Arthropod-Plant Interactions (2024) 18:469–478
https://doi.org/10.1007/s11829-024-10049-6

ORIGINAL PAPER

Beyond nectar: exploring the effects of ant presence on the interaction of flower visitors of a rosette in grassland

Daniel A. Carvalho[1] · **Lucas M. Costa**[2] · **Izadora M. Silva**[3] · **Natália A. Amoza**[4] · **Sebastian F. Sendoya**[4] · **Adriano Cavalleri**[5]

Received: 14 September 2023 / Accepted: 5 February 2024 / Published online: 13 April 2024

Abstract
Plants and ants engage in diverse mutualistic interactions that contribute to their adaptive fitness. However, the presence of ants in flowers can generate conflicts between plants and pollinators. These interactions are little studied in temperate grasslands, despite the ubiquitous interactions between ants and plants in this region. In this study, we investigated how the presence and mobility of *Camponotus termitarius* (Emery) ants on *Eryngium chamissonis* Urb. affect the frequency of insect visitation on the flowers of this plant. We constructed contrasts and tested using generalized linear mixed models (I) whether the presence of any organism in the inflorescences decreases insect visitation, (II) whether it is really the presence of ants that decreases visitor interaction, and (III) whether the ant behavior has a greater effect on potentially reducing visits. We showed that the interaction of ants with *E. chamissonis* affected the number of visits to flowers, mainly reducing the frequency of the two main groups, bees and flies. These effects were consistent regardless of the ants' behavior, indicating that the mere presence of these insects on flowers can alter the frequencies of floral visitors. Our work is one of the first to report the effects of the interaction between ants and flowers in temperate grasslands in southern South America. The observed effects may go beyond the simple risk of predation and competition for resources, involving broader ecological implications for this ant–plant interaction, including a negative impact on the reproduction of *E. chamissonis*.

Keywords Subtropical grasslands · Floral ecology · Ant aggressiveness · Pampa · Ant–plant interactions

Introduction

Plants and ants maintain a great diversity of mutualistic and antagonistic interactions with each other (Hölldobler and Wilson 2008). From the perspective of the plant, these interactions are usually associated with the indirect defense of vegetative and reproductive organs against herbivores (Rosumek et al. 2009), although there is a great debate about the effects of ants on plants (Oliveira 1997; Ohm and Miller 2014; Ibarra-Isassi and Oliveira 2018). The protective action of ants, however, can simultaneously involve several types of conflicts for plants in terms of pollination (Ness et al. 2006; Sendoya et al. 2009; Assunção et al. 2014; Ibarra-Isassi and Oliveira 2018; Villamil et al. 2019), exerting an important effect on the adaptive fitness of plants. Indeed, plant visitors may differentiate plants by the presence of ants, telling them apart from other organisms or even differentiating among ant species (Sendoya et al. 2009; Ibarra-Isassi and Oliveira 2018). It is often reported that ants negatively affect plants when interacting with flowers by reducing the frequency,

Handling Editor: Abel Bernadou.

✉ Daniel A. Carvalho
dandr29@outlook.com

[1] Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil

[2] Departamento de Botânica, Instituto de Biologia, Universidade Federal de Pelotas, Pelotas, Rio Grande do Sul, Brazil

[3] Programa de Pós-Graduação em Botânica, Setor de Ciências Biológicas Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[4] Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Pelotas, Rio Grande do Sul, Brazil

[5] Instituto de Ciências Biológicas, Universidade Federal do Rio Grande - Campus Carreiros, Rio Grande, Rio Grande do Sul, Brazil

duration, or diversity of flower visitors, especially other insects (Lach 2008; Hansen and Müller 2009; Junker et al. 2010; Gonzálvez et al. 2012; Souza et al. 2020). This may be attributed to factors such as their mere presence and aggressive behavior combined with chemical traces (Cembrowski et al. 2014; Li et al. 2014) and may lead to less effective pollination (Tsuji et al. 2004). However, there is evidence that the presence of ants on flowers can also benefit the plant if these insects repel less effective pollinators (Gonzálvez et al. 2012), floral herbivores (Oliveira 1997; Bleil et al. 2011), and seed predators (Higginson et al. 2010) or even act as primary pollinators in a few situations (Ibarra-Isassi and Sendoya 2016).

In recent decades, many studies on the interaction between ants and plants have been carried out in tropical forests and savannas (Rico-Gray and Oliveira 2007; Cembrowski et al. 2014; Belém et al. 2020; De Sousa-Lopes et al. 2020). Such studies have demonstrated that these organisms can form intricate networks that can be influenced by climate, latitude, forest cover, and landscape heterogeneity (Rico-Gray and Oliveira 2007). Conversely, temperate grasslands, spanning about 35% of our planet's surface, have been notably overlooked in understanding ant–plant interactions (Shantz 1954; Juárez-Juárez et al. 2023). An example of such landscapes is the Pampa, a prevalent vegetative cover extending across southern Brazil, Uruguay, and parts of Argentina, characterized by grasses, a few trees, and herbs (Fidelis et al. 2009; Pillar et al. 2009; Andrade et al. 2023). *Eryngium* (Apiaceae) is a genus of rosette-shaped plants that are particularly rich and abundant in temperate regions, comprising a total of 220 species, 100 of which are native to the Americas (Calviño et al. 2008). Due to their prominent presence in the Pampa's landscape, these plants are used as food and shelter for a wide range of animals. Their complex architectural structure and dense inflorescences benefit a large number of arthropods (Campos 2010; Campos and Fernández 2011; Oleques et al. 2021). The overlapping leaves of some *Eryngium* species can form a water-harvesting rosette known to amplify arthropod diversity within ecosystems (Gonçalves-Souza et al. 2010; Fernandez-Barrancos et al. 2017). Our field observations indicate a large number of ants foraging on these plants. In particular, we have found several nests of *Camponotus termitarius* (Emery) ants close to patches of *Eryngium chamissonis* Urb. in the extreme south of the state of Rio Grande do Sul, Brazil. Ant visitation to this plant is likely driven by multiple factors, such as the presence of floral resources, insect trophobionts (e.g., treehoppers, whiteflies, or aphids), and the plant's suitability as a microhabitat. Therefore, it is expected that ant presence or foraging behavior has consequences for other organisms associated with the plant.

