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ORIGINAL PAPER

Extrafloral nectaries exhibit dual ecological functions in a plant from the Brazilian Cerrado

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Abstract

Extrafloral nectaries (EFNs) are nectar-secreting plant glands not related to pollination. Several not mutually exclusive hypotheses explain the ecological function of EFNs. We focused on the (1) protection hypothesis, which predicts the attraction of natural enemies by the extrafloral nectar, providing indirect defense to plants against herbivores, and the (2) ant-distracting hypothesis, which predicts the distraction of ants away from sap-sucking herbivores secreting sugary rewards (honeydew). We aimed to test both hypotheses simultaneously to understand the relative ecological roles of EFNs in a model plant from the Brazilian Cerrado. We experimentally manipulated plant groups according to the presence or absence of EFNs and hemipterans during two years of field study (2018 and 2019). We found some support for both hypotheses. Extrafloral nectaries reduced the damage caused by herbivores by attracting predatory ants, although plants with both EFNs and hemipterans showed the highest herbivory reduction in 2018. The presence of neither EFNs nor hemipterans was associated with increased fruit production. The honeydew, which had higher sugar concentrations than the extrafloral nectar, was used by ants for longer periods. However, more than 70% of the ants were observed feeding on the extrafloral nectar instead of honeydew. We suggest that the relatively high quantity of EFNs can compensate for their lower quality and still reduce the number of ants attending and protecting hemipterans, ultimately mitigating plant damage. In summary, EFNs may fit multiple functions depending on the ecological context.

Keywords Brazilian savanna · Coevolution · Evolutionary ecology · Insect-plant plant defenses · Mutualism

Introduction

Extrafloral nectaries (EFNs) are plant glands that secrete nectar, a sugar-rich aqueous solution that also contains small amounts of amino acids, lipids, alkaloids, and volatile organic compounds (Bentley 1977; Koptur 1992; Blüthgen et al. 2004a). EFNs occur in more than 110 families of plants and 876 genera (Weber et al. 2015). In the Cerrado biome (Brazilian savanna), 25% of woody species have EFNs, representing about 30% of all trees found in that biome (Oliveira and Freitas 2004). Despite the similar chemical composition to floral nectar, extrafloral nectar usually has a higher sugar concentration (Koptur 1994) and is not related to pollination (Del-Claro et al. 2016). Due to their nutritional value (Blüthgen et al. 2004a; Byk and Del-Claro 2011; Calixto et al. 2021a), EFNs attract several animals, such as ants, spiders, and wasps (Nahas et al. 2012; Stefani et al. 2015; Moura et al. 2021). Some animals, especially ants, often attack and remove arthropod herbivores from those plants (Fagundes et al. 2017), reducing herbivory levels (Oliveira and Pie 1998; Schoereder et al. 2010; Gomes et al. 2021; Moura et al. 2022; Moura and Del-Claro 2023) and increasing fruit and seed production (Rosumek et al. 2009; Nascimento and Del-Claro 2010).

Extrafloral nectaries are thus mainly considered to be part of a plant's indirect defense system (Pearse et al. 2020),

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as predicted by the plant protection hypothesis (Bentley 1977; Calixto et al. 2018; Moura et al. 2021). Despite the enormous amount of evidence supporting this claim (e.g., Rosumek et al. 2009), other hypotheses propose alternative roles for the EFNs (Del-Claro et al. 2016), since ants do not always defend plants from herbivores. Such inconsistency is not surprising, since the outcomes of ant–plant interactions vary according to different ecological factors, including the involved plant (Trager et al. 2010; Baker-Méio and Marquis 2012), herbivore (Alves-Silva et al. 2015), and ant species (Ness et al. 2006; Del-Claro and Marquis 2015). For instance, many ant species occurring on EFN-bearing plants are simply unable to prey on or remove herbivores due to physical limitations (e.g., small size) or lack of aggressiveness (Fagundes et al. 2017). In addition, the quality and quantity of extrafloral nectar production strongly vary in time and space and among species (Lange et al. 2017; Calixto et al. 2021b), directly affecting ant community composition, visiting frequency, and, consequently, the effectiveness of ant protection (Pacelhe et al. 2019; Moura and Del-Claro 2023). For example, well-protected plants usually offer high-quality rewards (Pacelhe et al. 2019) and exhibit just a single or a few dominant ant species that are highly aggressive (Miller 2007).

