Sociobiology 72(4): e11715 (December, 2025) DOI: 10.13102/sociobiology.v72i4.11715

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Facilitative Interactions among Extrafloral Nectary-bearing Plants, Ants, and Neighboring Vegetation in the Brazilian Cerrado

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Article History

Edited by
Evandro Nascimento Silva, UEFS, Brazil
Received 23 April 2025
Initial acceptance 05 May 2025
Final acceptance 15 October 2025
Publication date 23 November 2025

Keywords
Byrsonima intermedia, *Peixotoa tomentosa*, herbivory, Malpighiaceae, plant–ant interactions, proximity.

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Abstract

Herbivory is a key plant–insect interaction that can have a negative impact on plant development. Some plants have evolved indirect defenses by attracting protective ants through extrafloral nectaries (EFNs). These mutualistic ants may extend their protective behavior to neighboring plants, generating facilitative interactions. This study investigated whether two Malpighiaceae species − one with EFNs (*Peixotoa tomentosa*) and one without (*Byrsonima intermedia* − benefit from proximity to EFN-bearing neighbors. We assessed herbivory, leaf loss, growth rate, and the number of young leaves in focal plants near EFN and non-EFN neighbors. *B. intermedia* produced more young leaves when close to EFN-bearing plants but fewer when near non-EFN plants; similarly, *P. tomentosa* experienced greater leaf loss when in proximity to non-EFN plants. Specifically, in *B. intermedia*, increasing the distance to EFN plants from 1 to 2 meters led to a reduction of approximately 1.57 young leaves (-27.2%), whereas increasing the distance to non-EFN plants resulted in a gain of 3.47 young leaves (+83.5%). In *P. tomentosa*, the same increase in distance to non-EFN neighbors reduced leaf loss by 4.84 leaves (-64.5%). These results highlight the ecological importance of neighboring plant identity at realistic spatial scales. Prior research suggests that EFN-bearing plants may promote anthill formation and enhance soil quality, potentially explaining the observed facilitation. Our findings underscore the role of ant-mediated facilitative interactions in shaping plant community dynamics and guiding ecosystem management.

Introduction

Plants interact with both animals and other plants, with outcomes that may be positive or negative. These interactions among plants themselves can take on diverse forms. For instance, there are inhibitory interactions, where a plant releases compounds into the soil that impede the growth and development of neighboring plant species, a phenomenon known as allelopathy (Cipollini et al., 2012). Conversely, plants also engage in facilitative interactions, where one plant supports the growth of another (Bruno et al., 2003). These contrasting interactions underscore the complexity and dynamic nature of plant communities.

Ecological facilitation refers to interactions in which at least one species benefits while none is harmed. Although its manifestations vary widely in nature, it often involves one species improving environmental or biotic conditions for another (Bruno et al., 2003; Lortie, 2007; Verdú et al., 2021).

Open access journal: http://periodicos.uefs.br/index.php/sociobiology
ISSN: 0361-6525

Facilitation is especially relevant in systems where one organism improves environmental conditions or modifies biotic interactions in ways that benefit others. Classic examples include nurse plants that create shaded microhabitats favorable to seedling establishment in arid ecosystems (Bruno et al., 2003), and ant-plant mutualisms in which extrafloral nectaries (EFNs) attract ants that defend plants from herbivores (Rosumek et al., 2009; Trager et al., 2010). These interactions demonstrate how a facilitating species can alter the local ecological context, thereby promoting the growth, survival, or reproduction of other species. Facilitation can also occur indirectly: when a third species benefits from the presence of a facilitator due to reduced competition or altered enemy pressure. Recognizing these dynamics is essential for understanding how ecological interactions structure plant communities.

This complexity is further evidenced by observations that facilitation can significantly enhance plant growth rates. For example, *Enchylaena tomentosa* has been found to thrive better in shaded areas (Hastwell & Facelli, 2003), while species such as *Symphoricarpos occidentalis* exhibit superior growth performance in the presence of grasses (Li & Wilson, 1998). Additionally, some studies indicate that certain forest tree species exhibit faster growth in environments with greater species diversity (Pretzsch, 2022). On the other hand, other species thrive better in environments with moderate shading (Semchenko et al., 2011). These findings highlight the influence of various factors, such as shading intensity, the presence of neighboring species, and environmental conditions, on plant growth rate. These diverse examples illustrate that the presence and identity of neighboring plants can significantly influence performance, but little is known about how this occurs through ant-mediated indirect defenses.

A less-explored form of ecological facilitation among plants involves the transfer of indirect defenses from plants with EFNs to those lacking these structures (Jezorek et al., 2011). EFNs are nectar-producing glands located outside flowers, typically on leaves, stems, and petioles, and are widely recognized for their role in mediating mutualistic interactions between plants and arthropods (Rico-Gray & Oliveira, 2007; Del-Claro & Torezan-Silingardi, 2012). EFNs secrete sugary liquids that attract a variety of predatory arthropods, such as ants (Rico-Gray & Oliveira, 2007; Del-Claro & Torezan-Silingardi, 2012), parasitoid wasps (Röse et al., 2006), and spiders (Nahas et al., 2012), which in turn provide biotic protection against herbivory. For instance, parasitoid wasps like *Microplitis croceipes* can use EFNs as their sole food source, exhibiting increased longevity and reproductive success compared to those lacking access to nectar (Röse et al., 2006). Moreover, these wasps are capable of learning and locating EFNs by olfactory cues alone, demonstrating enhanced foraging behavior after prior experiences with EFN-bearing plants (Röse et al., 2006). Similarly, spiders and ants interact in complex ways on EFN-bearing plants, with both groups contributing to herbivore suppression, albeit with context-dependent outcomes due to intraguild interactions (Nahas et al., 2012).