Our study aimed to evaluate whether the presence of *C. termitarius* ants on the inflorescences of *E. chamissonis* affects the number of insect visitation on flowers. We also determined whether the ant's effect on floral visitors may be derived from their physical presence only (in contrast to the presence of organisms other than ants) or from their behavior and mobility. We predicted that (I) plants with ants on their inflorescences would show a lower number of floral visitors when compared to plants without ants; (II) only the presence of ants and not other organisms on the inflorescences would have a negative effect on visitation. In other words, we expected the number of visits in plants with an organism other than ants to be higher when compared to plants with ants; and (III) the number of floral visitation in plants with active ants would be lower than in plants with dead pinned ants, suggesting that movement is an important visual cue for flower-visiting insects.

Materials and methods

Study site

This study was carried out between December 2022 and February 2023 in an area belonging to the Faculty of Veterinary Medicine of the Federal University of Pelotas, located in the city of Capão do Leão, Rio Grande do Sul (31° 80′ S–52° 41′ W). The predominant vegetation in this area is typical of the Pampa biome, including *E. chamissonis* and large nests of *C. termitarius*. This is a flat region with well-defined seasons and temperatures that can reach approximately 40 °C in the summer, as well as low rainfall, which is characteristic of this time of year. The study area is an occasionally flooded field, which is waterlogged in the winter and drier in the summer, typical of the regions south of the Coastal Plain of Rio Grande do Sul (Becker et al. 2007).

Study system

The plant *E. chamissonis* (Fig. 1a), known as Gravatá-do-banhado or Caraguatá (Fidelis et al. 2009), is restricted to flooded fields, usually forming dense clusters and conferring a typical appearance in moist areas (Joly 2005; Pillar et al. 2009). It is an erect rosette-shaped herb that stands out from other plants of genus *Eryngium* due to its larger and more robust size (Wanderley et al. 2005). It has rigid leaves with aculeate margins, and during the reproductive months (December to February), it produces dense inflorescences at the top of a rachis that can reach 4 m in height (Wanderley et al. 2005), which contain globular capitula of yellowish to light green colors with inconspicuous flowers (Cardozo et al. 2021; Oleques et al. 2021) (Fig. 1a, c, d). These plants in our study area are associated with *C. termitarius* ants (= *C. punctulatus* subsp. *termitarius*), which use the base of *E. chamissonis* leaves for building satellite nests, most likely

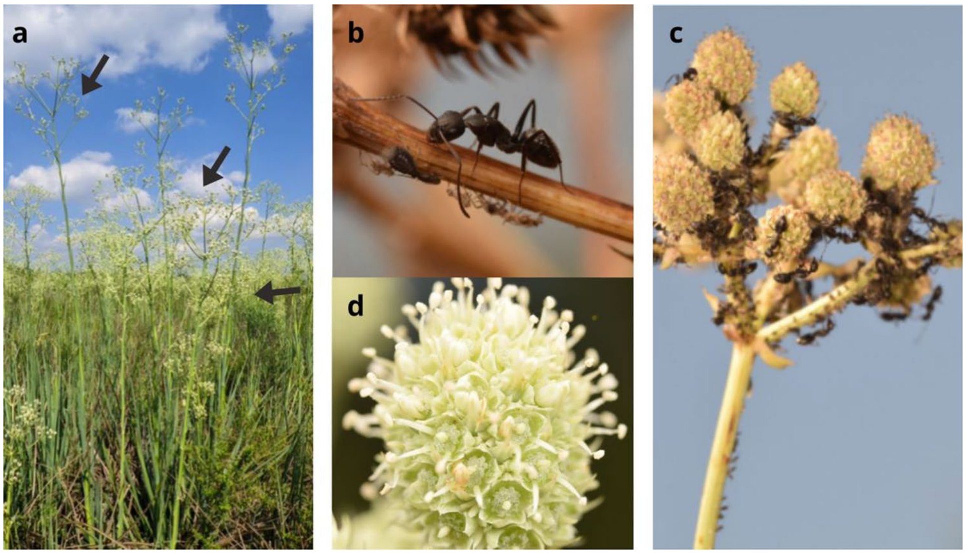

Fig. 1 Study system in Brazilian Pampa. **a** General view of the vegetation at the study site with the presence of *Eryngium chamissonis* in the reproductive period; arrows indicate their inflorescences. **b** *Camponotus termitarius* workers tending hemipterans on the inflorescences of *E. chamissonis*. **c** Workers of *C. termitarius* foraging on *E. chamissonis* inflorescences. **d** Globular flower head of *E. chamissonis*

as an adaptive strategy to environmental fluctuations caused by flooding (pers. obs.). These ants forage throughout the plant, including the inflorescences during the reproductive period, sometimes interacting with aphids (Fig. 1b). The pollinators of *E. chamissonis* remain unknown. Although *Camponotus* ants are often seen walking over its inflorescences, our observations suggest that they do not serve as primary pollinators of this plant. In fact, plants in the reproductive phase without ants were commonly observed in the study area, indicating that this interaction is facultative and further studies will test if *C. termitarius* can effectively pollinate *E. chamissonis*.

