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Ant–plant–herbivore interactions in the neotropical cerrado savanna

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Abstract The Brazilian cerrado savanna covers nearly 2 million km² and has a high incidence on foliage of various liquid food sources such as extrafloral nectar and insect exudates. These liquid rewards generate intense ant activity on cerrado foliage, making ant–plant–herbivore interactions especially prevalent in this biome. We present data on the distribution and abundance of extrafloral nectaries in the woody flora of cerrado communities and in the flora of other habitats worldwide, and stress the relevance of liquid food sources (including hemipteran honeydew) for the ant fauna. Consumption by ants of plant and insect exudates significantly affects the activity of the associated herbivores of cerrado plant species, with varying impacts on the reproductive output of the plants. Experiments with an ant–plant–butterfly system unequivocally demonstrate that the behavior of both immature and adult lepidopterans is closely related to the use of a risky host plant, where intensive visitation by ants can have a severe impact on caterpillar survival. We discuss recent evidence suggesting that the occurrence of liquid rewards on leaves plays a key role in mediating the foraging ecology of foliage-dwelling ants, and that facultative ant–plant mutualisms are important in structuring the community of canopy arthropods. Ant-mediated effects on cerrado herbivore communities can be revealed by experiments performed on wide spatial scales, including many environmental factors such as soil fertility and vegetation structure. We also present some research questions that could be rewarding to investigate in this major neotropical savanna.

Introduction

In the tropics many ant species use plant foliage as a foraging substrate to search for animal prey and plant-

derived food resources. The dominance of ant foragers on tropical vegetation is such that they can comprise 70% of the canopy-dwelling arthropods in Peruvian rainforests (Tobin 1991), where a single tree was reported to contain 43 ant species belonging to 26 genera, about equal to the entire ant fauna of the British Isles (Wilson 1987). Overall, ants and termites together compose nearly one-third of the entire animal biomass of the *terra firme* rainforest in central Amazon (Fittkau and Klinge 1973). Because ant species may nest in plant organs, the plant itself sometimes represents the core of a colony's patrolled area (Carroll and Janzen 1973). Ant foraging on leaves is further promoted by the presence of predictable and renewable food sources, including extrafloral nectar, honeydew from phloem-feeding hemipterans, and secretions from lepidopteran larvae (Way 1963; Bentley 1977; Buckley 1987; Pierce et al. 2002). Indeed, ant attractants are widespread amongst the flora of different vegetation physiognomies. Extrafloral nectaries (EFNs), for example, occur in 93 flowering plant and five fern families (Koptur 1992a). Plants bearing EFNs comprised 33% of the species (woody and climbing plants) surveyed in the rainforest of Barro Colorado Island in Panama (Schupp and Feener 1991), and 12% of the woody species in a rainforest reserve in West Malaysia (Fiala and Linsenmaier 1995). In different vegetation types of Amazonian Brazil, 18–53% of the woody species were found to possess EFNs, accounting for up to 50% of the individuals surveyed locally (Morellato and Oliveira 1991). As expected from these findings, the abundance and diversity of ant–plant interactions is particularly notable in tropical habitats in comparison with temperate areas (e.g., Pemberton 1998). For instance, Rico-Gray (1993) recorded a total of 312 ant–plant associations (i.e., use of plant-based food by ants) in one Mexican coastal site, whereas Fonseca and Ganade (1996) reported that myrmecophytic plants (i.e., those especially adapted to house ant colonies) occur at a density of 377 plants/ha in the Amazonian rainforest.

Recent studies have shown that the energy supply of foliage-dwelling ants depends largely on plant- and in-

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sect-derived liquid foods (Tobin 1995; Davidson et al. 2003). Although such carbohydrate-rich resources are more commonly consumed by arboreal species, ground-nesting ants frequently climb onto plants to search for this type of food (Oliveira and Brandão 1991; Del-Claro and Oliveira 1996; Blüthgen et al. 2000). Because the majority of ants appear to have an opportunistic diet that combines plant/insect exudates with animal prey (Kaspari 2000), their numerical dominance on foliage can have a dramatic impact – positive or negative – on the biology of insect herbivores (e.g., Oliveira et al. 2002).

From the plant's perspective, the outcome of ant–plant–herbivore interaction is markedly variable and will largely depend on how ant behavior at a food source can affect herbivore performance on a particular plant species. For example, while aggression towards herbivores by EFN-gathering ants can positively affect plant fitness by decreasing herbivore damage to the plant (see review by Koptur 1992a), protection of honeydew-producing hemipterans by tending ants can reduce plant fitness by increasing hemipteran damage to the host plant (Rico-Gray and Thien 1983). It may also happen that ant visitation to EFNs affords no apparent benefit to plants (Tempel 1983), or that ants tending hemipteran trophobionts positively affect the plant by deterring other herbivores (Oliveira and Del-Claro 2004). In recent years it has become increasingly apparent that the consequences of ant–plant–herbivore associations vary greatly in space and time, in association with factors such as identity, abundance, and behavior of species partners, type of plant damage inflicted by herbivores or pathogens, and joint effects with other arthropods (Thompson 1988; Cushman 1991; Bronstein 1998; Ruhren and Handel 1999; Bronstein and Barbosa 2002; Heil and McKey 2003; Cuautele and Rico-Gray 2003; and references therein).

We here provide an overview of our work in the cerrado savanna of Brazil, with emphasis on the interactions involving ants, plants bearing EFNs, and insect herbivores. We first summarize the data on distribution and abundance of EFNs in the woody flora of cerrado communities in the context of related work from other regions, and stress the relevance of liquid food sources (including hemipteran honeydew) for the ant fauna. In the second part we examine how consumption by ants of plant and insect exudates can affect associated herbivores of selected cerrado plant species, and how such impact can influence the plants' reproductive output. In the third part we show how predation pressure by ants can shape the behavioral biology of both immature and adult stages of a non-myrmecophilous butterfly species on a highly ant-visited host plant. We close by reviewing the role of such ant-centered, multitrophic systems in structuring herbivore communities, and by stressing the uniqueness of the cerrado for research on ant–plant–herbivore interactions. We also point out some promising research avenues that could be rewarding to investigate in this major neotropical savanna.

This review is not intended to cover all aspects of ant–plant–herbivore interactions in equal detail. We pay special attention to aspects important for our considera-

tions, observations, and experimental results in the cerrado. Because the amount of information available on ant–plant interactions is already vast and is increasing very rapidly, we have avoided a thorough review of the literature and sometimes used citations in a representative rather than a comprehensive manner. Excellent reviews on different aspects of the natural history and evolutionary ecology of ant–plant–herbivore associations have been published in the past two decades (Buckley 1982; Beattie 1985; Hölldobler and Wilson 1990; Huxley and Cutler 1991; Koptur 1992a; Davidson and McKey 1993; Bronstein 1998; Beattie and Hughes 2002; Pierce et al. 2002; Heil and McKey 2003; Wirth et al. 2003; Rico-Gray et al. 2004).

