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Ant–plant interactions: the importance of extrafloral nectaries versus hemipteran honeydew on plant defense against herbivores

Ricardo I. Campos · Gabriela P. Camacho

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Abstract The two most important ant–plant attractions are extrafloral nectaries (EFNs) and hemipteran honeydew. In both cases, ants may offer an effective protection against natural enemies of plants, in exchange for its sugar-rich exudates. The aim of this paper was to compare the efficiency of ant protection between plants with EFNs and with hemipteran honeydew. The study was carried out in the Amazonian Rain Forest Reserve at km 41 (02° 24'S, 59° 44'W), located 80 km from Manaus. We recorded 24 ant species in 25 plants species in the forest understory along two line transects of 5 km. The efficiency of ants in protecting plants was measured by an experiment of prey removal using isopteran workers. It was found that ants are more effective and faster in attacking termites when using honeydew rather than EFNs, probably due to the larger resource monopolization. This study further underlines the importance of experimental studies to elucidate the ecological and evolutionary importance of EFNs and honeydew in ant–plant defense against herbivores.

Keywords Ant food reward · Sugar-rich exudates · Arboreal ants · Termites · Myrmecophily · Amazonian Rain Forest

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R. I. Campos (✉)
Departamento de Biologia Geral, Universidade Federal de Viçosa (UFV), Viçosa, MG 36570-000, Brazil
e-mail: ricardo.campos@ufv.br

G. P. Camacho
Programa de Pós-Graduação em Entomologia, Departamento de Zoologia, Universidade Federal do Paraná (UFPR), Curitiba, PR 81531-980, Brazil
e-mail: gabieco.camacho@gmail.com

Introduction

Ants and plants can form mutualistic systems in which plants offer food (exudates) to the ants, which in turn protect plants against their natural enemies (Rico-Gray and Oliveira 2007; Nascimento and Del-Claro 2010). Considered one of the most important plant food rewards for ants (Bentley 1977; Nogueira et al. 2012), the nectar produced by extrafloral nectaries (hereafter EFNs) is used by a great variety of ants to supplement their diets (Oliveira and Brandão 1991). The great amount of sugar-rich exudates produced by these glands (Beattie 1985; Davidson and Mckey 1993) attracts different ant species (Blüthgen et al. 2000; Nogueira et al. 2012). Generally, these ants, by means of aggressive behavior, can generate protection against the plant's natural enemies, such as predators, parasites and/or competitors (Del-Claro and Santos 2000; Nascimento and Del-Claro 2010). Therefore, plants with extrafloral nectaries tended by ants generally experience less herbivory (Korndorfer and Del-Claro 2006; Nascimento and Del-Claro 2010).

Alternatively, many ant species can use a sugary substance excreted by hemipterans (“honeydew”) as the main source of carbohydrates in their diets, with these ants protecting hemipterans and their host plants from natural enemies (Buckley 1987; Cushman and Whitham 1991). Several hemipteran taxa, such as Coccidae, Psilidae and Membracidae, are attended by ants (Moya-Raygoza and Nault 2000; Delabie 2001). The conspicuous associations between ants and hemipterans (Order Hemiptera, Suborder Sternorrhyncha and Auchenorrhyncha; Carver et al. 1991) occur in the great majority of flowering plant families, which are widely distributed from tropical to temperate habitats (revision in Buckley 1987).

Despite the great importance of EFNs and hemipteran honeydew in structuring ant assemblages in plants

(Blüthgen et al. 2000), few studies have compared these two types of food rewards at a community level (Floren and Linsenmair 2000; Blüthgen et al. 2000). Studies with one species of Hemiptera and/or one species of plants demonstrate that ants generally shift between EFNs and honeydew depending on the most abundant resource available (Moya-Raygoza and Larsen 2001; Katayama and Suzuki 2003). Working with different species of ants, hemipterans and plants, Blüthgen et al. (2000) showed that honeydew may be a more valuable resource for ants than nectar from EFNs because the former is generally more abundant, nutritious and constant. Based on this, it is plausible to believe that ants attending hemipterans can increase the protection for plants, when compared with those using EFNs.