Experimental design

First, we established a total of 17 buffers, each with a radius of 10 m. These buffers were used in this study as experimental blocks, which were distanced from each other at intervals of no less than 30 m. In each block, we documented the occurrence of *E. chamissonis*, with and without active inflorescences (indicated by the presence of the inflorescence scape). Additionally, we recorded the number of *E. chamissonis* individuals with satellite *C. termitarius* nests in the vegetative sector of the plant. To test our hypotheses, we selected four individuals of *E. chamissonis* per experimental block, spaced at least 1 m apart, with inflorescences at the same phenological stage and a minimum height of 1.7 m. We defined as the same phenological stage those plants that presented open globular capitula. Any plant that was serving as a contact bridge for ants to reach the inflorescences of the selected plants in each block was pruned to avoid bridges for the ants to pass from the surrounding vegetation to the inflorescences of the selected plant. The selected individuals were randomly assigned to one of the following treatment groups: (I) inflorescence without ant presence, (II) inflorescence with active *C. termitarius* ants (i.e., plants where ants were foraging on the inflorescences at the time of selection), (III) inflorescence with dry dead *C. termitarius* ants that had been pinned, and (IV) inflorescence with another dry dead and pinned organism (*Ulomoides dermestoides* Fairmaire, Coleoptera: Tenebrionidae). For treatments III and IV, we attached eight *C. termitarius* workers and eight *U. dermestoides* individuals, respectively, on to the inflorescences for each observation session, ensuring that they were positioned in all cardinal and collateral directions. To prevent ant access to the inflorescences in treatments I, III, and IV, we applied the sticky resin Tanglefoot® (Tanglefoot Co., Grand Rapids, MI, USA) at the base of the inflorescences 24 h before the start of the experiment. Throughout this period, we also removed the ants in treatment I and any other associated insects from the selected plants' inflorescences. We applied a small dab of Tanglefoot® resin in treatment II, which did not inhibit the passage of ants, but controlled potential chemical or manipulative effects of the resin on floral visitors.

Observation and evaluation of floral visitors

In each block, the mounted treatments were observed by the same observer from December to February, with only one observation carried out per block during this period. For each plant, we counted the number of branches present in each inflorescence. Subsequently, we began the experiments by observing the floral visitation of insects for a period of 15 min per plant and registering the number of insect visitations on the inflorescences. During this time, we observed the insects from a distance of 1 m for 10 min, and in the remaining 5 min, we approached the plant to observe smaller and/or associated insects. Associated insects largely refer to small coleoptera and cockroaches that during our observations fed on the inflorescences and were not easily identified at a distance of 1 m. We considered any insect that touched the inflorescence to be a floral visitor (hence, it counts as a visit). When a given insect touched/landed on another branch of the same plant, we counted this interaction as a new visit. The floral visiting insects were grouped into the following major taxonomic groups: bees (Hymenoptera: Anthophila), flies (Diptera), wasps (Hymenoptera: Apocrita, excluding Formicidae and Anthophila), beetles (Coleoptera), cockroaches (Blattodea), and Other groups during the observation period. Due to the immense morphological variation of Diptera, in our observations, we counted those organisms with a morphology similar to the main representatives of the suborder Brachycera (Schiner) as flies. Those insects that could not be identified due to their fast flight and/or small size were allocated as 'Other groups'. All observations took place on sunny days between 10 a.m. and 3 p.m., totaling 17 h of observation. All treatments in the same experimental block were observed only once on the same day.

We performed three experimental comparisons within each block using different combinations of the selected plants. Our first experiment aimed to assess how the presence of any organism on the inflorescences influenced the floral visiting insect fauna. This was carried out by comparing the number of visits in treatment I with the number of visits in treatments II, III, and IV pooled together. In the second experimental comparison, we compared visitation between treatments III and IV to determine whether only ants (but not other insects of similar size) could influence the frequency of floral visitation by insects. The third experimental comparison aimed to determine whether ant mobility and foraging behavior affected the number of visits. In this case, we compared visitation between treatments II and III.

Statistical analyses

Premises

Considering the complexity of the study system, we verified whether the observed visitation to flowers was influenced by the number of plants in the reproductive stage in the block prior to the experimental comparisons. Generalized linear models assuming a negative binomial distribution of error were constructed for this purpose, using the number of floral visitations as a response variable and the total number of plants in the reproductive stage as a predictor variable. Since we did not identify significant relationships between these variables ($Z = 0.23$, $P = 0.817$, additional data are given in Online Resource Table 1), we did not consider the number of plants in the reproductive stage as a covariate in the subsequent models.

Testing our hypotheses

Experimental comparison data were analyzed using generalized linear mixed models (GLMMs). We used the Poisson distribution model, which was chosen based on the error dispersion and adequacy of the data in the models using the DHARma package (Hartig 2020). In these models, we compared the observed number of visitations of each group of insects between treatments. We used the visitation frequency of each group of visiting insects as the response variable and the treatments as fixed variables. The experimental block was taken as a random variable.

To facilitate the specific planned comparisons, we structured contrasts among the categorical predictor levels (treatment) before model fitting, following the methodology outlined by Crawley (2007). Three contrasts were constructed to encompass our specific planned experimental comparisons. The first contrast aimed to evaluate whether any organism attached to the inflorescences affected floral visitors (i.e., a contrast assuming positive values for treatment I without ant access and negative values for all other treatments). The second contrast aimed to assess the effect of *C. termitarius* on floral visitation against any other organism of similar size (i.e., a contrast assuming positive values for treatment IV with pinned *U. dermestoides* beetles and negative values for treatment III with pinned ants). The last contrast determined whether the behavior of live ants affected insect visitation (i.e., a contrast assuming positive values for treatment III with pinned ants and negative values for treatment II with live ants).

We built models for each category of the observed insect groups. We also built a model for the entire floral visitor dataset. All models followed the comparisons specified in the contrasts. We calculated the effect size for each comparison using the effect size package (Ben-Shachar et al. 2020). The modeling process was performed using glmer from the lme4 package (Bates et al. 2015). For other statistical inferences, we used likelihood comparisons via the Anova function from the Car package (Fox and Weisberg 2019) and graphical visualization with the ggplot2 package (Wickham 2016), all executed in R software version 4.2.2 (R Development Core Team 2023).

Results

After 1020 min of observation in 68 plant individuals, 2791 floral visits were recorded. The most frequently observed taxa were bees (42.8%), flies (37.9%), wasps (7%), and beetles (5.3%) (see Table 1 for more information).