Richness of liquid food rewards on cerrado foliage, and the associated ants

The Brazilian cerrado savanna covers nearly 2 million km², representing about 22% of the country's physical area (Oliveira and Marquis 2002). The whole biome is characterized by an extremely variable physiognomy ranging from open grassland to forest with a discontinuous grass layer. Between these two extremes lies a continuum of savanna formations spanning the entire range of woody plant density, collectively known as the *cerrados* (Oliveira-Filho and Ratter 2002).

Two main factors contribute to the dominance of ants on cerrado foliage. First, boring beetles hollow out the stems of many plants and leave galleries that are used as nest sites by numerous arboreal ant species, and this fact alone causes intense ant patrolling activity on leaves (Moraes and Benson 1988). For instance 136 live woody plants (27 species) and 17 dead standing trunks were found to house stem-nesting ants within 1,075 m² of cerrado in Mogi-Guaçu (SE Brazil), totaling 204 arboreal nests (Moraes 1980). Overall, the stem-nesting ant guild at Mogi-Guaçu comprised 27 species (Moraes 1980), a figure that rivals similar censuses undertaken in tropical forests (Carroll 1979). The occurrence of ant nests on cerrado foliage is further promoted by the high occurrence of insect galls, which are occupied by ant colonies after the emergence of the galling species (Fernandes et al. 1988; Araújo et al. 1995). Second, the wide occurrence of predictable liquid food sources in the form of extrafloral nectar and insect honeydew further promotes ant foraging on leaves (Fig. 1A–E). A total of 45 EFN-bearing woody species from 17 families were sampled in the cerrados of São Paulo and Mato Grosso (Oliveira and Leitão-Filho 1987, Oliveira and Oliveira-Filho 1991). The plant families most frequently having EFNs are the Mimosaceae (seven species), Bignoniaceae (six species) and Vochysiaceae (five species). Table 1 summarizes the proportion and abundance of plant species bearing EFNs within the woody floras of ten cerrado areas in southeast and western Brazil. The surveys revealed that 15.4–25.5% of the species were found to possess EFNs, accounting locally for 7.6–31.2% of the individuals surveyed. Although the frequency of EFN-bearing species clearly

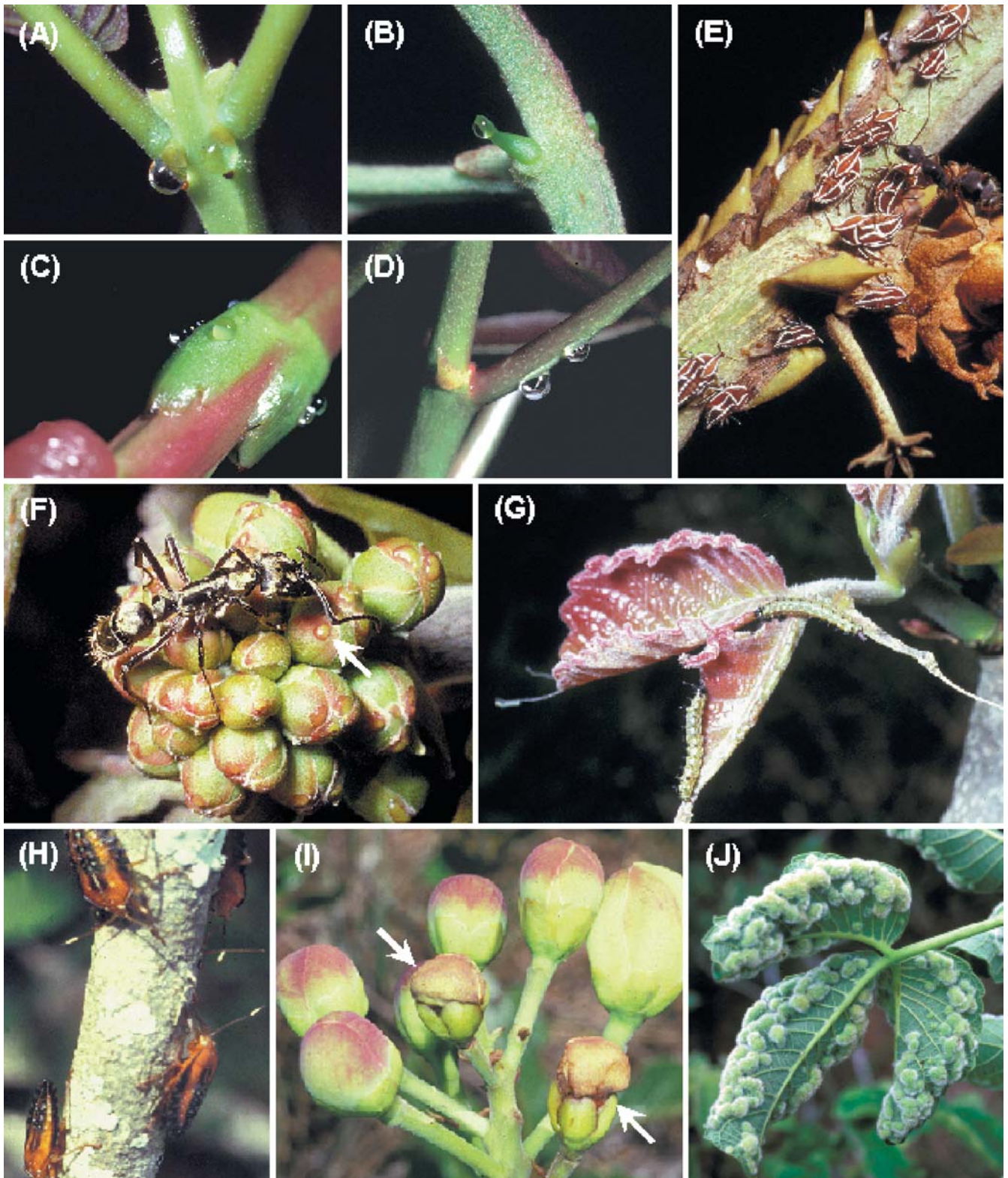


Fig. 1 A–D Accumulated extrafloral nectar produced by glands located at various plant organs. **A** Stem of *Qualea grandiflora* (Vochysiaceae). **B** Trichomes of *Bauhinia rufa* (Caesalpinaceae). **C** Stipules of *Ouratea spectabilis* (Ochnaceae). **D** Petiole of *Eriotheca gracilipes* (Bombacaceae). **E** Worker of *Camponotus rufipes* tending an aggregation of the honeydew-producing treehopper *Guayaquila xiphias*. **F–J** The extrafloral nectary shrub *Caryocar*

brasiliense, its visiting ants, and the associated insect herbivores. **F** Worker of *Pachycondyla villosa* collecting extrafloral nectar at glands (arrow) located on the bud sepals. **G** Caterpillars of *Eunica bechina* feeding on young leaves. **H** Nymphs of the bud- and fruit-sucking bug *Edessa rufomarginata*. **I** Damaged floral buds (arrows) infested by larvae of the fly *Prodiplosis floricola*. **J** Leaves severely damaged by galling wasps

