

Insights into a novel three-partner interaction between ants, coreids (Hemiptera: Coreidae) and extrafloral nectaries: implications for the study of protective mutualisms

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Abstract Extrafloral nectar of plants and honeydew of hemipterans are the common mediators of facultative interactions that involve ants as a mobile strategy of defence. The outcome of these interactions can vary from mutualistic to commensalistic or even antagonistic, depending on the ecological context and the interacting species. Here, we explore a novel, three-partner interaction involving ants, the coreid *Dersagrena subfoveolata* (Hemiptera) and the extrafloral nectaries (EFNs) bearing plant *Senna aphylla* (Fabaceae) in semi-arid Northwest Argentina. We surveyed natural areas and conducted ant exclusion experiments, to understand how each pairwise interaction influences the overall outcome among the three interacting parts. The outcome of the interactions was assessed for experimental plants as the reproductive output and herbivore abundances and for coreids as predator abundances. We found that the coreids occurred exclusively on *S. aphylla* plants and that at least nine ant species

interacted with the EFNs as well as with the coreids. Coreid occurrence and abundance depended on ant densities, which in turn, was determined by the presence of actively secreting EFNs. Coreid and ant presence did not influence plant reproductive success, and ants provided to coreids some biotic defence, mainly against vespidae predators, but had no effect on non-coreid herbivores. We conclude that the interaction outcome is commensalistic between ants and plants (assuming that EF nectar is not costly for the plant), antagonistic between coreids and plants, and mutualistic between coreids and ants. The sum of all outcomes is net positive effect for ants and coreids, and net slightly negative to neutral for plants.

Keywords Multitrophic interaction · Protection mutualism · Trophobiosis · Indirect defence

Introduction

Most mutualistic interactions between species are mediated by some kind of food reward (Wäckers et al. 2005). For facultative mutualisms that involve ants as partners, the rewards are sugar-rich liquids given in the form of nectar or honeydew (see Rico-Gray and Oliveira 2007; Del-Claro et al. 2016 and references therein). In the first case, ants consume the nectar secreted by extrafloral nectaries (hereafter EFNs) found on both reproductive and vegetative plant parts, but not related to pollination (e.g. Koptur 1992; Heil 2015). In the second case, ants consume the honeydew excreted by sap-sucking hemipterans and lepidoptera larvae (Way 1963; Buckley 1987). Ants involved in these interactions are not food specialized (Stradling 1978) and can feed on either EF nectar or honeydew, while they complete their diet by preying on living or dead

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insects (Davidson 1997). Due to this preying behaviour and on the basis that ants protect their food source against natural enemies (mainly other arthropods), these EFN plant and honeydew-producing insect interactions with ants are considered defence or protective mutualisms (Heil and McKey 2003; Wäckers et al. 2005; Grasso et al. 2015).

Species in over a hundred angiosperm families possess EFNs (Weber and Keeler 2013), and honeydew for ants is particularly common among sap-sucking hemipterans (Delabie 2001; Fagundes et al. 2013). Currently, strong consensus exists on considering both kinds of interactions as mutualistic (i.e. protection mutualisms), but whether both interacting parts benefit or not from the interaction highly depends on the ecological context in which this interaction takes place (Bronstein 1994; Kersch and Fonseca 2005; Chamberlain and Holland 2008). The identity, abundance, phenology and behaviour of the interacting species, herbivore and predator, pressure, quality and amount of the reward, and the influence of other mutualistic or trophic guilds on each pairwise relationship are all factors that produce variable outcomes of the interactions in time and space (Cushman and Addicott 1991; Bronstein and Barbosa 2002; Del-Claro et al. 2016).

The defensive benefits of ants on EFN plants have empirically been demonstrated in several studies (see meta-analyses by Rosumek et al. 2009; Trager et al. 2010). However, in many other cases, neutral or even negative effects on plant fitness were found (e.g. O'Dowd and Catchpole 1983; Rashbrook et al. 1992; Ruhren 2003; Miller et al. 2010; Alves-Silva and Del-Claro 2014; Alma et al. 2015). For honeydew-producing hemipterans, ant-derived benefits often increase their survival (Queiroz and Oliveira 2001), but these benefits may vary yearly (Del-Claro and Oliveira 2000), and a high degree of conditionality in the outcome of the interactions also exists (Cushman and Addicott 1991; Billick and Tonkel 2003).

From the host plant's standpoint, harbouring ant-tended hemipterans becomes beneficial when tending ants deter other, non-hemipteran herbivores (Carroll and Janzen 1973; Styrsky and Eubanks 2007). In such cases, the tri-trophic association can be regarded as a three-partner mutualism, with benefits for ants, hemipterans and the host plant (Compton and Robertson 1988; Moreira and Del-Claro 2005). However, ants that defend the hemipterans, by increasing their survival, may consequently augment their deleterious effect on plants through their phloem feeding and also because they are potential vectors of plant pathogens (Delabie 2001). Moreover, ant–plant–hemipteran interactions may increase in complexity and uncertainty when host plants bear EFNs. For instance, conflicts may arise if the presence of hemipterans disrupts the EFN–ant interaction by offering food of better quality, thus distracting ants from protecting valuable organs such

as reproductive structures or new leaves (Buckley 1983; Rico-Gray and Thien 1989). Also, because ants exhibit constancy for a predictable, renewable food source, as is EF nectar, then EFN plants may indirectly benefit hemipterans aggregations by supporting higher ant abundances of would-be tending ants than plants lacking these glands (Buckley 1987; Cushman and Addicott 1991; Bächtold et al. 2014).