Table 1 Number of visits to flowers of *Eryngium chamissonis* by each group of insects per experimental group

	All visits	%	Treatment I (without ants)	Treatment II (with access to ants)	Treatment III (with pinned ants)	Treatment IV (with pinned beetles)
Bees	1196	42.85	437	173	251	335
Flies	1059	37.94	327	239	188	305
Wasps	198	7.09	56	41	52	49
Beetles	150	5.37	45	26	43	36
Cockroaches	46	1.64	23	6	11	6
Other groups	142	5.08	37	26	49	30
All visitors	2791		925	511	594	761

Manipulation experiment

Our results demonstrated that plants without ants had a higher number of floral visits when compared to plants with any experimental organism (live ants, pinned ants, or pinned *U. dermestoides*). This result held for flies ($Z = 4.04$, $P < 0.01$, Fig. 2a), bees ($Z = 9.26$, $P < 0.01$, Fig. 2c), and cockroaches ($Z = 3.78$, $P < 0.01$, Fig. 2e), as well as when

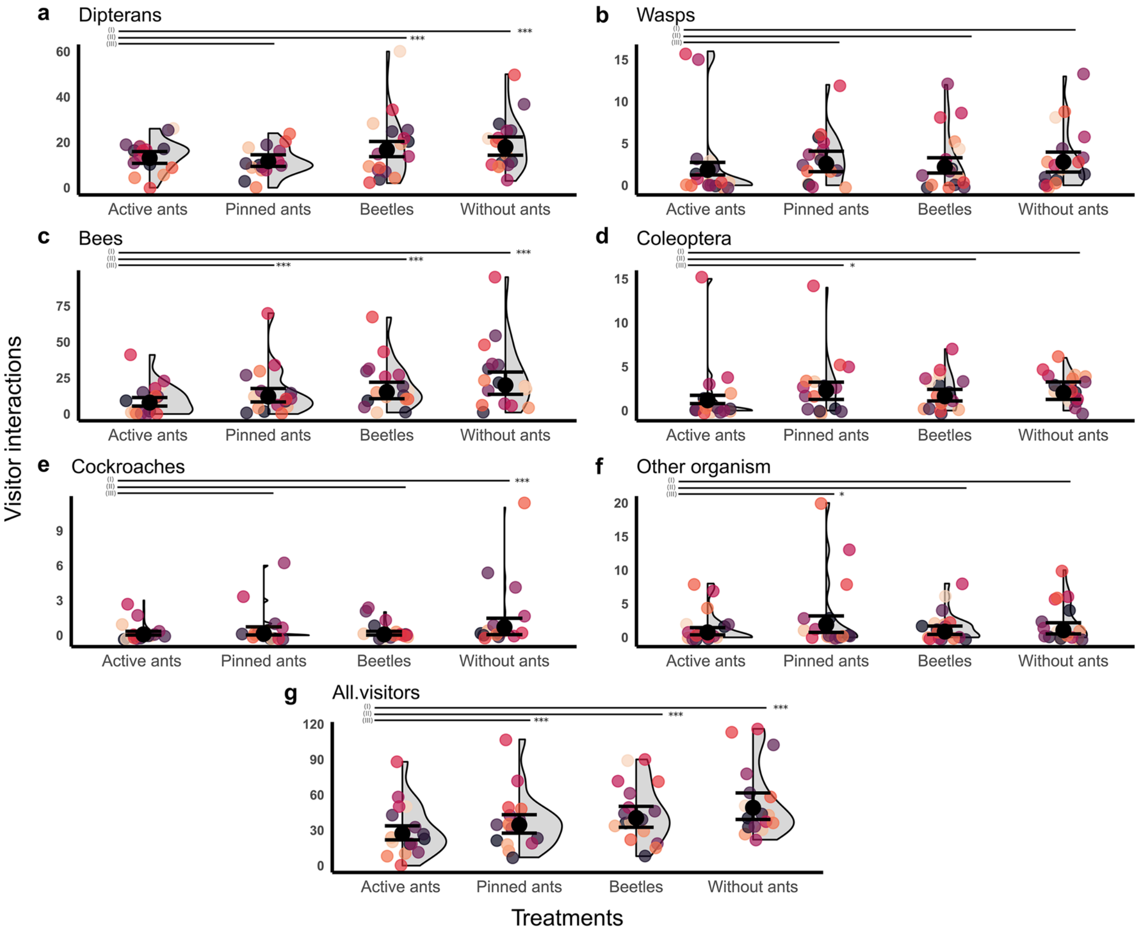

Fig. 2 Results presented by the models built to investigate the effects of the proposed treatments on *Eryngium chamissonis* floral visitors. Each colored circle represents one of the 17 experimental blocks. The upper bars refer to the following experiments carried out: (I) comparison between plants without ants with the other treatments (the first contrast—Any organism), (II) comparison between plants with pinned ants against those with the pinned beetle *Ulomoides dermestoides* (the second contrast—Ant presence), and (III) comparison between plants with live, pinned ants (the third contrast—Ant mobility). The variation in gray, throughout the plots, represents the probability density estimated via Kernel, that is, the highest frequency of results predicted by the model, for each treatment and the asterisks refer to the significance values presented by the model (***$P < 0.01$; *$P = 0.05$)

considering the whole group of visitors ($Z = 9.42$, $P < 0.01$, Fig. 2g; for additional details, see Online Resource Table 2). The remaining insect groups did not exhibit differences among the experimental treatments.

Regarding the specific presence of ants (compared with pinned *U. dermestoides*), we identified a lower number of visits to plants with pinned ants for bees ($Z = 6.06$, $P < 0.01$, Fig. 2c), flies ($Z = 4.00$, $P < 0.01$, Fig. 2a), and the whole insect community model (Fig. 2g). This result was not observed for the other insect groups. We also observed a negative effect on the total number of insect visits caused by ant activity (i.e., live ants) for the bee fauna ($Z = 6.30$, $P < 0.01$, Fig. 2c), beetles ($Z = 1.95$, $P = 0.05$, Fig. 2d), and other visitors ($Z = 1.94$, $P = 0.05$, Fig. 2g).