Table 1 Occurrence of plants with extrafloral nectaries (EFNs) in different vegetation types in tropical, subtropical, and temperate habitats worldwide. Frequency of plants is expressed as a percentage of species and/or individuals (cover). Unless otherwise indicated, surveys include all plant life forms. See original sources for details on sampling methods

Region and type of vegetation	% of species with EFNs	% cover of plants with EFNs	Source
Tropical and subtropical			
Brazilian cerrado			
Southeast Brazil, São Paulo (5 sites; woody species)	15.4–21.9	7.6–20.3	Oliveira and Leitão-Filho 1987
Western Brazil, Mato Grosso (5 sites; woody species)	16.5–25.5	14.2–31.2	Oliveira and Oliveira-Filho 1991
Brazilian Amazon			
Terra firme forest (woody species)	17.6	19.1	Morellato and Oliveira 1991
Successional forest (woody species)	18.5	42.6	Morellato and Oliveira 1991
Buriti-rana (palm) vegetation (woody species)	33.3	29.7	Morellato and Oliveira 1991
Shrub canga (woody species)	53.3	50	Morellato and Oliveira 1991
Mexico			
Coastal vegetation (forest, sand dune, grassland, water marsh)	14.8	–	Díaz-Castelazo et al. 2004
Costa Rica			
Tropical dry forest hillside	–	30–80	Bentley 1976
Tropical riparian forest	–	10–40	Bentley 1976
Lowland rain forest	–	1–8	Koptur 1992a
Lower montane cloud forest	–	3–22	Koptur 1992a
High montane oak forest	–	0–3	Koptur 1992a
Panama			
Rainforest (shrubs and trees)	14–34	–	Schupp and Feener 1991
Rainforest (climbing plants)	44	–	Schupp and Feener 1991
Venezuela			
Rainforest (epiphytes)	19	28	Blüthgen et al. 2000
Jamaica			
Second growth forest (sea level)	–	28	Keeler 1979a
Second growth forest (montane)	–	0	Keeler 1979a
Florida (USA)			
Sawgrass prairie	–	2	Koptur 1992b
Rockledge pinelands	–	34	Koptur 1992b
Hardwood hammock	–	23	Koptur 1992b
Cameroon			
Rainforest (trees)	41.8	55.7	Dejean et al. 2000
Rainforest (climbing plants)	44.4	70	Dejean et al. 2000
East Asia			
Bonin islands (forest, sclerophyll shrub)	7.5	40.2	Pemberton 1998
Malaysia rainforest (woody species)	12.3	19.3	Fiala and Linsenmair 1995
Australia			
Rainforest (trees)	16.9	14.4	Blüthgen and Reifenrath 2003
Rainforest (climbing plants)	21.3	19.2	Blüthgen and Reifenrath 2003
Polynesia			
Hawaii (native species)	1.2	–	Keeler 1985
Temperate and cold			
North America			
Southern California (desert communities)	–	0–27.7	Pemberton 1988
Northern California (grassland, forest, chaparral)	0	0	Keeler 1981a
Nebraska (forest, prairie)	3.8	0–14.2	Keeler 1979b, 1980
Nebraska (forest, prairie) (woody plants only)	2.3	–	Keeler 1979b
Arizona (forest, desert, chaparral)	–	0–39	Keeler 1981b
Russia			
Tundra	0.3	10.3	Pemberton 1998
Cool-cold temperate forest	0.6–1.2	12.3–12.5	Pemberton 1998
Korea			
Deciduous forest	4.1	0.5–55	Pemberton 1990
Warm temperate forest	3–4	14.6	Pemberton 1998

varies among plant life forms (Koptur 1992a), the values obtained in cerrado and in many other regions worldwide (Table 1) in general support the contention that EFNs are more common in tropical than in temperate communities (Bentley 1977; Oliveira and Leitão-Filho 1987; Schupp and Feener 1991; Coley and Aide 1991; Pemberton 1998).

Coupled with the high incidence of plant exudates, persistence of ants on cerrado foliage is further promoted

by the occurrence of insect-derived liquid food sources in the form of honeydew from sap-feeding hemipterans (Dansa and Rocha 1992; Del-Claro and Oliveira 1999), and secretions of myrmecophilous butterfly larvae (Diniz and Morais 1997). Indeed, quantitative surveys performed by Lopes (1995) over a 3,600 m transect in the cerrado revealed that ant-tended treehoppers (Membracidae) occurred on 30% (27 out of 93) of the plant species exam-

ined (total of 1,025 plants monitored). Recent samplings of arboreal ant communities in cerrado areas of central Brazil (Ribas et al. 2003; Ribas and Schoereder 2004) have revealed that ant species richness in this biome is high when compared to that of Australian savannas (Andersen 1991a, 1991b; Andersen and Patel 1994), and even tropical rainforests (Majer 1990; Majer and Delabie 1994; Blüthgen et al. 2000; Soares et al. 2001). As stressed by Ribas et al. (2003), the richness of foliage-dwelling ants in cerrado sites (64 and 95 species in two localities) can be attributed among other things to the high availability of extrafloral nectar and hemipteran honeydew on vegetation. Such liquid food sources have been regarded as key resources for ant mosaics in the cerrado savanna (Ribas and Schoereder 2004), and rainforests as well (Blüthgen et al. 2000; Dejean et al. 2000).

The attractiveness of plant and insect exudates to cerrado ants is high enough to maintain constancy of ant attendance to the food source over 24 h. Sequential samplings at these stable food sources showed that attracted ant assemblages are diverse, with a clear daily turnover in the species composition of the principal ant visitors. For instance, across diurnal and nocturnal censuses, a total of 34 species of ants were recorded visiting the EFNs of *Caryocar brasiliense* (Oliveira and Brandão 1991), a range of ant species surpassed only by the EFN-bearing hemi-epiphyte *Philodendron fragrantissimum* in Amazonian rainforest (Blüthgen et al. 2000). Likewise the treehopper *Guayaquila xiphias* is tended day and night on shrubs of *Didymopanax vinosum* by an assemblage of 21 species of honeydew-gathering ants, the highest number ever recorded for a single ant-tended hemipteran species (Del-Claro and Oliveira 1999). The species composition of cerrado ant assemblages at EFNs and honeydew-producing hemipterans is very similar, and dominant *Camponotus* species (Formicinae) are by far the best represented during both day and night (Fig. 1E). During the day the most frequent visitors are *Camponotus crassus* and *C. aff. blandus*, whereas at night *C. rufipes*, *C. renggeri*, and *C. pallidus* are among the most dominant species at these liquid food sources. Samplings on foliage using pitfall traps and/or food baits have also confirmed *Camponotus* as the best represented arboreal ant genus in different cerrado sites in central and southeast Brazil (Morais 1980; Ribas et al. 2003; Ribas and Schoereder 2004). Although formicine ants are clearly the predominant group, ants in the subfamilies Myrmicinae (*Cephalotes*), Ponerinae (*Ectatomma*), and Dolichoderinae (*Azteca*) also commonly feed on plant and insect exudates on cerrado foliage (for detailed faunal accounts, see Oliveira and Brandão 1991; Dansa and Rocha 1992; Oliveira et al. 1995; Oliveira and Pie 1998; Del-Claro and Oliveira 1999; Santos and Del-Claro 2001).