A second hypothesis through which EFNs can be beneficial for plants is the ant-distracting hypothesis. This hypothesis was first proposed by Becerra and Venable (1989) and suggests that EFNs may have evolved in response to the negative effects of honeydew-producing hemipterans (trophobionts) on plants (Pierce et al. 2002). Some hemipterans offer sugary rewards (e.g., honeydew) to lure ants and use them as bodyguards against predators, parasitoids, and pathogens (Stadler and Dixon 2005; Nielsen et al. 2010). Thus, under the protection of tending ants, hemipteran populations may grow dramatically (Rice and Eubanks 2013), spreading plant diseases and inflicting high damage to leaves and reproductive structures (Rico-Gray and Castro 1996; Delabie 2001; Nelson and Mooney 2022). Some researchers have acknowledged that EFNs can be as rich or richer in nutrients than honeydew (Engel et al. 2001; Katayama et al. 2013; Chanam et al. 2015) and hypothesized that EFNs may serve as an alternative resource to disrupt ant–hemipteran mutualisms. This particular role of EFNs could be valuable for plants since developing chemical defenses against sap-sucking insects imposes many physiological constraints (Züst and Agrawal 2016). Furthermore, the peak production of EFNs is relatively predictable in space and time (Lange et al. 2017), and the extrafloral nectar is usually more abundant and easier to consume than honeydew (Becerra and Venable 1989). In comparison to the protection hypothesis, however, the ant-distracting hypothesis has been much less tested, and there is no consensus on the relative importance of the latter to ant–plant–hemipteran interactions (Del-Claro and Oliveira 1993; Katayama and Suzuki 2003; Blüthgen et al. 2004a). The outcomes of ant–plant–hemipteran interactions are also highly contextual. For instance, ants may simply fail to protect hemipterans and eventually prey on them (Billick et al. 2007; Schifani et al. 2023). However, some studies further suggest that, in certain contexts, trophobiont hemipterans are ecologically analogous to EFNs and provide indirect plant defenses against non-tended herbivores via ant attraction (Moura et al. 2021).

Considering the high variability of studies evaluating the effects of EFNs on plants (Trager et al. 2010), testing alternative hypotheses for the role of EFNs may help explain why some published studies have not found mutualistic effects between ants and plants with EFNs. While many studies have investigated alternatives to the protection hypothesis (Del-Claro et al. 2016), we are not aware of any study that has experimentally investigated the effects of multiple hypotheses. Here, we investigated the ecological role of EFNs by experimentally testing both the protection and ant-distracting hypotheses in a system involving a native extrafloral-bearing species from the Brazilian Cerrado that commonly hosts honeydew-producing hemipterans.

Material and methods

Study area

This study took place at the Clube Caça e Pesca Itororó (CCPIU) reserve, west of Uberlândia city (18° 59’ S, 48° 18 W), Minas Gerais. The site was chosen for having an extensive area of 628 ha, mainly characterized by typical Cerrado vegetation (Brazilian Savanna). This is the largest remnant of the natural Cerrado within the limits of Uberlândia, bearing trees and shrub species ranging between 2 and 8 m in height. The climate is characterized by a dry (May–September) and a wet (October–April) season, with an average temperature of 22.7 °C (Velasque and Del-Claro 2016).

Study species

We chose *Banisteriopsis malifolia* (Malpighiaceae) (Fig. 1a, b) as a model species. It is a shrub species (about 2 m tall) that bears two extrafloral nectaries (EFNs) on the base of each leaf (Fig. 1e). This species is abundant and easy to access at the study site, which allowed us to carry out the proposed experiments simultaneously. Trophobiont hemipterans are commonly found on the reproductive parts of this plant (Fig. 1c), and many ants feed on the honeydew produced by them (Fig. 1d) (Alves-Silva 2011; Alves-Silva et al. 2013). Other common herbivores are endophytic beetles that

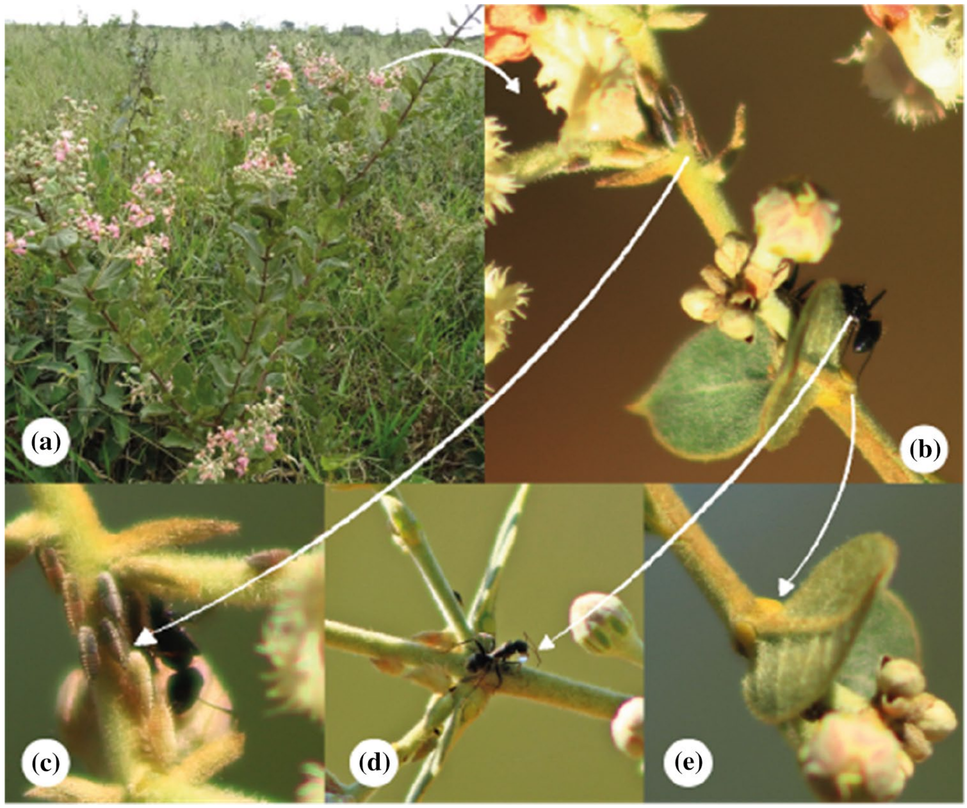


Fig. 1 Pictures of *Banisteriopsis malifolia* (Malpighiaceae) (**a**), a common shrub with different ant resources (honeydew-producing hemipterans and extrafloral nectaries) (**b**). Trophobiont hemipterans on flowers (**c**), ants feeding on extrafloral nectar (**d**), and a pair of extrafloral nectaries (**e**)

consume flower buds (Torezan-Silingardi 2011; Mendes-Silva et al. 2021).