When examining the magnitude of effects observed in each experiment, the fly fauna was prominently affected by the presence of insects on inflorescences, especially by pinned ants (Fig. 3a). Conversely, bees showed a more pronounced response to the presence of live ants on plants compared to other contrasts (Fig. 3c), a trend also evident within the overall floral visitor community (Fig. 3g). In the case of cockroaches, the presence of any organism on the plants had a greater effect on this group of insects, causing them to visit the inflorescences less (Fig. 3d). Similarly, the same occurred for beetles and other groups, where the presence of live ants was the only factor that most influenced these groups of insects to visit the inflorescences less (Fig. 3e, f).

Discussion

Our study revealed that the presence of the experimental insects on *E. chamissonis* inflorescences had a detrimental impact on floral visitors. Specifically, we observed a

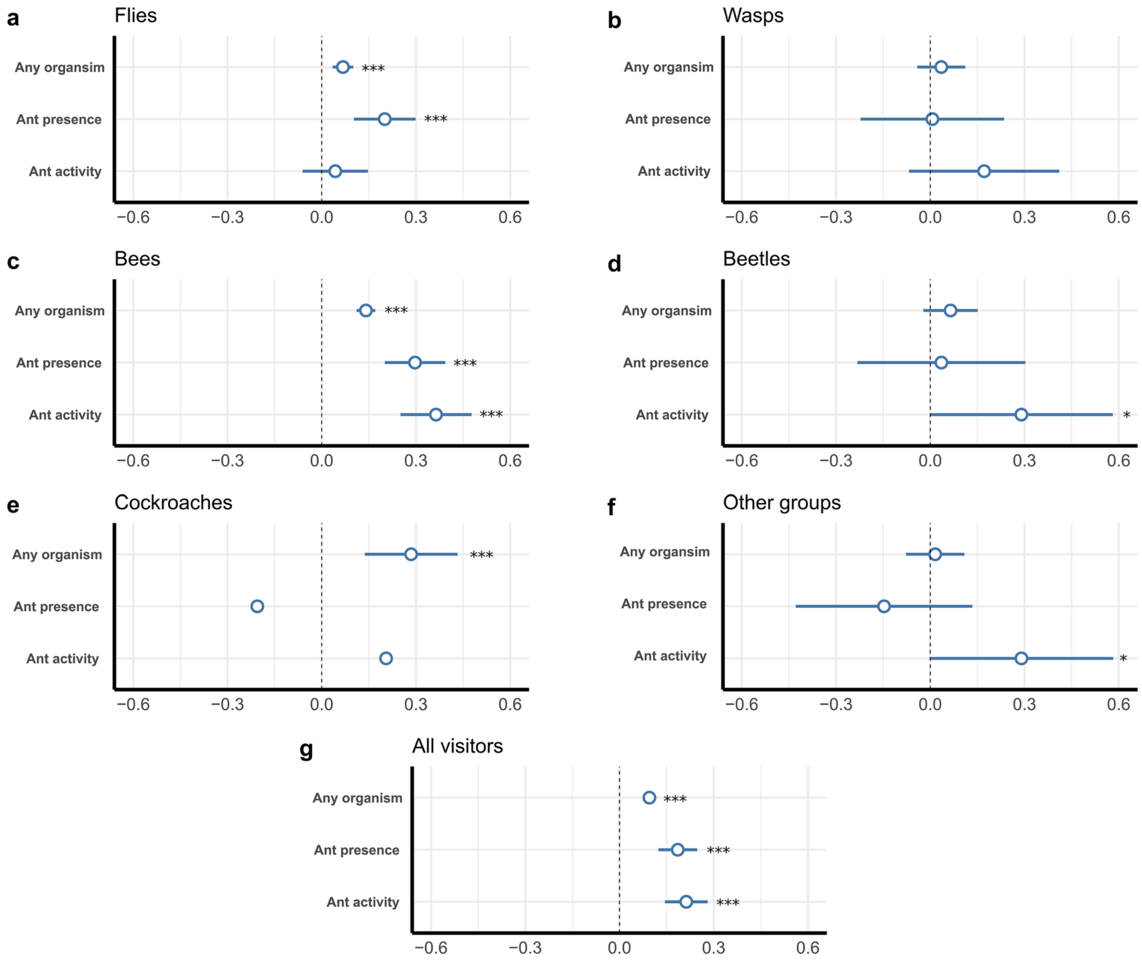

Fig. 3 Standardized coefficients (x-axis) for each constructed contrast used for hypothesis testing (y-axis) in GLMMs. Any organism—comparison between inflorescences without ant access versus inflorescences with live ants, pinned ants, and pinned *Ulomoides dermestoides*. Ant presence—comparison between inflorescences with ants and pinned *U. dermestoides*. Ant activity—comparison between inflorescences with live ants and pinned ants. The asterisks refer to the significance values presented by the model (***$P < 0.01$; *$P = 0.05$) and 95% confidence intervals are shown by blue bars (absent when intervals are extremely low)

prominent negative effect of ant presence on the floral visitation by bees and flies, compared to the presence of the beetle *U. dermestoides*. The interactions between flowers and floral visitors may depend on the presence of potential antagonists on the flowers (Romero et al. 2011; Benoit and Kalisz 2020). These antagonists can alter visitor behavior, either through aggressiveness or resource competition (Grether et al. 2009; Benoit and Kalisz 2020). In this context, we highlight that potential competition between *C. termitarius* ants and floral visitors results in a decrease in the interaction of these organisms with the inflorescences of *E. chamissonis*.

The influence of *C. termitarius* on *E. chamissonis* floral visitors was not similar for all visiting insects. Wasps, for example, were not influenced by the experiments proposed in this work. These predatory insects are highly aggressive and as such may not feel threatened by the presence of other insects on *E. chamissonis* inflorescences. However, the influence of *C. termitarius* on the other visitors may be derived from the behavior of these ants, since the presence of live ants negatively affected bee visitation. This effect was also observed in the visitation by beetles and other groups with no identification in the field, extending to the entire community of visiting insects. This effect is likely to be linked to the foraging and aggressive behavior of *C. termitarius*, which has been observed to consume floral nectar, attacking visitors and intimidating other visiting insects. Furthermore, when we observe the results of the effects of ants on the community, this directly reflects the essentially concentrated effect on bees and dipterans that together represented a large part of the floral visitor fauna of *E. chamissonis*. Therefore, these two groups may represent the insects that are most affected by the behavior and presence of *C. termitarius*.