Evidence for ant-derived protection to cerrado plants

As opposed to myrmecophyte symbioses in which plants possess specialized organs to house ant colonies (Davidson and McKey 1993), nonsymbiotic ant–plant mutu-

alisms are mediated solely by the supply of food rewards to a number of ant species nesting elsewhere (Koptur 1992a). In the latter case many opportunistic ants are attracted to foliage via plant- and insect-derived rewards, and the outcomes of such facultative ant–plant associations may depend on a number of factors. For instance, benefits to EFN-bearing plants by visiting ants have been shown to vary with time (Tilman 1978), habitat type and intensity of herbivory (Barton 1986; Cogni et al. 2003), abundance and identity of ant visitors (Inouye and Taylor 1979; Rico-Gray and Thien 1989), herbivore vulnerability to ant predation (Hedges and Lawton 1985; Koptur 1984), presence of associated wasps (Cuautle and Rico-Gray 2003), and even with abiotic factors (De la Fuente and Marquis 1999; Wirth and Leal 2001). Moreover, the degree to which herbivore deterrence by visiting ants can affect plant fitness may depend largely on the type of tissue being damaged through herbivore activity (Marquis 1992; Oliveira et al. 1999, see Fig. 1G–H).

In this section we provide a general picture of the facultative, reward-mediated interactions between cerrado plants and their ant visitors. We present the experimental results separately for two groups of interaction systems: those mediated by the direct supply of extrafloral nectar by the plant, and those in which ants are attracted to the plant because of insect exudates.

Extrafloral nectary-mediated interactions

Experimental field studies in the cerrado have supported the idea that ant visitation to EFN-bearing plants results in decreased herbivore damage to the plant, and may also positively affect fruit set (Table 2). The deterring potential of ants against herbivores on plants with EFNs in the cerrado was first examined for the common tree *Qualea grandiflora* (Fig. 1A). The results from this study indicated that frequency of ant occupancy and levels of ant visitation were much higher on *Q. grandiflora* than on neighboring plants lacking EFNs. A field experiment using simulated herbivores (live termites) further demonstrated that common EFN-gathering *Camponotus* ants (*C. rufipes*, *C. crassus* and *C. aff. blandus*) could potentially act as anti-herbivore agents on *Q. grandiflora* leaves due to their overt aggressive behavior toward intruders near the food source (Oliveira et al. 1987). This was confirmed through a 2-month ant-exclusion experiment demonstrating that prevention of ant visitation to *Q. grandiflora* indeed significantly increased levels of leaf damage by specialist *Compsolechia* lepidopteran larvae (Gelechiidae), and by witnessing EFN-gathering ants attacking caterpillars on the host plant (Costa et al. 1992). An unequivocal demonstration of a positive effect from visiting ants to plant fitness in *Qualea* trees came from the study of Del-Claro et al. (1996), in which reduced damage to leaves and reproductive plant organs on ant-visited *Q. multiflora* trees translated into a 40% increase in fruit set when compared with ant-excluded trees (Table 2).

The most detailed study on an ant–plant–herbivore system in the cerrado involves the EFN-bearing shrub

Table 2 Summary of the main experimental results obtained in cerrado vegetation on ant-plant-herbivore interactions

Plant species (Family)	Type of ant reward ^a	Site of ant reward	No. of ant species	Herbivore	Plant organ consumed	Effect from ant visitation	Source
<i>Qualea grandiflora</i> (Vochysiaceae)	EFN	Stem, pedicel	12 ^b	Lepidopteran larvae	Leaves	Reduced folivory	Costa et al. (1992)
<i>Q. multiflora</i>	EFN	Stem, pedicel	8	Lepidopteran larvae Beetles	Leaves Buds, flowers	Reduced folivory Increased fruit set	Del-Claro et al. (1996)
<i>Ouratea spectabilis</i> (Ochnaceae)	EFN	Stipules, pedicel	26 ^c	Lepidopteran larvae	Leaves	Reduced folivory	Ferreira (1994)
<i>Caryocar brasiliense</i> (Caryocaraceae)	EFN	Buds, shoot tip	34 ^d	Lepidopteran larvae	Leaves	Reduced damage to stem and buds	Oliveira (1997)
				Galling wasps Hemipterans Dipterans	Leaves, stem Buds, fruits Buds	Increased no. of flowers and juvenile fruits	
<i>Didymopanax vinosum</i> (Araliaceae)	HEM	Branch	21 ^e	Beetles Leaf-mining dipterans	Leaves	Reduced folivory Reduced damage to apical meristem	Oliveira and Del-Claro (2004)
<i>D. vinosum</i>	LEP	Buds, flowers	7	Thrips Lepidopteran larvae	Shoot tips Buds, flowers	Decreased fruit set	Oliveira and Del-Claro (2004)

^a EFN = extrafloral nectaries; HEM = hemipteran honeydew; LEP = secretion from lepidopteran larvae^b Oliveira et al. (1987) have shown that ants attack simulated herbivores on leaves. List of ant species is given in Oliveira and Brandão (1991)^c Oliveira et al. 1995 have shown that ants (24 species) attack simulated herbivores on leaves of *Ouratea hexasperma*.^d For an account of the associated ant fauna, see Oliveira and Brandão (1991)^e For an account of the associated ant fauna, see Del-Claro and Oliveira (1999)

Caryocar brasiliense, which is intensively patrolled both day and night by many nectar-gathering ants (Fig. 1F). The plant is infested by five species of specialist insect herbivores that consume different types of plant tissue (Fig. 1G–J). Larvae of the butterfly *Eunica bechina* (Nymphalidae) feed on young leaves; nymphs and adults of the sucking bug *Edessa rufomarginata* (Pentatomidae) feed on buds and fruits; larvae of the fly *Prodiplosis floricola* (Cecidomyiidae) consume and destroy developing buds; and two species of galling wasps (Chalcidoidea) heavily attack branches and leaves. Ant-exclusion experiments have demonstrated that ant foraging activity on *C. brasiliense* significantly reduces the infestation levels by four of the herbivore species monitored, but had no effect on the leaf-galling wasp (Oliveira 1997). However, contrary to the results obtained for *Qualea multiflora* by Del-Claro et al. (1996), herbivore deterrence by EFN-gathering ants did not translate into a higher final fruit set by ant-visited *C. brasiliense* shrubs compared with ant-excluded ones. Despite producing significantly more flowers and initial fruits, higher rates of fruit abortion in ant-visited shrubs resulted in similar final fruit sets for plants in either experimental category (Table 2).

