individuals of both plant species were carefully examined always in the morning

TABLE 1: Frequency of occurrence of ants and myrmecophilous hemipterans on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil. Comparisons made with contingency tables.

Characteristics	Roupala	Solanum	χ^2	P
Examined plants	327	431		
Plants with ants	218	226	15.517	0.0001
Plants with myrmecophilous hemipterans	139	188	0.094	0.816
Co-occurrence of ants and hemipterans	115	143	0.328	0.620
Plants with hemipterans without ants	24	45	2.161	0.141
Plants with ants without hemipterans	103	83	15.046	0.0001

period. Every ant observed on the plant was collected and the occurrence of myrmecophilous hemipterans registered. *Roupala montana* plants ($n = 327$) were examined between April and September (dry season) of 2007 in a typical cerrado vegetation area of 2 ha. Previous surveys in the same study area were made on this species during the wet season of 2006, when the focus was to collect the ants tending nymphs of *Rotundicerus* sp. ($n = 116$). *Solanum lycocarpum* plants ($n = 431$) were inspected between March 2007 and March 2008 along dirt roads that cross a mosaic of environments, including typical and “campo sujo” (a physiognomy dominated by herbaceous vegetation) native cerrado areas, pastures and cultures of coffee, sorghum, and pine. The sampling area of *S. lycocarpum* was more widely spread than that of *R. montana*.

The mean similarity of ant species composition between the two plant species was calculated by grouping the samples of each month from April and October ($n = 7$). The similarity indexes and rarefaction curves were generated using EstimateS [39]. The frequency tests were made using BioEstat 5.0 [40].

3. Results

Ants were more frequent on *R. montana* (67%) as compared to *S. lycocarpum* (52%) and this difference was due to higher occurrence of ants on *R. montana* plants without myrmecophilous hemipterans (Table 1). Along the study we collected a total of 45 ant species from 11 different genera. We recorded 35 species on *R. montana* and 26 on *S. lycocarpum*, with estimated richness (first order Jackknife \pm standard deviation) of 40 (± 2.6) and 29 (± 2.3), respectively, (Figure 1; Table 2).

The frequency of occurrence of the most common ant species were different on the two plant species (Table 2) and the mean similarity (\pm sd) of the ant assemblages for the dry season was low (Sorensen Index = 0.419 \pm 0.078), especially when the frequency of occurrence of ant species was considered (Morisita-Horn Index = 0.372 \pm 0.167).

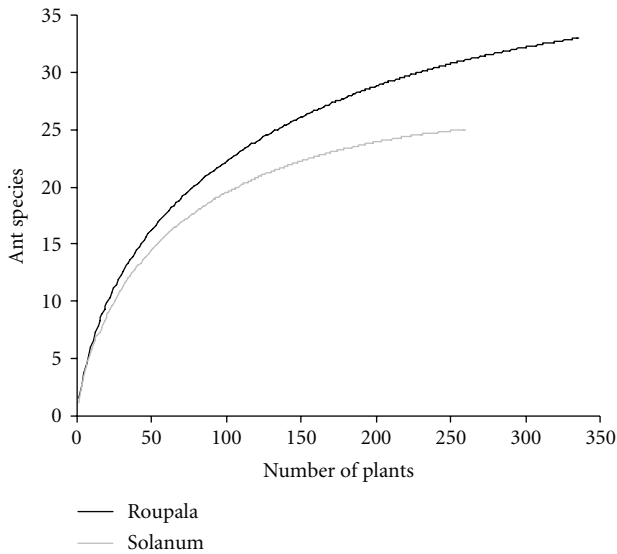


FIGURE 1: Rarefaction curves of ant species collected on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil.

Scale insects were an abundant resource in the leaves of *R. montana*, being found throughout the sampling period and 21% of ants in this plant were exploring this resource. We found 15 species of ants attending scale insects, and the most frequent were *Cephalotes pusillus* (Klug, 1824) (17 occurrences), *Camponotus crassus* (Mayr, 1862) (8), *Brachymyrmex* sp. (7), *Crematogaster evallans* (Forel, 1907) (6), and *Solenopsis* sp. (5). Some individuals of *R. montana* were flowering between April and July 2007 and developing inflorescences were explored by aphids, associated to four ant species, mainly *Cr. evallans* (4) and *Camponotus (Myrmaphaenus)* sp.2 (3). Seven species were recorded exploring mature floral nectaries, mostly *Ce. pusillus* (5) and *Camponotus (Myrmaphaenus)* sp.2 (4).