In this work, we aim to disentangle the possible outcomes of ant–EFN plant–hemipteran interactions by studying a novel, three-partner interaction involving the EFN plant *Senna aphylla* (Cav.) H.S. Irwin & Barneby (Fabaceae), the honeydew-producing coreid *Dersagrena subfoveolata* (Berg) (Hemiptera: Coreidae) and their associated ants, in an arid environment of Northwest Argentina. By conducting field observations and manipulative experiments, we test the hypothesis that the interaction among the three partners is mutualistic (i.e. beneficial to the three partners involved). Specifically, we address the following questions: Is the occurrence of coreids on the EFN plant determined by the presence of EFN-feeding ants? Do ants provide benefits to both plants and hemipterans? Does the coreid–ant interaction have a negative effect on plants? And finally, can we consider this three-partner relationship as a “multiple” mutualism?

Materials and methods

Study area and study species

The study was conducted from October 2013 to February 2015 in undisturbed natural sites nearby Anillaco, La Rioja, Northwest Argentina (28°48'S, 66°56'W, ca. 1300 m a.s.l.). The area is within the Monte Desert biome, a shrubby steppe of perennial xerophyte shrubs and cacti, with *Larrea cuneifolia* Cav. (Zygophyllaceae) as the dominant plant species (Abraham et al. 2009). The climate is arid, with average annual temperature of 16.6 °C, average annual precipitation of 272 mm and a marked seasonality with a dry season from May to November and a wet season from December to April (Anillaco Meteorological Station, series from 1999 to 2012).

Senna aphylla (Fabaceae: Caesalpinoideae) is a leafless xerophytic shrub (up to 2 m tall), widely distributed in the Monte Desert of Argentina (Aranda-Rickert 2014). It is characterized by nectarless, buzz-pollinated flowers (Buchmann 1974; Irwin and Barneby 1982). It bears un conspicuous EFNs consisting of multicellular glandular trichome-like structures concentrated at the base of bracts subtending inflorescences or flowers (Aranda-Rickert et al. 2014).

The Coreidae, commonly called leaf-footed bugs, are heavy bodied heteropterans that include species considered crop pests of economic importance (Carpintero and Dughetti 2012). *Dersagrena subfoveolata* belongs to the Acanthocerini, an exclusively American tribe, and is prevalent in semi-arid Northwest Argentina (Pall and Coscarón 2013). Like other sap-sucking insects, they take phloem from the green tissues of plants with their stylet, leaving a small dark dot on the plant surface. Nymphs are wingless, while adults can fly over short distances.

Observational studies

The interaction between ants, coreids and plants was examined in four *S. aphylla* populations growing in natural areas of the study region (each population separated by at least 10 km). Observations were made in January 2015 (which corresponds to the summer season) on a total of 134 plants at least 10 m apart from each other. Each plant was surveyed once, during the morning or afternoon hours (8.30–10.30 and 17.00–19.00 h), by recording the number of each ant species and the number of coreids (nymphs and adults) in a 10-min search of the plant. We also noted the phenology of the plant (with buds, flowers or fruits), positioning of coreids and ants on the plant and occurrence of interactions. For each examined plant, an interaction was marked when at least one ant was observed feeding on an EFN (i.e. an EFN–ant interaction) or antennating and/or consuming the honeydew excreted by the coreids (i.e. a coreid–ant interaction). The frequency of occurrence of each interaction is calculated as the number of plants in which at least one interaction was recorded over the total number of plants studied. The abundance of ants involved in the interaction is calculated as the number of workers of each species in which at least one interaction was recorded. For plants in which both interactions co-occurred (i.e. ants interacted with both EFNs and coreids switching constantly from one resource to the other), we considered ant abundance as a single value.

Ant exclusion experiments

The field experiment was carried out on a natural population of *S. aphylla* plants (a different one than that of the observational studies) occurring in approximately 1 ha of the experimental field of the CRILAR Institute, located within the study site and consisting of natural Monte Desert vegetation. We surveyed a total of 40 experimental paired stems, compared on 20 plants. Before the beginning of the growing season (August), we tagged 20 healthy shrubs of *S. aphylla* of similar height (mean \pm SD = 199.3 \pm 30.5 cm), at the same phenological stage (i.e. no reproductive structures), at least 5 m apart from each other and under similar light

conditions. The most similar stems (length and number of branches) were paired and assigned either as control (ant-access plants) or treatment (ant-excluded plants) by the flip of a coin. To prevent ant access, a 2-cm-wide layer of non-toxic resin (Hormigel[®]) was applied on a tape surrounding the base of treatment stems. Vegetation bridges were removed regularly during the experiment. By the time the experiment was set up, EFN secretion was null, and no ants or coreids were present on the experimental plants. Because adult coreids are able to fly over short distances, the ant exclusion treatment did not impede them to colonize and move across plants.

From September to December 2015, every two weeks, we surveyed each experimental plant for two minutes at the same time of day (17:00–18:30 h during the spring and 18:30–20 h during the summer; which is when ant activity and diversity is the highest, and both crepuscular and diurnal species are active; Aranda-Rickert et al. 2014). During each of the 12 total censuses, we recorded the number and taxonomic identity of ants (all omnivorous species that interacted with EFNs, coreids or both), coreids (nymphs and adults), non-ant EFN consumers, potential herbivores and potential coreid predators. For each group, we combined all species or morphospecies and computed their densities as the number of individuals per stem per census.