Sampling procedure

Most of the methods described below were carried out in two flowering periods of *Banisteriopsis malifolia*: between March and April 2018 and 2019, although we performed some additional experiments in 2021 and 2022 (see below). During these periods, we used different plant individuals to test each hypothesis. All marked individuals of *B. malifolia* were at least three meters apart, were between 1.5 and 2 m in height, and had leaves in the sprouting stage. After establishing all treatments, we performed manipulative experiments to test the ecological hypothesis of the EFNs. For logistical and time-optimization reasons, we selected two study sites 100 m apart, one for each hypothesis test. We studied 90 *B. malifolia* plants to test the protection and ant-distracting hypotheses (30 and 60 plants, respectively). Voucher specimens of all observed ant species were collected for posterior identification in the laboratory.

Protection hypothesis

Between 2018 and 2019, we randomly divided 30 plants into two groups (n = 15): no ants (exclusion) and Control. The study site was visited three times a week, and each plant was observed for 5 min. We manually removed all ants from plants in the Exclusion group and used a non-toxic sticky resin (Tanglefoot®), applied on masking tape positioned on the base of the plant stem, to restrict the access of ants to the EFNs. In the Control group, the resin was only partially applied to the stem so ants could freely pass. In both groups, we marked three branches on each plant, and in each branch, we counted the number of ants and herbivores. In each branch, young leaves were tagged (six per branch) to estimate leaf area loss after two months of observation. Leaves were photographed on the tagging day and after the two-month period. Leaf area loss was estimated with ImageJ software (Schneider et al. 2012). The percentage of leaf area loss was calculated by dividing the total leaf area by the estimated area loss.

Ant-distracting hypothesis

In 2018 and 2019, we studied 60 plants divided into four groups: Exclusion, Hemipteran (*Enchenopa* sp., Membracidae), EFN, and EFN + Hemipteran (n = 15 for each group). For each plant, we randomly selected three branches to work with. The Exclusion group had all hemipterans manually removed from the selected branches, while all EFNs were obstructed with the aid of colorless nail polishes. The EFN group had all hemipterans removed, but the EFNs were preserved. The Hemipteran group had all hemipterans preserved, while all EFNs were obstructed. Finally, the EFN + Hemipteran group had all components preserved and was characterized as our control. In this group, we applied colorless nail polish just beside the EFNs. After establishing all plant groups, we performed one-minute observations on each plant. During the observations, we counted the number of ants on the EFNs and the number of hemipterans found on the sampled branches. For all sampled branches, fruit production was evaluated by the end of the experiment, and the percentage of leaf herbivory was calculated according to the methods used to test hypothesis 1 (above).

In 2021, we repeated the same treatments: EFN, Hemipteran, and EFN + Hemipteran ($n = 10$ for each group) to assess the time ants spent using each resource (honeydew or extrafloral nectar) and moving around the plant. For this, we randomly selected one ant from each plant and observed it for 3 min. During this observation period, we recorded how much time the ants spent tending trophobiont hemipterans, feeding on the EFNs, and moving around the plant.

Sugar concentrations in honeydew and extrafloral nectar

In 2022, we replicated treatments EFN, Hemipteran, and EFN + Hemipteran ($n = 10$ for each group) to measure the sugar concentrations of the honeydew and extrafloral nectar. Branches with Hemipterans and/or EFNs were bagged with polyester fabrics between 7:00 and 8:00 am. Polyester bags minimize water evaporation from nectar and ease the sampling process of extrafloral nectar and honeydew without interference from ants and other arthropods. After 24 h, we returned to the field to collect the nectar and honeydew. Hemipterans were held laterally with flexible forceps and lightly pressed for honeydew secretion, which was collected with a graduated microcapillary tube (5 µL). The same types of tubes were used to collect nectar from EFNs. Finally, we used a manual refractometer (Eclipse model) to measure the sugar concentrations of the honeydew and the extrafloral nectar of each plant (see Lange et al. 2017, for details).

