RESEARCH ARTICLE

Alien vs. herbivore: ant-mediated plant defense as an option for biological control of leafcutter ants

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Abstract

Leafcutter ants are a major pest in vineyards in Argentina, but their damage to vine plants has not been sufficiently quantified. Biological control against leafcutter ants has not been successful so far. Sugary rewards can trigger ants to act as plant bodyguards against a wide range of herbivores. The Argentine ant *Linepithema humile* (Mayr) is a common invader of vineyards worldwide and has a strong preference for carbohydrates. In a first 10-week field experiment, we attracted *L. humile* ants to a group of plants using sugar feeders, while no feeders were used for a second group. Ant-excluded control plants were also deployed. We quantified the damage inflicted by the leafcutter ant *Amoimyrmex bruchi* (Forel) on potted vines with and without *L. humile* ants. In a second short field experiment, we evaluated the impact of *L. humile* on *A. bruchi* foraging through the quantification of foraging activity and the amount of transported material as a function of *L. humile* presence. We found that *A. bruchi* caused >90% leaf area reductions in plants without *L. humile*, while plants where the species was present were rarely attacked and leaves developed similar to those of ant-excluded controls. Active interaction with *L. humile* decreased *A. bruchi*'s foraging activity and the amount of material transported by it. This is the first report of *A. bruchi* as a vineyard pest and the first quantification of the damage inflicted by a leafcutter ant on organic grapevines. We demonstrate that *L. humile* defends vine plants against herbivore pests and artificial sugar sources boost can this defense service. The development of biological control strategies that include the ecological services of ants as natural enemies of herbivorous pests could become a useful tool in sustainable viticulture and horticulture.

Keywords *Amoimyrmex bruchi* · *Linepithema humile* · *Vitis vinifera* · Ant-mediated plant defence · Biological control · Sugar feeders · Grapevine

1 Introduction

Leafcutter ants (Formicidae: Attini) are dominant herbivores in Neotropical ecosystems and play a central role in nutrient cycling (Hölldobler and Wilson 2011). In an agroecological context, they can become important herbivore pests in a number of tropical and subtropical crops, including grapevine (Dagatti et al. 2019; Montoya-Lerma et al. 2012; Rosado et al. 2012). Biological control of leafcutter ants is challenging. Although experiments with entomopathogenic fungi and phorid flies showed promising results (de Britto et al. 2016; Folgarait et al. 2020; Goffre and Folgarait 2019), leafcutter ant control relies chiefly on pesticides and labor-intensive physical methods (de Britto et al. 2016). Leafcutter ant herbivory can be reduced by hemipteran-tending ants (Jutsum et al. 1981; Folgarait et al. 1994). These ants engage in a mutualism where they protect sap-feeding hemipterans against natural

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enemies in exchange for honeydew and extent their protective services to the host plant (by-product or indirect mutualism) (Rico-Gray and Oliveira 2007). Plant defense by ants has been studied over decades, and many studies suggest possible applications of this interaction in agriculture (Anjos et al. 2021; Carroll and Janzen 1973; Offenberg 2015; Way and Khoo 1992). Ants are important natural enemies of fruit fly larvae in coffee and fruit orchards (Eskafi and Kolbe 1990; Fernandes et al. 2012), and prey on lepidopteran and coleopteran pests in soybean, cotton, peanuts, and cauliflowers, among others (Agarwal et al. 2007; Baldwin et al. 2020; Vinson 2013). Tree-nesting weaver ants (*Oecophylla* sp.) are employed as biological pest control agents in tropical tree crops (Offenberg 2015; Thurman et al. 2019). Recent studies show that ant-mediated plant protection can also be encouraged by supplementation of sugar feeders that attract ants of various genera to trees in temperate apple and pear orchards (Parrilli et al. 2021; Pérez-Rodríguez et al. 2021; Offenberg et al. 2019; Schifani et al. 2020). This kind of conservation biological control supports and conserves natural enemy populations and could be a sustainable pest management tool in the future.