In addition, Oliveira et al. (1987a) demonstrated that ant patrolling on plant foliage is related to the distribution of extrafloral nectaries among the branches of *Qualea grandiflora* in *Cerrado* vegetation. In this work, the authors have shown that the leaf age did not affect the rate of prey attack by ants, but the greater patrolling activity was correlated with greater availability of food resources (e.g., density of EFNs). Furthermore, another study with plants of the genus *Triplaris* showed that the ants tend to be more aggressive close to their nest or to food sources, especially if food is scarce, or has a permanent location (Oliveira et al. 1987b). This is the case for EFNs that produce a small amount of nectar source and have a fixed position, which differs from honeydew that is an abundant resource and tends to move throughout the plant branches. However, no experimental study has compared the plant defense behavior by ants between these two types of carbohydrate sources. We believe that making this comparison, we will generate some basic information that could help to solve at least some part of the controversy among researchers who are trying to explain the influence of EFNs on the evolution of the ant–hemipteran interaction and vice versa (Becerra and Venable 1989, 1991; Gaume et al. 1998; Offenbergl 2000; Blüthgen et al. 2004).

Therefore, the purpose of this study was to compare ant efficiency in protection between plants with EFNs and hemipteran honeydew. Specific aims are based on the following questions: (1) Do ants attending hemipterans generate a stronger and faster response in the protection for plants, when compared with those using EFNs? (2) Are there differences in plant protection by ants according to the distance from the food source (EFNs or hemipteran honeydew)?

Methods

The study was carried out in July 2003 in the Amazonian Rain Forest Reserve at km 41 (02° 24'S, 59° 44'W), which

Table 1 Number of plant individuals recorded with ants visiting extrafloral nectaries (EFNs) or attending hemipterans (AHI)

Plants		Number of individuals	
Family	Species	EFNs	AHI
Bignoniaceae	<i>Arrabidaea</i> sp.	2	
Boraginaceae	<i>Cordia</i> sp.		1
Clusiaceae	<i>Vismia cayannensis</i>		4
	<i>Vismia guianensis</i>		4
	<i>Vismia japurensis</i>		6
Euphorbiaceae	<i>Aparistimum cordatum</i>	2	
Leguminosae	<i>Acacia multipinnata</i>	1	
	<i>Inga</i> sp. 1	3	
	<i>Inga</i> sp. 2	4	
	<i>Inga</i> sp. 3	4	
	<i>Machaerium multifoliolatum</i>	1	
Lauraceae	<i>Stryphnodendron pulcherrimum</i>	2	
	<i>Mimosa guilandinae</i>	4	
	<i>Ocotea</i> sp.		1
	<i>Platymicium</i> sp.	1	
Malpighiaceae	<i>Piptadenia minutiflora</i>	4	
	<i>Piptadenia</i> sp.	1	
	<i>Byrsonima duckeana</i>		2
Melastomataceae	<i>Byrsonima</i> sp.		2
	<i>Bellucia dichotoma</i>		6
Myrtaceae	<i>Miconia</i> sp.		1
	<i>Eugenia</i> sp.		1
Sapotaceae	<i>Diliocarpus</i> sp.		2
Siparunaceae	<i>Siparuna</i> sp.		1
Violaceae	<i>Rinorea</i> sp.	1	

belongs to the Biological Dynamics of Forest Fragments Project (PDBFF/INPA), located 80 km from Manaus, Brazil. Ant sampling was conducted along ZF3 (an unpaved road) in two parallel 5-km transects placed on both sides of the road. Inter-transect distance was 100 m (50 m from the road on both sides), in order to avoid edge effects. Along these transects, all plants (young trees or shrubs) that possessed ants on EFNs or attending hemipterans were recorded, totalling 61 plant individuals spaced by at least 20 m from each other.

The 61 plant individuals belonged to 25 species, 18 genera and 12 families. All of the Leguminosae plant species and almost all of the Lauraceae were recorded presenting interaction with EFNs, and all of the Melastomataceae and Clusiaceae presented ant–hemipteran interactions. No plant species sampled presented both interactions (Table 1).

The efficiency of ant–plant protection was measured by a prey removal experiment, which used isopteran workers

(Jeanne 1979). For this experiment, two live termites were pasted on the upper face of two different leaves on the same plant individual. The termites were pasted on their backs with white glue. In total, 122 termites were fixed to 61 plant individuals. The experiment was divided in two treatments with two levels. Treatment one consisted of 30 plants with EFNs and treatment two, 31 plants with ant-hemipteran interactions (hereafter AHI). There were no plants with both interactions at the same time. For each plant, a termite was glued to the nearest leaf to the interaction (EFNs or AHI), the “close” level, and another termite was glued to the most distant leaf from the interaction (at least 1 m), named as the “far” level. The “far” level was distant at least 1 m from other interactions that may be occurring in the plant.

