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The arboreal ant community visiting extrafloral nectaries in the Neotropical cerrado savanna

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Summary

The cerrado savanna of Brazil embraces an area of approximately 2 million km^2, in which vegetation physiognomies may vary from open grassland to forest with a discontinuous herbaceous layer. Here we describe the main ecological factors accounting for the prevalence of ants on cerrado foliage, and present a general characterization of the arboreal ant fauna of this savanna. The high incidence of ants on cerrado foliage results mostly from the wide occurrence of predictable liquid food sources in the form of extrafloral nectaries (EFNs) and insect honeydew, which act as efficient promoters of ant activity on vegetation. In addition, stem galleries and cavities constructed by boring beetles and insect galls create a nesting space frequently used by arboreal ants. Specific studies involving ants, herbivores and plants are reported to demonstrate the impact that foliage-dwelling ants can have on phytophagous insects, herbivory levels, and ultimately on host plants. These studies show that: (i) ants visit EFNs and likely benefit from this resource; (ii) EFN-gathering ants can benefit particular plant species by reducing herbivory and increasing plant fitness; (iii) presence of EFNs does not affect ant species richness within a given tree; (iv) there is not a particular ant species composition typical of plants with EFNs; (v) although plants with EFNs are visited by more ant individuals than non-nectariferous plants, this visitation pattern does not translate into lower numbers of herbivores on the nectariferous plant community. We suggest some promising research avenues to elucidate how community-level parameters can be tied to the ecology of ant-plant associations in cerrado.

Keywords

Ant community; ant-plant interactions; cerrado savanna; extrafloral nectaries; herbivory; insect honeydew; species richness

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Introduction

Ants outnumber all other terrestrial animals and their supremacy in terrestrial habitats is combined with a broad taxonomic diversity and a widespread occurrence around the globe (Wheeler, 1910; Hölldobler and Wilson, 1990). According to Wilson (1987), the ecological success of ants can be ascribed mostly to their eusocial organization, local abundance, and diversity of adaptations. Indeed, ants present a broad diversity of feeding habits and foraging strategies, which include the use of foliage as a foraging substrate (Carroll and Janzen, 1973). The numerical and behavioral dominance of ants on vegetation have been repeatedly documented in different tropical habitats (Adis et al., 1984; Majer, 1990; Tobin, 1991, 1994; Davidson et al., 2003). The ant fauna exploiting the canopy environment includes not only typical arboreal species (i.e., that nest inside plant structures), but also ground-nesting ones that regularly climb on plants to search for animal prey and plant-derived food resources (Rico-Gray et al., 1998; Blüthgen et al., 2000; Davidson et al., 2003). Ant foraging on tropical vegetation is encouraged by the prevalent occurrence of predictable and renewable plant- and insect-derived exudates such as extrafloral nectar, honeydew from sap-feeding hemipterans, and secretions from lepidopteran larvae (Figure 1; see Bentley, 1977; Díaz-Castelazo et al., 2004; Koptur, 2005; Styrsky and Eubanks, 2007; Stadler and Dixon, 2008). Indeed, extrafloral nectaries (EFNs) are widely distributed amongst the flora of different vegetation types worldwide (Rico-Gray and Oliveira, 2007), and surveys on foliage have shown that exudate-producing insects are abundant in the canopy of tropical habitats (e.g., Rico-Gray, 1993; Blüthgen et al., 2000; Dejean et al., 2000).

Studies with foliage-dwelling ants have shown that their foraging ecology is largely mediated by the offer of plant- and insect-derived liquid food, and that the most abundant species in canopy samples are typically exudate-consumers (Davidson, 1997; Blüthgen et al., 2000; Dejean et al., 2000). Using the ratio of N isotopes ($^{15}N/^{14}N$, formulated as $\delta^{15}N$), Davidson et al. (2003) investigated the causes of the dominance of ants in rainforest canopies in Peru and Borneo. Because animal tissues are almost always enriched in ^{15}N compared to plants, there is a progressive upgrading of $\delta^{15}N$ at successive trophic levels (e.g., Post, 2002) that permits to compare N sources among ant species with different foraging modes. Davidson et al. (2003) showed that despite the very low concentrations of nitrogenous compounds in plant tissues, exudate-consuming ant species – particularly those in the subfamilies Formicinae and Dolichoderinae – obtain their nitrogen lower in the trophic chain compared to sympatric carnivorous species (see also Blüthgen et al., 2003).

These findings support Tobin's (1991, 1994) hypothesis that the extraordinary abundance of canopy-dwelling ants in tropical forests occurs because they act chiefly as herbivores (i.e., consumers of plant-derived exudates), rather than as predators or scavengers of animal matter as previously assumed (Hölldobler and Wilson, 1990). Presence of extrafloral nectaries and honeydew from sap-feeding hemipterans on foliage can be relevant for the structure of food webs in tropical habitats by fueling costly prey-hunting activities by ants (Figure 1), which in turn can positively affect some plant