In the past, two species of leafcutter ants have been reported in Argentine and Brazilian vineyards: *Amoimyrmex striatus* and *Acromyrmex lobicornis* (Amatta et al. 2015; Dagatti 2015; Paris 2011; Rosado et al. 2012). In Chile, which also produces wine, leafcutter ants do not exist, probably due to the geographical barrier of the Andes mountains. Leafcutter ants damage vines by cutting all green plant parts, including flowers and leaves (Amatta et al. 2015). Repeated attacks are fatal for vine plants especially if plants are young (personal observation). Leafcutter ants are generalist herbivores that forage on an ample range of plant substrates including both monocots and dicots (Farji Brener and Ruggiero 1994). Grapevine herbivory might be opportunistic, a study by Dagatti et al. (2019) pointed out that in vineyards with cover crops *A. striatus* prefers monocots. The present study focuses on *Amoimyrmex bruchi*, a species that is distributed in Argentina and Bolivia (Cristiano et al. 2020) but has not been reported as a grapevine pest yet. *Amoimyrmex bruchi* is morphologically similar to *A. striatus*; in the light of the recent taxonomic changes in the *Amoimyrmex* genus (Cristiano et al. 2020), it appears possible that some of the *A. striatus* records correspond to *A. bruchi*.

The hemipteran-tending Argentine ant *Linepithema humile* is a common non-native ant species in vineyards worldwide (Daane et al. 2007; Mgocheki and Addison 2009; Westermann et al. 2016). This ant is native to the Paraná River watershed (Wild 2004), but it is non-indigenous in the wine-producing area in north-western Argentina, where we carried out the present study. *Linepithema humile* is characterized by high interspecific aggressiveness, activity, abundance, fast mass recruitment, and a very pronounced

preference for carbohydrates, such as honeydew excreted by hemipterans (Holway et al. 2002). Although *L. humile* does not damage grapes or vine plants directly, in viticulture it is infamous for its food-for-protection mutualism with vineyard mealybugs that can lead to mealybug outbreaks and interfere with biological control (Daane et al. 2007; Mgocheki and Addison 2009). On the other hand, it has been recognized that *L. humile*'s protective services can include the host plants and result in a benefit through herbivore reduction (Ludka et al. 2015; Stanley et al. 2013; Way et al. 1999). In 2011, a report described the aggressive behavior of *L. humile* against native leafcutter ants in northern Argentina (Paris 2011).

The present study aims to explore antagonistic and beneficial ant-plant interactions in a grapevine-based ecosystem through (i) the quantification of *A. bruchi* herbivory in grapevine with and without *L. humile* and (ii) the evaluation of the impact of *L. humile* on *A. bruchi* foraging patterns to explore the underlying mechanism of the potential herbivory mitigation (Fig. 1). We hypothesize that *A. bruchi* herbivory substantially damages vines and expect that *L. humile* presence lowers this damage and affects *A. bruchi*'s foraging in the field.

2 Materials and methods

2.1 Study site

Our study was carried out near Cafayate, Salta, Argentina (Fig. 2), situated in the Calchaqui valley at 1700 m above sea level. The valley is characterized by a temperate desert climate (rainfall <200 mm/year) which is ideal for grape and wine production. As leafcutter ants are managed with pesticides in local vineyards, we chose two sites adjacent to but outside the vineyards for our experiments (Fig. 2). In an initial visual scan, we georeferenced all *A. bruchi* colonies in our experimental sites. The colony size of mature colonies of the same leafcutter ant species is usually similar (Beckers et al. 1989). While there is no data available for *A. bruchi*, the closely related species *Acromyrmex striatus* forms colonies of approx. 10^3–10^4 workers (Nobua Behrmann 2014). Both sites had a history of extensive livestock grazing and had comparable *A. bruchi* colony densities (Table 1). Vegetation (e.g., *Cercidium praecox*, *Prosopis ferox*, *Acacia caven*, *Senna* sp.) of both sites was considered to be similar in the two most common vegetation layers (vegetation strata 0–15 and 15–150cm height), as Hutcheson's *t* test for Shannon diversity did not show significant variations in plant communities across 27 5m-by-5m squares (site 1:18 squares, site 2: 9 squares) during peak vegetation season (0–15-cm-height-stratum: $t = 1.71$, df = 74.35, $p = 0.10$; 15–150-cm-height-stratum: $t = 0.07$, df = 91.72, $p = 0.95$). To measure the impact of