The experiment itself consisted of measuring the time interval from gluing the termite on the leaf until the first ant attack on the termite. It was not considered as an attack when the ant just located the termites, not biting them nor recruiting other workers. The maximum time established for an attack was 10 min; after that, the termite was considered non-attacked. For analyses, the variable “time” was transformed into seconds and the time considered for the termites non-attacked was 600 s (10 min). After the experiment, at least three individuals of each ant species and a sample of each individual plant were collected for identification.

In order to compare ant species richness between plants with EFNs or AHI, we used a generalized linear model (GLM, see Crawley 2013). For this GLM model, we used the number of ant species per plant as response variable and the type of interaction (EFN and AHI) as explanatory variable. In order to deal with a count data (number of ants species), we used Poisson error distribution in software R (R development Core Team 2009). We compare the ant efficiency protection between plants with EFNs and hemipteran honeydew using a regression analysis following a Weibull survival distribution (Weibull 1951). For this survival model, we used the proportion of termites attacked by ants and the time of attack as response variables and the type of interaction (EFNs or AHI) and distance from interaction (close or far) as explanatory variables. We used the survival function in software R for this analysis (R development Core Team 2009). Finally, the ant species similarity between plants with EFNs and AHI was calculated by the binary index of Jaccard (Zar 1999).

Results

In total, 24 ant species, representing 15 genera and 5 subfamilies, were recorded (see Table 2) from 61 plant individuals. The richest genera were *Camponotus* Mayr

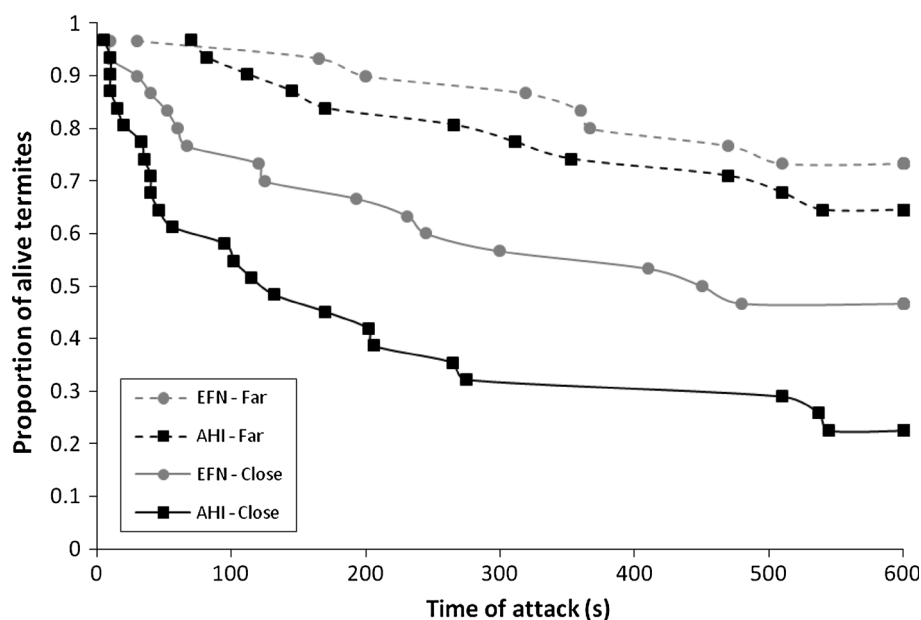
Table 2 Ant species recorded visiting extrafloral nectaries (EFNs), attending hemipterans (ant-hemipteran interaction-AHI) or just foraging on the leaves (others)

Ants		Interactions		
Subfamily	Specie	EFN	AHI	Others
Dolichoderinae	<i>Azteca</i> sp.	X		
	<i>Dorymyrmex</i> sp.		X	
	<i>Dolichoderus</i> sp.	X	X	
Formicinae	<i>Brachymyrmex</i> sp.			X
	<i>Camponotus retangularis</i>			X
	<i>Camponotus</i> sp. 1		X	
	<i>Camponotus</i> sp. 2			X
	<i>Camponotus</i> sp. 3	X		
	<i>Camponotus</i> sp. 4		X	
	<i>Gigantiops destructor</i>			X
Myrmicinae	<i>Nylanderia</i> sp.			X
	<i>Crematogaster</i> sp. 1	X	X	
	<i>Crematogaster</i> sp. 2	X	X	
	<i>Cephalotes pusillus</i>			X
	<i>Pheidole</i> sp. 1	X	X	
Ectatomminae	<i>Pheidole</i> sp. 2		X	
	<i>Wasmannia</i> sp.			X
	<i>Ectatomma tuberculatum</i>	X	X	
	<i>Ectatomma</i> sp. 1	X	X	
Pseudomyrmecinae	<i>Ectatomma</i> sp. 2	X	X	
	<i>Pseudomyrmex gracilis</i>			X
	<i>Pseudomyrmex</i> sp. 1			X
	<i>Pseudomyrmex</i> sp. 2			X
	<i>Pseudomyrmex</i> sp. 3			X