Although the number of studies on ant–flower–floral visitor interactions in temperate regions is limited, previous research has demonstrated the impact of various ant species on flower-visiting insects in other geographical locations, specifically tropical and subtropical areas (Gonzálvez et al. 2012; Villamil et al. 2019; Belém et al. 2020; Souza et al. 2020). Ants can compete with floral visitors through exploratory competition (consuming floral rewards and reducing resource availability) and interference competition (directly excluding pollinators from flowers) (Cembrowski et al. 2014). Our findings indicate that *C. termitarius* influences floral visitors to *E. chamissonis* through both mechanisms, particularly affecting bees and flies, which accounted for over 80% of the visits.

Exploring the effects of *Camponotus termitarius* on floral visits to insects

An extremely generalist pollination is reported for the Apiaceae family (Lindsey 1984), including other *Eryngium* species that occur in grasslands in southern Brazil (see Oleques et al. 2021). We suggest that bees and flies might be the primary pollinators of *E. chamissonis*, mainly based on their high frequencies and behavioral strategies (see Herrera 1987; Rodríguez-Rodríguez et al. 2013). The small and numerous flowers in the inflorescences of this plant with exposed nectar and pollen facilitate its use by these organisms, which are hampered by the presence of the ant *C. termitarius*.

For bees, both the presence and activity of ants were factors in these insects reducing the number of visits to inflorescences. In contrast, fly visitation was only reduced by the presence of ants on flowers, but not by their activity. Although few studies have directly assessed the role of ant behavior in flower visitation, decreased visits by bees and flies have been frequently observed (Romero et al. 2011). Ants are considered important predators in many cases (Cuny et al. 2021), which even generate negative effects on the reproductive fitness of plants by driving away or preying on pollinators (Ohm and Miller 2014; Benoit and Kalisz 2020). The perceived risk of predation is well known to influence wildlife behavior (Palmer et al. 2017; Prugh et al. 2019), creating a “landscape of fear” where species alter their behavior or avoid areas with a higher perceived risk (Laundré et al. 2010). Some studies indicate that pollinators can identify the presence of a predator on flowers (e.g., Romero and Koricheva 2011; Assunção et al. 2014) and the bees and flies observed here might interpret the presence of ants as a threat.

In the case of flies, viewing an ant's silhouette appears to be the key to modifying their behavior when trying to interact with flowers. We observed that this group showed less interactions with plants that had ants attached than with *U. dermestoides*, although they also exhibited less interactions when the plants had any organism on the inflorescences. As for bees, one of their foraging strategies is the chemical detection of occupied flowers, both to avoid predators and to identify a potential available resource (Leonard et al. 2011; Li et al. 2014; Su et al. 2022). In this sense, we demonstrate that bees can also be deterred from visiting flowers due not only to the silhouette of ants but also to the presence of live ants, which can chemically make flowers less attractive. Ants have glands in their bodies that secrete substances detectable by bees (Cembrowski et al. 2014). Furthermore, ants can reduce nectar availability by acting as thieves while occupying inflorescences (Lach 2008; Irwin et al. 2010). Miner and Wilson Rankin (2023) demonstrated that bees modify their foraging behavior due to the presence of ants, but mainly because they are capable of chemically detecting the presence of these insects. Thus, our results might reflect a difference between bees and flies regarding the identification of potential predators in inflorescences. Bees reduce their visits to inflorescences with live ants because they quickly perceive these insects, both by chemical and visual signaling, with the latter perception being the dominant cue for flies (Agrawal et al. 2014).

Final considerations

Our data demonstrated that individuals of *E. chamissonis* with ants had less floral insect visitation, potentially arising from the visual or chemical detection of ant presence by visitors or their active behavior. Considering the overall impact observed, future studies should investigate whether the presence of ants reduces the pollination and reproductive success of *E. chamissonis*. In a broader context, the interaction between these plants and *C. termitarius* could affect not only plant reproduction but also the acquisition of food resources by floral visitors. Given the study site's characteristics, inflorescences may be among the few available floral resources for visiting insect fauna. It is worth noting that the similar floral morphology of Eryngium species suggests that associations with ants in other contexts may yield comparable results (Cardozo et al. 2021).

Furthermore, understanding that the effects of *C. termitarius* on *E. chamissonis* inflorescences result from competition through interference or exploitation (Cembrowski et al. 2014), limited to two groups of floral visitors, prompts the question of whether the presence of this species and its active behavior on flowers influence the structure of the floral visiting insect community. Examining how groups of organisms interacting with *E. chamissonis* inflorescences are morphologically organized for ant identification is essential. For instance, does the morphology found in flies and bees contribute to the accurate identification of ants on plants, leading them to visit other inflorescences in the absence of ants? Therefore, potential studies that evaluate this interaction from a community perspective may provide crucial insights into the potential effects of ants on the community of floral visiting insects and the possible adaptations of these organisms in their interaction with *E. chamissonis* and *C. termitarius*.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11829-024-10049-6.

Acknowledgements We thank Helena Romanowski and Viviane Ferro for laboratory support and other essential activities related to this research, the entire team of the Ant Ecology and Behavior Laboratory (LACEF/UFPel) for their assistance in the field expeditions, the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for promoting this research (process number 88887.667264/2022-00), and the Graduate Program in Animal Biology—UFRGS.

Author contributions AC, SFS, and DAC contributed to the conception and sampling design of the study. Material preparation and data collection were carried out by DAC, LMC, IMS, and NAA. The organization, data analysis, and preparation of the graphs were carried out by DAC, AC, and SFS. The first draft of the manuscript was written by DAC, and all authors commented on earlier versions of the manuscript. All authors read and approved the final manuscript.

Data availability Not applicable.

Declarations

Conflict of interest We declare that our work has no conflicts of interest. This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) by a Brazilian government agency.