Fig. 1 A Leafcutter ant (*A. bruchi*) herbivory on a grapevine plant. **B** Leafcutter ant herbivory on a grapevine plant with *L. humile* attraction treatment.
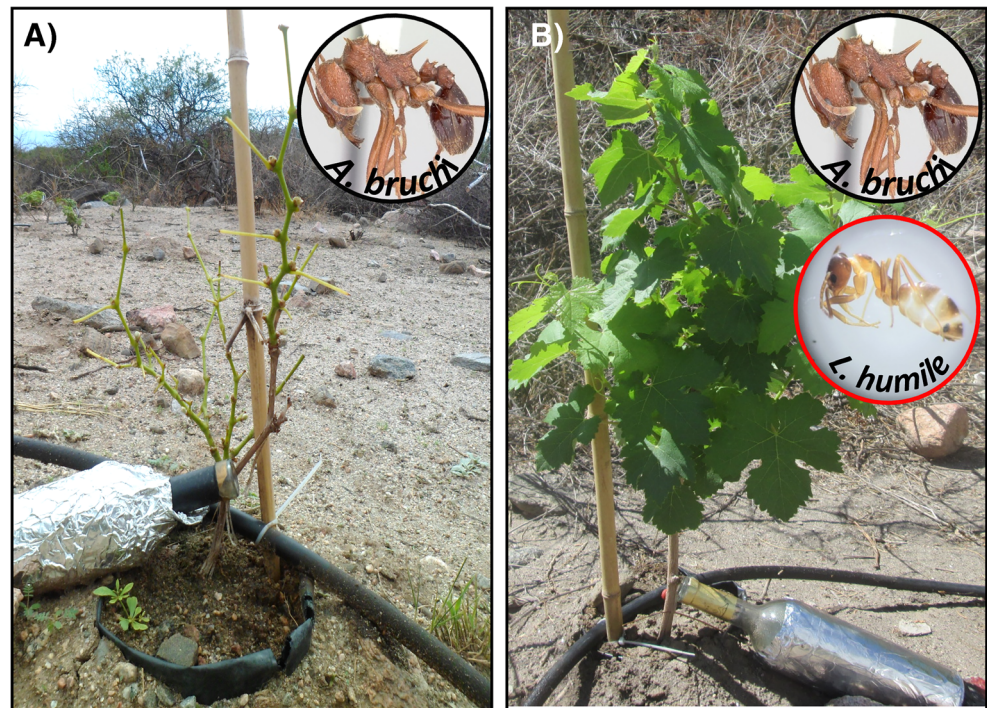
L. humile on *A. bruchi* foraging and grapevine herbivory, two field experiments were conducted.

2.2 Vine plant damage by *Amoimyrmex bruchi* and plant defense by *Linepithema humile*

Most field studies on ant-mediated plant defense either report observational data (Folgarait et al. 1994; Ludka et al. 2015) or use ant exclusion experiments (Janzen 1966; Jutsum et al. 1981; Koptur 1979; Stanley et al. 2013; Way et al. 1999). However, in the present study, both herbivores and plant bodyguards were ants; hence, we relied on ant attraction rather than exclusion to obtain treatments. In July 2015, 130 2-year-old vine plants (*cv. Torrontes*) were transferred from the field to 30 × 50 cm polyethylene flowerpots containing a mixture of local soil and mulch. All plants were pruned to one spur and were left to grow until the start of the experiment. Both experimental sites were fenced to prevent the entry of livestock, and

all *A. bruchi* colonies were marked (site 1: 18 colonies, site 2: 11 colonies; Table 1). In October 2015 (spring of the southern hemisphere), upon the experiment's onset, we selected a total of 18 colonies (site 1: 12 colonies, site 2: six colonies) and eight control spots (four in each site) (Fig. 2B). We selected mature leafcutter ant colonies with more than three entrance holes and with sufficient distance (> 5 m) among colonies to ensure independence among *A. bruchi* colonies with respect to *L. humile* activity (Bronstein and Lanan 2013). Five potted vine plants were implanted at surface level forming a circle with approximately 1 m distance between plants around each of the 18 colonies and eight control spots (Fig. 3). The circle had a diameter of approx. 2 m, distance from each of the five vines to the nest was approx. 1 m (Fig. 3).

Test colonies with their respective vine plants were assigned to two treatments following a randomized stratified design. One treatment received sugar solution feeders to attract *L. humile* to the plants (treatment Ab + Lh, N = 9, Fig. 3B), while the other received empty feeders (treatment Ab, *N* = 9, Fig. 3A). Additionally, a control treatment excluding all ants was deployed applying non-toxic insect glue (CeroPestes Hormiga, Sanipro SRL, Buenos Aires, Argentina) on the upper margins of the flowerpots of five vines with empty feeders (control treatment, *N*= 8, Fig. 3C). The glue was renewed every month to maintain its properties over time. Vines of the control treatments were not placed around a LCA nest, like in the other treatments. For all treatments, we planted the five vines in a circle with 1 m among plants and 2 m circle diameter. Generally, treatments were separated by at least 5 m from each other.