Data analyses

All tests were performed using R statistical software (R Core Team 2020, version 4.0.0). We used analysis of variance (ANOVA) and linear mixed model (LMM) procedures to test the two hypotheses in two years of study (2018 and 2019). To test the protection hypothesis, we conducted two one-way ANOVAs between the Control (no manipulation) and Exclusion (no ants) groups using leaf herbivory proportion and the production of fruits as response variables. To evaluate the ant-distracting hypothesis, we first conducted a set of two-way ANOVAs testing for the effects of both the presence of EFNs and hemipterans (EFN, Hemipteran, Exclusion, and Control groups) on leaf herbivory proportion and fruit production. We also evaluated interaction effects (EFNs × hemipteran factors) and performed Tukey post-hoc tests when necessary. Afterward, we performed two LMMs evaluating the mean proportion of ants observed attending either EFNs or hemipterans on plants from three groups: EFN + Hemipteran (Control), EFN, and Hemipteran. We used plant identity and the number of hemipterans as random factors: $y \sim x + (1|\text{plant ID}) + (1|\text{n}^{\circ}\text{ hemipterans})$ (Bates et al. 2015). The goal here was to verify whether ants prefer a specific resource when both occur in the same plant (EFN + Hemipteran group) and how ants use those resources when they occur apart (EFN and Hemipteran groups), while controlling for potential effects of the number of hemipterans. Using the same plant groups, we performed another LMM to test for differences in the time ants spent using each resource type (honeydew or extrafloral nectar) and moving on the plant. Finally, we used a t-test to analyze the possible differences between the sugar concentrations of honeydew and extrafloral nectar.

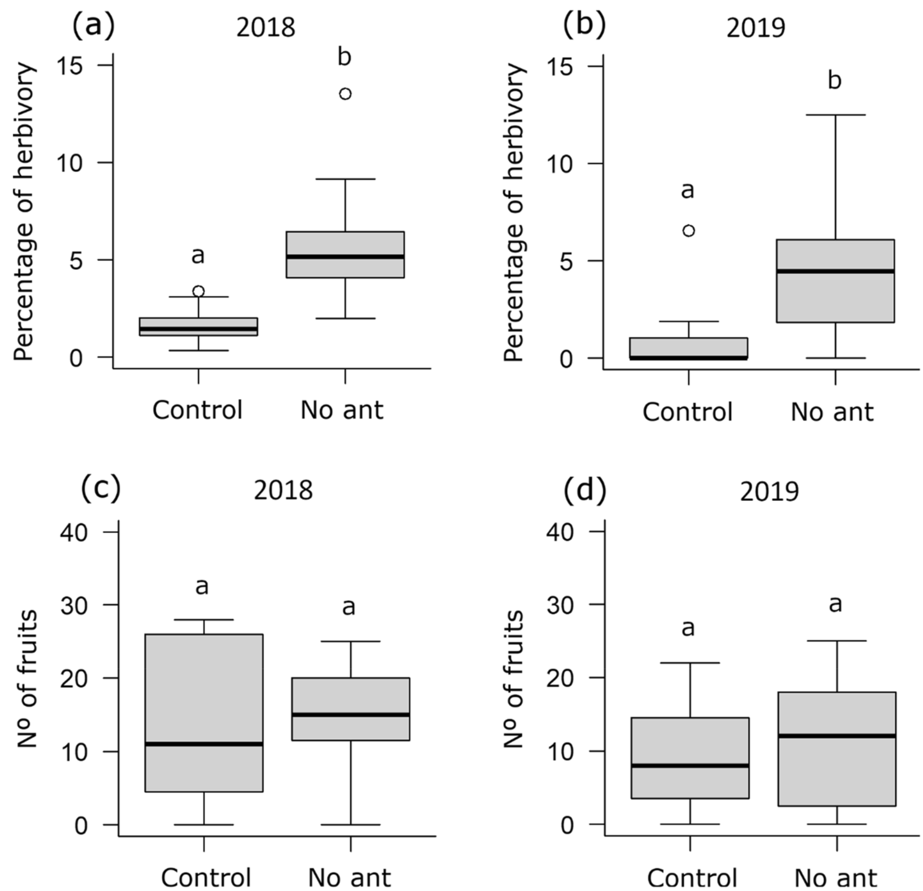
We performed a set of analyses of similarity (ANOSIM; Clarke 1993) to test for differences in the species composition of ants among plant groups (Control, Hemipteran, and EFN) from each year of the study. The ANOSIM set was performed using the "vegan" package of R (Oksanen et al. 2013). We first used the Hellinger transformation on our data (square root of the sample total standardized data). Then, the Bray–Curtis distance was calculated, and 999 permutations were performed based on the number of vising ants per plant (Santos and Moura 2021). From the total number of individuals ($n = 45$), we excluded plants that were not visited by any ant (2018: $n = 6$; 2019: $n = 3$). After ANOSIM, we generated a set of nonmetric multidimensional scaling (NMDS) graphs to visualize the results.

All statistical assumptions were verified according to Zuur et al. (2010). Data normality was assessed using boxplots, histograms, and Lilliefors normality tests. Variance homogeneity was verified using the function "var. test" from the "stats" package and the function "simulateResiduals" from the "DHARMa" package. Variability signs and values in the Results section depict the standard error of the mean (SEM).

Results

We observed a total of 10 morphospecies of ants visiting *B. malifolia*. The most common ants were *Camponotus* species and *Ectatomma tuberculatum*.

Fig. 2 Percentage of herbivory (a and b) and fruit production (c and d) in groups of *Banisteriopsis malifolia* (Malpighiaceae) where ants were maintained (Control; n = 15) or excluded (No ant; n = 15) in 2018 and 2019. Distinct letters indicate statistically different groups according to α = 5%



Protection hypothesis

In 2018 and 2019, leaf herbivory was greater in plants without ants (Exclusion group) (2018: $F_{1,28} = 27.78$; $p = 0.001$; 2019: $F_{1,28} = 13.97$; $p < 0.001$; Fig. 2a and b). However, fruit production did not differ between the groups (2018: $F_{1,28} = 0.031$; $p = 0.86$; 2019: $F_{1,28} = 0.30$; $p = 0.58$; Fig. 2c and d).