The frequency of occurrence of the commonest ant species was different on *R. montana* with and without *Rotundicerus* sp. A large proportion (67%) of the *R. montana* individuals examined during the dry season had ants, and 68% of the groups of *Rotundicerus* sp. on the same plant species and in the same area where tended by ants during the rainy season of 2006. Although the occurrence of the leafhopper did not enhance the frequency of visits of ants, it altered the composition of the ant fauna. The most notable cases were *Ca. crassus* and *Azteca instabilis* (Smith, 1862), which increased their frequency on the plants when *Rotundicerus* sp. was present, from 4 to 28% and 0 to 10%, respectively. *Cephalotes pusillus* and *Crematogaster stollii* Forel, 1885, on the other hand, decreased their frequency from 19% to 8% and from 7% to 0%, respectively.

Major resources explored by ants in *S. lycocarpum* were two species of Membracidae, each one present in 23% of the examined plants and *Ca. crassus* was the most frequent ant found in association with them. One species of Aetalionidae and scale insects were infrequent on this plant, being seen three and seven times, respectively. We lack nutritional information of glandular trichomes of *S.*

lycocarpum, but small ants, like some species belonging to the genera *Brachymyrmex*, *Dorymyrmex*, *Pheidole*, and *Solenopsis*, possibly use this resource. *Pseudomyrmex* spp. were generally present (68%) on plants without myrmecophilous hemipterans.

4. Discussion

We found a high frequency of plants visited by ants, showing the prevalence of ants foraging on cerrado plants, even during the dry season, when *R. montana* plants were examined. The high availability of potential resources for ants [2, 13, 41], especially myrmecophilous hemipterans in the cerrado vegetation [21, 22, 42, 43], makes this stratum attractive to ants. Even with the predominance of liquid diet, it is important to stress that various species of ants forage for preys on plants, including myrmecophilous hemipterans [44]. In an urban area of Campinas (SP), for example, 70% of the diet of *Pseudomyrmex gracilis* (Fabricius, 1804) was based on arthropods, primarily a Psyllidae species (Hemiptera and Sternorrhyncha) [45]. This can explain the high frequency of *Pseudomyrmex* spp. in the samples, as well as the presence of *Pachycondyla* spp., a genus of predator ants [46]. Besides, some genera (e.g., *Cephalotes* and *Pseudomyrmex*) nest in dried plant branches, and this too can affect the ant assemblage that forage on an individual plant.

Richness of ants was high in both plant species, especially considering that the surveys were conducted only in the morning. Studies including day and night time observations, showed an average of 21 ant species visiting EFNs on six species of cerrado plants, with a minimum of nine on *Qualea multiflora* Mart. (Vochysiaceae) and a maximum of 34 on *Caryocar brasiliense* Camb. (Caryocaraceae) (Appendix 6.1 in [1]). Sequential samplings on *Schefflera vinosa* (Cham. & Schltdl.) Frondin and Fiasch (Araliaceae) revealed that *Guayaquila xiphias* (Fabricius, 1803) treehoppers are attended day and night by 21 species of honeydew-gathering ants [42], whereas shrubs of *Solanum lycocarpum* hosting *Enchenopa brasiliensis* treehoppers are regularly visited by 10 ant species [22]. Campos et al. [19], using pitfall traps in a cerrado area of the state of Goias, found 16 species of ants on the shrub stratum (height between 0.5 and 1.5 m) and 28 on the arboreal stratum (dominated by taller, mature trees).

As expected, ant fauna between the two plants species investigated showed small similarity. The different habitats of occurrence of the plants undoubtedly had an effect on this result [47–50], but variation on resource availability might have an important influence on the composition of ant species [41]. So there must be a particular ant species composition typical of plants with these kinds of resources (e.g., big groups of myrmecophilous hemipterans and active EFNs) even though for a limited period of time. Probably the fidelity of dominant ants plays a key role in structuring assemblages of tending ants on this rich food resource. Hence, comparisons on the frequency of occurrence and composition of species of ants on plants with and without these resources need to be done when they are present

TABLE 2: Ant species and its occurrence on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil. The most frequent species are highlighted.