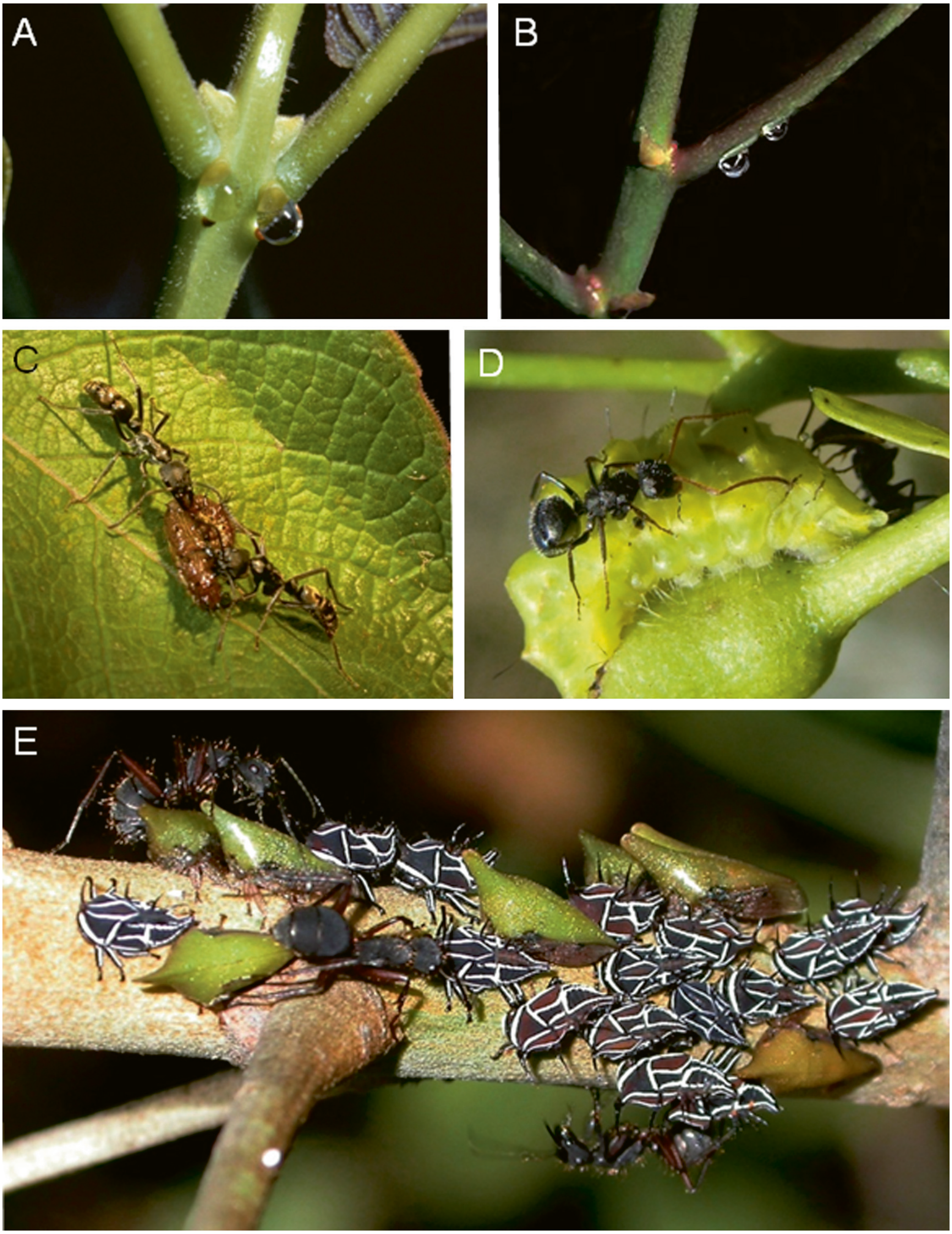

Figure 1. Accumulated extrafloral nectar on the (A) stem of *Qualea grandiflora* and (B) leaf petiole of *Eriotheca gracilipes*. (C) Workers of *Pachycondyla villosa* attacking a caterpillar of the butterfly *Eunica bechina* on a young leaf of the EFN-bearing plant *Caryocar brasiliense*. (D) Workers of *Camponotus crassus* collecting sugary secretions from a myrmecophilous caterpillar of the riodinid butterfly *Synargis* sp. (E) Workers of *Camponotus rufipes* tending an aggregation of the honeydew-producing treehopper *Guayaquila xiphias*. Photographs (C), (E) courtesy of A. V. L. Freitas; (D) courtesy of L. A. Kaminski.

species through predation on herbivores (Davidson and Patrell-Kim, 1996; Davidson, 1997; Tillberg, 2004; Koptur 2005).

The Brazilian Cerrado

The cerrado savanna embraces an area of approximately 2 million km^2, which corresponds to nearly 22% of Brazil (Oliveira and Marquis, 2002). The physiognomy of the cerrado biome varies from open grassland to forest with a discontinuous herbaceous layer. Between these two extremes lies a continuum of savanna formations that extends throughout the entire range of woody plant density, which is called together as the *cerrados* (Oliveira-Filho and Ratter, 2002).

The purpose of the current review is to describe the main ecological factors accounting for the prevalence of ants on the foliage layer of cerrado, and to present a general characterization of the arboreal ant fauna of this savanna. We also report on specific study cases involving ants, herbivores and plants, and demonstrate the potential effects of ants on phytophagous insects as well as on plant fitness in cerrado. Finally we test the importance of EFNs on ant species richness and composition in cerrado vegetation, and suggest some promising research avenues to shed light on how such community-level parameters are linked with the ecology of ant-plant associations in this neotropical savanna.

Liquid food sources as promoters of ant activity on cerrado foliage

The high incidence of ants on cerrado foliage results mostly from the wide occurrence of predictable liquid food sources in the form of extrafloral nectaries (EFNs) and insect-derived secretions, which act as promoters of ant activity on plants (Figure 1; see also Ribas et al., 2003; Oliveira and Freitas, 2004). For instance, a total of 45 EFN-bearing woody species from 17 families were recorded in 10 areas of cerrado in southeast and west Brazil, and quantitative samplings of the local floras revealed that 15 to 25% of the species have EFNs, representing up to 31% of the plant individuals surveyed (Oliveira and Leitão-Filho, 1987; Oliveira and Oliveira-Filho, 1991). Ant censuses carried out over 24 hours on EFN-bearing *Caryocar brasiliense* plants (Caryocaraceae) recorded a total of 34 species of visiting ants (Oliveira and Brandão, 1991), whereas on *Ouratea hexasperma* (Ochnaceae) a total 24 nectar-gathering ant species were registered day and night by Oliveira et al. (1995). For a list of studies on plants bearing EFNs and associated ant fauna at diverse habitats, see Rico-Gray and Oliveira (2007).

Hemipteran honeydew and secretions from myrmecophilous butterfly larvae also play an important role as ant attractants in cerrado (Figure 1D, E; see also Del-Claro and Oliveira, 1996; Diniz and Morais, 1997; Rico-Gray and Morais, 2006; Kaminski et al., 2009). Surveys carried out by Lopes (1995) revealed that ants associated with honeydew-producing treehoppers (Membracidae) are present on 30% of the plant species monitored (1025 plants) over a 3600 m transect in the cerrado. Sequential samplings on *Schefflera vinosa* (Araliacae) revealed that *Guayaquila xiphias* treehoppers are

Figure 2. Close-up view of a colony of *Cephalotes pusillus* inside a stem gallery of a live plant species in cerrado. Photograph courtesy of H. Soares Jr.

attended day and night by 21 species of honeydew-gathering ants (Del-Claro and Oliveira, 1999), whereas shrubs of *Solanum lycocarpum* (Solanaceae) hosting *Enchenopa brasiliensis* treehoppers are regularly visited by 10 ant species (Moreira and Del-Claro, 2005).

Finally, an additional factor accounting for ant predominance on cerrado foliage is the frequent occurrence of stem galleries constructed by boring beetles, which create a potential nesting space for numerous arboreal ant species (Figure 2; see also Morais and Benson, 1988; Ribas et al., 2003; Ribas and Schoereder, 2004). Nesting on vegetation is further promoted by the cavities left by insect galls after emergence, which are commonly occupied by ant colonies (Fernandes et al., 1988, Araújo et al., 1995).

The role of exudate-feeding ants as herbivore deterrents in cerrado

Case study 1: Ants at extrafloral nectaries of Caryocar brasiliense *(Caryocaraceae)*

The interaction system involving the EFN-bearing shrub *Caryocar brasiliense* and its associated nectar-gathering ants and insect herbivores has been studied in detail for nearly 20 years. The plant is visited day and night by a diverse ant assemblage (Oliveira and Brandão, 1991), and is infested by the following insect herbivores: the butterfly *Eunica bechina* (Nymphalidae), whose larvae feed on young leaves; the stink bug *Edessa rufomarginata* (Pentatomidae) that feeds on sap from buds and fruits; the dipteran *Prodiplosis floricola* (Cecidomyiidae), whose larvae consume developing buds; and two species of galling wasps (Chalcidoidea) that infest branches and leaves. Controlled field experiments using ant-visited and ant-excluded plants showed that ant foraging on *C. brasiliense* reduces infestation levels by four of the herbivore species examined, resulting in increased production of flowers and initial fruits by ant-visited plants (Oliveira, 1997).

Aggression by ants towards larvae of *Eunica bechina* frequently kills the caterpillars (Figure 1C), and field experiments have further demonstrated that ant presence on leaves inhibits oviposition by female butterflies (Freitas and Oliveira, 1992, 1996). More recently, using dried ant specimens pinned to leaves to signal predation risk, Sendoya et al. (2009) showed that gravid butterflies use size and form as visual recognition cues to distinguish deadly from innocuous ants, and avoid ovipositing on plant locations occupied by aggressive ants more likely to kill larval offspring. Herbivore deterrence by ants on EFN-bearing plants in cerrado has also been demonstrated for *Qualea grandiflora* and *Q. multiflora* (Vochysiaceae) (Figure 1A; Oliveira et al., 1987; Costa et al., 1992; Del-Claro et al., 1996), and *Lafoensia pacari* (Lythraceae) (Korndörfer and Del-Claro, 2006).