(five species) and *Pseudomyrmex* Lund (four species). Among the 24 ant species collected, 11 were foraging on the leaves (not assessing alimentary sources), seven used the two types of resources, two only used EFNs and four only used hemipterans honeydew (Table 2). From all 122 termites, 59 were attacked. There was a larger number of ant species associated with plants that possessed AHI ($N = 31$; median = 2; range = 1–5) when compared with plants with EFNs ($N = 30$; median = 1; range = 1–3; deviance_{1,60} = 4.55; $p = 0.032$). There was also a relatively high species similarity between ant fauna visiting EFNs and honeydew, where seven out of 13 species visited both food sources (Jaccard = 53.8 %; Table 2).

Regarding our two main questions, the survival analysis model showed that the proportion of alive termites (termites not attacked by ants) decreased faster and in a greater proportion in plants with AHI than with EFNs (Deviance_{1,119} = 3.87; $p = 0.049$; Fig. 1) and also when they were placed close than far from the interaction

Fig. 1 Survival curves showing the proportion of alive termites (termites not attacked by ants) decreasing in function of time. This curves were constructed with the time taken by the ants to attack and kill the termites glued in plant leaves close and far from extrafloral nectaries (EFNs) and ant–hemipteran interactions (AHIs)



(deviance_{1,118} = 20.45; $p \ll 0.001$; Fig. 1). The model also showed that regardless the type of interaction (AHI and EFNs), the termites were attacked more and faster when placed close to the interaction (absence of statistical interaction between the two variables: deviance_{1,117} = 0.46; $p = 0.499$; Fig. 1).

Discussion

Higher ant richness was found in plants with AHI in comparison with plants with EFNs. This result could be considered controversial since only one ant species was found attending hemipterans on the same plant, which indicates that ants tend to strongly monopolize this type of resource (Blüthgen et al. 2000; Delabie 2001). A possible explanation could be related to less movement of ants attending hemipterans when compared with those using EFNs (Delabie 2001; Oliveira and Pie 1998). Possibly, ants harvesting honeydew tend to reduced mobility on the plant due to a clumped distribution of hemipterans. This behavior would allow a larger number of other ants to forage on the plant, since they do not interfere with the attended hemipterans. As EFNs generate a good distribution of exudates with high quality (Oliveira and Pie 1998), it seems that a few dominant species would monopolize these plants and exclude other several non-dominant ant species from the plant that would be forced to use suboptimal resources (Dattilo et al. 2014). Inversely, for the Amazonian rainforest canopy, lower ant richness in plants with AHI than EFNs was found (Blüthgen et al. 2000). One possible explanation is related to the higher hemipteran

abundance found in the canopy than in the understory. Probably, there is a higher number of hemipteran aggregations on plants in the canopy compared with the understory. Consequently, in the tree canopy, ants attracted by honeydew would be present all over the plant, decreasing the number of other ant species.

A relatively high similarity was observed between ant species visiting EFNs and hemipteran honeydew (54 %). Ants that explored these two types of food sources possess similar food characteristics (Hölldobler and Wilson 1990; Oliveira and Pie 1998; Delabie 2001) which makes a high similarity likely between that fauna. Dattilo et al. (2013, 2014) showed that in general terms, the ant–plant networks are formed by a small subset of generalist ant species composing an interactive core. These authors argue that it could be explained by the fact that few ant species present a set of feeding adaptations related to the exploitation of liquid sources (Eisner 1957). It is also important to point out that there are also a few ant genera that do not have any adaptation for liquid feeding but can still carry that externally to the nest, but these less specialized species and weak competitors only participate in the networks as peripheral species (Dattilo et al. 2014).

Although few studies directly compare AHI and EFN, Blüthgen et al. (2000) working in the canopy of the Amazonian Rain Forest found a lower ant species similarity (27 %). This might have been influenced by the spatial distribution of food sources for these ants in the canopy habitat, where most of the EFNs are restricted to epiphytes and lianas, while the majority of hemipterans are restricted to trees. Moreover, completely different habitat conditions are expected in the canopy and understory of

tropical forests (Erwin 1983). Hence, since we only sampled short trees in the understory, factors such as smaller habitat complexity and more stable climatic conditions could have influenced the greater similarity found here.