Ant-distracting hypothesis

In 2018, the highest herbivory was found in plants without EFNs and hemipterans (Exclusion), while the lowest herbivory was observed in plants bearing both EFNs and hemipterans (2018: $F_{2,57} = 14.40$; $p < 0.001$; Fig. 3a). In 2019, the EFN + Hemipteran and EFN groups had herbivory values close to zero (2019: $F_{2,57} = 56.24$; $p < 0.001$; Fig. 3b). In both years, we did not observe significant differences in fruit production (2018: $F_{2,57} = 0.56$; $p = 0.57$; Fig. 3c; 2019: $F_{2,57} = 2.68$; $p = 0.077$; Fig. 3d).

Ants showed a preference for EFNs compared to hemipterans. In both years, about 70% of ants, on average, were observed feeding on EFNs when both EFNs and hemipterans occurred on the same plant (Control), while less than 30% of them were observed feeding on hemipterans (2018: $F_{1,28} = 17.38$; $p < 0.001$; Fig. 4a; 2019: $F_{1,28} = 16.08$; $p < 0.001$; Fig. 4c). Interestingly, ants showed no preference when resources occurred separately on plants (only hemipterans or only EFNs) (2018: $F_{1,28} = 0.66$; $p = 0.43$; Fig. 4b; 2019: $F_{1,28} = 1.69$; $p = 0.20$; Fig. 4d).

When we compared ant activity between plant groups (Control, Hemipteran, and EFN) and the time spent using each resource type (honeydew or nectar) or moving on the plant, we found that ant activity differed according to the plant group and food resource ($F_{2,129} = 4.05$; $p = 0.019$; Fig. 5). In the Control and Hemipteran groups, the ants spent most of their time feeding on honeydew (Control: Honeydew = 74.5% ± 4.32 SEM, Control: Nectar = 6% ± 1.66 SEM; Fig. 5a; Hemipteran: Honeydew = 82% ± 2.26 SEM; Fig. 5b). In the EFN group, the ants spent almost the same amount of time foraging or feeding on extrafloral nectar (Nectar = 52% ± 4.3 SEM; Fig. 5c).

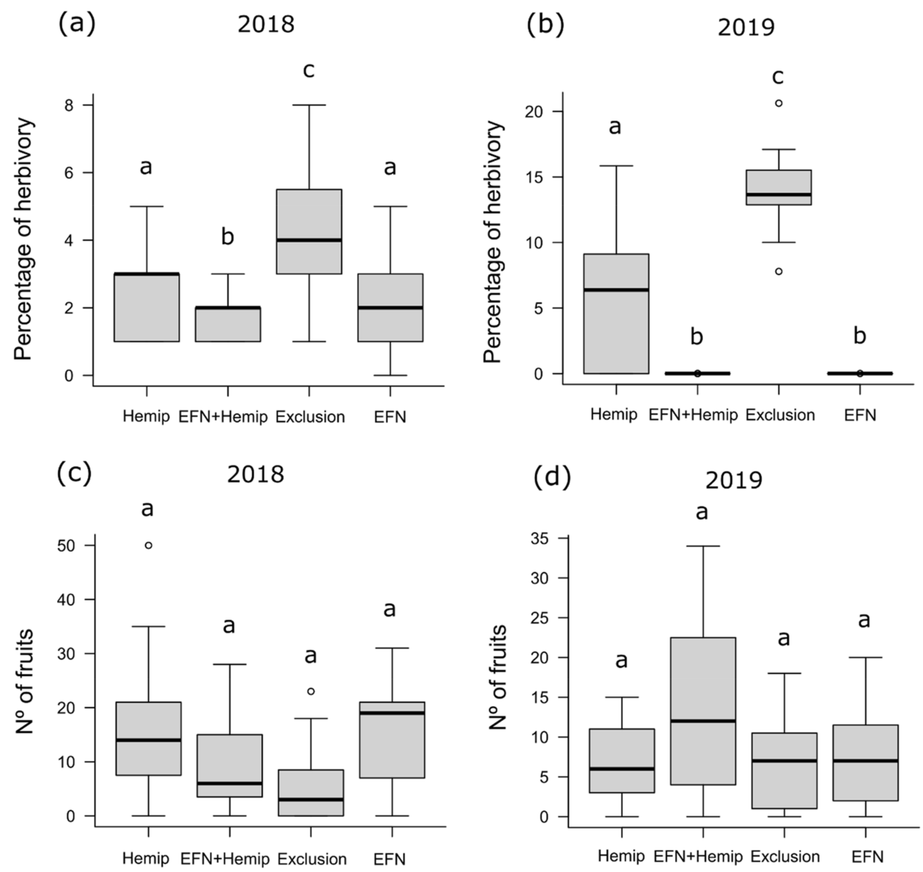


Fig. 3 Mean percentage of leaf herbivory (a and b) and fruit production (c and d) observed in four plant groups of *Banisteriopsis malifolia* (Malpighiaceae) during the two years of the study (n per group = 15). Hemip = only honeydew-producing hemipterans; EFN + Hemip = extrafloral nectaries and hemipterans on the same plant; Exclusion = both hemipterans and extrafloral nectaries excluded; EFN = only extrafloral nectaries. Distinct letters indicate statistically different groups according to α = 5%

Sugar concentrations in honeydew and extrafloral nectar

We observed that honeydew had a higher sugar concentration, on average, than extrafloral nectar (Honeydew: 24.25% ± 1.61 SEM, n = 20; EFNs: 18.71% ± 0.65 SEM, n = 20; $t_{2,38} = 3.19$, $p = 0.003$).