The contrasting consequences of ant-derived protection against herbivore damage for the reproductive output of EFN-bearing *Qualea* and *Caryocar* are possibly related to differences in resource allocation to fruits by each type of plant. Cerrado soils are characteristically poor (Motta et al. 2002), and nutrient deficiency is known to affect growth and biomass allocation in cerrado woody species (Franco 2002). While *Q. multiflora* trees produce many dry 'cheap' fruits each with 10–18 wind-dispersed seeds, *C. brasiliense* shrubs produce up to four fleshy drupes (weight 400 g) each containing 1–4 large vertebrate-dispersed seeds (Gottsberger and Silberbauer-Gottsberger 1983). Given that lack of soil nutrients is known to negatively affect final seed set in plants (Stephenson 1981), low soil fertility in cerrado possibly constrains the ability of *Caryocar* shrubs to provide the resources necessary for growth and development of their heavy fleshy fruits. Thus a higher production of initial fruits by ant-visited shrubs would be neutralized by competition among developing fruits and subsequent abortion. Resource limitation has already been suggested as a possible factor affecting the reproductive output in EFN-bearing plants protected by ants (Kelly 1986). The nutrient deficiency hypothesis for the ant–*Caryocar* system would require further confirmation using soil-enrichment experiments (Willson and Price 1980). Even if not translated into an increased final fruit set, reduction of herbivore damage by EFN-gathering ants may allow shrubs of *C. brasiliense* to overcome periods of intense herbivore attack as the plant grows larger. Thus ant-derived benefits could ultimately increase overall lifetime fitness of the plant even if seed set is not increased over a single ecological time point. Possible additional ant-derived benefits include a larger floral display and increased attractiveness to bat pollinators, production of surplus hermaphroditic flowers and increased male contribution to fitness through pollen

donation, and selective abortion of genetically inferior progeny as the maternal investment is adjusted to match available resources (Oliveira 1997).

Interactions mediated by ant attraction to insect exudates

The behavioral traits of foliage-dwelling ants causing herbivore deterrence on EFN-bearing plants are similar to those associated with protection of ant-tended insects from their natural enemies, and in either case the ants' ownership behavior near the food source is sufficient to repel intruders from the immediate vicinity (DeVries 1991; Koptur 1992a). Indeed, abundant and aggressive *Camponotus rufipes* are very effective at chasing intruders near both EFNs and honeydew-producing hemipterans in the cerrado (Oliveira et al. 1987; Del-Claro and Oliveira 2000; Sobrinho et al. 2002). Thus increased alertness and aggression by tending ants near trophobionts can potentially increase plant fitness if ant-derived benefits from herbivore deterrence outweigh losses resulting from hemipteran feeding (Carroll and Janzen 1973; Messina 1981).

The sap-feeding treehopper *Guayaquila xiphias* (Membracidae) commonly infests shrubs of *Didymopanax vinosum* in the cerrado, and is tended day and night by a diverse assemblage of honeydew-gathering ants (Del-Claro and Oliveira 1999). The treehoppers frequently aggregate close to the inflorescence at the apex of the single reproductive branch. The importance of *G. xiphias* honeydew as an energy supply for ants in the cerrado is such that species like *C. rufipes* (Fig. 1E) and *Ectatomma edentatum* extend their tending activities for 24 h. Field experiments demonstrated that tending ants decrease the abundance of the treehopper's natural enemies on the host plant, and have a positive impact on *G. xiphias* survival (Del-Claro and Oliveira 2000).

Apart from ant-tended *Guayaquila*, shrubs of *D. vinosum* are infested by four species of specialist insect herbivores. The thrips *Liothrips didymopanicis* (Phlaeothripidae) feeds on apical shoot tips, and severe thrips-induced damage may kill the host plant (Del-Claro and Mound 1996). Leaf damage is caused mainly by chewing *Caralauca olive* beetles (Chrysomelidae), and by mining/feeding activity of developing lepidopteran larvae. Myrmecophilous larvae of *Panthiades polibetes* (Lycaenidae) consume floral buds and are tended by *Camponotus*, *Cephalotes*, and *Ectatomma* ants, which actively feed on secretions from caterpillars. Thus, if co-occurring with *G. xiphias* on a plant, *P. polibetes* shifts ant attention partly away from the treehoppers towards the liquid-rewarding caterpillars. Results from field experiments with manipulated plants revealed that the occurrence of ant-*Guayaquila* interactions can have contrasting effects on the abundance and damage caused by associated herbivores of *D. vinosum* (Table 2). While ants tending *G. xiphias* treehoppers significantly decreased damage by thrips to the growing meristem and by chewing and mining insects to leaves, higher infestation levels by ant-

tended *P. polibetes* larvae on plants with treehoppers reduced fruit set of *D. vinosum* by 84% (Oliveira and Del-Claro 2004).

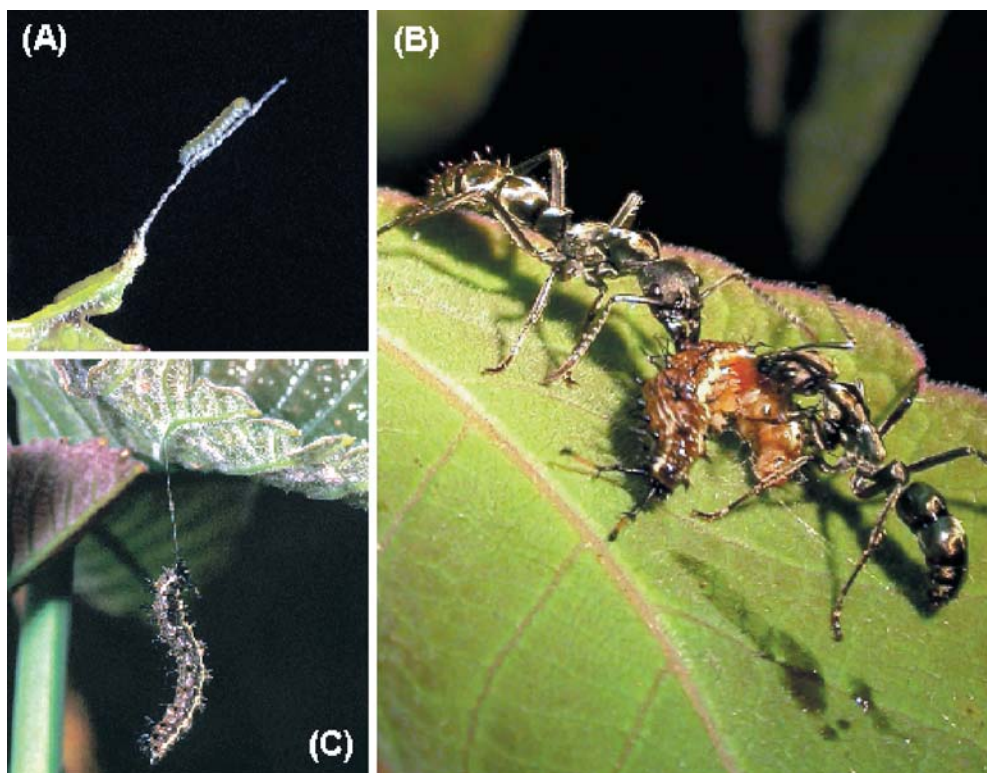
Extrafloral nectaries, predation pressure by ants, and herbivore behavior: a tale of a butterfly