Regarding our main questions the removal experiments using termites indicated that close to the interaction, hemipteran honeydew produced a more effective and faster ant protection against plant natural enemies than EFNs. Firstly, a greater ant density near hemipteran aggregations when compared with EFNs could increase the probability of ants finding termites. Unfortunately, we did not measure the ant abundance near the interactions, but personal observations strongly indicate that the ant density near hemipterans was always greater than close to the NEFs. Secondly, the ants that use honeydew can attack more and faster as a simple protection to the mutualist. Blüthgen et al. (2000), by means of behavioral observations in Amazonian rainforest canopy, point out that ants associated with hemipterans are usually more aggressive and protect the food resource more effectively than those that visit EFNs. However, this was the first time that such comparison had been explicitly examined experimentally.

Without excluding the above hypotheses, other factors related to nectar quantity, quality and constancy are also able to explain our results. Blüthgen et al. (2000) point out that the honeydew seems to be more nutritious (with a larger quantity of amino acids), more predictable and more abundant than nectar from EFNs, and so it would be better defended by ants (Cushman and Beattie 1991). Studies conducted in Southeast Asia also showed that honeydew from hemipterans may provide a more constant food source for ants when compared with nectar from extrafloral nectaries (Fiala 1990). However, before accepting these hypotheses, it is important to consider that there is a high variation in nectar quality and quantity secreted by these two food sources (Becerra and Venable 1991; Shenoy et al. 2012).

It was also demonstrated here that ants locate potential herbivores quickly when prey is placed close to an interaction. Oliveira et al. (1987a) found similar results, indicating that ant aggressiveness is directly related to resource or nest proximity. However, it is important to make clear that the non-encounter of termites far from interactions can vary merely as a function of ant density on the plant. Probably, few plants with naturally high ant densities were sampled, and this fact itself could explain the low encounter frequencies of termites placed far from the interaction. Another fact to be considered is the time of waiting in termite removal experiment. Ten minutes was probably insufficient time for ants to find the termites placed distant from EFNs and AHL.

We consider our study as a first step toward a better understanding of the balance between the plants, benefits derived from these two resources. Our study has revealed

that close to interactions, ants attending hemipterans seem to generate a more effective protection for plants than ants feeding on EFNs. We have attributed this finding to a larger ant monopolization of nectar from hemipterans. We may therefore predict that there is an evolutionary advantage for plants with hemipterans than with EFNs. However, this may not be so simple since hemipterans feed on plant phloem and can also act as plant parasite vectors. That fact generates considerable controversy among researchers who are trying to explain the influence of EFNs on the evolution of the ant-hemipteran interaction and vice versa (Becerra and Venable 1989; 1991; Fiala 1990; Gaume et al. 1998; Offenberg 2000; Blüthgen et al. 2004). This study further underlines the importance of other experimental studies to compare the importance of these two nectar sources on plant fitness.

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References

- Beattie AI (1985) Evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge Massachusetts
- Becerra JX, Venable DL (1989) Extrafloral nectaries: a defence against ant-homoptera mutualism? *Oikos* 55:276–280
- Becerra JX, Venable DL (1991) The role of ant-homoptera mutualisms in the evolution of extrafloral nectaries. *Oikos* 60:105–106
- Bentley BL (1977) The protective function of ants visiting extrafloral nectarines of *Bixa orellana* L. (Bixaceae). *J Ecol* 65:27–38
- Blüthgen N, Verhaagh M, Goitia W, Jaffe K, Morawetz W, Barthlott W (2000) How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia* 125:229–240
- Blüthgen N, Stork NE, Fiedler K (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos* 106:344–358
- Buckley RC (1987) Ant-plant-homopteran interactions. *Adv Ecol Res* 16:53–85
- Carver M, Gross GF, Woodward TE (1991) The insects of Australia. Cornell University Press, Ithaca
- Crawley MJ (2013) The R book. Wiley, Hoboken
- Cushman JH, Beattie AI (1991) Mutualisms: assessing the benefits to hosts and visitors. *Trends Ecol Evol* 6:193–195
- Cushman JH, Whitham TG (1991) Competition mediating the outcome of a mutualism—protective services of ants as a limiting resource for membracids. *Am Nat* 138:851–865
- Dattilo W, Marquitti FMD, Guimarães PR Jr, Izzo TJ (2014) The structure of ant-plant ecological networks: is abundance enough? *Ecology* 95:475–485
- Dáttilo W, Guimarães PR, Izzo TJ (2013) Spatial structure of ant-plant mutualistic networks. *Oikos* 122:1643–1648
- Davidson DW, McKey D (1993) The evolutionary ecology of symbiotic ant-plant relationships. *J Hym Res* 2:13–83