Formicidae	Roupala	Solanum
Myrmicinae		
<i>Cephalotes adolphi</i> Emery	2	0
<i>Cephalotes atratus</i> Linnaeus	0	2
<i>Cephalotes betoi</i> De Andrade	3	0
<i>Cephalotes depressus</i> (Klug)	5	10
<i>Cephalotes grandinosus</i> (Smith)	6	0
<i>Cephalotes liepini</i> de Andrade & Baroni Urbani	2	0
<i>Cephalotes pusillus</i> (Klug)	147	18
<i>Crematogaster distans</i> Mayr	3	6
<i>Crematogaster evallans</i> Forel	11	3
<i>Crematogaster stollii</i> Forel	14	0
<i>Crematogaster victima</i> (Smith)	1	0
<i>Crematogaster</i> sp.	3	0
<i>Nesomyrmex pleuriticus</i> (Wheeler)	1	0
<i>Nesomyrmex tristani</i> Emery	1	0
<i>Pheidole capillata</i> Emery	10	7
<i>Pheidole</i> sp.1 grupo <i>fallax</i>	2	1
<i>Solenopsis substituta</i> (Santschi)	0	9
<i>Solenopsis</i> sp.	12	0
Formicinae		
<i>Brachymyrmex</i> sp.	14	9
<i>Camponotus arboreus</i> (Smith)	4	0
<i>Camponotus atriceps</i> (Smith)	2	0
<i>Camponotus blandus</i> (Smith)	1	2
<i>Camponotus crassus</i> Mayr	64	105
<i>Camponotus fastigatus</i> Roger	0	2
<i>Camponotus melanoticus</i> Emery	1	5
<i>Camponotus novogranadensis</i> Mayr	3	0
<i>Camponotus rufipes</i> Fabricius	0	38
<i>Camponotus</i> (<i>Myrmaphaenus</i>) sp.1	1	3
<i>Camponotus</i> (<i>Myrmaphaenus</i>) sp.2	34	2
<i>Camponotus</i> (<i>Myrmaphaenus</i>) sp.3	0	1
<i>Camponotus</i> (<i>Myrmaphaenus</i>) sp.4	0	3
<i>Camponotus</i> (<i>Myrmobrachys</i>) sp.1	1	0
<i>Camponotus</i> (<i>Myrmobrachys</i>) sp.2	2	0
<i>Camponotus</i> (<i>Tanaemyrmex</i>) sp.	4	2
Dolichoderinae		
<i>Azteca instabilis</i> (Smith)	19	0
<i>Azteca</i> sp.	14	0
<i>Dorymyrmex</i> sp.1	0	6
Pseudomyrmecinae		
<i>Pseudomyrmex gracilis</i> (Fabricius)	0	14
<i>Pseudomyrmex pupa</i> (Forel)	0	2
<i>Pseudomyrmex termitarius</i> (Smith)	0	1
<i>Pseudomyrmex tenuissimus</i> (Emery)	7	2
<i>Pseudomyrmex rufiventris</i> (Forel)	1	4
<i>Pseudomyrmex</i> sp. gp. <i>Pallidus</i>	1	4
Ponerinae		
<i>Pachycondyla inversa</i> (Smith)	1	0
<i>Pachycondyla villosa</i> (Fabricius)	3	0

(e.g., active EFNs) and, preferentially, carefully choosing the species of plants, as phylogeny and genetic distance have a known influence in herbivore communities [51, 52].

Most studies about ant-hemipteran associations do not take into account records of ants on plants during periods of absence of these sap-sucking insects. Nevertheless they feed on young tissues of the host plant [9, 21, 22, 42, 43], so plant phenology has a direct effect on their occurrence and their potential association with ants. *Solanum lycocarpum* continuously produces leaves that are consumed by treehoppers practically throughout the year, while *R. montana* produces leaves roughly around September and November, period when its main sap-sucking insect, the myrmecophilous hemipteran, *Rotundicerus* sp., achieves its development and leaves the host plants. In any case, both plant species are patrolled by ants in the absence of their main hemipteran resources and other apparent ones. Plant phenology and seasonality have an effect on availability of resources exploited by tree-dwelling ants, producing a dynamics of niches occupied by a turnover of ant species. This yearly variation can reveal the strength of mutualistic associations between ants and myrmecophilous hemipterans and plants with or without EFNs, being important to understand the patterns of ant-plant-herbivore interactions.

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