To estimate the effect of ant exclusion on reproductive success of the plants, we calculated the survival of flowers to fruits (fruit set number of fruits/flowers), seed set (number of seeds/fruit) and seed damage (number of damaged seeds/total seeds). On each pair of experimental stems, we counted every two weeks the number of flowers (in September–October) and the number of fruits (in November–December). For the analysis, we used the maximum value obtained during each survey. At the end of the fruiting season (December), we randomly collected 20 pods from each experimental stem (stems producing about 50–70 pods) and, under binocular lens, we recorded total seeds, herbivory-damaged seeds and presence of seed predators per pod.

Data analyses

For the observational data, we used a generalized linear model (GLM) with Poisson distribution and log link function to analyse the relationship between the abundance of ants (only those species recorded interacting with coreids) and the abundance of coreids on *S. aphylla* plants, with the number of ants as predictor of the number of coreids (as dependent variable).

For the experimental data, we used generalized linear mixed models (GLMM) with Poisson distributions to analyse how ants influenced the occurrence of coreids, non-

ants EFN consumers (flies and wasps), non-coreid herbivores (including leaf-cutting ants) and potential coreid predators on *S. aphylla* experimental stems. In each model, we included plants as random factors, and sampling date and treatment (ant access and ant exclusion) as fixed factors. We conducted three separate analyses, one with ant, fly and wasp densities as predictor variables and coreid density as dependent variable, one with ant and wasp densities as predictors and non-coreid herbivores as dependent variable, and a third one with ant and density as predictor and coreid predators as dependent variable. The model included the interactions between factors and selection was based on the Akaike Information Criterion (AIC). Non-significant interactions between fixed effects ($p < 0.05$) were dropped from the final model.

We compared the plant reproductive success between the matched pairs of experimental stems (ant exclusion and ant access) using Wilcoxon signed-rank test, as the data did not satisfy the normality and homogeneity of variances assumptions. We conducted three separate analyses for each of the following variables: fruit set, seed set and seed damage. For seed set and seed damage we used the average number of 20 fruits per experimental stem. All analyses were performed using the statistical computing language R v. 3.0.6 (R Development Core Team 2009) and standard packages.

Results

Coreid occurrence and patterns of interaction with ants

During 5 years spent at the study site in Anillaco, La Rioja, the first author consistently found the coreid *D. subfoveolata* exclusively on *S. aphylla* (ca. 150 plant species inspected; see Aranda-Rickert 2014). The coreid occurred in all four *S. aphylla* examined populations and (totally) on 50% of the 134 plants. We recorded a total of 211 coreids (143 nymphs and 48 adults), with up to 10 coreids per plant (mean \pm SD, 3.18 ± 2.03 , $n = 67$). In 44 out of 67 plants, coreids formed clusters which consisted of cohorts of one to five adults and one to eight nymphs. Each plant harboured one to three clusters of coreids.

EFN-feeding ants were present on 72.4% of the 134 inspected plants, and coreids co-occurred with them on 64.94% of the 97 plants with ants. Of the 37 plants which harboured no ants, 21 lacked buds and flowers, then plants had no EFN secretory activity. We recorded a total of nine species and 741 individuals feeding on the EFNs of *S. aphylla*, in which six species and 354 individuals were observed also interacting with the coreids (Table 1). Ants and coreids formed aggregations that were spatially

restricted to the reproductive branches (with flowers or developing fruits), coinciding with the plant parts bearing the EFNs. The number of ants within each aggregation ranged from one to 31 (mean \pm SD, 5.42 ± 5.01 , $n = 63$). The most common ant interacting with the EFNs as well as with the coreids was *Camponotus blandus* Smith, both in terms of frequency (number of plants in which they occurred, 53.6% of the total) and abundance (number of interacting workers, 39.8% of the total), followed by *C. mus* Roger (16.3 and 21.8%) and *Dorymyrmex planidens* Mayr (7.3 and 13.4%). These three species were apparently mutually exclusive as they were consistently found on different plants, while the other ant species were observed in low number together with the dominant species.

We found higher coreid abundances on plants that had a greater number of ants. The GLM analysis showed a significant and positive relationship between the number of ants and the number of coreids per plant (coeff. 0.171, 95% CI 0.092–0.249; $t = 4.277$, $p < 0.0001$, $N = 134$).

Ants displayed no aggressive behaviour towards the coreids nor did the coreids appear disturbed or molested by the ants. Instead, the ants commonly stayed beside the coreids and even crawled over them, forming an aggregation of ants and coreids (Fig. 1a, b). We also observed *C. blandus* individuals touching with their antennae and forelegs the coreids' dorsum and anus (Fig. 1c), similarly to when ants solicit honeydew from other hemipteran species as well as from myrmecophilous lepidoptera. However, we did not observe the ants consuming the droplets directly from the coreids' anus, as happens with the former examples. Most commonly, coreids flicked the honeydew away by contracting the rectum or the entire abdomen; afterwards, the droplets falling on the plant surface were rapidly collected by patrolling ants with their mouthparts (Fig. 1d), as when they collect EF nectar droplets. We also observed some ants closely approaching the stylet while coreids were feeding on the plant, suggesting that they were taking some of plant phloem.