Ant species composition

We found no differences in ant species composition among plant groups (Control, Hemipteran, and EFN) either in 2018 (ANOSIM: $R = 0.022$, $p = 0.27$; Fig. 6a) or 2019 (ANOSIM: $R = -0.064$, $p = 0.99$; Fig. 6b).

Discussion

Our results provide partial support for both the protection and ant-distracting hypotheses, indicating that EFNs may possess multiple ecological roles. The protection hypothesis was supported, as we observed increased herbivory values in the absence of ants (Fig. 2a, and c), although the influence of ants was not converted into a higher reproductive output for *Banisteriopsis malifolia* (Fig. 2c and d). In the first year of the study, we also observed that the simultaneous presence of hemipterans and EFNs was associated with the lowest values of foliar herbivory (Fig. 3a), although differences in the reproductive output were not detected (Fig. 3b and d). We found some support for the ant-distracting hypothesis since more than 70% of ants were registered feeding on the extrafloral nectar instead of honeydew when both resources were offered together (Fig. 4a and c). When offered separately (i.e., different plant groups), the resources were equally used by ants (Fig. 4b and d). However, we also observed that the ants fed for longer periods of time on honeydew, which contained, on average, 29.6% more sugar than the extrafloral nectar (Fig. 5).

The complex interactions involving plants, hemipterans, and ants partially explain why our study supported, at least partially, both hypotheses. EFNs may have evolved multiple ecological roles in regions where plants with EFNs co-occur with sap-sucking insects (Chanam et al. 2015). In addition to the protection role, EFNs can distract ants that could potentially be attending hemipterans. While hemipterans have also been associated with a reduction in herbivory, we speculate that EFNs may help control hemipteran populations, thus minimizing plant damage due to overpopulation, as large numbers of sap-sucking hemipterans are associated with diseases and increased plant damage (Delabie 2001;

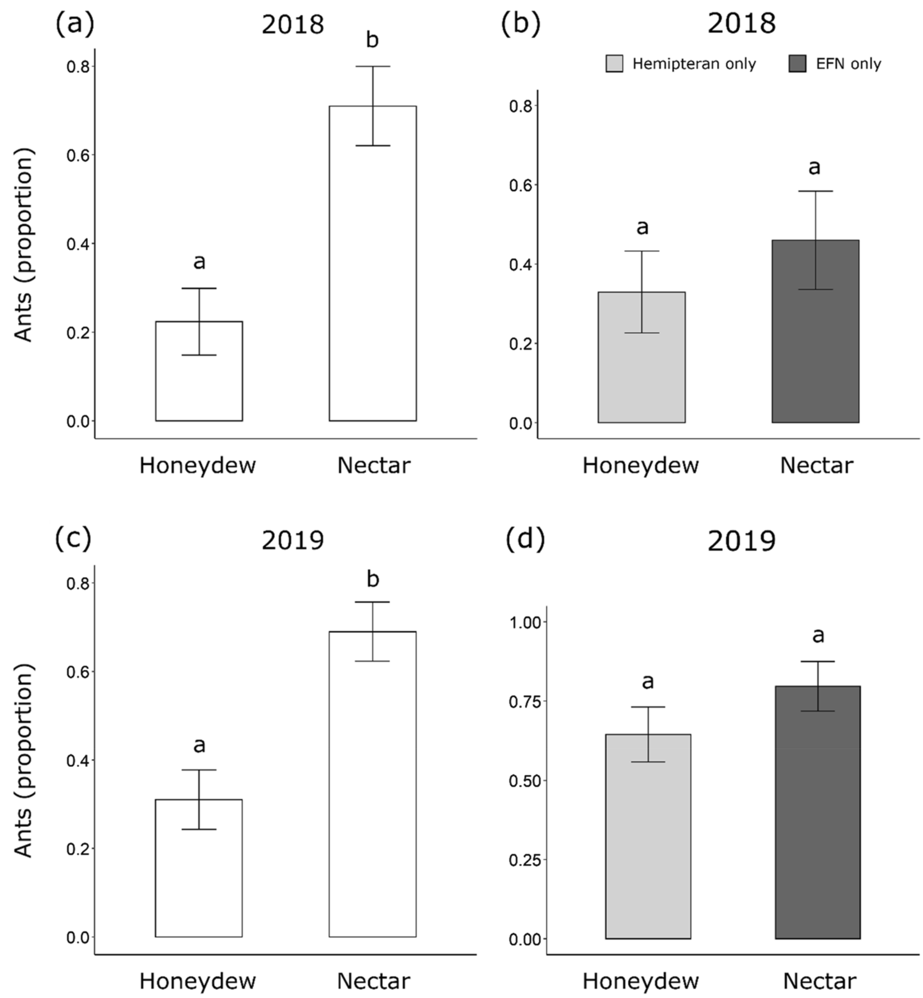


Fig. 4 Proportion of visiting ants using resources (honeydew or extrafloral nectar) of *Banisteriopsis malifolia* (Malpighiaceae) exhibiting the simultaneous presence of extrafloral nectaries and hemipterans (a and c; EFN + Hemipteran group; n = 15) and in plants where only one type of resource was offered (b and d; Hemipteran or EFN groups; n per group = 15). Distinct letters indicate statistically different groups according to α = 5%