Case study 2: Ants tending honeydew-producing Guayaquila xiphias *(Membracidae)*

The honeydew-producing treehopper *Guayaquila xiphias* is tended day and night by a diverse assemblage of honeydew-gathering ants on shrubs of *Schefflera vinosa*, a relationship known as trophobiosis (Figure 1E; see Del-Claro and Oliveira, 1999). By flicking accumulated honeydew to lower leaves and ground, brood-guarding females and incipient treehopper aggregations are able to effectively attract potential tending ants to the host plant (Del-Claro and Oliveira, 1993, 1996). Some ant species may tend *G. xiphias* aggregations continuously for 24 hours, and often construct shelters of dry grass to house the treehoppers (Oliveira et al., 2002). Ant-exclusion experiments demonstrated that aggressive honeydew-gathering ants ward off nearby predators and parasitoids and positively affect treehopper survival. Ant attendance can also increase treehopper fecundity if brood-guarding females transfer parental care to ants and lay an additional clutch (Del-Claro and Oliveira, 2000).

Shrubs of *S. vinosa* can benefit from hosting treehopper aggregations because patrolling and deterring behavior by tending ants negatively affect different types of leaf herbivores (thrips, chewing beetles, and mining caterpillars), and decrease their damage to the plant (Oliveira and Del-Claro, 2005). The myrmecophilous bud-destroying butterfly *Parrhasius polibethes* (Lycaenidae), on the other hand, frequently infests plants with ants and *G. xiphias* and shifts ant attention partly away from treehoppers towards its liquid-rewarding caterpillars. Thus the multitrophic system around ant-*Guayaquila xiphias* associations can produce variable outcomes relative to ant-derived effects on leaf and flower herbivores, which makes uncertain the overall impact on *Schefflera vinosa* host plants (Oliveira and Del-Claro, 2005).

Because ants commonly prey on phytophagous insects, hemipteran honeydew has been proposed to play an appeasement role by restraining aggression by ants, which would then begin tending activities (Hölldobler and Wilson, 1990). In a recent experimental study involving the manipulation of cuticular chemical profiles of freeze-dried prey, Silveira et al. (2010) demonstrated that chemical background matching with the host plant (i.e., chemical camouflage) protects *G. xiphias* treehoppers against predation by the tending ant *Camponotus crassus*, regardless of honeydew supply. Indeed, if treehoppers are transferred to a plant species with which they have a low chemical similarity, predation by ants is augmented. Additionally, experimental manipulation of moth larvae to match the chemical background of the treehopper's host plant (*Schefflera vinosa*) decreased ant predation compared to unchanged controls. *Guayaquila* treehoppers receive a range of benefits from attendance by aggressive ants, and even attract the latter onto host plants through honeydew flicking (Del-Claro and Oliveira, 1996, 2000). However, because honeydew-gathering ants may occasionally prey on hemipteran trophobionts (Sakata, 1994; Offenberg, 2001), chemical camouflage decreases the risk of ant predation to *Guayaquila* treehoppers and enhances the variable character of the outcomes of such ant-trophobiont associations (see Rico-Gray and Oliveira, 2007; Stadler and Dixon, 2008).

From tritrophic interactions to ant and plant communities

Most studies on ant-plant interactions focus on the effects of ants on plant fitness, reporting which ant species are present on the plants, their aggressiveness, and their effect on plant survival and reproduction (Del-Claro et al., 1996; Oliveira et al., 1987; Oliveira, 1997; Oliveira et al., 1999; Stephenson, 1982; Sobrinho et al., 2002; Rosumek et al., 2009). Exclusion experiments are extremely effective in such studies to detect the possible advantages obtained by the plants due to ant visitation. In contrast, studies investigating the advantages of the interactions to the ants are rare (Lach et al., 2009). In addition, there is a lack of information of the role of tri-trophic interactions to the understanding of the structure of cerrado communities (Del-Claro and Torezan-Silingardi, 2009). Here we use data of cerrado arboreal ant communities to understand whether plant-ant-herbivore systems can contribute to the cerrado biodiversity.

Because the abundance and frequency of EFN-bearing plants in cerrado is relatively high (Oliveira and Freitas, 2004), it is expected that such liquid resources would influence the structure of ant communities. It is also known that plant species richness and density correlates with ant species richness (Ribas et al., 2003), although the mechanism behind this pattern remains unexplained. The question is: Why do ants forage on plants? As stressed above, ants may use EFNs when they are available, or may forage on other resources such as insect exudates, animal prey, seeds, and even use plants as refuge or nesting sites (Figures 1, 2). Most of these resources are present in almost all habitats, but the proportion of plants bearing EFNs is generally higher in cerrado than in other habitats (see Rico-Gray and Oliveira, 2007). The presence of this energy-rich resource on foliage could increase ant species richness, or change ant species composition in cerrado. On the other hand, the presence EFNs could attract dominant ant species, which would competitively exclude more submissive species, and thus decrease ant species richness. Because nectar secretion is usually related with plant phenology and increases in the pre-reproductive phase (Bentley, 1977), ant communities are also expected to vary according to nectar abundance (Campos et al., 2008). If extrafloral nectar is available throughout the year, ants are expected to visit plants for a longer period. However, if the resource is ephemeral, ants would abandon the plant when nectar production decreases to a level that no longer represents a profitable food resource (see Rico-Gray, 1993; Rico-Gray et al., 1998).

Recently, Rosumek et al. (2009) revised the effect of ants on plant herbivory. The removal of ants had a strong effect on herbivory, and plants without ants suffered 97% more herbivory and presented 53% more herbivores than plants visited by ants. Moreover, the presence of ants positively affected plant biomass (leaf production) and reproduction. The observed effects are always more expressive on plants from tropical regions than from temperate ones.

The benefits acquired by ants through foraging on plants can be quite distinct. Ant-visited plants can be classified into myrmecophytes (plants bearing structures, known as domatia, which house ant colonies) or myrmecophiles (plants presenting EFNs, food bodies, or other ant attractants). Rosumek et al. (2009) consider the myrmecophytes as the most effective cost-benefit system. It is expected that ants associated with myrmecophytes are more specialized, because these systems usually result from co-evolutionary changes of both plants and ants (Fonseca and Ganade, 1996), while the in the myrmecophiles there are no expected evolutionary changes in ants in response to plant adaptations. The intimate interactions between ants and myrmecophytes have been studied both in cerrado and in sites in which plants have been introduced. *Tococa formicaria* (Melastomataceae) is a myrmecophyte from cerrado that attracts several ant species, but mainly two species in the genus *Azteca* (Bizerril and Vieira, 2002). The presence of ant domatia does not implicate in an obligatory interaction between ants and the plant. Nevertheless, when *Azteca* ants are present the plants suffer less herbivory compared to other species of ant occupants. Similar results have been found by Wetterer (1997) with introduced myrmecophytes of the genus *Cecropia* (Cecropiaceae) in Hawaii.

Myrmecophilous plants providing liquid food (e.g., EFN-bearing plants), on the other hand, tend to attract more generalist ant species (Blüthgen et al., 2000; Goitia and Jaffé, 2009). The effectiveness of ants as anti-herbivore agents is higher for myrmecophytic than for myrmecophilous plants (see Heil and McKey, 2003; Rico-Gray and Oliveira, 2007, and included references). Indeed, following the ant-exclusion treatment, Rosumek et al. (2009) recently reported that myrmecophytes suffered four times more herbivory than myrmecophilous plants. This may be due to the fact that ant species inhabiting myrmecophytes are more specialized and/or more aggressive towards herbivores than those visiting myrmecophilous plants (see also Heil and McKey, 2003).