Exclusion experiment

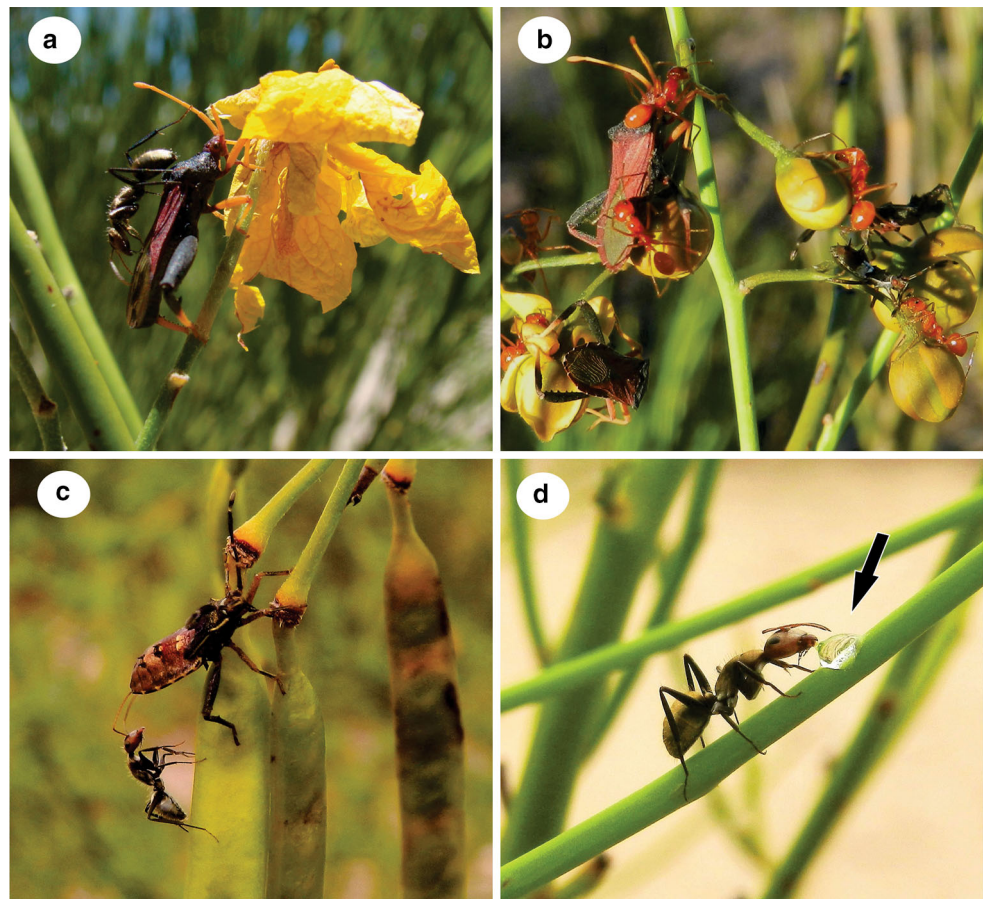
Five experimental plants (both control and ant-excluded stems) were left completely flowerless by leaf-cutting ants (*Acromyrmex lobicornis* Emery and *A. striatus* Roger) during the first month of the experiment; hence, the final sample size was lowered to 15 experimental plants. The arthropod fauna recorded on the experimental *S. aphylla* plants across all censuses (i.e. treatment and control plants) consisted mostly of ants (443 individuals), followed by *D. subfoveolata* coreids (64), while the rest included non-ant EFN consumers (42 and 45 individuals of wasps and flies of Diptera order, respectively), flower visitors (14 bumblebee individuals), non-coreid herbivores (29) and non-

Table 1 Ant species observed feeding on extrafloral nectaries (EFNs) of *S. aphylla* and interacting with the coreid *D. subfoveolata*

Ant species	Frequency		Abundance	
	EFNs	EFNs + coreids	EFNs	EFNs + coreids
Subfamily Formicinae				
<i>Camponotus blandus</i> Smith	16	50	60	235
<i>Camponotus mus</i> Roger	12	8	83	79
<i>Camponotus punctulatus</i> Mayr	3	1	20	5
<i>Brachymyrmex patagonicus</i> Mayr	3	–	25	–
Subfamily Myrmicinae				
<i>Crematogaster quadriformis</i> Roger	3	–	58	–
Subfamily Dolichoderinae				
<i>Dorymyrmex exsanguis</i> Forel	5	2	14	2
<i>Dorymyrmex planidens</i> Mayr	6	3	76	23
<i>Dorymyrmex spurius</i> Santschi	4	2	33	10
<i>Forelius albiventris</i> Forel	5	–	18	–
Total	57	66	387	354

Frequencies are the number of spatially independent occurrences (number of plants in which the interactions were observed), and abundances are the total number of ant workers observed interacting with the EFNs or with both EFNs and coreids ($N = 134$ inspected plants)

Fig. 1 Ant, coreid and EFN plant interactions in northern Argentina. **a** A *Camponotus blandus* ant crawls over the coreid *Dersagrena subfoveolata* on a *Senna aphylla* plant; **b** an aggregation of *Dorymyrmex exsanguis* ants and *D. subfoveolata* nymphs and adults; **c** a *C. blandus* ant antennates a *D. subfoveolata* nymph; **d** a *C. blandus* ant foraging a honeydew droplet that has just been expelled by a *D. subfoveolata*



wasp predators (11) of three orders (Hemiptera, Coleoptera and Arachnidae)—A complete list is provided as Online Resource 1.