The mutualistic association between plants and these arthropods is influenced by multiple ecological and evolutionary factors, including phenological variation, species identity, and environmental conditions, which can modulate the nature and outcome of interactions over time and space (Del-Claro et al., 2016). Plants with EFNs consistently attract a greater abundance and diversity of ants compared to those without EFNs, even when other floral resources are available, and this elevated ant activity is correlated with reduced levels of herbivory (Del-Claro & Torezan-Silingardi, 2012). As highlighted by Heil and McKey (2003), EFN-mediated mutualisms represent experimentally tractable systems for investigating resource allocation strategies, multi-trophic interactions, and the evolutionary dynamics of interspecific cooperation, offering a valuable framework for understanding the ecological significance and evolutionary stability of indirect plant defenses. However, these ant-plant mutualisms may also incur indirect costs, such as negative effects on pollination when ants interfere with pollinator visitation to flowers (Nogueira et al., 2021), highlighting the complexity of balancing multiple interactions in EFN-bearing plants.

Despite these potential costs, plants with EFNs can indirectly confer protection to neighboring plants lacking EFNs through ant sharing. Ants attracted to EFN-bearing plants may forage beyond the host plant in search of additional resources, leading them to patrol adjacent vegetation and reduce herbivory in nearby non-rewarding plants (Moura & Del-Claro, 2023; Souza et al., 2024). Experimental evidence shows that ants frequently visit neighboring plants without EFNs and that proximity to an EFN-bearing plant increases ant abundance and decreases herbivore damage (Jezorek et al., 2011; Moura & Del-Claro, 2023). However, there is no universally defined minimum distance for this facilitation to occur. Some studies suggest effects within one meter (Jezorek et al., 2011), while others report indirect benefits up to 10 meters from the focal EFN plant (Moura & Del-Claro, 2023), depending on the foraging range of the ant species involved. The identity and behavior of ant species play a crucial role, as more aggressive and efficient mutualists, such as species of *Camponotus* and *Ectatomma*, provide better protection than non-mutualistic ants like *Crematogaster* or *Pseudomyrmex gracilis* (Moura & Del-Claro, 2023; Souza et al., 2024).

Despite increasing interest, several knowledge gaps remain. These include the spatial and temporal extent of ant-mediated indirect protection, the influence of ant nest distribution, the interplay between competition and facilitation among neighboring plants, and the impact of ant community composition on facilitation strength. Further studies are needed to clarify how widespread and consistent these facilitative effects are across systems and ecological contexts.

Furthermore, biotic protection can be more effective in reducing herbivory levels than other types of plant defenses, such as physical traits (e.g., trichomes), which may only partially deter herbivores or affect specific guilds (Pereira et al., 2020). Plants bearing EFNs not only benefit individually from attracting protective arthropods but may also confer indirect protection to neighboring plants lacking EFNs through a process known as associational resistance. This phenomenon has been demonstrated in multiple systems. Jezorek, Stiling, and Carpenter (2011), for example, showed that *Opuntia* species growing near *Chamaecrista fasciculata* – a legume with EFNs – experienced higher ant abundance, lower herbivory by the invasive moth *Cactoblastis cactorum*, and increased growth rates compared to isolated *Opuntia* individuals. Their experimental manipulations confirmed that ant predation on moth eggs and pupae was significantly higher on *Opuntia* plants near *C. fasciculata*, suggesting that the presence of EFNs in the community can mediate the spatial distribution of herbivory pressure. More recently, Moura and Del-Claro (2023) found that *Smilax polyantha*, a liana without EFNs, exhibited nearly threefold reductions in foliar herbivory when associated with EFN-bearing support plants. These EFN-bearing neighbors indirectly benefited *S. polyantha* by increasing ant visitation and species richness on its leaves. Notably, the experimental addition of artificial nectaries to *S. polyantha* further enhanced ant activity on surrounding vegetation, resulting in a 2.5-fold increase in ant abundance on neighboring plants. These findings illustrate how the sharing of biotic defenses can create localized networks of protection, with potential implications for plant community dynamics and species coexistence. Sharing biotic defenses thus represents a promising facilitation mechanism that may enhance the survival and reproductive success of plants lacking EFNs through spatially mediated mutualistic spillovers.

Given that ecological facilitation is less studied than interactions such as competition (Callaway & Pugnaire, 2007; Bronstein, 2009; Butterfield & Callaway, 2012), and facilitation via shared biotic defenses is even more poorly understood (e.g., Jezorek, Stiling and Carpenter 2011; Moura & Del-Claro, 2023), this study aimed to investigate whether the presence or absence of neighbors with EFNs can influence the growth and production of leaves of plants from the Brazilian Cerrado (Savanna). Given the potential significance of facilitation in preserving ecological niches over time and in species conservation (Valiente-Banuet & Verdú, 2007), this research sought to shed light on this lesser-explored facet of plant interactions.

Considering that plants equipped with EFNs attract ants, which can be shared with neighboring plants that lack EFNs, the proximity between plants can significantly impact their performance. This ant-sharing can lead to enhanced protection against herbivores, thereby potentially improving the performance of the plants. Thus, we hypothesized that *Byrsonima intermedia* (without EFNs) plants located near those with EFNs will exhibit lower leaf loss, greater growth rates, and increased young leaf production compared to those situated near plants without EFNs. Conversely, we expect that *Peixotoa tomentosa* (with EFNs) plants located near plants without EFNs will show higher leaf loss, reduced growth rates, and decreased young leaf production compared to those near plants with EFNs.