Are EFNs important to structure cerrado ant communities?

The structure of arboreal ant communities in cerrado have recently been investigated in association with a number of parameters of the vegetation (Ribas et al., 2003; Ribas and Schoereder, 2004; Campos et al., 2008). Ant species richness is correlated with

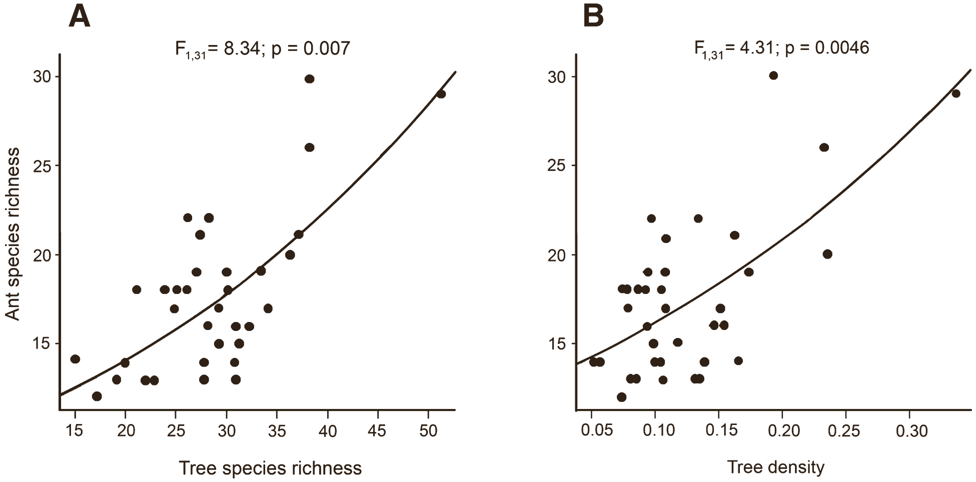

Figure 3. Relationship between ant species richness and (A) tree species richness and (B) tree density in two areas of cerrado, at Paraopeba and Distrito Federal (Brazil). Modified from Ribas et al. (2003).

both plant species richness and tree density (Figure 3) (Ribas et al., 2003). Although ant species have been found to occur in a mosaic spatial distribution in many habitats (reviewed by Rico-Gray and Oliveira, 2007), this pattern was not found to apply to cerrado arboreal ants (Ribas and Schoereder, 2004). Therefore, processes such as competition, behavioral dominance and species-specific relationships between ants and plants seldom explain ant species richness and composition in cerrado. Moreover, processes related to plant architecture and trunk characteristics such as bark thickness also did not correlate with ant species richness (Santos et al., 2008).

Because the usual described pattern is linked to tree species richness and abundance (Ribas et al., 2003), it is expected that this pattern is associated with resource abundance. Because EFNs represent a relevant plant-derived resource to ants, we used data from two studies to evaluate the importance of the presence of EFNs for the structure of ant communities.

The first study describes the arboreal ant communities in the cerrado reserve of Paraopeba, Minas Gerais (southeast Brazil), where we tested the hypotheses that EFN-bearing trees have (i) more species-rich ant communities, and (ii) more distinctive ant species compositions compared to non EFN-bearing species.

The second study describes the ant communities on shrub species with and without EFNs in the Parque Nacional da Serra do Cipó (Minas Gerais), where we tested the hypotheses that EFN-bearing plants have (i) more ant foragers, and (ii) lower numbers of herbivores compared to plants lacking EFNs. Additionally, the aggressiveness of ants towards live baits placed on plants with and without EFNs was also evaluated. This study was carried out in two seasons (dry/cold, and rainy/hot period), in order to investigate a possible relationship between ant behavior and phenological plant traits.

Arboreal ant species richness and composition in cerrado

To test the hypotheses that ant species richness and composition are different in trees with and without EFNs, arboreal ants were sampled using baited pitfall traps, in 352 individuals from 48 plant species (Table 1). From these, 11 species (22.9%) and 96 individuals (27.3%) have EFNs. These differences in the proportion of species and individuals with and without EFNs were considered in the analyses, because the higher number of samples from plants without EFNs could bias the results. A total of 92 ant species were sampled on plants lacking EFNs (Table 2). Only three ant species – *Leptothorax* sp., *Nesomyrmex asper*, and *Wasmannia auropunctata* – occurred exclusively on plants with EFNs. Plants with and without EFNs presented similar ant species richness ($F_{1,44}=0.07$; $p=0.78$), although ant richness was significantly affected by the number of plant individuals checked, indicating an effect of sampling effort ($F_{1,45}=90.69$; $p<0.001$; Figure 4). Furthermore, there was no significant difference of ant species composition between plants with and without EFNs (NMDS, followed by ANOSIM; $p>0.05$; Figure 5). These results suggest that ants visit cerrado trees independently of the presence of EFNs. Indeed, plants may offer several potential resources for the ants, including nesting sites and seeds, and other food sources are also found on foliage, such as honeydew, insect prey, and fungal hyphae. Furthermore, the absence of a particular ant species composition foraging on plants with EFNs indicates that the relationship between ants and plants is facultative. The seasonality of extrafloral nectar production, associated with the rarity of ant domatia among plant species, may impair the establishment of an obligatory relationship between EFN-bearing plants and ants in cerrado. When nectar secretion is abundant, the plants are visited by opportunistic ants, which may defend them against herbivores. However, when nectar is produced in lower quantity and/or quality, ant foraging may be reduced and/or ants may use other resources available on foliage (see Rico-Gray et al., 1998). Therefore, even though several studies report this interaction to be advantageous for certain EFN-bearing plant species in cerrado (Oliveira and Freitas, 2004), the benefits received by foliage-dwelling ants deserve further investigation: resources other than EFNs are apparently intensively utilized by ant foragers as well.

Foliage-dwelling ants and herbivore numbers across seasons

To test the hypotheses that shrubs and young trees with EFNs present higher ant abundance and lower herbivore numbers, 64 shrubs (33 with and 31 without EFNs) were sampled with a beating umbrella to collect both ants and herbivores. All sampled plants were in the vegetative phase and the most frequent EFN-bearing plant species were *Qualea grandiflora*, *Q. parviflora* (Vochysiaceae), *Stryphnodendron adstringens* (Mimosaceae) and *Lafoensia pacari* (Lythraceae). Ant aggressiveness was tested using leaf-cutting ant workers as live baits for foliage-dwelling ants. Leaf-cutters were glued on the leaves of ant-visited plant species with and without EFNs. Live baits were monitored during 15 minutes or until they were attacked by an ant forager. A total of twelve ant species were observed during trials, with eight species occurring simultaneously on plants with and without NEFs (Figure 6). The number of ants visiting plants with

Table 1. Tree species sampled for ants in the cerrado of Paraopeba, Minas Gerais, Brazil. The location of extrafloral nectaries (EFNs) is indicated for plants bearing such ant attractants. A hyphen ("-") indicates absence of EFNs