References

Agrawal S, Safarik S, Dickinson M (2014) The relative roles of vision and chemosensation in mate recognition of *Drosophila melanogaster*. J Exp Biol 217(15):2796–2805. https://doi.org/10.1242/jeb.105817

Andrade BO, Dröse W, Aguiar CAD et al (2023) 12,500+ and counting: biodiversity of the Brazilian Pampa. Front Biogeogr. https://doi.org/10.21425/F5FBG59288

Assunção MA, Torezan-Silingardi HM, Del-Claro K (2014) Do ant visitors to extrafloral nectaries of plants repel pollinators and cause an indirect cost of mutualism? Flora 209:244–249. https://doi.org/10.1016/j.flora.2014.03.003

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Becker FG, Ramos RA, Moura LA (2007) Biodiversidade: Regiões da Lagoa do Casamento e dos Butiazais de Tapes, planície costeira do Rio Grande do Sul. Porto Alegre, Brazil, Brasília, DF

Belém SO, Guia BP, Campbell AJ et al (2020) Effects of ants (Hymenoptera: Formicidae) on flying insect visitor behaviour and fruit production in açaí palm (*Euterpe oleracea* Martius). Austral Entomol 59(3):612–618. https://doi.org/10.1111/aen.12458

Ben-Shachar MS, Lüdecke D, Makowski D (2020) "Effect size: estimation of effect size indices and standardized parameters. J Open Source Softw 5(56):2815. https://doi.org/10.21105/joss.02815

Benoit AD, Kalisz S (2020) Predator effects on plant-pollinator interactions, plant reproduction, mating systems, and evolution. Annu Rev Ecol Evol Syst 51:319–340. https://doi.org/10.1146/annurev-ecolsys-012120-094926

Bleil R, Blüthgen N, Junker RR (2011) Ant-plant mutualism in Hawai? Invasive ants reduce flower parasitism but also exploit floral nectar of the endemic shrub *Vaccinium reticulatum* (Ericaceae). Pac Sci 65(3):291–300. https://doi.org/10.2984/65.3.291

Calviño CI, Martínez SG, Downie SR (2008) The evolutionary history of *Eryngium* (Apiaceae, Saniculoideae): rapid radiations, long distance dispersals, and hybridizations. Mol Phylogenet Evol 46:1129–1150. https://doi.org/10.1016/j.ympev.2007.10.021

Campos RE (2010) *Eryngium* (Apiaceae) phytotelmata and their macroinvertebrate communities, including a review and bibliography. Hydrobiologia 652:311–328. https://doi.org/10.1007/s10750-010-0364-y

Campos RE, Fernández LA (2011) Coleopterans associated with plants that form phytotelmata in subtropical and temperate Argentina, South America. J Insect Sci 11:147. https://doi.org/10.1673/031.011.14701

Cardozo AL, Goldenberg R, Fiaschi P, Labiak P (2021) *Eryngium* (Apiaceae, Saniculoideae) in the state of Paraná, southern Brazil. Phytotaxa 507(1):1–50. https://doi.org/10.11646/phytotaxa.507.1.1

Cembrowski AR, Tan MG, Thomson JD, Frederickson ME (2014) Ants and ant scent reduce bumblebee pollination of artificial flowers. Am Nat 183:133–139. https://doi.org/10.1086/674101

Crawley MJ (2007) The R book. England, Chichester

Cuny MAC, Bourne ME, Dicke M, Poelman EH (2021) The enemy of my enemy is not always my friend: negative effects of carnivorous arthropods on plants. Funct Ecol 35(11):2365–2375

De Sousa-Lopes B, Calixto ES, Torezan-Silingardi HM et al (2020) Effects of ants on pollinator performance in a distylous pericarpial nectary-bearing Rubiaceae in Brazilian Cerrado. Sociobiology 67(2):173–185. https://doi.org/10.13102/sociobiology.v67i2.4846

Fernandez-Barrancos EP, Reid JL, Aronson J (2017) Tank bromeliad transplants as an enrichment strategy in southern Costa Rica. Restor Ecol 25(4):569–576. https://doi.org/10.1111/rec.12463

Fidelis A, Overbeck GE, Pillar VD, Pfadenhauer J (2009) The ecological value of *Eryngium horridum* in maintaining biodiversity in subtropical grasslands. Austral Ecol 34(5):558–566. https://doi.org/10.1111/j.1442-9993.2009.01959.x

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks CA

Gonçalves-Souza T, Brescovit AD, Rossa-Feres DDC, Romero GQ (2010) Bromeliads as biodiversity amplifiers and habitat segregation of spider communities in a Neotropical rainforest. J Arachnol 38(2):270–279. https://doi.org/10.1636/P09-58.1

Gonzálvez FG, Santamaría T, Corlett RT, Rodríguez-Gironés MA (2012) Flowers attract weaver ants that deter less effective pollinators. J Ecol 101(1):78–85. https://doi.org/10.1111/1365-2745.12006

Grether GF, Losin N, Anderson CN, Okamoto K (2009) The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biol Rev 84(4):617–635

Hansen DM, Müller CB (2009) Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. Biotropica 41(2):202–208. https://doi.org/10.1111/j.1744-7429.2008.00473.x

Hartig F (2020) DHARma residual diagnostics for hierarchical (multi-level/mixed) regression models. 2020. R package version, v. 320.