Table 1 Site information. Sites as per Fig. 2.

	Site 1	Site 2
Perimeter (m)	255	202
Area (m²)	3555	2536
Amoimyrmex bruchi colonies	18	11
Nest density per hectare	50.63	43.38
Amoimyrmex bruchi colonies used in the study	12	6

Fig. 2 A Study sites and general location of the area in Argentina and the region. **B** Detailed view of study sites showing *A. bruchi* colonies (all circles) and experimental treatments (filled circles = Ab + Lh, open circles = Ab, squares = No-ant controls. Note that the real distance between sites 1 and 2 has not been kept on the lower map. Ab = *Amoimyrmex bruchi*; Lh = *Linepithema humile*. See main text for details on how treatments were achieved.
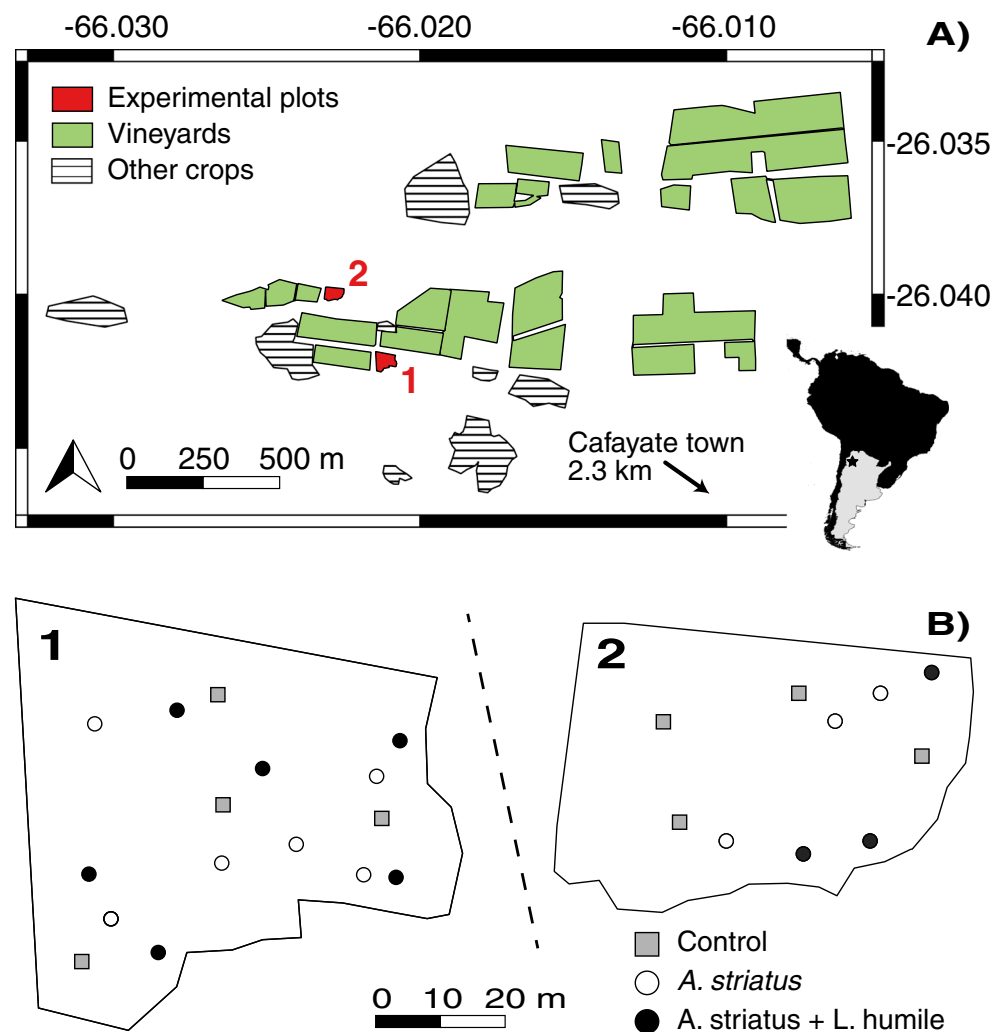
The plants were irrigated twice per week for 1 h with rainwater using drip irrigation (CORONA 2L/h, EURODRIP, Inofyta, Greece). Drip lines were painted with insect glue to prevent the ants from using them as "highways" to move between the plants. We measured the leaf surface fortnightly for 10 weeks by taking photos of all the leaves on all plants between October and December 2015. Photos were taken perpendicular to the leaf surface and included a scale in every picture. Images were processed to quantify the surface of each leaf using the software ImageJ (available at https://imagej.nih.gov/ij/). Feeders, 750-ml glass bottles containing 25% sucrose solution covered with cotton, dispensed artificial nectar to the ants (Reierson et al. 1998) of treatment Ab+Lh. We placed the feeders on the ground, next to the plant. To avoid high temperatures inside the feeders, we wrapped bottles in aluminum foil.