Plant species (Family)	Location of EFNs
Acosmium dasycarpum (Vog.) Yakovl. (Fabaceae)	-
Agonandra brasiliensis Benth. & Hook. f. (Opiliaceae)	-
Alibertia sessilis (Vell.) K. Schum. (Rubiaceae)	-
Annona crassiflora Mart. (Annonaceae)	-
Aspidosperma macrocarpon Mart. (Apocynaceae)	-
Astronium fraxinifolium Schott. (Anacardiaceae)	-
Bowdichia virgilioides H. B. & K. (Fabaceae)	-
Byrsonima coccolobifolia H. B. & K. (Malpighiaceae)	-
Byrsonima verbascifolia (L.) Rich. ex A. L. Juss. (Malpighiaceae)	-
Caryocar brasiliense Camb. (Caryocaraceae)	Buds, shoot tips
Curatella americana L. (Dilleniaceae)	-
Dimorphandra mollis Benth. (Mimosaceae)	-
Diospyros hispida A. DC. (Ebenaceae)	-
Enterolobium gummiferum (Mart.) Macb. (Mimosaceae)	Rachis
Erythroxylum cuneifolium (Mart.) Schult. (Erythroxylaceae)	-
Erythroxylum daphnites Mart. (Erythroxylaceae)	-
Erythroxylum suberosum St. Hil. (Erythroxylaceae)	-
Erythroxylum tortuosum Mart. (Erythroxylaceae)	-
Eugenia dysenterica DC. (Myrtaceae)	-
Guapira noxia (Netto) Lund (Nyctaginaceae)	-
Hymenaea stigonocarpa Mart. ex Hayne Caesalpinaceae)	Leaf blade
Hyptis cana Pohl ex Benth. (Lamiaceae)	-
Kielmeyera cf grandiflora (Wawra) Saddi (Clusiaceae)	-
Machaerium opacum Vog. (Fabaceae)	-
Magonia pubescens St. Hil. (Sapindaceae)	-
Miconia cf ligustroides (DC.) Naud. (Melastomataceae)	-
Myrcia lingua Berg (Myrtaceae)	-
Myrsine cf umbellata Mart. (Myrsinaceae)	-
Pera glabrata (Schott.) Baill. (Euphorbiaceae)	-
Piptocarpha rotundifolia (Less.) Baker (Asteraceae)	-
Plathymenia reticulata Benth. (Mimosaceae)	Stem
Qualea grandiflora Mart. (Vochysiaceae)	Stem, pedicel
Qualea multiflora Mart. (Vochysiaceae)	Stem, pedicel
Qualea parviflora Mart. (Vochysiaceae)	Stem, pedicel
Roupala montana Aubl. (Proteaceae)	-
Rudgea viburnoides (Cham.) Benth. (Rubiaceae)	-
Salvertia convallariaeodora St. Hil. (Vochysiaceae)	-
Schefflera (*Didymopanax*) *macrocarpa* (Seem.) D. C. Frodin (Araliaceae)	-
Sclerolobium paniculatum Vog. (Caesalpinaceae)	-
Stryphnodendron adstringens (Mart.) Cov. (Mimosaceae)	Rachis
Styrax camporum Pohl (Styracaceae)	-
Tabebuia aurea (Manso) Benth. & Hook.f. ex S. Moore (Bignoniaceae)	Leaf blade
Tapirira guianensis Aubl. (Anacardiaceae)	-
Terminalia argentea Mart. & Zucc. (Combretaceae)	Petiole
Tibouchina sp. (Melastomataceae)	-
Vochysia rufa Mart. (Vochysiaceae)	-
Xylopia aromatica (Lam.) Mart. (Annonaceae)	-
Zeyheria digitalis (Vell.) Hoehne (Bignoniaceae)	Leaf blade

Table 2. Ant species sampled at the cerrado reserve in Paraopeba, Brazil, on trees with and without extrafloral nectaries (EFNs)

Subfamily	Occurrence on plants	
Species	With EFNs	Without EFNs
Dolichoderinae		
Azteca sp. 1	x	x
Dolichoderus lamellosus (Mayr)	x	x
Dolichoderus lutosus (Smith)		x
Dorymyrmex jheringi Forel		x
Forelius sp. 1		x
Forelius sp. 2	x	x
Linepithema humile (Mayr)	x	x
Linepithema sp. 1		
Tapinoma melanocephalum (Fabr.)	x	x
Tapinoma sp. 1	x	x
Formicinae		
Brachymyrmex sp. 1	x	x
Brachymyrmex sp. 2	x	x
Brachymyrmex sp. 3		x
Brachymyrmex sp. 4	x	x
Camponotus (Myrmaphaenus) blandus (Smith)	x	x
Camponotus (Myrmaphaenus) leydigi Forel	x	x
Camponotus (Myrmaphaenus) novogranadensis Mayr	x	x
Camponotus (Myrmaphaenus) sp. 1	x	x
Camponotus (Myrmaphaenus) sp. 2		x
Camponotus (Myrmaphaenus) sp. 3	x	x
Camponotus (Myrmaphaenus) sp. 4	x	x
Camponotus (Myrmaphaenus) sp. 5	x	x
Camponotus (Myrmaphaenus) sp. 6		x
Camponotus (Myrmepomis) sericeiventris (Guérin)	x	x
Camponotus (Myrmobrachys) crassus Mayr	x	x
Camponotus (Myrmobrachys) sp. 1	x	x
Camponotus (Myrmobrachys) sp. 2		x
Camponotus (Myrmobrachys) sp. 3		x
Camponotus (Myrmobrachys) trapezoideus Mayr	x	x
Camponotus (Myrmothrix) atriceps (Smith)	x	x
Camponotus (Myrmothrix) cingulatus Mayr		x
Camponotus (Myrmothrix) renggeri Emery	x	x
Camponotus (Myrmothrix) rufipes (Fabr.)	x	x
Camponotus (Tanaemyrmex) agra (Fr. Smith)	x	x
Camponotus (Tanaemyrmex) melanoticus Emery	x	x
Camponotus (Tanaemyrmex) sp. 1	x	x
Camponotus (Tanaemyrmex) sp. 2	x	x
Camponotus (Tanaemyrmex) sp. 3		x
Camponotus (Tanaemyrmex) sp. 4	x	x
Camponotus (Tanaemyrmex) sp. 5	x	x
Myrmelachista sp. 1	x	x
Paratrechina sp. 1	x	x

Table 2. (*Cont.,*)

Subfamily	Occurrence on plants	
Species	With EFNs	Without EFNs
Myrmicinae		
Acromyrmex subterraneus Forel	x	x
Atta rubropilosa Forel	x	x
Cephalotes atratus (L.)	x	x
Cephalotes borgmeieri (Kempf)	x	x
Cephalotes clypeatus (Fabr.)	x	x
Cephalotes goeldii (Forel)	x	x
Cephalotes grandinosus (Smith)	x	x
Cephalotes pallens (Klug)	x	x
Cephalotes pusillus (Klug)	x	x
Crematogaster sp. 1		x
Crematogaster sp. 1 (*quadriformis* group)	x	x
Crematogaster sp. 2	x	x
Crematogaster sp. 2 (*quadriformis* group)	x	x
Crematogaster sp. 3		x
Leptothorax sp. 1		x
Leptothorax sp. 2	x	
Leptothorax sp. 3		x
Leptothorax tristani		x
Mycocepurus goeldii		
Nesomyrmex asper (Mayr)	x	
Ochetomyrmex sp. 1	x	x
Pheidole falax Mayr	x	x
Pheidole sp. 1	x	x
Pheidole sp. 2		x
Pheidole sp. 3		x
Pheidole sp. 4	x	x
Pheidole sp. 5	x	x
Pheidole sp. 6		x
Pheidole sp. 7	x	x
Pheidole sp. 8	x	x
Solenopsis sp. 1 (*diplorhoptrum* group)	x	x
Solenopsis sp. 1 (*solenopsis* group)		x
Solenopsis sp. 2 (*diplorhoptrum* group)		x
Solenopsis sp. 3 (*diplorhoptrum* group)	x	x
Solenopsis sp. 4 (*diplorhoptrum* group)		x
Trachymyrmex sp. 1		
Wasmannia auropunctata (Roger)	x	
Wasmannia sp. 1	x	x
Xenomyrmex sp. 1	x	x
Ectatomminae		
Ectatomma brunneum (Smith)	x	x
Ectatomma planidens Borgmeier	x	x
Ectatomma tuberculatum (Olivier)	x	x
Gnamptogenys sulcata (Smith)		x