To test this hypothesis, we studied these two typical species from the Brazilian Cerrado. In our study, we measured the distance from non-EFN plants in addition to the distance between EFN-bearing plants because this parameter is critical for understanding the dual nature of ant-mediated facilitation. On one hand, the proximity of non-EFN plants to those with EFNs may allow them to benefit from shared protective ants and improved soil conditions resulting from increased ant activity. On the other hand, this same interaction could potentially disadvantage the EFN-bearing plants by diverting some of their mutualistic ants to neighboring non-EFN plants. By evaluating the effect of distance from non-EFN plants on both vegetative performance and herbivory, we aim to determine whether the indirect facilitative benefits of ant sharing might be offset by a reduction in the protective services available to the EFN-bearing plants themselves. This approach enables us to assess whether ant-mediated facilitation represents a net benefit or a trade-off for plants within mixed-species neighborhoods.

Methods

Study Location

The present study took place from the second half of 2020 to the end of 2021 in a neotropical savanna region located within the Brazilian Cerrado. Specifically, this area is located within the ecological reserve of Clube Caça e Pesca Itororó, situated in Uberlândia, a city in the state of Minas Gerais, Brazil (18° 59’ S, 48° 18’ W). The cerrado biome in this region, dominated by cerrado *stricto sensu* vegetation, experiences two distinct seasons: a rainy and warm season extending from October to March, characterized by an average rainfall of 270 ± 50 mm and an average temperature of 23 ± 5 ºC; followed by a dry and cool season spanning from April to September, with an average rainfall of 22 ± 20 mm and an average temperature of 19 ± 3 ºC (Vilela et al., 2017). This climate aligns with Köpen’s Aw classification. Pastures and properties with varying levels of conservation surround the study area.

Plant Species

B. intermedia A. Juss. is a bushy member of the Malpighiaceae family, known for its leaves generally covered with trichomes (Santos et al., 2020). It exhibits unguiculate, hermaphroditic, zygomorphic, and pentamerous flowers featuring yellow petals and sepals equipped with a pair of elaiophores, which signifies that it produces oil as one of the floral resources to attract pollinators. The pollen is of a whitish hue and has a viability rate of approximately 90%. The ovary is superior, tricarpellate, and trilocular, and the gynoecium consists of three elongated styles. The yellow flower buds are fused, and these blooms usually last for only one day (Oliveira et al., 2007). It is worth noting that this species lacks EFNs. Flowering predominantly takes place during the rainy season, spanning from October to March (Boas et al., 2013). The main herbivore of *B. intermedia* is *Cerconota achatina* (Oecophoridae), a moth caterpillar (Velasque & Del-Claro, 2016). Common ants associated with this species include *Ectatomma brunneum* and *Camponotus rufipes* (Ibarra-Ibassi & Oliveira, 2017).

P. tomentosa A. Juss. is a deciduous subshrub of the Malpighiaceae family, typically reaching heights between 0.5 and 2.5 meters, although some individuals may grow up to 3 meters tall (Pereira et al., 2020). This species possesses a pair of EFNs at the base of each leaf, on the abaxial face, which are active primarily in the early stages of leaf development and are mainly active at the beginning of the rainy season (Del-Claro, 1998; Pereira et al., 2020). These EFNs attract ants from a variety of genera, including *Camponotus*, *Ectatomma*, *Pseudomyrmex*, *Brachymyrmex*, and *Zacryptocerus* (Del-Claro, 1998; Vilela et al., 2014; Bächtold et al., 2017; Pereira et al., 2020), which may act as protective mutualists by patrolling the plant and deterring or removing herbivores. The flowering period of *P. tomentosa* extends from April to July, peaking between May and June (Del-Claro & Marquis, 2015), and the flowers have five yellow petals arranged in a panicle-type inflorescence (Del-Claro et al., 1997). During this reproductive phase, the most frequent herbivores include thrips (Thysanoptera), particularly *Heterothrips peixotoa*, followed by orthopterans, hemipterans, coleopterans, and lepidopteran larvae (Del-Claro et al. 1997; Vilela et al., 2014). Experimental studies have demonstrated that the presence of ants significantly reduces both leaf and floral herbivory, particularly during years with high herbivore pressure. For example, Del-Claro (1998) found that small ant species capable of accessing internal floral structures were particularly effective in removing thysanopterans, resulting in increased seed and fruit production. However, the effectiveness of ant protection can vary depending on factors such as ant species composition, herbivore pressure, and environmental conditions (Del-Claro 1998, 2004). In contrast, in areas with high densities of leaf-cutting ants (*Atta laevigata*), the presence of generalist ants was insufficient to prevent extensive damage to leaves, buds, and flowers. These findings suggest that the protective benefits provided by ants to *P. tomentosa* are context-dependent, modulated by both biotic interactions and spatiotemporal variation in the Cerrado environment.

Experiment

In this study, a total of 15 plants belonging to the species *P. tomentosa* and 15 plants of the species *B. intermedia* were selected and marked with numbered aluminum plates. Individuals of the same species were spaced at least ten meters apart. For clarity, we refer to *P. tomentosa* and *B. intermedia* as the "main plants". For each main individual plant, two additional plants were marked nearby, one with EFNs and the other without EFNs. The distances between each main plant and its two close neighbors, whether they had EFNs or not, were measured using a measuring tape. The two neighboring plants of each main plant were chosen at a maximum distance of five meters, but as close as possible to the main plants. Among these additional plants, the neighbors without EFNs included *B. intermedia* and *Miconia albicans*, while those with EFNs included *P. tomentosa* and *Banisteriopsis malifolia.* We refer to these nearby plants as "neighboring plants". This resulted in a total of 30 plants with EFNs and 30 without EFNs among these neighboring plants. *B. malifolia* attracts ants that contribute to a reduction in herbivory on its leaves (Vilela et al., 2014). The study area comprises typical Cerrado vegetation, which includes several plant species bearing EFNs. However, to minimize potential interference from other neighboring EFN-bearing species, we selected focal individuals of *P. tomentosa* and *B. intermedia* located in relatively open areas or natural clearings. Additionally, when necessary, surrounding vegetation within a 2-meter radius of the focal plants was manually removed prior to the start of the experiment. These precautions were taken to reduce external influences on ant activity and plant performance, thereby ensuring that the observed patterns were primarily related to the experimental treatments.