Among the ants, eight species (five genera and three subfamilies) were observed feeding on the EFNs of experimental stems (Fig. 2). The exclusion protocol

effectively prevented ants to access treatment stems: ant density was significantly higher on ant-access than on ant exclusion stems (mean individuals/census/stem ($\pm 95\%$ CI), $N = 360$, ant-access = 2.29 (1.73–2.85), ant-excluded = 0.08 (0.03–0.14), GLMM, $Z = -12.93$, $p < 0.0001$, Fig. 3a). *Camponotus blandus* was by far the most common EFN consumer ant (68.96% of the ant individuals). It was the largest species and behaved aggressively towards the other ant species as well as other non-ants EFN consumers. The most frequent non-ant EFN consumers were camaoti wasps (*Polybia scutellaris*, Hymenoptera: Vespidae) and flies (*Musca* sp., Diptera: Muscidae). In both cases, their densities were significantly higher on ant-excluded than on ant-access stems (mean individuals/census/stem ($\pm 95\%$ CI), $N = 360$, wasps: ant-access = 0.06 (0.01–0.11), ant-excluded = 0.17 (0.09–0.24), GLMM: $Z = 2.95$, $p < 0.001$, flies: ant-access = 0.07 (0.03–0.11), ant-excluded = 0.15 (0.08–0.22), GLMM: $Z = -2.28$, $p < 0.01$, Fig. 3b).

The density of *D. subfaveolata* coreid was 95% lower in ant-excluded stems than ant-access stems (mean individuals/census/stem ($\pm 95\%$ CI), $N = 360$, ant-access: 0.77 (0.55–0.98); ant-excluded: 0.04 (0.01–0.06); GLMM: $Z = 6.31$, $p < 0.0001$, Fig. 3a). The exclusion treatment (which was correlated with ant density) as explanatory variable best explained the increase in coreid densities on experimental plants, with no significant effect of vespid wasps and flies (Table 2; Fig. 4, AIC values are given as Online Resource 2). In fact, wasps and flies were rarely observed by the coreid aggregations and did not interact with them.

Overall, the total number of non-coreid herbivores (Lepidoptera larvae, Coleoptera, leaf-cutting ants and

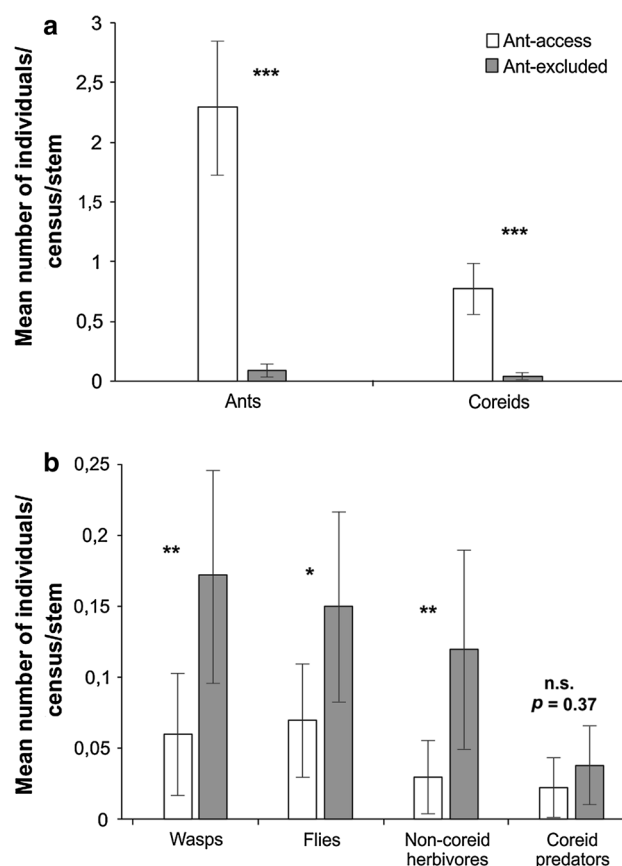


Fig. 3 Densities (means $\pm 95\%$ CI) of **a** ants and coreids, and **b** wasps, flies, non-coreids' herbivores and coreids' predators on *Senna aphylla* ant-access and ant-excluded experimental stems. Data correspond to two min census/stem on 15 experimental plants for a total of 12 censuses ($N = 180$). Asterisks indicate significant differences between treatments: * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$ (GLMM)

Fig. 2 Cumulative abundance (number of individuals) of each nectarivorous ant species on experimental ant-access and ant-excluded *Senna aphylla* stems during two min census/stem on 15 experimental plants for a total of 12 censuses ($N = 180$). Total number of ants is given for each species at the individual bars

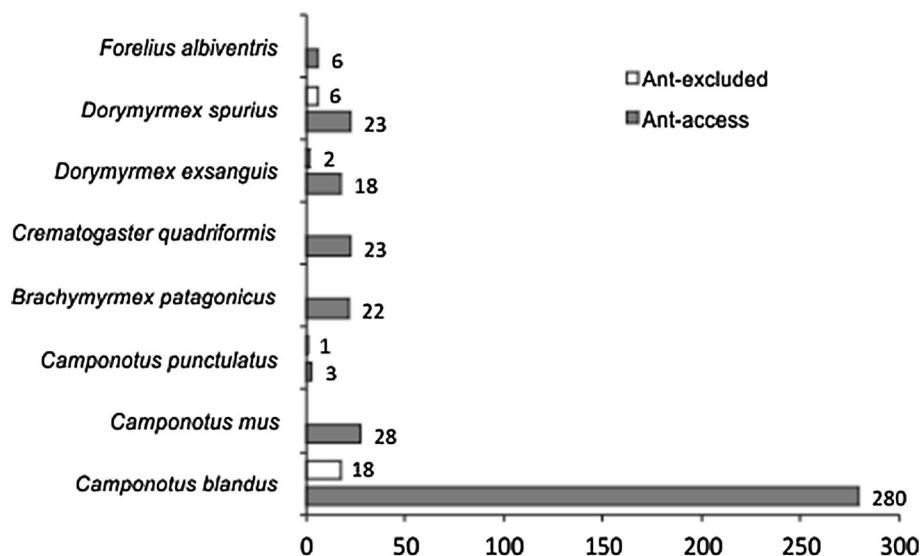


Table 2 Results of the Poisson GLMMs separately testing for the effect of the exclusion treatment on coreid (Model 1), no-coreid herbivore (Model 2) and coreid predator densities (Model 3) on *S. aphylla* experimental plants