(*Continued*)

Table 2. (*Cont.*,)

Subfamily Species	Occurrence on plants With EFNs	 Without EFNs
Ponerinae		
Pachycondyla villosa (Fabr.)	x	x
Pseudomyrmecinae		
Pseudomyrmex elongatus (Mayr)	x	x
Pseudomyrmex filiformis (Fabr.)		x
Pseudomyrmex gracilis (Santschi)	x	x
Pseudomyrmex kuenckeli (Emery)		x
Pseudomyrmex pisinnus Ward	x	x
Pseudomyrmex pupa (Forel)	x	x
Pseudomyrmex sp. 1 (*palidus* group)		x
Pseudomyrmex sp. 2 (*palidus* group)	x	x
Pseudomyrmex termitarius (Smith)	x	x

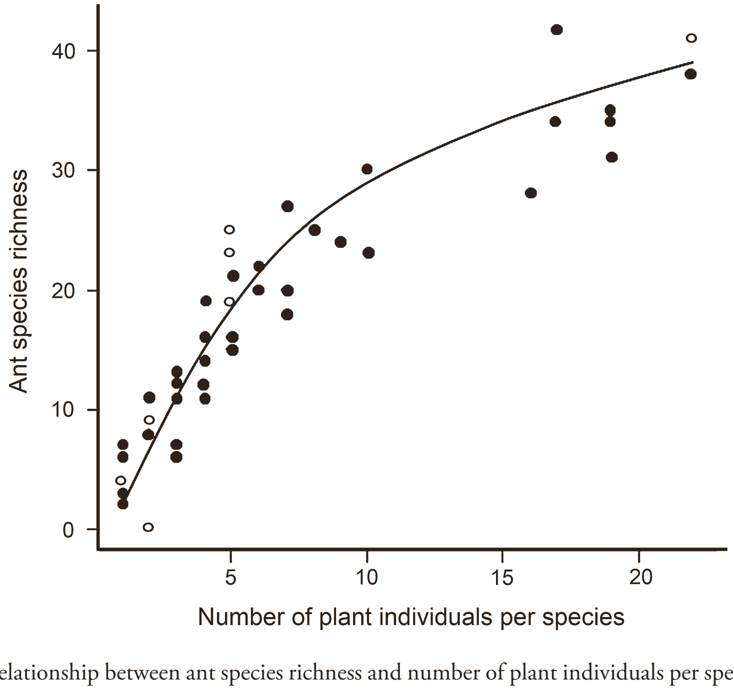

Figure 4. Relationship between ant species richness and number of plant individuals per species in which ants have been sampled at the cerrado reserve of Paraopeba (Brazil). Ant species richness was significantly affected by sampling effort ($F_{1,45}$=90.69; p<0.001). Presence (white) or absence (black) of EFNs on plants had no effect on ant species richness ($F_{1,44}$=0.07; p=0.78).

EFNs was higher compared to plants without EFNs ($F_{1,61}$=13.91, p=0.0004; Figure 7A), although the number of herbivores did not vary with the presence of EFNs ($F_{1,61}$= 0.21, p=0.65; Figure 7B). The number of ants foraging on plants was higher in the dry/cold season than in the rainy/hot season ($F_{1,60}$=9.73, p=0.003; Figure 8A), but the

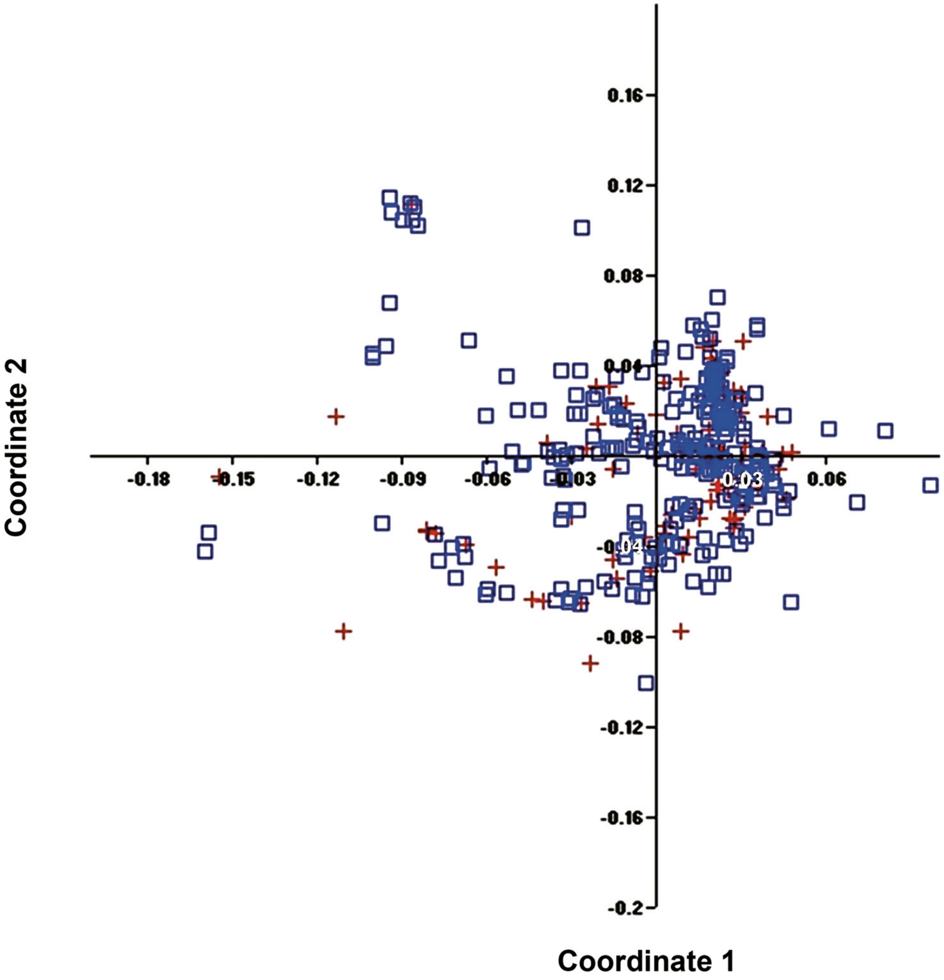

Figure 5. Non-metric multidimensional scaling (NMDS) obtained from ant species composition sampled on plants with (red crosses) and without (blue squares) EFNs. Ants were sampled in the cerrado reserve of Paraopeba (Brazil). The composition of ant species visiting plants with and without EFNs does not differ (p>0.05).