These distances were then related to five dependent variables: natural leaf herbivory, leaf loss, growth rate (using a measuring tape), and production of young leaves. Natural leaf herbivory was quantified by measuring the percentage of leaf area lost. Photographs of five leaves per plant were taken and analyzed using Bioleaf software to assess the damaged area. This analysis focused on the physical loss of leaf tissue and did not include damage caused by insects with sucking mouthparts, as this type of damage does not result in a visible reduction of leaf area. This software has high accuracy in estimating foliar damage, comparable to professional equipment such as the LI-COR 3100 and the CI-202 LAM (Machado et al., 2016; Ullah et al., 2020). This level of precision ensures reliable and robust results, essential for a detailed analysis of herbivory impacts. Within each species, leaves of similar age were randomly selected. Subsequently, the average herbivory level was calculated based on the leaves analyzed for each plant. This assessment took place in May 2021, marking the end of the peak herbivory period in the Cerrado (December to May), after which herbivory levels tend to decline sharply (Calixto et al. 2020), coinciding with the onset of the southern hemisphere's winter. Regarding leaf loss, leaf counts were conducted in December 2020 (the peak of the rainy season) and in May 2021 (the beginning of the dry season), with the difference in leaf count between these two seasons calculated.

For growth measurements, plant height was assessed from the base of the stem at soil level to the highest point of the plant using a measuring tape in both December 2020 and June 2021. The growth rate was calculated as the difference in height between these two periods. The number of young leaves was counted for each plant in May 2021. In addition to the descriptions provided, a graphical diagram illustrating the experimental design is available in the supplementary material (Figure S7). Moreover, all variables, including leaf loss, growth rate, young leaf production, and leaf herbivory, along with their means and respective standard errors, are summarized in Table 2. During data collection visits, we recorded opportunistic observations of the most common herbivore taxa and ant species found on the study plants. These observations were not conducted through formal sampling protocols but were noted incidentally during measurements of distances, leaf loss, young leaf production, and other study variables.

Statistical Analyses

The distances from each main species (*P. tomentosa* and *B. intermedia*) to the neighboring plants with and without EFNs were the independent variables in all models analyzed. The leaf loss, growth rate, young leaf production, and leaf herbivory were the dependent variables. To verify the independence between the distances to neighboring plants with and without EFNs and the possible influence of autocorrelation on the results, we performed the Durbin-Watson test for both species studied, *B. intermedia* (DW = 2.4242, p = 0.7805) and *P. tomentosa* (DW = 2.4284, p = 0.7884). These results indicated no significant spatial autocorrelation between distances to neighboring plants. These findings are supported by the scatterplots of the distances to plants with and without EFNs, which showed no clear patterns of collinearity (see Supplementary Material). Therefore, we concluded that variable independence was maintained and that multicollinearity did not affect model performance. Natural leaf herbivory on each plant was assessed through a multiple linear regression test that considered the distances to plants with and without nectaries as independent variables. We rigorously tested and satisfied all assumptions in our models, including linear relationships between the dependent variable and independent variables, lack of correlation between independent variables, normally distributed residuals with constant variance, and no autocorrelation (see Supplementary Table 1). Although some residuals exhibited slight deviations from normality, these did not compromise the validity of the linear models. It is well-established that linear models, such as ANOVA and linear regression, are robust to mild and moderate deviations from normality, particularly when the sample size is sufficiently large (Rochon and Kieser 2010; Schmider et al. 2010). Furthermore, Sainani (2012) emphasizes that the normality assumption is often less critical in large samples, where standard statistical tests tend to perform reliably even in the presence of non-normal distributions.

The analysis of leaf loss was conducted using a quasipoisson test for both *B. intermedia* and *P. tomentosa*, due to overdispersion. Additionally, since several values were negative due to substantial leaf loss in many plants, a simple transformation was applied by adding a constant to all values, making them positive and allowing for the quasipoisson analysis. Growth rate was analyzed using multiple linear regression, with distances to plants with and without nectaries as predictors, after verifying model assumptions. Regarding the number of young leaves in both species, a zero-inflated negative binomial test was employed. This approach was chosen because the data exhibited a significant number of zeros, as indicated by the DHARMa zero-inflation test (ratioObsSim = 2.133, p-value < 0.001 for *P. tomentosa* and ratioObsSim = 8.695, p-value < 0.001 for *B. intermedia*). All statistical analyses were conducted using R software (version 4.2.2), with the "car", "zoo", "lmtest" and "DHARMa" packages employed in most tests.

To complement the interpretation of model estimates, we translated the significant regression coefficients into biologically meaningful values by calculating the relative and percentage changes in leaf dynamics over a realistic spatial gradient. Specifically, we used the predict() function from base R to compare the expected values of foliar production or loss when the distance to neighboring plants increased from 1 to 2 meters. The absolute difference between predictions was used to calculate the percentage change in leaf production or loss. Predicted responses across the distance gradient were visualized using response curves, with the plot() function from the base graphics package, based on predicted values calculated along a continuous sequence of distances using seq() and predict(), within the R environment.

Results

The most common herbivores observed foraging on the study plants belonged to the insect orders Phasmatodea, Orthoptera, Lepidoptera, and Hemiptera. The most prevalent ant species observed on the study plants were *Camponotus aff. blandus*, *Ectatomma brunneum*, and *Ectatomma tuberculatum* (Figure 3).