Linepithema humile activity on feeders was monitored on three occasions. For this, we replaced glass-bottle-feeders with preweighed tube-feeders (50-ml Falcon tubes filled with 25% sucrose solution). The tube-feeders were weighed before (initial weight) and after spending 24 h in the flowerpots (final

weight). We used additional, ant-excluded tube-feeders to quantify evaporation (evaporation weight). A single *L. humile* ant is known to consume 0.3 μL of sugar solution per visit (Reierson et al. 1998; Rust and Hooper 1998), equivalent to a weight of 0.33 mg (density of 25% sugar solution: 1104 g / mL). Therefore, the number of visits was calculated as:

L.humile visits

$$= \frac{(\text{initial weight} - \text{final weight} - \text{evaporation weight})}{0.00033\ g}$$

2.3 *Amoimyrmex bruchi* foraging

In a second experiment, we evaluated if *A. bruchi* foraging simply deviated from vine plants of the Ab+Lh treatment, or if *L. humile* affected *A. bruchi* foraging in a more general way, e.g., in terms of forager activity and transported material. For this, the beforementioned 18 *A. bruchi* colonies used for the Ab and Ab + Lh treatments were sampled during maximum

Fig. 3 General scheme of experiment 1. **A** Treatment Ab, five vines planted adjacent to an *A. bruchi* colony (ant in circle), with free access for all ants, and empty feeders (clear bottles). **B** Treatment Ab + Lh, five vines planted adjacent to an *A. bruchi* colony (ant in circle), with free access for all ants, and sugar feeders (filled bottles) to attract *L. humile* (filled, red ant). **C** Treatment control, five ant-excluded vines with empty feeders. The distance among vines and the distance between each vine and the nest was approximately 1 m.
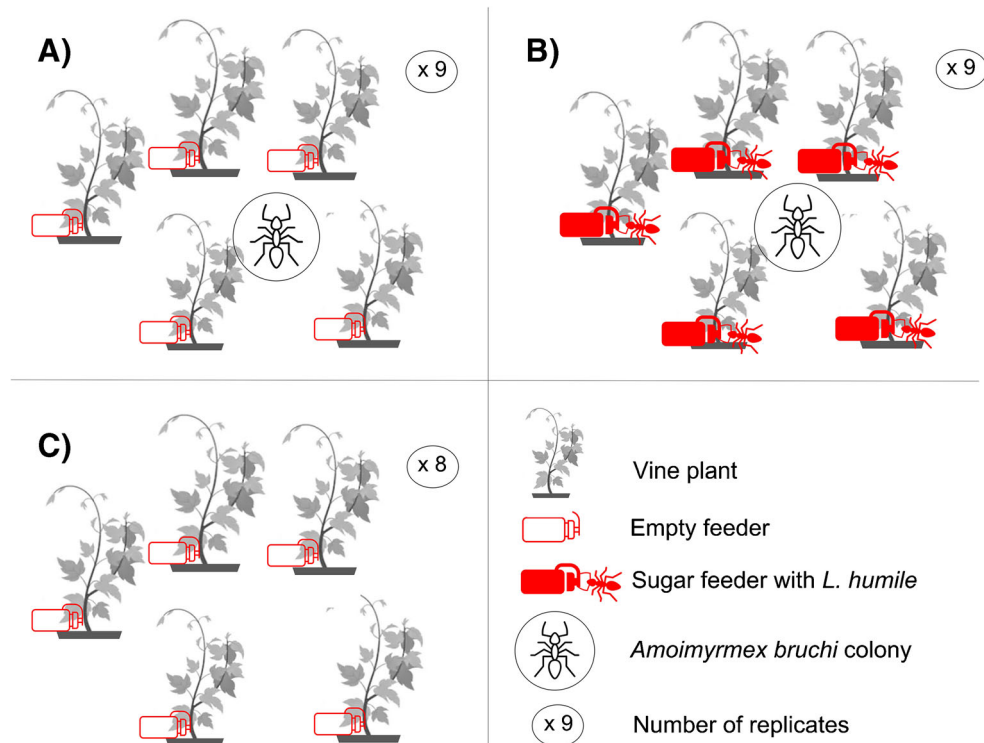
A. bruchi activity on three occasions between October 2015 and February 2016. The most active foraging trail of each colony was selected and traced until ants dispersed after approximately 5–15 m. We recorded for 5 min all ants passing an imaginary point on a foraging trail at a 1 m distance from the nest entrance and counted the number of transported pieces on this foraging trail for 10 min. We also recorded if the sampled foraging trail was intercepted by *L. humile* at the moment of data collection, i.e., if there was any interaction between *A. bruchi* and *L. humile* while sampling.