Moura et al. 2021). Furthermore, EFNs might reduce the number of ants visiting flowers, thus minimizing potential conflicts between ants and pollinators. Otherwise, hemipterans are commonly found on flowers; thus, attracted ants may interfere with pollinator services (Ibarra-Isassi and Oliveira 2018).

EFNs and hemipterans exhibited additive protective effects on plants in the first year of our study. In 2018, we observed that the lowest herbivory values were associated with plants producing both extrafloral nectar and honeydew, although we did not observe any differences in fruit production. This similar productivity might be explained by the fact that *B. malifolia* is constantly attacked by endophytic beetles that consume flower buds and bypass ant defenses (Torezan-Silingardi 2011; Mendes-Silva et al. 2021). Nevertheless, it is important to notice that we did not measure seed production, so we do not know whether herbivore damage could have caused changes in the number of viable seeds, for instance. Although trophobiont hemipterans can eventually provide benefits to plants (see Styrsky and Eubanks 2010; Vilela and Del-Claro 2018), their positive effects do not always stack when combined with other resources, such as EFNs (Savage and Rudgers 2013). The effects of combining hemipterans and EFNs are thus largely dependent on the ecological context, such as resource availability, the involved ant species, and herbivore pressure (Davidson et al. 2003; Rudgers et al. 2010; Chanam et al. 2015; Lange et al. 2017). Such conditional scenarios may explain why plants with only EFNs already showed virtually no herbivore damage in the second year of study. Furthermore, as we observed that the ant community composition did not change depending on the offered resource, eventual differences among plant treatments in terms of resource use and protection can be mostly attributed to unequal ant recruitment.

The greater abundance of ants feeding on extrafloral nectar than honeydew was somewhat surprising, given the higher sugar concentration in the honeydew, although the available evidence in the literature is conflicting. While some studies have shown that honeydew tends to attract more ants, as they are usually richer in nutrients than EFNs (Blüthgen et al. 2004a)—they may even contain addictive chemicals (Kudo et al. 2021)—other studies have demonstrated that

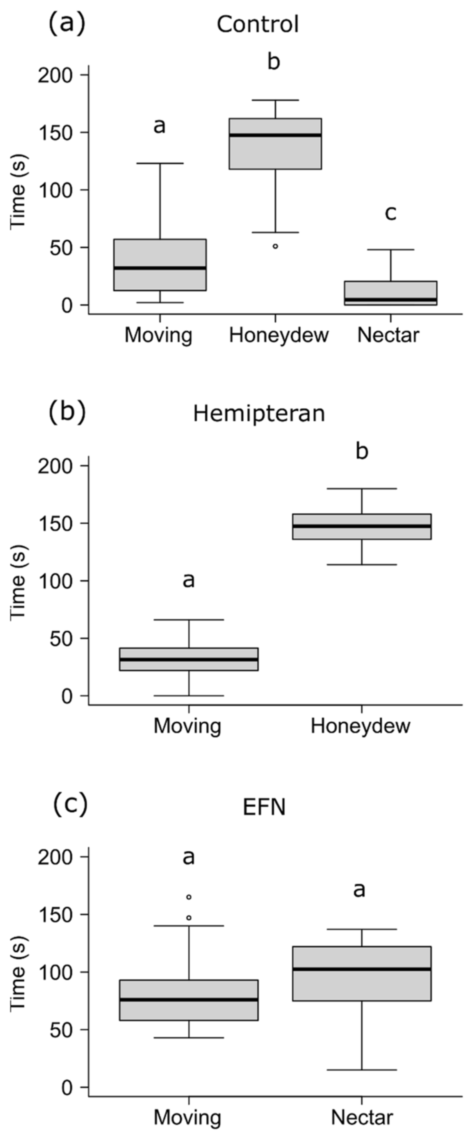


Fig. 5 Time spent by ants moving around the plant and feeding on honeydew or extrafloral nectar from the three groups of *Banisteriopsis malifolia* (Malpighiaceae): Control (no manipulation; n = 10), Hemipteran (only honeydew-producing hemipterans; n = 10), and EFN (only extrafloral nectaries; n = 10) (**a–c,** respectively). Distinct letters indicate statistically different groups according to α = 5%