All statistical tests and their respective results are summarized in Table 1. Distances to neighboring plants with EFNs of *P. tomentosa* ranged from 20 to 480 cm (mean ± SE = 245.6 ± 36.13 cm), whereas those without EFNs ranged from 10 to 180 cm (78.07 ± 14.25 cm). Similarly, distances to neighboring plants with EFNs of *B. intermedia* ranged from 32 cm to 478 cm (227.47 ± 37.23), and from 18 cm to 210 cm (87.2 ± 18.92) for those without EFNs. At the beginning of the experiment, the initial heights of the focal plants were measured in centimeters. *P. tomentosa* individuals ranged from 108 to 242 cm in height, while *B. intermedia* ranged

Table 1 - Statistical tests used and their respective results in *P. tomentosa* and *B. intermedia.* Significant values are indicated with asterisks (*<0.05, **<0.01, ***<0.001), while italic values indicate marginally significant results.

Dependent Vairable	Independent Variable	Plant Species	Used Test	Estimate ± SE	Statistic value	p-value
Leaf Loss	Distance with EFNs	*P. tomentosa*	Quasipoisson	0.000105 ± 0.001461	t = 0.072	0.944
	Distance without EFNs	*P. tomentosa*		-0.010362 ± 0.004631	t = -2.237	0.045*
Growth Rate	Distance with EFNs	*P. tomentosa*	Multiple linear regression	-0.03727 ± 0.03026	t = -1.232	0.2417
	Distance without EFNs	*P. tomentosa*		-0.03296 ± 0.07672	t = -0.430	0.6751
Production of Young Leaves	Distance with EFNs	*P. tomentosa*	Zero-inflated negative binomial	-0.008721 ± 0.005120	z = -1.705	*0.0881*
	Distance without EFNs	*P. tomentosa*		0.007203 ± 0.004009	z = 1.796	*0.0724*
Herbivory	Distance with EFNs	*P. tomentosa*	Multiple linear regression	-0.0000427 ± 0.0000274	t = -1.554	0.1462
	Distance without EFNs	*P. tomentosa*		0.0000346 ± 0.0000696	t = 0.497	0.6285
Leaf Loss	Distance with EFNs	*B. intermedia*	Quasipoisson	-0.000471 ± 0.002152	t = -0.219	0.830
	Distance without EFNs	*B. intermedia*		-0.003163 ± 0.0047997	t = -0.659	0.522
Growth Rate	Distance with EFNs	*B. intermedia*	Multiple linear regression	0.003339 ± 0.012775	t = 0.261	0.798
	Distance without EFNs	*B. intermedia*		0.035156 ± 0.025139	t = 1.398	0.187
Production of Young Leaves	Distance with EFNs	*B. intermedia*	Zero-inflated negative binomial	-0.003170 ± 0.001065	z = -2.976	0.0029**
	Distance without EFNs	*B. intermedia*		0.006069 ± 0.001527	z = 3.975	< 0.001***
Herbivory	Distance with EFNs	*B. intermedia*	Multiple linear regression	0.000021 ± 0.0000279	t = 0.753	0.467
	Distance without EFNs	*B. intermedia*		-0.0000337 ± 0.000051	t = -0.66	0.523

from 97 to 192 cm. These measurements provided a baseline for plant size before treatments, with no substantial structural asymmetry among individuals of the same species.

Considering leaf loss in *P. tomentosa*, the closer the distance to plants without EFNs, the greater the leaf loss, indicating an inversely proportional relationship (t = -2.237, p = 0.045, see Figure 2). However, the distance from plants with EFNs was not a significant predictor of this variable (t = 0.072, p = 0.944). For the growth rate of this species, no significant association was detected between the distance from plants with EFNs (t = -1.232, p = 0.242) and the distance from plants without EFNs (t = -0.430, p = 0.675).

Table 2 - Mean and standard error of each variable measured in *P. tomentosa* and *B. intermedia*.

Variable	Species	Mean	Standard Error
Leaf Loss	*P. tomentosa*	-6.27	2.37
	B. intermedia	-63	19.04
Growth Rate (cm)	*P. tomentosa*	13.93	3.98
	B. intermedia	4.6	1.75
Production of Young Leaves	*P. tomentosa*	1.8	0.84
	B. intermedia	4.53	1.83
Herbivory (%)	*P. tomentosa*	0.96	0.37
	B. intermedia	1.03	0.35

Regarding the production of young leaves in *P. tomentosa*, the distance to both plants with and without EFNs did not have explanatory power for this variable (z = -1.705, p = 0.088, for the distance from plants with EFNs, and z = 1.796, p = 0.072, for the distance from plants without EFNs). Likewise, for herbivory in this species, none of the distance variables were significant, and they did not explain the variation in herbivory among the study plants (t = -1.554, p = 0.146, for the distance from plants with EFNs, and t = 0.497, p = 0.629, for the distance from plants without EFNs).

For leaf loss in *B. intermedia*, neither the distance from plants with EFNs (t = -0.219, p = 0.83) nor the distance from plants without EFNs (t = -0.659, p = 0.522) was a significant predictor of leaf production in this species. Similarly, for the growth rate of this species, neither the distance from plants without EFNs (t = 1.398, p = 0.187) nor the distance from plants with EFNs (t = 0.261, p = 0.798) adequately explained this variable.

In contrast, the production of young leaves in *B. intermedia* was significantly explained by both distance variables (z = -2.976, p = 0.003, for the distance from plants with EFNs, and z = 3.975, p < 0.001, for the distance from plants without EFNs). An inverse relationship was found between the distance to EFN-bearing plants and the production of young leaves, with shorter distances favoring higher output. In contrast, greater distances from non-EFN neighbors enhanced young leaf production (Figure 1a-b).