2.4 Statistical analysis

Treatment effects on the average leaf area per plant between October and December were analyzed using a two-way repeated-measures ANOVA. Similarly, *L. humile* activity on both sites was compared with a two-way repeated-measures ANOVA. Deviations from sphericity were quantified and corrected using Greenhouse and Geisser's epsilon ($\varepsilon = = 0.42$ and 0.76, respectively). Foraging data (activity and transported pieces) of *A. bruchi* was log-transformed to obtain normal distributions. We used two-way ANOVAs to detect treatment effects (Ab + Lh, Ab) and effects of *L. humile* interaction. Multiple comparisons were performed using Sidak's test. Data were tested for normality using Shapiro-Wilks test. The analyses were performed with GraphPad Prism (GraphPad Prism 8.4.2, LaJolla, CA, USA).

3 Results

At the beginning of the experiment, in October, the plants of all treatments had low leaf areas. By November, however, leaves had visibly developed in the plants with sugar feeders (Ab + Lh) and in ant-excluded controls, while the leaf area of Ab treatment plants remained small due to the grazing by leafcutter ants. This difference was even greater on the following sampling date (end of November) and then remained constant until the end of the experiment. At this point (end of December), plants of the Ab + Lh treatment had 670 ± 189 cm^2 (mean ± SD) more leaf area than plants without sugar feeders in the Ab treatment, which equals a reduction in herbivory of 93% in plants with *L. humile* attraction (Fig. 4). The observed treatment effects were highly significant ($F_{2,\ 23} = 14.54$, $p < 0.001$) (Fig. 4).

Sugar feeders received approximately 30,000 *L. humile* visits per day, with no differences between sites ($F_{1,\ 7} = 1.45$, $p = 0.27$) or dates ($F_{2,\ 14} = 2.76$, $p = 0.12$) (Table 2). *Linepithema humile* was the only ant species observed on the sugar feeders.

The foraging of *A. bruchi* ants was significantly affected by *L. humile* interaction with the evaluated *A. bruchi* foraging line, but not by the nominal treatment used (i.e., with/ without sugar feeder). Thus, *A. bruchi* foragers of both treatments (Ab and Ab + Lh) transported 65% fewer pieces ($F_{1,\ 26} = 5.12$, $p = 0.032$) and had 64% fewer individuals on the trail ($F_{1,\ 24} = 7.98$, $p = 0.009$) when *L. humile* workers were interacting with