By producing sweet appeasing substances, ant-tended lepidopteran larvae can avoid ant attacks on the host plant (Malicky 1971), and numerous studies have shown that myrmecophilous larvae may also benefit from ant attendance in several ways, including protection from natural enemies, enhanced growth, and increased fecundity (Pierce et al. 2002, and references therein). On the other hand, due to the threat of ant predation, non-myrmecophilous caterpillars feeding on ant-visited plants must possess morphological and behavioral mechanisms to cope with frequent encounters with ants on foliage (Salazar and Whitman 2001). Experimental research on the negative effects of ants on butterfly behavioral biology, however, is scarce and mostly confined to the Heliconiini (Benson et al. 1976; Brown 1981; Smiley 1985). By attracting persistent ant assemblages to their foliage (Oliveira and Brandão 1991), plants bearing extrafloral nectaries provide an ideal opportunity for testing defensive mechanisms exhibited by non-myrmecophilous insect herbivores as they select host plants and/or feed on plant tissue. In this section we use the *Caryocar brasiliense* – ant system described above to gather data on behavioral patterns of an insect herbivore before (during the oviposition process) and after (as immature on host plant) it arrives on foliage and faces the threat of predation on a highly ant-visited plant.

Larvae of the non-myrmecophilous nymphalid butterfly *Eunica bechina* feed on young leaves of the ant-visited EFN-bearing shrub *C. brasiliense* (Fig. 1G). Caterpillars of 1st to 4th instars rest on the tip of stick-like frass chains constructed at leaf margins (Fig. 2A). While walking on leaves the caterpillars risk being killed by patrolling ants that are attracted to the plant's nectary secretions, and ant-excluded shrubs are more infested by eggs and larvae of *E. bechina* than plants with free ant access (Oliveira 1997). Although ant foragers attack and remove caterpillars from *C. brasiliense* (Fig. 2B), we here show that *E. bechina* may circumvent ant predation on this highly ant-visited host plant through behavioral traits exhibited by both larval and adult stages. Controlled field experiments enabled us to identify some of the selective forces underlying this ant-plant-butterfly system, and to demonstrate how certain behavioral patterns of an insect herbivore can markedly affect the chance of encountering its natural enemies on foliage (Freitas and Oliveira 1992, 1996). The main behavioral observations and experimental results are summarized here.

Ant foragers are known to consume and remove eggs of a variety of insect taxa, including lepidopterans (Kluge 1991; Goebel et al. 1999). However, possibly due to their toughness and firm attachment to leaves, *E. bechina* eggs

Fig. 2 Interaction between ants and caterpillars of *Eunica bechina* on *Caryocar brasiliense*. **A** First-instar larva rests motionless on its frass chain. **B** Workers of *Pachycondyla villosa* fiercely attack a fourth-instar caterpillar on a leaf; note signs of larval bleeding in the foreground caused by successive bites by the ants. **C** Third-instar larva hangs by a silken thread after jumping off the leaf upon attack by a large ant



were ignored by foraging ants on host plants and egg removal was not affected by ant presence over an observation period of 24 h (Freitas and Oliveira 1996). On the other hand ants did affect the oviposition behavior of *E. bechina* females, but this was shown to depend on the level of ant visitation to the host plant, with females laying fewer eggs on plant branches highly visited by ants than on ant-excluded ones (Table 3A). Similarly, caterpillar mortality on foliage was significantly affected only at high ant densities on the host plant, and vulnerability to ant predation decreased with larval size (Table 3B, C). Whereas small larvae can be easily subdued and carried by ant foragers, large caterpillars regurgitate or bleed upon disturbance (Fig. 2B) and this may provoke avoidance reactions by the ant and inhibit further attack. Jumping off the leaf and hanging on a silk thread may also occur if large ants continually bite the caterpillar (Fig. 2C).

The role of stick-like frass chains built by caterpillars (Fig. 2A) against ant predation on *C. brasiliense* was tested by attaching with nail polish live termites to the end of abandoned frass chains, and on leaves of ant-patrolled host plants. The frass chains were demonstrated to be a safe refuge against ant predation; ants attacked termites on leaves in significantly greater numbers than on frass chains (Table 3D). Caterpillars of *E. bechina* normally feed next to the frass chain and when perceiving the approach of ants, possibly by substrate-borne vibrations, they retreat to the tip of the frass chain in time to avoid predation (see Fig. 3).

Because ants do not chase ovipositing *E. bechina* and because egg-laying lasts only 1–3 s, the differential oc-

currence of butterfly eggs on ant-visited and ant-excluded *C. brasiliense* reported by Oliveira (1997) was hypothesized to result from a decision by the ovipositing females. Since butterflies are known to use visual cues prior to oviposition (Williams and Gilbert 1981), we tested whether *E. bechina* females would visually avoid ant-occupied plant locations. Indeed, egg-laying females were shown to visually inspect the host plant prior to oviposition (Fig. 4). Plant locations containing artificial rubber ants were significantly less infested over a 24 h period than locations with rubber circles used as controls, indicating that ant presence alone is enough to provoke an avoidance response by ovipositing females (Table 3E).

The experimental results with this ant–plant–butterfly system unequivocally demonstrate that the behavior of both immature and adult *E. bechina* is closely related to the utilization of a risky host plant, where intense visitation by ants can have a strong impact on caterpillar survival. Although larval defensive behaviors are probably more clear-cut (i.e., hanging on a silk thread, making a frass chain) due to direct predation pressure from ants, our data show that an appropriate choice of oviposition site by the gravid female can be crucial for the survival chances of her offspring.

Contrary to *E. bechina*, in which encounters with ants on foliage are discouraged by both larvae and adults, myrmecophilous butterfly species may actually promote contact with them by attracting nearby ants through substrate-borne vibration calls from larvae and pupae (Pierce et al. 2002), or by laying eggs on ant-occupied host plants (Atsatt 1981; Pierce and Elgar 1985). Promotion of contact with potential tending ants, by both

Table 3 Summary of the field experiments on the interaction between *Eunice bechina* and ants, on shrubs of *Caryocar brasiliense* (after Freitas and Oliveira 1996)

Experiment	Variable	Low ant density ^a		High ant density ^a		P ^c
(A) Effect of ant occupation on butterfly oviposition	No. of eggs laid in 24 h	Ants present (n=24) 0.96 ± 0.20	Ants excluded (n=24) 1.46 ± 0.31	Ants present (n=24) 0.58 ± 0.18	Ants excluded (n=24) 1.67 ± 0.22	** (U test)
(B) Effect of ant occupation on larval mortality	No. of larvae disappearing in 24 h	Ants present (n=32) 12	Ants excluded (n=32) 6	Ants present (n=33) 20	Ants excluded (n=33) 8	** (G test)
(C) Vulnerability to ant predation versus larval size	Percentage of larvae attacked	Caterpillar size class ^b 1st–2nd instars 70 (n=26)				** (G test)
(D) Role of frass chain as a refuge against ant predation	No. of termites attacked in 10 min	Location of termite on host plant Frass chain (n=30) 3			5th instar 0 (n=26)	** (G test)
(E) Response by egg-laying females to visual stimuli (ant image) on host plant	No. of eggs laid in 24 h	Type of rubber object (n=15 plants) 'Ant' 0.73 ± 0.21		Leaf (n=30) 20 Circle 1.6 ± 0.30		** (G test) * (U test)