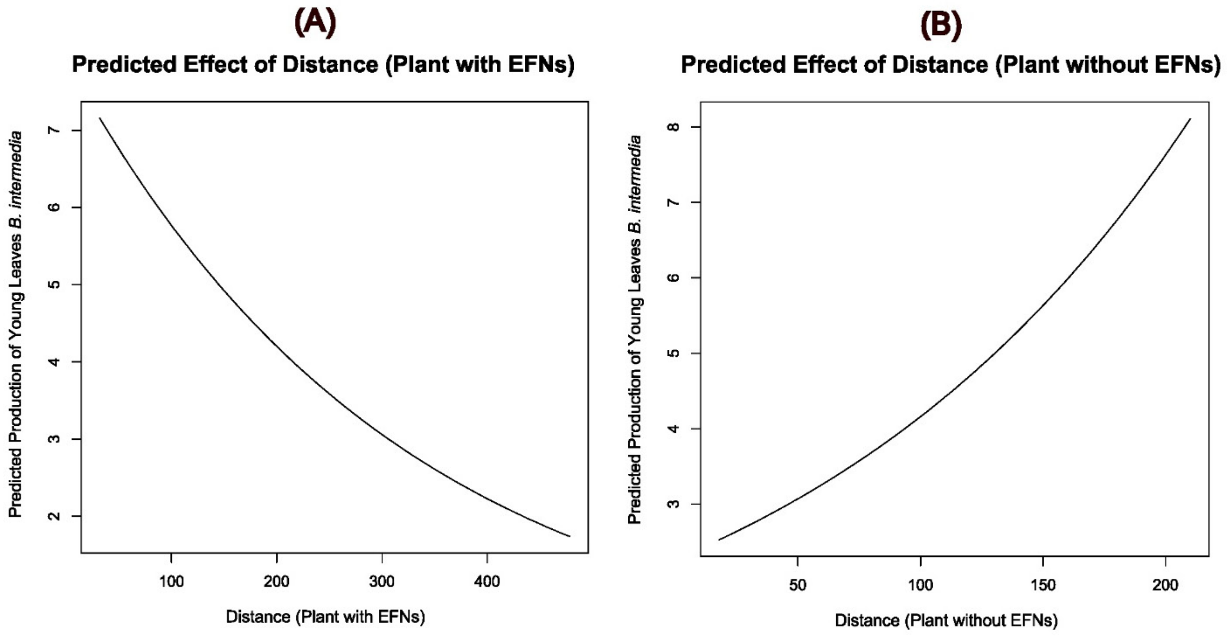

Fig 1. Predicted number of young leaves produced by *B. intermedia* as a function of neighbor identity and spatial arrangement. (a) Effect of distance (in cm) from neighboring plants with EFNs, holding the distance from non-EFN plants constant at its mean value. (b) Effect of distance (in cm) from neighboring plants without EFNs, while keeping the distance from EFN plants constant at its mean. Predictions are based on a zero-inflated negative binomial generalized linear model.

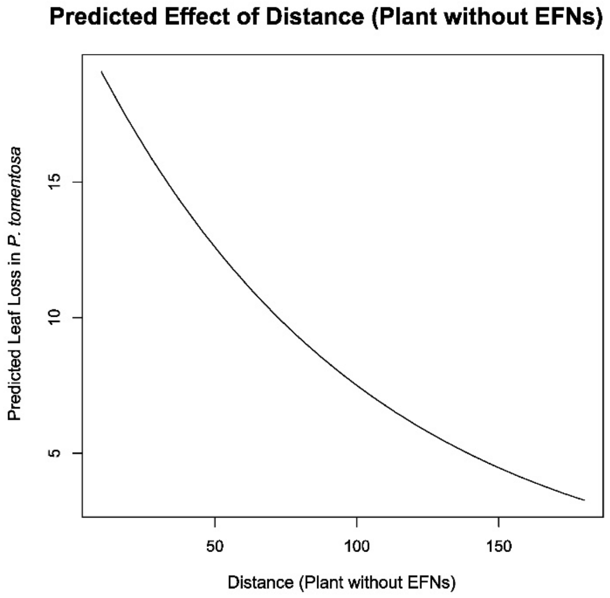

Fig 2. Predicted leaf loss in *P. tomentosa* in response to the distance (in cm) from neighboring plants without EFNs, with the distance from EFN plants held constant at its mean value. Predictions are based on a generalized linear model with a quasipoisson error distribution.

Regarding herbivory in this species, neither of the distance variables were significant, and they did not effectively explain the variation in herbivory among the study plants (t = 0.753, p = 0.467, for the distance from plants with EFNs, and t = -0.66, p = 0.523, for the distance from plants without EFNs).

When expressed as relative and percentage changes, model predictions revealed pronounced ecological effects associated with the spatial distribution of neighboring plants. In *B. intermedia*, increasing the distance to EFN-bearing neighbors from 1 to 2 meters led to a predicted reduction of