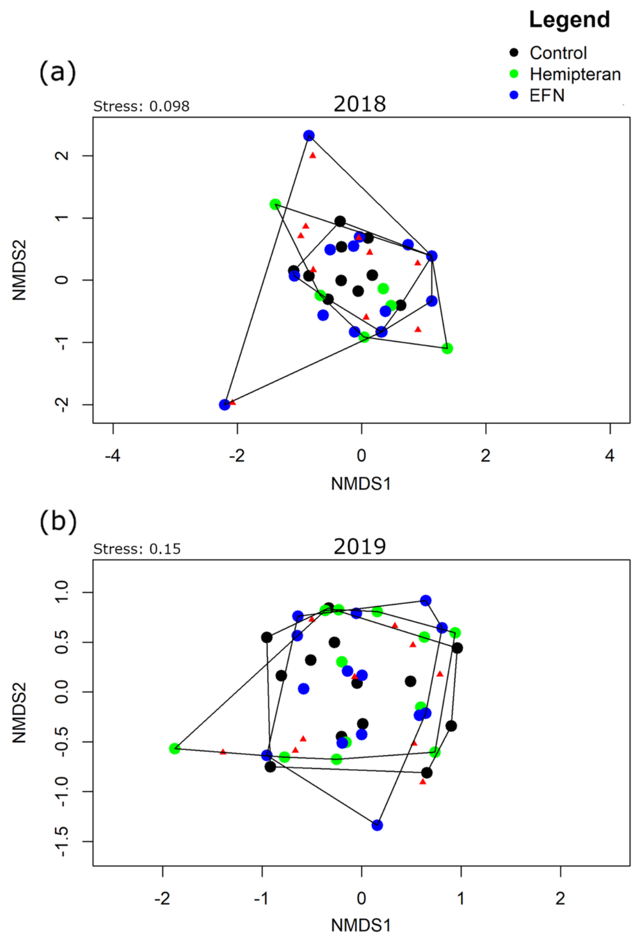


Fig. 6 Species composition of ants visiting three plant groups of *Banisteriopsis malifolia* (Malpighiaceae) in 2018 (**a**) and 2019 (**b**). Control = no manipulation (n_{2018} = 14; n_{2019} = 14); Hemipteran = only honeydew-producing hemipterans (n_{2018} = 11; n_{2019} = 14); EFN = only extrafloral nectaries (n_{2018} = 14; n_{2019} = 14). Ant species composition was not different among the groups (α = 5%) either in 2018 (ANOSIM: R = 0.022, p = 0.27) or 2019 (ANOSIM: R = −0.064, p = 0.99). Red triangles represent the ant species distribution

ants are less attracted by the complex sugars found in honeydew (Blüthgen and Fiedler 2004a). Although 70% of the total ants were observed feeding on EFNs instead of hemipterans when both resources were available, we showed that the ants spent more time tending hemipterans than feeding on EFNs. We believe that the relative abundance of EFNs and hemipterans on *B. malifolia* might explain this apparent paradox. While high-quality resources can trigger intense competition among ants, having enough power to structure whole ant communities (Blüthgen et al. 2004b; Orivel et al. 2018), they are not the sole meaningful factor influencing foraging decisions among ants. Ants make foraging decisions based on their preferences and the availability and distribution of resources (Davidson et al. 2003; Blüthgen and Fiedler 2004b; Savage and Rudgers 2013). Even though EFNs produced nectar with lower sugar concentrations than honeydew, they were more abundant on the plant (two EFN glands per leaf) and produced a larger reward volume (personal observation). Thus, ants might be willing to use the first encountered food resource, regardless of the quality, which by a simple matter of probability will most likely be the extrafloral nectar. The apparent collective preference for EFNs might reflect their high availability on the plant. This also explains why ants used extrafloral nectar and honeydew equally when no alternatives were offered. This reasoning is strengthened by the fact that plants with either EFNs or hemipterans were visited by similar ant communities, suggesting that the observed feeding preferences cannot be attributed to interspecific differences.

From an evolutionary perspective, the quantitative investment of *B. malifolia* in EFNs might be beneficial in two ways. First, abundant EFNs may still distract ants from hemipterans—and minimize their potential damage to plants—despite the putative inferior nutritious value of extrafloral nectar compared to honeydew. We hypothesize that resources of medium quality may foster ant protection since ants have to move around the plant in search of additional resources. Otherwise, resources of high quality could reduce ant movement (see Fig. 5b and c) and consequently the defensive potential of ants. Second, having more EFNs scattered on plants means that more ants can simultaneously visit the plant, which may improve indirect defenses. We also argue that a strong preference for hemipterans over EFNs would most likely be an unstable evolutionary strategy—for both ants and plants—since ants can stimulate the overgrowth of hemipteran populations, rapidly reducing plant fitness and ultimately ant fitness. Still, our results suggest that keeping hemipteran populations under control by reducing hemipteran attendance to stable levels via ant-distracting mechanisms may actually improve plant defenses. In summary, *B. malifolia* investment in EFNs is in line with both the protection and ant-distracting hypotheses.

We concluded that EFNs may suit more than a single ecological role in plants (e.g., indirect defense), strengthening the importance of these structures for plant populations and possibly plant communities. We also concluded that honeydew-producing hemipterans are not intrinsically negative for plants, and under certain circumstances, they may even foster indirect defenses provided by ants. As for future perspectives, the next step is to understand how the relative quantity, productivity, and positioning of both EFNs and honeydew-producing hemipterans affect ant–plant–hemipteran interactions.

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Declarations

Competing interests The authors declare no competing interests.

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