- Delabie JHC (2001) Trophobiosis between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an overview. *Neotrop Entomol* 30:501–516
- Del-Claro K, Santos JC (2000) A função de nectários extraflorais em plantas do cerrado. In: Cavalcanti TB (ed) Tópicos atuais em botânica. Embrapa, Brasília, pp 84–89
- Eisner T (1957) A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bull Mus Comp Zool* 116:441–490
- Erwin TL (1983) Tropical forest canopies: the last biotic frontier. *Bull Ent Soc Amer* 29:14–19
- Fiala B (1990) Extrafloral nectaries vs ant-homoptera mutualisms: a comment on Becerra and Venable. *Oikos* 59:281–282
- Floren A, Linsenmair KL (2000) Do ant mosaics exist in pristine lowland rain forests? *Oecologia* 123:129–137
- Gaume L, Mckey D, Terrin S (1998) Ant-plant-homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. *Proc R Soc Lond* 265:567–575
- Hölldobler B, Wilson EO (1990) The ants. The belknap press of harvard university press, Cambridge Massachusetts
- Jeanne RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224
- Katayama N, Suzuki N (2003) Changes in the use of extrafloral nectaries of *Vicia faba* (Leguminosae) and honeydew of aphids by ants with increasing aphid density. *Ann Entomol Soc Am* 96:579–584
- Korndorfer AP, Del-Claro K (2006) Ant defense versus induced defense in *Lafoensia pacari* (Lythraceae), a myrmecophilous tree of the Brazilian Cerrado. *Biotropica* 38:786–788
- Moya-Raygoza G, Larsen KJ (2001) Temporal resource switching by ants between honeydew produced by the fivespotted gama grass leafhopper (*Dalbulus quinquenotatus*) and nectar produced by plants with extrafloral nectaries. *Am Midl Nat* 146:311–320
- Moya-Raygoza G, Nault LR (2000) Obligatory mutualism between *Dalbulus quinquenotatus* (Homoptera: Cicadellidae) and attendant ants. *Ann Entomol Soc Am* 93:929–940
- Nascimento EA, Del-Claro K (2010) Ant visitation to extrafloral nectaries decreases herbivory and increases fruit set in *Chamaecrista debilis* (Fabaceae) in a Neotropical savanna. *Flora* 205:754–756
- Nogueira A, Guimarães E, Machado SR, Lohmann LG (2012) Do extrafloral nectaries present a defensive role against herbivores in two species of the family Bignoniaceae in a Neotropical savannas? *Plant Ecol* 213:289–301
- Offenberg J (2000) Correlated evolution of the association between aphids and ants and the association between aphids and plants with extrafloral nectaries. *Oikos* 91:146–152
- Oliveira PS, Brandão CRF (1991) The ant community associated with extrafloral nectaries in the Brazilian cerrados. In: Cutler DF, Huxley CR (eds) Ant-plant interactions. Oxford University, England, pp 198–212
- Oliveira PS, Pie MR (1998) Interaction between ants and plants bearing extrafloral nectaries in cerrado vegetation. *An Soc Entomol Bras* 27:161–176
- Oliveira OS, da Silva AF, Martins AB (1987a) Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in Cerrado vegetation: ants as potential anti-herbivore Agents. *Oecologia* 74:228–230
- Oliveira PS, Oliveira-Filho AR, Cintra R (1987b) Ant-foraging on ant-inhabited *Triplaris* (Polygonaceae) in western Brazil: a field experiment using live termite baits. *J Trop Ecol* 3:195–200
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rico-Gray V, Oliveira PS (2007) The Ecology and evolution of ant-plant interactions. The University of Chicago Press, Chicago
- Shenoy M, Radhika V, Satish S, Borges RM (2012) Composition of extrafloral nectar influences interactions between the myrmecophyte *Humboldtia brunonis* and its ant associates. *J Chem Ecol* 38:88–99
- Weibull WA (1951) A statistical distribution of wide applicability. *J Appl Mech* 18:293–297
- Zar JH (1999) Biostatistical analysis. Prentice-Hall, Englewood Cliffs