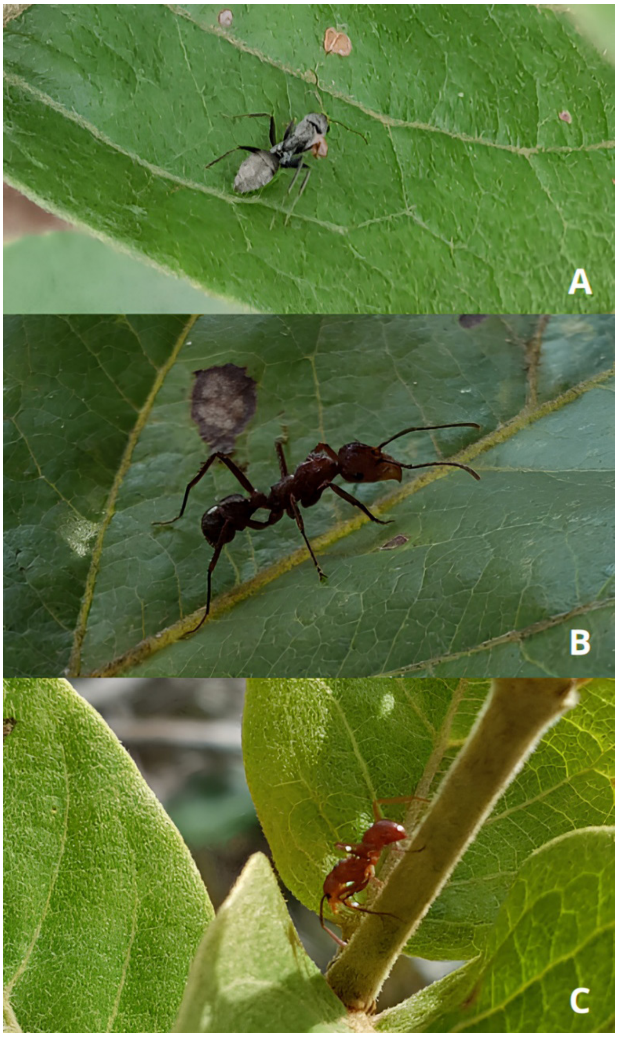

Fig 3. Frequent ant visitors recorded on the study plants: *Camponotus aff. blandus* (A), *Ectatomma brunneum* (B), and *Ectatomma tuberculatum* (C), all observed actively foraging during the sampling period.

1.57 young leaves, corresponding to a 27.2% decrease. In contrast, distancing from non-EFN neighbors over the same interval increased young leaf production by approximately 3.47 leaves, an 83.5% increase. For *P. tomentosa*, individuals located 2 meters from non-EFN neighbors exhibited a loss of 4.84 fewer leaves compared to those at 1 meter, representing a 64.5% reduction in leaf loss.

Discussion

In this study, we investigated whether facilitation interactions can occur via shared indirect biotic defenses (ant sharing) among plants with and without EFNs. We hypothesized that *B. intermedia* would exhibit lower leaf loss, increased growth rates, and higher young leaf production when in proximity to neighboring plants with EFNs, while *P. tomentosa* would show higher leaf loss, reduced growth rates, and decreased young leaf production when near neighboring plants without EFNs. For *P. tomentosa*, the leaf loss was inversely related to the distance from plants without EFNs. In other words, the closer the plants without EFNs are, the greater the leaf loss in this species, suggesting that *P. tomentosa* is sharing its ants with plants without EFNs. Distance from plants with EFNs had no significant impact. The growth rate and production of young leaves were not influenced by distance from plants with or without EFNs. For *B. intermedia*, the production of young leaves increased with proximity to plants with EFNs and with greater distance from plants without EFNs. Leaf loss and growth rate were not significantly affected by any of the distances in this species. None of the distance variables explained the variation in herbivory for both species. Thus, our hypothesis was only partially supported. These findings underscore that facilitative interactions via ant sharing are species-specific and may not equally benefit all neighboring plants.

The ant species that were commonly found on the plants in our study (*Camponotus aff. blandus*, *Ectatomma brunneum* and *Ectatomma tuberculatum*) are known for their aggressive behavior and active role in plant protection (Bächtold and Alves-Silva 2012; Melati and Leal 2018; Souza et al. 2024). For instance, *Camponotus aff. blandus* has been shown to deter herbivores by attacking both termites and butterflies that attempt to access floral resources, being responsible for over 50% of attacks in an experimental study with *Pseudabutilon coccinea* (Leal et al. 2006). Similarly, in *Qualea grandiflora*, a cerrado species with EFNs, *C. aff. blandus* − along with other *Camponotus* species − was among the most aggressive ants, accounting for most termite removals in simulated herbivory tests (Oliveira and Pie 1998). *Ectatomma* species, on the other hand, are also known for their dominance and high aggressiveness in interspecific interactions, further supporting their effectiveness as defenders of plants (Leal et al. 2006). These behavioral traits suggest that the ant species observed in our study are effective biotic defenders that are likely to contribute to reducing herbivory pressure on the focal plants.

To aid the interpretation of effect sizes, we translated the model estimates into biologically meaningful values. For *B. intermedia*, when the distance to plants with EFNs increased from 1 to 2 meters, the expected number of young leaves decreased by approximately 1.57 leaves, corresponding to a 27.2% reduction in leaf production. In contrast, increasing the distance to neighboring plants without EFNs over the same range resulted in an estimated increase of 3.47 young leaves, representing an 83.5% increase in young leaf production. Similarly, for *P. tomentosa*, increasing the distance to neighboring non-EFN plants from 1 to 2 meters led to a reduction of approximately 4.84 lost leaves, corresponding to a 64.5% decrease in foliar loss. These results indicate that proximity to non-EFN plants can negatively affect leaf dynamics in both species − by reducing young leaf production in *B. intermedia* and increasing leaf loss in *P. tomentosa*. These findings highlight the substantial ecological impact of neighboring plant identity when interpreted over realistic spatial scales in the field.

Our results differ from some of the few studies that investigated similar variables. For instance, facilitation mechanisms through EFNs were observed to increase ant species richness, visitation, biomass and reduce leaf herbivory in some studies (Moura et al. 2021; 2022; Moura and Del-Claro 2023; Staab et al. 2023). Our results also differ from those presented by Jezorek, Stiling and Carpenter (2011), in which *Opuntia* plants situated near *Chamaecrista fasciculata* (a plant that has EFNs) exhibited greater growth during the growing season. To the best of our knowledge, that study is the only one, beside ours, which investigated the effect of neighboring plants with EFNs on growth rates of main plants. Although we did not record detailed measures of ant activity or EFN productivity throughout the experiment, previous studies have established that *P. tomentosa* possesses EFNs at the base of young leaves and inflorescences, which remain active during the early stages of leaf development (Del-Claro, 1998). In our study, most focal individuals exhibited numerous young leaves and showed consistent ant attraction (personal observation), indicating that EFNs were active during the experimental period. Therefore, the conditions necessary for ant-mediated facilitation were likely present, supporting the ecological plausibility of our findings. Moreover, our results align with recent findings by Souza et al. (2024), who demonstrated that while EFN-bearing plants can influence the visitation patterns of protective ants to neighboring plants via ant sharing, such indirect interactions do not necessarily lead to reduced herbivory, suggesting that the benefits of this facilitation mechanism may be context-dependent and limited in some ecological settings.