Herrera CM (1987) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50(1):79–90. https://doi.org/10.2307/3565403

Higginson AD, Ruxton GD, Skelhorn J (2010) The impact of flower-dwelling predators on host plant reproductive success. Oecologia 164:411–421. https://doi.org/10.1007/s00442-010-1681-6

Hölldobler B, Wilson EO (2008) The superorganism: the beauty, elegance, and strangeness of insect societies. Cambridge

Ibarra-Isassi J, Oliveira PS (2018) Indirect effects of mutualism: ant–treehopper associations deter pollinators and reduce reproduction in a tropical shrub. Oecologia 186(3):691–701. https://doi.org/10.1007/s00442-017-4045-7

Ibarra-Isassi J, Sendoya SF (2016) Ants as floral visitors of Blutaparon portulacoides (A St-Hil) Mears (Amaranthaceae): an ant pollination system in the Atlantic Rainforest. Arthropod-Plant Interact 10(3):221–227. https://doi.org/10.1007/s11829-016-9429-9

Irwin RE, Bronstein JL, Manson JS, Richardson L (2010) Nectar robbing: ecological and evolutionary perspectives. Annu Rev Ecol Evol Syst 41:271–292

Joly AB (2005) Introdução À Taxonomia Vegetal. São Paulo

Juárez-Juárez B, Dáttilo W, Moreno CE (2023) Synthesis and perspectives on the study of ant-plant interaction networks: a global overview. Ecol Entomol 48:269–283. https://doi.org/10.1111/een.13227

Junker RR, Bleil R, Daehler CC, Blüthgen N (2010) Intra-floral resource partitioning between endemic and invasive flower visitors: consequences for pollinator effectiveness. Ecol Entomol 35(6):760–767. https://doi.org/10.1111/j.1365-2311.2010.01237.x

Lach L (2008) Argentine ants displace floral arthropods in a biodiversity hotspot. Divers Distrib 14(2):281–290. https://doi.org/10.1111/j.1472-4642.2007.00410.x

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. Open Ecol J 3:1–7. https://doi.org/10.2174/1874213001003030001

Leonard AS, Dornhaus A, Papaj DR (2011) Flowers help bees cope with uncertainty: signal detection and the function of floral complexity. J Exp Biol 214(1):113–121. https://doi.org/10.1242/jeb.047407

Li J, Wang Z, Tan K et al (2014) Giant Asian honeybees use olfactory eavesdropping to detect and avoid ant predators. Anim Behav 97:69–76. https://doi.org/10.1016/j.anbehav.2014.08.015

Lindsey AH (1984) Reproductive biology of Apiaceae. I. Floral visitors to Thaspium and Zizia and their importance in pollination. Am J Bot 71(3):375–387. https://doi.org/10.1002/j.1537-2197.1984.tb12524.x

Miner MC, Wilson Rankin EE (2023) Bumble bee avoidance of Argentine ants and associated chemical cues. J. Insect Behav. 36:20–32. https://doi.org/10.1007/s10905-023-09815-w

Ness JH, Morris WF, Bronstein JL (2006) Integrating quality and quantity of mutualistic service to contrast ant species protecting *Ferocactus wislizeni*. Ecology 87(4):912–921. https://doi.org/10.1890/0012-9658(2006)87[912:IQAQOM]2.0.CO;2

Ohm JR, Miller TEX (2014) Balancing anti-herbivore benefits and anti-pollinator costs of defensive mutualists. Ecology 95(10):2924–2935. https://doi.org/10.1890/13-2309.1

Oleques SS, Souza-Chies TTD, Avila RS Jr (2021) Elucidating plant-pollinator interactions in South Brazilian grasslands: What do we know and where are we going? Acta Botanica Brasilica 35(3):323–338. https://doi.org/10.1590/0102-33062020abb0225

Oliveira PS (1997) The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). Funct Ecol 11:323–330. https://doi.org/10.1046/j.1365-2435.1997.00087.x

Palmer MS, Fieberg J, Swanson A et al (2017) A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecol Lett 20(11):1364–1373. https://doi.org/10.1111/ele.12832

Pillar VP, Müller SC, Castilhos ZMS, Jacques AVÁ (2009) Campos Sulinos: Conservação e Uso Sustentável da Biodiversidade. Brazilia

Prugh LR, Sivy KJ, Mahoney PJ et al (2019) Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol Conserv 232:194–207. https://doi.org/10.1016/j.biocon.2019.02.011

R Development Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rico-Gray V, Oliveira PS (2007) The Ecology and evolution of ant-plant interactions. Chicago United States.

Rodríguez-Rodríguez MC, Jordano P, Valido A (2013) Quantity and quality components of effectiveness in insular pollinator assemblages. Oecologia 73(1):179–190. https://doi.org/10.1007/s00442-013-2606-y

Romero GQ, Antiqueira PA, Koricheva J (2011) A meta-analysis of predation risk effects on pollinator behaviour. PLoS ONE. https://doi.org/10.1371/journal.pone.0020689

Romero GQ, Koricheva J (2011) Contrasting cascade effects of carnivores on plant fitness: a meta-analysis. J Anim Ecol 80(3):696–704. https://doi.org/10.1111/j.1365-2656.2011.01808.x

Rosumek FB, Silveira FAO, Neves FS et al (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. Oecologia 160(3):537–549. https://doi.org/10.1007/s00442-009-1309-x

Sendoya SF, Freitas AVL, Oliveira PS (2009) Egg-laying butterflies distinguish predaceous ants by sight. Am Nat 174(1):134–140. https://doi.org/10.1086/599302

Shantz HL (1954) The place of grasslands in the earth's cover of vegetation. Ecology 35(2):142–145. https://doi.org/10.2307/1931110

Souza CS, Baronio GJ, Weirich CE et al (2020) Ants climb plants because they cannot swim: ant presence on flowers during the flood season reduces the frequency of floral visitors. Ecol Entomol 45(6):1337–1345. https://doi.org/10.1111/een.12917

Su W, Ma W, Zhang Q et al (2022) Honey bee foraging decisions influenced by pear volatiles. Agriculture 12(8):1074. https://doi.org/10.3390/agriculture12081074

Tsuji K, Hasyim A, Nakamura H, Nakamura K (2004) Asian weaver ants, *Oecophylla smaragdina*, and their repelling of pollinators. Ecol Res 19(6):669–673. https://doi.org/10.1111/j.1440-1703.2004.00682.x

Villamil N, Boege K, Stone GN (2019) Testing the Distraction Hypothesis: do extrafloral nectaries reduce ant-pollinator conflict? J Ecol 107(3):1377–1391. https://doi.org/10.1111/1365-2745.13135

Wanderley MGL, Shepherd GJ, Melhem TS, Giulietti AM, (2005) Flora fanerogâmica do Estado de São Paulo. Volume 4. São Paulo

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York