Model	Response variable	Estimate	95% CI	Z	p
1	Coreids	-2.95	-0.88, -0.49	-7.82	<0.0001
2	Herbivores	1.299	0.01, 0.16	2.822	<0.001
3	Predators	0.63	-0.01, 0.05	0.99	0.31

Densities are number of individuals/census/stem ($N = 180$). Significant terms are highlighted in bold. Successful models were selected through comparisons of AIC values. All other non-significant terms of the models are not shown

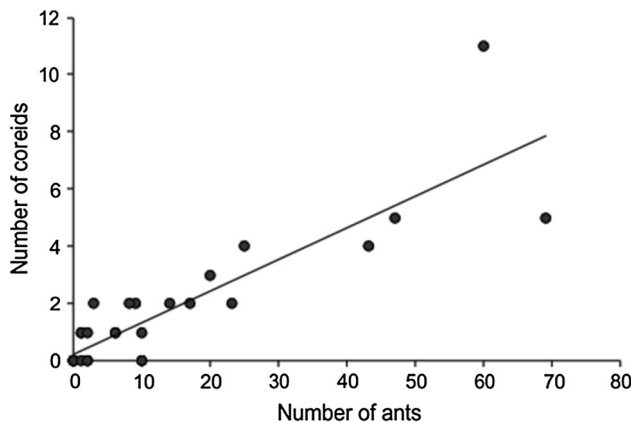


Fig. 4 Relationship between the number of ants and coreids on experimental (ant access and ant exclusion) stems of *S. aphylla*. Data are the cumulative number of ants and coreids counted over two min census/stem on 15 experimental plants for a total of 12 censuses ($N = 30$). Regression equation: $y = 0.24 + 0.12x$, Adj. $r^2 = 0.73$, $p < 0.0001$

Pentatomidae hemipterans) and coreid predators (Coccinellidae, Arachnidae and Reduviidae hemipterans) observed over the course of the experiment was low, both groups accounting together only 6.6% of the total number of arthropods observed on the experimental plants. Ant-excluded stems had 4 times as much non-coreid herbivore densities as ant access treatments (mean individuals/census/stem ($\pm 95\%$ CI), $N = 360$, ant-access: 0.03 (0.01–0.05); ant-excluded: 0.12 (0.04–0.19); GLMM: $Z = 2.82$, $p < 0.001$, Fig. 3b), and these differences were largely determined by ant presence (Table 2). The most abundant herbivore other than coreids were the leaf-cutting ants, which made up to ca. 45% of the total non-coreid herbivore individuals. Potential coreid predators did not differ in their densities between treatments (ant-access: 0.02 (95% CI 0.01–0.04); ant-excluded: 0.04 (0.01–0.06); GLMM: $Z = 0.89$, $p = 0.37$, Fig. 3b), and neither did ants or wasps have a significant effect on their densities (Table 2). The only event of predation we observed was that of two *Cosmoclopius* sp. individuals (Hemiptera: Reduviidae) which fed on an adult coreid while copulating.

The exclusion experiment had no effect on plant fitness in terms of reproductive success. No significant differences

in fruit set (Wilcoxon test: $W = 99$, $N = 15$, $p = 0.58$), seed set ($W = 126$, $N = 15$, $p = 0.58$) and seed damage by herbivory ($W = 111$, $N = 15$, $p = 0.96$) were found between control and ant exclusion treatments. A similar proportion of seeds (ant-access 14.2% of 4993 seeds; ant exclusion 16.4% of 5051 seeds) were damaged in both treatments. The most common seed predator was a bruchid beetle larvae (Coleoptera: Chrysomelidae, Bruchinae), which made up to 55.3% of total arthropods found inside the examined pods. To a lesser extent, microhymenoptera larvae (Hymenoptera: Chalcidoidea) of families Eurotomidae (1 sp.), Eulophidae (1 sp.), Torymidae (2 spp.) and Eupelmidae (1 sp.) also damaged the seeds by developing inside them (Online Resource 1).

Discussion

Plants supporting ant–hemipteran associations generally experience neutral, positive or negative effects depending on the ecological context and the interacting species (Del-Claro 2004; Chamberlain and Holland 2009). In addition, these possible outcomes may vary in space and time due to contingencies and environmental constraints (Menzel et al. 2014; Del-Claro et al. 2013; Del-Claro and Marquis 2015). In this study, we aim to disentangle the possible outcomes of a novel, three-partner interaction involving ants, coreids and EFNs bearing plants, as well as to identify sources of variation (i.e. conditionalities) in such outcomes.

Mutualistic relationships between ants and hemipterans of the former suborder Homoptera (currently suborders Auchenorrhyncha and Stenorrhyncha that include aphids, mealybugs, scale insects, and membracids) are widespread and have been well described for a number of systems worldwide (reviewed by Delabie 2001; Del-Claro et al. 2016). In contrast, reports of mutualism between ants and hemipteran true bugs (suborder Heteroptera) are scarce, either because they are rare or because simply overlooked. They have been reported in few systems in tropical forests from Asia and Africa (seven species of Plataspidae and six species of Coreidae; see Silva and Fernandes 2016), and in the Americas, they have only been documented

recently—to our knowledge—for two Pentatomidae species in the Cerrado area of Brazil (Guerra et al. 2011; Silva and Fernandes 2016). In this study, we report for the first time a new case of interaction between coreids and ants for the Americas, that also involves EFN-bearing plants as a third partner.