Fig. 4 Leaf area of grapevine plants between October and December (spring to early summer of the southern hemisphere) in different ant treatments. Ab (grey bars): Free access for all ants; Ab + Lh (black bars): Free access for all ants with sugar feeders attracting *L. humile*; Control (white bars): Ant exclusion. Bars are mean values (± SD) of 9 replicates (consisting of 5 plants each) of Ab and Ab + Lh treatments, and 8 replicates of the control treatment. Letters represent statistical differences at a significant level of $\alpha = 0.05$. Treatments as per Fig. 2.
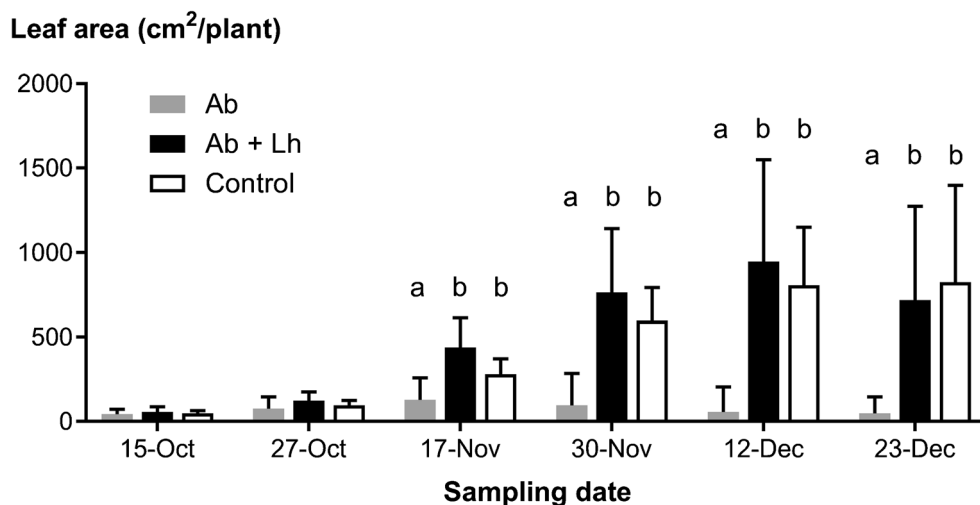
the trail (Fig. 5A, B) than when no interaction occurred. No such differences were observed between the nominal treatments themselves (number of foragers: $F(1, 24) = 0.3154$, $p = 0.58$; Transported pieces: $F(1, 26) = 1.416$, $p = 0.25$; Fig. 5).

4 Discussion

Considering our results in light of the proposed hypotheses, we confirm that leafcutter ants can cause great damage to grapevine plants and illustrate how *L. humile* acts as a plant bodyguard who greatly reduces this damage in plants that offer sugary rewards, i.e., sugar feeders. Apart from this direct bodyguard service, *L. humile* also impacted *A. bruchi* foraging in more general terms throughout the whole experimental area.

4.1 *A. bruchi* damage to plants

Vineyard managers control leafcutter ants thoroughly with reiterated pesticide applications or physical methods, in consequence, it is difficult to obtain quantifications of leafcutter ant damage under "natural", i.e., unmanaged, conditions. Amatta et al. (2015) estimated that leafcutter ants cause approx. 6% damage to leaves and inflorescences in

commercial vineyards with conventional pest control in San Juan, Argentina. The present study is the first report of *A. bruchi* as a grapevine pest and the first to quantify the impact of leafcutter ants on grapevine without pest control against these ants. The observed leaf damage was high: by the end of the experiment, the average plant without *L. humile* protection had 93% less leaf area than plants with *L. humile* and 94% less than completely ant-excluded control plants. During the experiment, some, but not all, defoliated plants budded again and were defoliated again by leafcutter ants. Although we did not continue our observations after the end of the experiment, these continued attacks might eventually lead to the plant's death. In other perennial crops such as the Argentine willow (*Salix nigra*), *Acromyrmex lundii* leaf damage has recently been estimated to be between 80 and 100% within 85 days after plantation (Jiménez et al. 2021); and citrus farmers estimated losses due to foraging by *Atta* and *Acromyrmex* ants up to 30% in new seedlings despite conventional pest management practices (Cherrett and Jutsum 1983). However, we advise that our results need to be considered with caution. Our experimental set-up aimed to test the defense potential of *L. humile*; hence, we used a scenario where leafcutter ant herbivory was likely to occur. Even if leafcutter ants do not necessarily prefer the closest plants (Cherrett 1968; Rockwood and Hubbell 1987), it is probable that a palatable

Table 2   Number of *L. humile* visits to sugar feeders placed on experimental plants of the Ab + Lh treatment during 24 h. Treatments and study sites as per Fig. 2.