^a Ant density per plant: low (0.25 ± 0.20, n=56); high (1.25 ± 1.19, n=57)^b Size of larval instars: 1st–2nd (<6 mm), 3rd–4th (6–20 mm), 5th (>20 mm)^c ns = not significant, * <0.05, ** <0.01

hemipteran trophobionts through honeydew flicking, and myrmecophilous lycaenids through preferential oviposition on ant-visited plants, has also been demonstrated in the cerrado (see Del-Claro and Oliveira 1996; Oliveira and Del-Claro 2004).

Liquid food rewards, facultative ant–plant systems, and the community

Recent studies have provided strong evidence that the occurrence of liquid rewards on leaves plays a key role in mediating the foraging ecology of foliage-dwelling ants, and that facultative ant–plant mutualisms are important in structuring the community of canopy arthropods. Ants comprise a major part of the arthropod fauna occupying the canopy of tropical forests, and the numbers and biomass of ant foragers greatly surpass those of their potential herbivore prey (Tobin 1995). This inverted biomass pyramid has been explained by recent evidence showing that the dietary requirements of many foliage-dwelling ants consist mostly of plant- and insect-derived exudates such as extrafloral nectar, hemipteran honeydew, and lepidopteran secretions (Davidson 1997; Davidson et al. 2003). Indeed, although the abundance of EFN-bearing plants is relatively well documented for a number of habitats (Table 1), knockdown samples have apparently underestimated the occurrence of honeydew-producing insects in the canopy of tropical environments (see Lopes 1995; Dejean et al 2000). Davidson (1997) has suggested that the high abundance of liquid food rewards on leaves plays an important role in shaping the food web structure in tropical forests by fueling costly prey-hunting activities by foliage-dwelling ants, especially if the ants are physiologically adapted to a diet of low nitrogen content. At high densities on foliage, exudate-fueled ant foragers would keep prey species at lower numbers than expected from an ant diet entirely dependent on animal prey.

In contrast to other types of interactions (e.g., Barbosa and Benrey 1998; Barbosa and Wratten 1998), few studies have addressed the role of mutualism in shaping communities (Gilbert 1980). In particular, ant–plant systems in which herbivore deterrence by visiting ants reduces herbivore damage are surprisingly poorly represented among community level studies. However, because such mutualistic systems frequently involve a range of direct and indirect effects encompassing multiple trophic levels, their impact on community structure can be strong due to the cascading effects (top-down and bottom-up) produced beyond the pairwise interaction (see Bronstein and Barbosa 2002; Dyer and Coley 2002).

The impact of ants on community organization derives largely from an opportunistic diet that simultaneously makes them the main predators of arthropods on tropical foliage (Jeanne 1979), as well as prime consumers of carbohydrate-rich plant and insect exudates (Blüthgen et al. 2000; Davidson et al. 2003). Indeed, this dietary attribute has set the scenario for the involvement of ants in protection mutualisms with plants via ant attraction

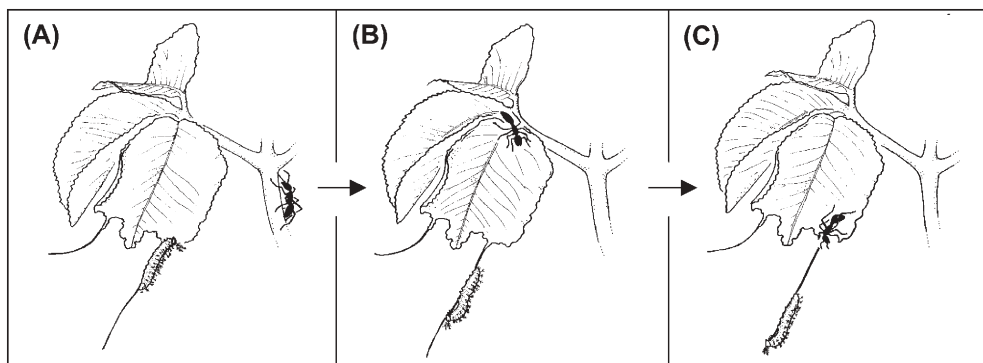


Fig. 3 Behavior of *Eunica bechina* caterpillars on ant-visited shrubs of *Caryocar brasiliense*. **A** While feeding at leaf margins, the caterpillar typically remains on its frass chain. **B** As a foraging ant reaches the leaf, the caterpillar immediately walks to the end of the frass chain and remains motionless. **C** The ant may chase the

caterpillar but eventually walks away after a few attempts to reach the larva. Field experiments have shown that the frass chain represents a safe refuge against ant attacks on the host plant; see Table 3D

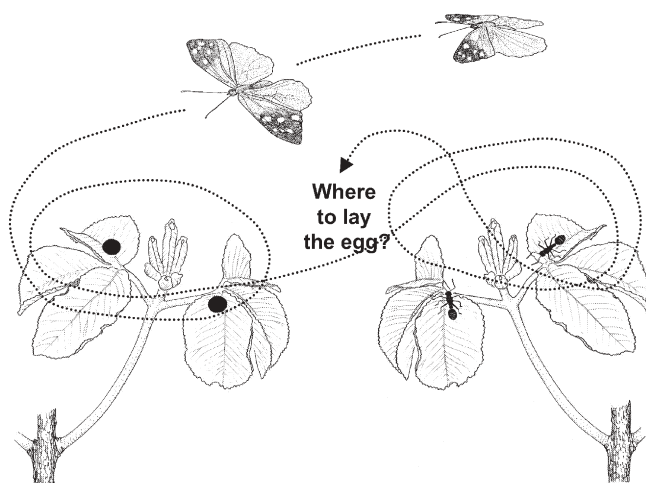


Fig. 4 Experimental setup used in the field to test whether females of the butterfly *Eunica bechina* visually avoid ovipositing on ant-occupied locations of its host plant, the shrub *Caryocar brasiliense* (after Freitas and Oliveira 1996). Visual cues to ovipositing females consisted of similar-sized (1 cm) black rubber ants (right) and black rubber circles (left) placed simultaneously on neighboring branches of ant-excluded, egg-free shrubs. After 24 h, more eggs had been laid on plant locations with rubber circles than with rubber ants; see Table 3E

through the offer of extrafloral nectar or food bodies (Koptur 1992a), and with insect trophobionts whose energy-rich exudates induce ant attendance (Buckley 1987; Pierce et al. 2002). Moreover, trophobionts themselves may act as insect analogs of extrafloral nectaries because tending ants may deter other herbivores on the plant (Messina 1981; Oliveira and Del-Claro 2004). By feeding on these carbohydrate-rich secretions, however, exudate-foraging ants may require help from associated endosymbionts to upgrade their nitrogen from lower trophic levels (Davidson 1997), which further enhances the interconnected and multispecific character of the mutualisms centered around foliage-dwelling ants (see Bronstein and Barbosa 2002).