number of herbivores on the plants did not vary with season ($F_{1,60}$=0.04, p=0.85; Figure 8B). The presence of EFNs did not affect ant aggressiveness towards live baits (χ^2=0.68, p=0.41; Figure 9), suggesting that this plant trait was not responsible for the overall aggressiveness of ant species on vegetation. These results suggest that EFNs may be an important resource for the ants, because their abundance is higher on EFN-bearing plants. Furthermore, the seasonal differences of ant abundance may account for differences in the availability of other resources during the year, with EFNs being more important to ants during the dry season than in the rainy season. Possibly when the ants find such a resource, they increase their recruitment towards the plants to maximize

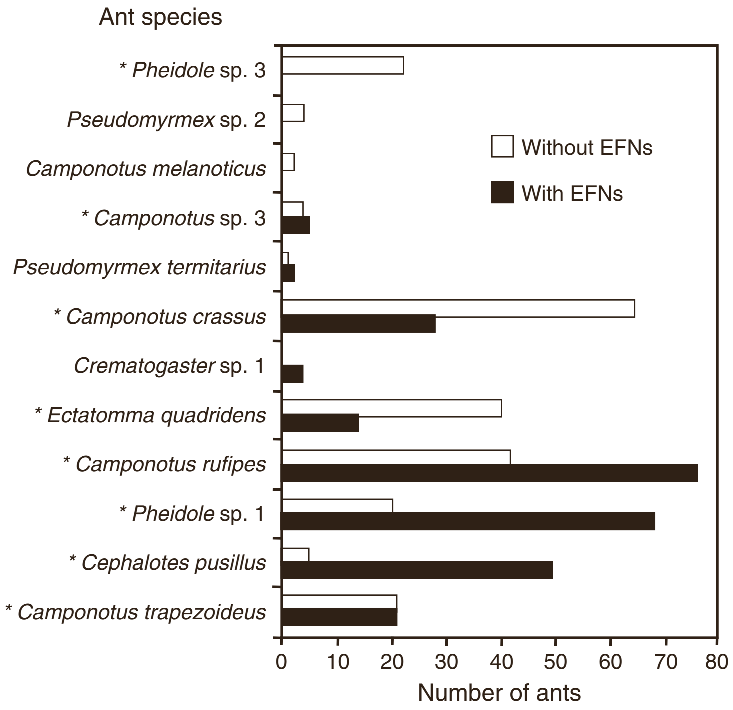

Figure 6. Number of ant workers sampled on plants with and without EFNs at the Parque Nacional da Serra do Cipó (Brazil). An asterisk indicates that the ant species attacked live baits experimentally placed on plants.

nectar collecting and energetic gain. Moreover, the higher abundance of ants visiting plants with EFNs during the dry/cold season compared with the rainy/hot season, may be due to variation in nectar quality throughout the year. Indeed, Díaz-Castelazo et al. (2004) found that abundance of EFN-bearing plants may vary seasonally in coastal Mexico, and suggested that extrafloral nectar from vegetative and reproductive structures are available at different periods of the year. There is also evidence that the nectar produced in the dry season is more concentrated than in the wet season due to the low water availability in the soil, which increases sugar and amino acid contents in the nectar (Blüthgen and Fiedler, 2004) and makes the plant more attractive to ant foragers.

Although the presence of ants on plants tends to reduce herbivory (Rosumek et al., 2009), this study reveals that at the community level foliage-dwelling ants may not defend the EFN-bearing plants against herbivores. It is possible that some plants bearing EFNs attract mostly nectarivorous ants that ignore herbivores, which may also explain our results with the aggressiveness tests (see Sendoya et al., 2009). Presence of EFNs normally increases ant aggressiveness towards live baits due to the attraction of noxious ants to the plants and/or due to changes in the behavior of ants near nectar

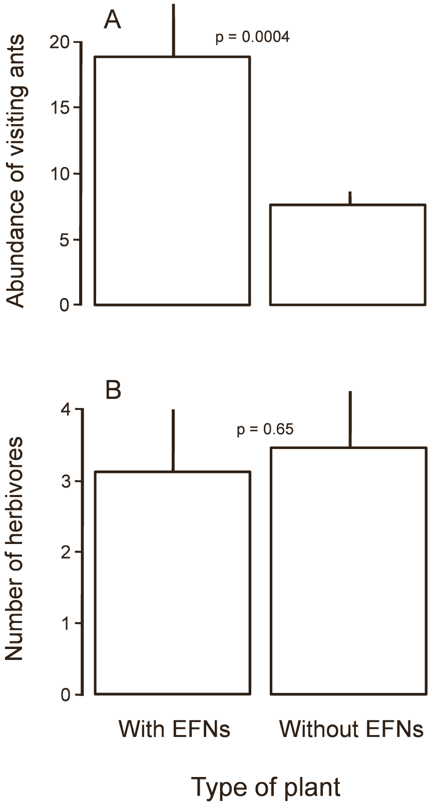

Figure 7. (A) Abundance of ants and (B) herbivores on plants with and without EFNs at the Parque Nacional da Serra do Cipó (Brazil). Data are means ± SE.

sources ("ownership behavior"; see Way, 1963; Bentley, 1977; Oliveira et al., 1987). In our case, because trials evaluating ant aggressiveness were performed on the general plant community with and without EFNs (and not on particular plant species), it is possible that the number of ants on vegetation was not high enough to reduce overall herbivore numbers, despite the higher ant visitation levels to EFN-bearing plants compared to non-nectariferous plants. Indeed, a number of factors may account for the lack of ant-derived protection to EFN-bearing plants worldwide, including interspecific differences in ants' deterring traits (Rico-Gray and Thien, 1989; Mody and Linsenmair, 2004; Sendoya et al., 2009), interhabitat variation in ant or herbivore activity on foliage (Bentley, 1976; Barton, 1986; Cogni et al., 2003; Koptur 1985), temporal variation (Heil et al., 2001; Wirth and Leal, 2001), or counteradaptations of herbivores to circumvent ant predation on foliage (Koptur, 1984; Heads and Lawton, 1985; Freitas and Oliveira, 1996; Sendoya et al., 2009). The diverse sources of variation inherent to interactions involving ants and plants with EFNs are discussed by Koptur (1992, 2005), Bronstein (1998), Beattie and Hughes (2002), Rico-Gray and Oliveira (2007).

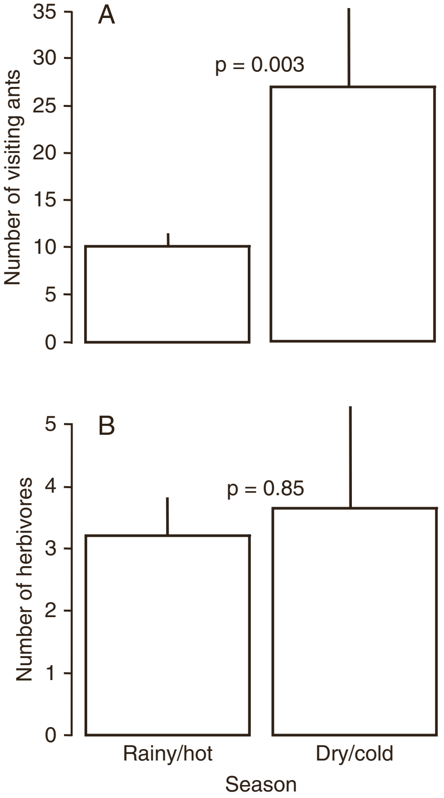

Figure 8. (A) Abundance of ants and (B) herbivores on plants with and without EFNs at the Parque Nacional da Serra do Cipó (Brazil), in the rainy/hot and dry/cold season. Data are means ± SE.