Most Hemiptera species are specialized feeders restricted to a single plant genus or family (Blackman and Eastop 1994). Mashwitz et al. (1987) and Blüthgen et al. (2006) found that coreids were exclusively present on two species of bamboo (Poaceae) in Malaysia and Borneo, respectively, though these species are not reported to possess EFN (Weber et al. 2015). In our study, *D. subfaveolata* coreids are specific and consistent with respect to the host species they choose, and they were found exclusively on *S. aphylla* plants, regardless of the presence of other plant species with EFNs and their associated ants. This suggests that the interaction between coreids and *Senna* plants is obligate and that in the selection of the host plant, not only ant presence, but also visual and chemical cues related to the plant are involved. Our field observations and experimental manipulations showed that coreid density on the plant increased with increasing levels of ant activity, which in turn, was determined by the presence of actively secreting EFNs. Therefore, coreids' choice for colonizing a *Senna* plant should reflect the following algorithm: (1) is it a *Senna* plant? When answer is yes, then follows (2) are there ants on it? Such cues should be reinforced for plants where ants are more abundant compared to those that harbour fewer nectarivorous, potential tending ants.

Apparently, the coreids' choice is not influenced by what ant species is on the plant. In our study, at least six ant species interacted with the coreids, and *Camponotus blandus* was the most common. This is an aggressive and large ant (Aranda-Rickert and Fracchia 2011), and together with other *Camponotus* species, has been repeatedly reported in the Neotropics as effectively guarding mutualist partners, such as lycanid larvae, hemipterans and EFN plants (e.g. Del-Claro et al. 1996; Oliveira 1997; Gibernau and Dejean 2001; Kaminski et al. 2010). Despite its aggressiveness, *Camponotus* ants did not display predatory or antagonistic behaviour towards the coreids (both adults and nymphs). Conversely, coreids did not attempt to escape nor did they seem to be bothered by ant presence; instead, they formed aggregations with their offspring and with the ants as well. Honeydew (and EF nectar) is an essential resource to ants (Davidson 1997; Lach et al. 2009; Byk and Del-Claro 2011), and its offering has been interpreted as a strategy to appease aggressive ants (Stadler and Dixon 2008; Silva and Oliveira 2010). Indeed, in our study, ants readily collect the honeydew droplets flicked away by the coreids and antennated them similarly to when they solicit food from other honeydew-producing hemipterans.

Although, beyond the aims of our study, another mechanism for avoiding ant aggression could be, for example, a chemical matching with its host plant that camouflages them as insect analogues of EFNs (Portugal and Trigo 2005).

Ant exclusion affected arthropod activity on the examined *S. aphylla* plants. For instance, it led to an increase in the number of vespid wasps and Diptera flies, both EFN consumers and potential competitors for this resource. The reduction of these wasps by ants could represent a cost of ant presence to the plants, because they can act as effective plant defenders by preying on herbivores (Koptur 1985; Cuautele and Rico-Gray 2003). Nevertheless, by deterring predacious wasps, ants could also indirectly increase coreids' survival probability. Nevertheless, the abundance of all other non-EFN-consuming coreids' potential predators, considered as a whole, was overall low and was not influenced by ant presence. Therefore, ants appear to effectively guard coreids only when coreids' predators act as competitors for food resources.

Our manipulative experiments under field conditions show that ant presence is not related to a decrease in the abundance of non-coreid herbivores and seed predators, and that the impact of the ant–coreid interaction is neutral for the plant in terms of fruit and seed production. For instance, the most common cause of seed damage in our study, namely pre-dispersal seed loss by bruchid seed predators, is not lessened by guarding ants. Apparently, ants do not interfere with the adult females that oviposit in the young fruits, where larvae can develop undisturbed and protected against ant attack. Similarly to our results, Ruhren (2003) found that ants did not deter bruchid seed predation in the EFN plant *Chamaecrista nictitans*. In general, it is not always clear, that EFN consumer ants provide benefits for the plants in terms of decreased herbivore damage, increased plant growth and/or increased reproductive success (e.g. Rashbrook et al. 1992; Ruhren 2003; Chamberlain and Holland 2008; Miller et al. 2010; Alves-Silva and Del-Claro 2014; Alma et al. 2015). Furthermore, a number of studies have found that honeydew-producing hemipterans can impose costs on plant fitness via plant sap consumption or transmission of plant pathogens (Buckley 1987; Delabie 2001). Our results do not provide evidence of such negative effects by coreids. The fact that each *S. aphylla* plant in our study harboured up to 10 coreids rather suggests that these hemipterans become harmful to the plant only when they reach high densities, typically in non-natural, low-biodiversity systems such as orchards, greenhouses or crop fields (Janzen 1972).