Neighboring plants with EFNs had a positive association with young leaf production in *B. intermedia*, while nearby plants without EFNs had a negative production, suggesting that plants without EFNs are being facilitated by the proximity of plants with EFNs. However, the mechanism behind this facilitation should be further investigated.

A possible avenue for future research is the influence of soil characteristics and quality on leaf production results. Previous studies have suggested that areas with a higher abundance of plants with EFNs may also have more mutualistic ant nests, and the soil surrounding these nests is often enriched with organic debris, potentially increasing its fertility (Cammeraat and Risch 2008; Wagner and Nicklen 2010; Farji-Brener and Werenkraut 2014), which may affect the vegetative and reproductive performance of plant species. Although soil variables were not measured in this study, all observations were conducted within a contiguous area of *cerrado sensu stricto*, minimizing large-scale environmental heterogeneity. Nonetheless, small-scale differences in soil properties may still have contributed to the observed patterns, and future studies should include direct measurements of edaphic conditions to better distinguish between biotic and abiotic influences.

Given the potential for ants to defend plants with EFNs more efficiently under certain conditions, such as when plants have a higher abundance of EFNs, which attract aggressive ants in high numbers (Del-Claro et al. 2016, Calixto; Lange and Del-Claro 2018; Nogueira et al. 2020; Gijsman et al. 2021), a possible mechanism for the observed patterns could involve enhanced protection from herbivory. Specifically, the observed patterns refer to *B. intermedia* plants showing greater production of young leaves when in proximity to plants with EFNs, while the proximity of plants without EFNs increased the leaf loss in *P. tomentosa*. Since plants with EFN can potentially attract more ants and foster the establishment of ant nests nearby (Wagner and Nicklen 2010), we suggest that plants with EFNs might have assisted in reducing herbivore damage on *B. intermedia* when both plants were close, allowing for greater investment in young leaf production. Conversely, as *B. intermedia* moves further from plants with EFNs and their potential ant nests, it may be more exposed to herbivores (see Inouye and Taylor 1979), which could explain the observed reduction in young leaf production.

Interestingly, the relatively low levels of leaf herbivory observed in this study may themselves reflect the effective protective role of ants attracted by EFNs. Rather than indicating a lack of herbivore pressure, such low damage levels might result from a preventive deterrent effect by ant partners, consistent with previous findings in mutualistic ant-plant systems. Therefore, the absence of strong herbivory signals does not necessarily preclude the activation or relevance of indirect defenses. Future studies should explore thresholds of herbivore pressure required to induce jasmonate-mediated responses and examine how ant-mediated protection might buffer such induction.

While leaf herbivory did not show a significant relationship with distances to neighboring plants with or without EFNs for either plant species, it is important to note that this study did not collect data on floral herbivory, such as by Thrips, which are known to attack the flowers of *P. tomentosa* (Vilela et al. 2014). Although there was no significant effect of leaf herbivory in relation to distances, floral herbivory may have been influenced by the possible sharing of ants from EFN-bearing plants to non-EFN-bearing plants (Staab et al. 2023). This interaction could have affected floral protection through ant-mediated defense, despite the lack of a detectable impact on leaf herbivory. Future studies could explore the potential influence of soil properties and ant behavior in shaping these interactions, specifically investigating how spatial variability in ant nests and their foraging habits might affect both plants with and without EFNs.

In conclusion, our study explored facilitation interactions mediated by plants with EFNs among species in the Brazilian Cerrado, more specifically on *B. intermedia* and *P. tomentosa*. We found that while proximity to plants with EFNs positively influenced young leaf production in *B. intermedia*, it had no significant effect on growth rates in either species. Conversely, proximity to plants without EFNs increased the leaf loss in *P. tomentosa*. These results suggest that plants with EFNs may indirectly facilitate neighboring plants by enhancing soil quality or ant sharing. However, further investigation is needed to elucidate the exact mechanisms underlying these facilitative interactions and their broader ecological implications in plant communities. Since frost and fire events in the study area prevented the analysis of buds, flowers, and fruits, it is still necessary to investigate potential facilitation effects on reproductive structures. Although we did not quantify ant abundance or visitation rates, the observed patterns in vegetative traits are consistent with indirect facilitation mediated by shared ant species, as reported in similar systems (e.g., Jezorek, Stiling and Carpenter 2011; Moura et al. 2021, Moura and Del-Claro 2023; Staab et al. 2023), or may also be explained by better soil quality near ant nests. Thus, the absence of abundance data does not preclude interpretation of facilitative effects, but future studies could benefit from incorporating behavioral observations and more detailed assessments of ant activity. These findings emphasize the importance of considering the overall plant community structure in habitat management and conservation programs for degraded areas, helping environmental managers make informed decisions about species management to maximize restoration efforts.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. The authors gratefully acknowledge CAPES for financial support, Clube Caça e Pesca Itororó de Uberlândia for granting access to its ecological reserve, and the University of São Paulo for research infrastructure. One of the authors wishes to thank his family for motivational support during challenging periods, including the frost and fire events at the study site in 2021.

Funding statement

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

Competing interests

There are no competing interests to declare.

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