Conclusion and prospects

This review attempted to summarize the current knowledge regarding the interactions between arboreal ants and cerrado plants, with two different approaches. The study of the interactions, focusing particularly on the benefits obtained by the plants due to the presence of visiting ants have received considerable attention in the last few decades (reviewed by Rico-Gray and Oliveira 2007). On the other hand, the community-level effect of EFN-bearing plants on ants, and their reverse impact, needs further investigation.

The vast number of plant species and individuals with EFNs in cerrado in comparison with other vegetation types (Oliveira and Freitas, 2004) raises a few hypotheses regarding their influence on the composition of the ant communities in this neotropical savanna. For instance, if there are ant species specialized in drinking liquid resources, either in the form of EFNs or insect honeydew (see Davidson et al., 2003), we would be expect to find a higher abundance of these species in cerrado than in other Brazilian biomes. Studies comparing arboreal ant species composition in adjoining biomes such as cerrado and Atlantic forest for instance, would allow the testing of this hypothesis

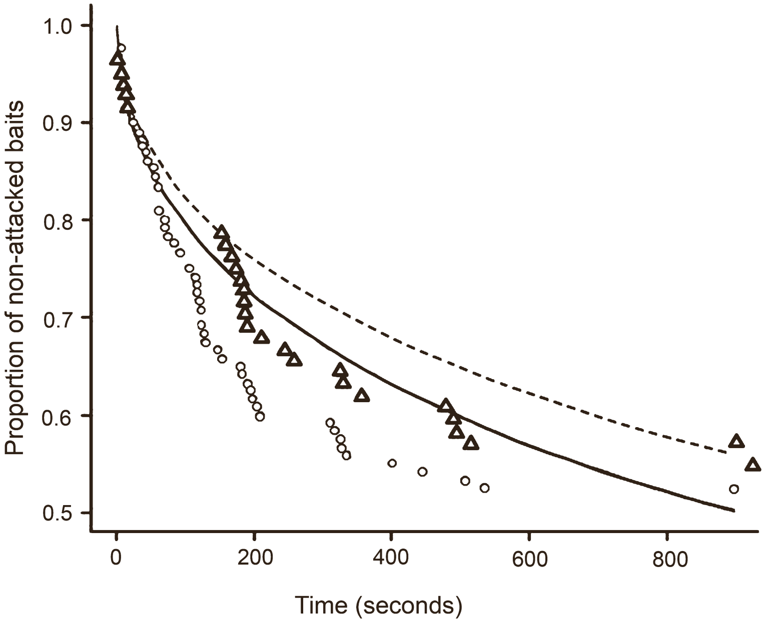

Figure 9. Relationship between the proportion of live baits not attacked and the time spent for the attack by foliage-dwelling ants. The curves were generated by the Weibull distribution. The proportion of baits attacked do not differ between plants with (circles and continuous line) and without EFNs (triangles and dashed line) ($\chi^2 = 0.68$, p = 0.41).

by removing the effects of regional differences in species composition. Based on the current knowledge about the fauna that visits EFNs in cerrado (Ribas et al., 2003; Ribas and Schoereder, 2004), it is possible to predict that these differences would not occur, that ants would use EFNs as an additional resource, and that the presumed mutualism between ants and plants would be at least very asymmetrical.

Most studies of ant-plant mutualisms concentrate their efforts on the effects that the presence of ants has on plant fitness. Recently, Lach et al. (2009) have produced the first experimental study comparing the survival of ants that foraged on plants with and without EFNs. In addition, because their experiments were carried out using native and non-native ants, they were able to test the physiological adaptations of ant species to EFN-bearing plants and could indicate evolutionary specializations of the ants. Lach et al. (2009) did not find increased survival of ants foraging on plants with EFNs compared to non-nectariferous plants. Moreover, they found no difference between native and non-native ant species, indicating that neither physiological adaptations nor the sharing of an evolutionary history is necessary for recognizing or digesting extrafloral nectar. The pioneering approach by Lach et al. (2009) stimulates future studies testing the reciprocal effects of ant-plant relationships so as to identify the actual nature of these associations.

Three further efforts should be made to clarify the relationships between ants and plants with EFNs: (i) the overall effect of ants on herbivore communities, (ii) the overall effect of ants on plant communities, and (iii) the effect of the regional plant species pool on ant species composition. Although the study described here did not find an effect of ant abundance on herbivore numbers in the cerrado plant community, our design was rather generalized in that it investigated such relationships in many plant species, which hosted many insect species. The ability to attract ants, nonetheless, does vary among plant species and may depend strongly on the presence of EFNs (Koptur, 2005; Rico-Gray and Oliveira, 2007, and included references). On the other hand, some herbivore species or guilds may be more prone to be attacked by the ants (Mody and Linsenmaier, 2004). Insect herbivores that are highly mobile, that are morphologically protected, or that possess accurate vision can escape the attack of ants and stay on the plants despite their presence (Heads and Lawton, 1985; Freitas and Oliveira 1992, 1996). Therefore it is predicted that herbivore species composition, or guild composition, may be affected by the presence of foliage-dwelling ants, and this pattern could result in differential herbivory levels for plants with EFNs compared to plants lacking ant attractants.

Although the influence of leaf-cutting ants on species composition of plant communities has already been demonstrated (Wirth et al., 2003), the potential effect of nectar-feeding ants on plant communities is unknown. It is expected that EFN-bearing plants would receive increased ant-derived protection in cerrado sites with higher numbers of ant species and/or higher ant abundance (see Barton, 1986; Cogni et al., 2003). Therefore, the structure of the ant species assembly could potentially influence the assembly of plants in cerrado. This hypothesis could be tested by experiments employing exclusion or addition of ant species.

Finally, the question of spatial scale must be considered when analyzing the distribution of ant species on cerrado trees. Ant species richness and composition within a given cerrado tree should mirror two factors: the local characteristics of the tree and the regional pool of ant species. Because cerrado vegetation is formed by several physiognomies ranging from grasslands to forests (see Oliveira-Filho and Ratter, 2002), it is possible that ant-derived protection against herbivores varies across cerrado physiognomies inhabited by ant assemblages that differ in species richness and/or species composition (see Horvitz and Schemske, 1984). Therefore, the assembly of arboreal ants in cerrado may be a result of regional species composition, and the proportional influence of local and regional factors deserves further study. A first attempt to investigate such spatial patterns in ant-plant interactions across vegetation physiognomies was made by Díaz-Castelazo et al. (2004) in coastal Mexico, and revealed that different vegetation types within a relatively small area (< 100 ha) can generate considerable variation that affect ant-plant associations.

The studies in cerrado summarized here indicate that: (i) ants visit EFNs and possibly obtain some individual benefit from this resource; (ii) EFN-gathering ants can benefit particular plant species by reducing herbivory levels and increasing plant fitness; (iii) presence of EFNs does not affect the richness of ant species that visit a given tree; (iv) there is not a particular ant species composition typical of plants with EFNs; (v) plants with EFNs are visited by more ant individuals than non-nectariferous plants, although this visitation pattern does not necessarily imply an overall reduction in the abundance of herbivores in the nectariferous plant community. Despite the vast literature on ant-plant associations (see Rico-Gray and Oliveira, 2007), there are several avenues of investigation that remain unexplored, especially at the level of the community. Future investigation in cerrado should focus especially on the mechanisms affecting species richness and composition of arboreal ant communities, and on how such community-level parameters are tied with the ecology of ant-plant associations in this neotropical savanna.

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