In our study, the most important herbivores were leaf-cutting ants. An attack from these ants on the *S. aphylla* plants usually resulted in the complete loss of flowers, obviously affecting the plants' reproductive output

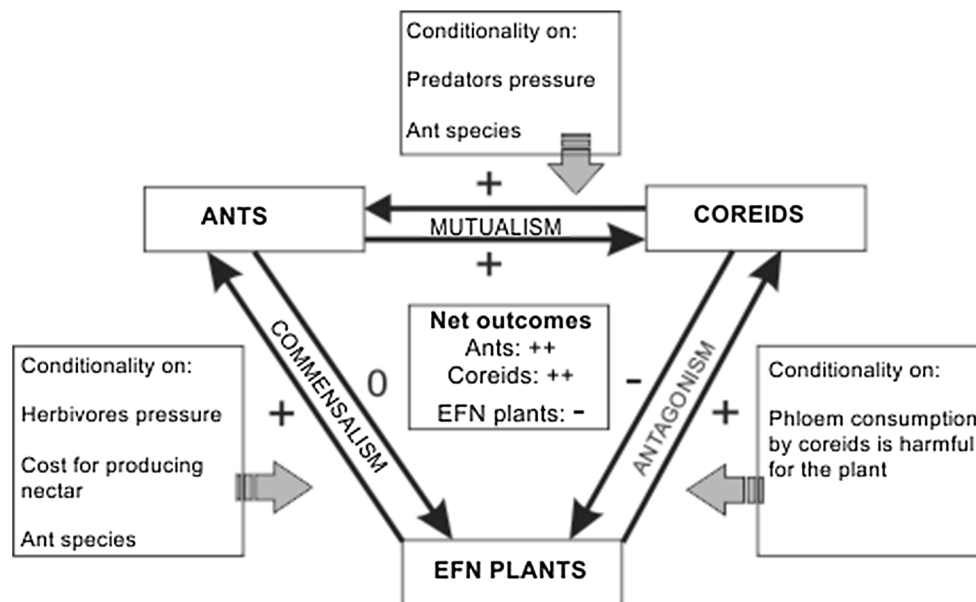


Fig. 5 Ecological complexity of the interaction between ants, *D. subfaveolata* coreids and *S. aphylla* EFN plants. Positive outcomes are indicated by (+), neutral by (0) and negative by (-)

(though not their survival). Because our manipulative experiments exclude ants and also other non-ant crawling insects, they cannot disentangle the role of nectarivorous ants as plant defenders from the role of leaf-cutting ants as plant enemies. Nevertheless, because both group of ants search for food at the same location on the plant (EFNs are outside the flowers), we could expect that at least the most aggressive and bigger EFN consumer ant species (e.g. *Camponotus* spp.) play a defensive role by repelling the scouts, i.e. the leaf-cutting ant workers that first search for a potential food resource and then reclude their mates back to the nest. But, this needs to be investigated further.

Interactions outcomes

In the ant–EFNs system and considering that EF nectar is cheap to produce (see O’Dowd 1979), the outcome is neutral for the plant, because it receives no indirect benefit through ant protection from herbivores, and positive for the ant, because it gains a high-energy food. Thus, the relationship is commensalistic. However, conditionalities must be considered too, and the ones on this outcome are imposed especially by the ant species involved (their aggressiveness, i.e. whether the ants are aggressive or not, and their effectiveness to deter herbivores, including seed predators) and the herbivore pressure on the plant (i.e. the abundance of herbivores and/or vulnerability of the plant to them). In the ant–coreid system, ants benefit in the form of honeydew, and coreids in the indirect form of protection against predacious wasp. Therefore, this relationship is

mutualistic. In this case, conditionalities are analogous to the former system: the ant species involved (aggressiveness and effectiveness) and the predators’ pressure on the coreids.

Finally, in the coreid–EFN plant system, coreids gain food in the form of plant sap and indirectly benefit from the EFNs that attract more potentially guarding ants. But, because plants suffer from the sap sucking, the relationship is antagonistic. Conditionality in this system is given by the assumption that phloem consumption by the coreids has a negative effect on the plant. However, because we could not find any evidence for any such negative effect, it is possible that the costs of sap sucking are negligible; thus, the relationship would be commensalistic. By integrating the three partners in this system, the sum of all outcomes gives net positive effects for ants and for coreids, and possibly neutral effects for the plant (Fig. 5).

Conclusions

A mutualistic relationship is defined as a reciprocally beneficial interaction between individuals of different species. Our results show that net benefits for the three partners that are involved in our study system (EFN plant–ant–hemipteran coreid) do not support the hypothesis that the relationship is mutualistic for the three-partner system as a whole. In fact, the individual two-partner relationships differ in their outcomes, particularly because of the indirect forms of benefits that ants (may or may not) provide when interfering with the plants’ or coreids’ enemies.

In general, context dependency is a common feature of facultative ant interactions with plants and other animals (Bronstein 1994). Under average environmental conditions, mutualist ant guarding is suggested to rather be neutral, with positive effects on the plant only when facing rare but important events such as herbivore outbreaks or years of high seedling recruitment (Ford et al. 2015). Indeed, meta-analyses of EFN–ant interaction studies (Chamberlain and Holland 2009; Trager et al. 2010) indicate that such interactions are usually beneficial to plants. Yet, it is possible that this is biased by (1) the fact that systems with more aggressive nectarivorous ants are usually more attractive study systems and, thus, receive more attention than systems with less or non-aggressive ants that are probably rather overlooked; (2) most studies assess the impact of ant guarding as defence against herbivory, only a few report effects on both herbivory and reproduction, and even more fewer analyse the net effect of ants on long-term population dynamics (e.g. Ford et al. 2015) and (3) few studies evaluate the net outcome of the mutualistic relationship with ants with a multispecies approach, i.e. taking into account the coexisting arthropod community and the whole network of interactions in which they exist. In any case, field studies that examine how the mutualist ants affect the partner plants' and hemipterans' population dynamics in the long-term would be a valuable tool to evaluate the ultimate impact of ant guarding with a demographic approach.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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