The interaction scenario in cerrado: uniqueness and perspectives

Beattie and Hughes (2002) state that particular habitats may generate similar traits among highly disparate plant families that inhabit them, and that local ant assemblages taking advantage of such traits may generate a continuum of interactions that may vary from antagonism to mutualism. The cerrados constitute a unique biome for studies on ant–plant–herbivore interactions due to a few key traits of the plant community that make ants especially prevalent on foliage. In particular, the richness of the arboreal ant fauna in the cerrado (Ribas et al. 2003; Ribas and Schoereder 2004), and the high occurrence on vegetation of predictable liquid food sources in the form of extrafloral nectar (Oliveira and Leitão-Filho 1987; Oliveira and Oliveira-Filho 1991; Paiva et al. 2001) and insect-derived secretions (Dansa and Rocha 1992; Lopes 1995; Diniz and Morais 1997) generate intense ant activity on cerrado foliage and, as a result, make ant–plant–herbivore interactions especially pervasive in this biome (Oliveira and Del-Claro 2004).

Although the bulk of information accumulated over the past two decades in cerrado indicate that ants can be key participants in the selective processes operating at the plant–herbivore interface (Freitas and Oliveira 1996; Oliveira et al. 2002), more basic natural history and quantitative data are essential for a better understanding of their role in structuring cerrado herbivore communities. For instance, what is the proportion of ants in both numbers and biomass compared to their potential herbivore prey in cerrado communities? In the only case of myrmecophyte symbiosis so far reported in the cerrado region, Bizerril and Vieira (2002) showed that *Tococa formicaria* plants inhabited by *Azteca* ants had lower levels of herbivory than plants occupied by other ant species. The degree to which occurrence of arboreal ant nests inside hollowed out stems of non-myrmecophytic plants can reduce herbivore activity as a result of increased ant foraging on leaves awaits further investigation. Despite the abundance of liquid rewards on the plant

surface and the constancy and diversity of ant attendants at such food sources, it is still unclear how simultaneous ant visitation to plant and insect exudates on a given plant can affect herbivore performance in cerrado (see Bécerra and Venable 1989; Fiala 1990; Del-Claro and Oliveira 1993). Moreover, although attractiveness of plant and insect exudates is high enough to induce ant attendance over 24 h (Oliveira and Brandão 1991; Del-Claro and Oliveira 1999), the relative importance of liquid rewards as an energy supply of foliage-dwelling ants and their specific effects on the ant colony remain to be evaluated in cerrado (see Pierce and Nash 1999).

Besides deterring herbivores and/or removing their eggs on the leaf surface, foliage-dwelling ants can also influence the egg-laying process by disturbing ovipositing females (see Janzen 1967). Our experimental results on ant–butterfly interactions provide additional insights about the behavioral response of insect herbivores to ant presence, and to host-plant traits. Although ants provide a consistent defense system relatively immune to evolutionary changes by the herbivore (Schemske 1980), it has already been shown that immature and adult herbivores present morphological and behavioral traits that markedly reduce ant interference on foliage (Hedges and Lawton 1985; Freitas and Oliveira 1992, 1996; Machado and Freitas 2001; Salazar and Whitman 2001). Results of the field experiment on oviposition preference by *Eunica bechina* females suggest that the use of visual cues prior to oviposition can be relevant not only to increasing offspring survival on a risky ant-visited plant, but to evaluating plant quality as well. All known species of *Eunica* oviposit on new leaves and/or buds (DeVries 1987; Oliveira and Freitas 1991; Freitas and Oliveira 1992), and these plant organs in general present a contrasting reddish appearance (Fig. 1F, G). Since butterflies can use a variety of visual cues such as color, shape, and presence of special structures while selecting host plants (Rauscher 1978, 1979; Williams and Gilbert 1981; Shapiro 1981), it is possible that *Eunica* females use color discrimination while choosing appropriate plant organs for oviposition. Additionally, because the negative impact of ants on *Eunica* caterpillars varies among different ant species (Freitas and Oliveira 1992), it would be worth exploring whether egg-laying females are able to discriminate between ant species based on their external appearance on foliage, and can respond differently to these during the oviposition process. One can also predict that ant avoidance by females through visual cues, and/or construction of frass chains by larvae, would be more common and notable in butterfly species using plants with high ant visitation rates. As an ant-rich environment, the cerrado savanna offers an ideal opportunity for research on behavioral ecology of ant–herbivore interactions.

Concluding remarks

Ecological communities based on terrestrial plants involve at least three interacting trophic levels – plants,

herbivores, and natural enemies of herbivores – and in recent years a consideration of the third trophic level has been regarded as crucial for understanding not only plant–animal interactions but also entire communities (Price et al. 1980; Thompson 1988). Because multitrophic/multi-species mutualisms (including ant–plant systems) entail a range of direct and indirect effects among many participant species, their outcomes can be highly variable (Bronstein and Barbosa 2002). Since direct and indirect effects can cascade up and down across different trophic levels, the identification of which populations within a trophic web can be controlled by resource availability (bottom-up effect), and which can be regulated by higher trophic levels (top-down effect) has become a central issue in community ecology (Pace et al. 1999). Bottom-up and top-down effects can follow different trends along a latitudinal gradient (Dyer and Coley 2002), and ant-mediated effects on the structure of herbivore communities in cerrado are more likely to be revealed by experiments performed on wider spatial scales, and considering environmental factors such as climate, soil fertility, and vegetation structure (see Beattie and Hughes 2002). In fact, available evidence from the ant–*Caryocar brasiliense* system suggests that soil fertility may play a role in determining ant-derived benefits to the plant's reproductive output by constraining maternal investment in fleshy fruits (Oliveira 1997). Moreover, long-term studies in this system might explain the evolutionary forces maintaining interactions that have only minor short-term effects. The Brazilian cerrados cover a vast geographic extension, and vegetation physiognomies may also vary markedly on a regional scale (Oliveira-Filho and Ratter 2002). Thus, the occurrence of extrafloral nectary plants along both local and latitudinal (subtropical to tropical) gradients of cerrado communities need to be assessed in connection with abiotic factors and with parameters associated with ant prevalence on foliage (e.g., species richness, frequency of arboreal nests), ant-derived herbivore deterrence (rates of ant predation), herbivore activity, and plant performance (Pemberton 1998; Coley and Aide 1991). However, continual fragmentation of the cerrado biome caused by intense human use is currently destroying the integrity of the savanna's rich habitat matrix, and threatens the “interaction biodiversity” within the cerrado landscape (Thompson 1997). This threat raises a major concern as to how complex multispecies systems such as those reported here will respond, and ultimately whether cerrado communities will remain viable.

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