Date	Site 1 Mean ± SD (N)	Site 2 Mean ± SD (N)	Total Mean ± SD (N)
11-Nov	25 561.85 ± 15 233.89 (6)	40 150.97 ± 15 818.04 (3)	30425 ± 16149.55 (9)
18-Nov	23 057.57 ± 14152.15 (6)	37 393.32 ± 17 714.22 (3)	27836 ± 15968.84 (9)
24-Nov	31 781.4 ± 18 280.87 (6)	41 245.97 ± 9239.36 (3)	34936 ± 15893.55 (9)

Fig. 5 Impact of *L. humile* interacting with the foraging lines of *A. bruchi* colonies of the Ab and Ab + Lh treatments. **A** Number of *A. bruchi* foragers on one foraging trail in the course of 5 minutes. **B** Number of pieces transported on one *A. bruchi* foraging line in 10 min. Bars are mean values (± SD) across all sampling dates (*n* = 9). Different letters indicate statistical differences at a significant level of α = 0.05. Treatments as per Fig. 2.
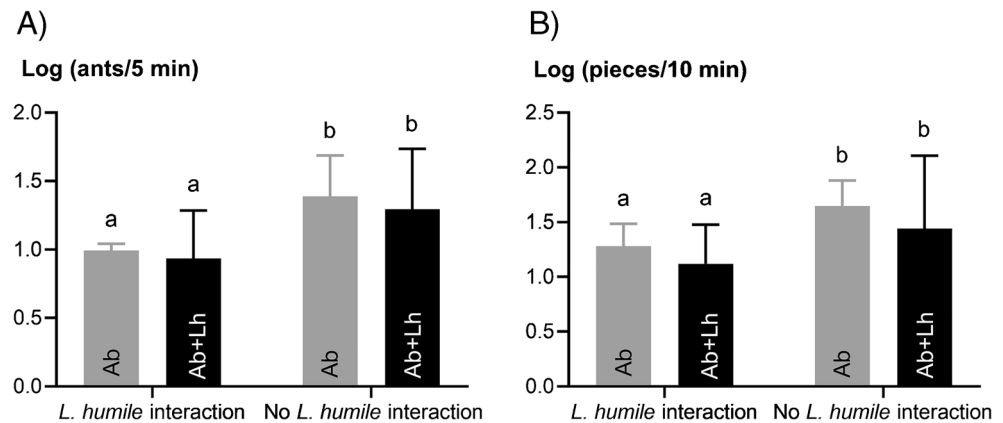
plant in direct vicinity to a leafcutter ant colony is discovered and cut. This might contribute to a potential overestimation of leafcutter ant herbivory. In vineyards, not all ant colonies are located so close to the vine plants, and ants in our study might have been particularly attracted to this new palatable resource.

4.2 Plant defense by *L. humile* and the role of sugar feeders

The present study clearly shows that *L. humile* can repel *A. bruchi* ants from vine plants and greatly reduce their herbivory. Given that vine plants were placed in direct proximity of leafcutter ants' nests, it is very impressive that plant defense was effective over the complete duration of the experiment (10 weeks). This is a promising result for vine-growers in this region, especially since the experiment was conducted during the spring when vines are especially vulnerable to defoliation by leafcutter ants. Although these ants forage on vines throughout the entire vegetative cycle, the greatest damage might occur during the spring when the ants forage on the inflorescences and young leaves (personal communication from local vine growers). Interestingly, autumn, winter, and spring are dry seasons in Argentina's wine-producing areas, marked by scarce precipitations and very limited vegetation. Vineyards are irrigated throughout the year; in spring, they are the first green vegetation within the natural Monte desert which is very attractive to leafcutter ants.

It is widely recognized that ants can act as bodyguards of plants in exchange for nutritional rewards or shelter, and several publications describe ant-mediated plant defense against leafcutter ants. *Dolichoderus attelaboides* and *Azteca alfari* ants deterred or removed individuals of *Atta laevigata* and *Atta cephalotes* from trees in Brazil and Venezuela (Leston 1978; Michelangeli 2006; Vasconcelos and Casimiro 1997). *Azteca* sp. and *Dolichoderus bidens* deterred *Atta cephalotes* leafcutter ants from defoliating citrus trees in Trinidad (Jutsum et al. 1981); and *Camponotus blandus* was reported as a biotic defense against *A. striatus* of trees and shrubs in a forest reserve in Argentina (Folgarait et al. 1994). Interestingly,

Amazonian indigenous communities were reported to use *Azteca* ants to repel leafcutter ants (*Atta* sp.) from their crops in Brazil (Anderson and Posey 1985). Ant-mediated defense against herbivores is not uncommon, but our study is the first to provoke this interaction against leafcutter ants. On the other hand, a study by Rezende et al. (2021) showed that extrafloral nectaries of *Inga* trees function as natural sugar feeders in coffee plantations which eventually led to enhanced biological control and bigger fruit size.

Sugar feeders readily attracted *L. humile* to vine plants. Feeders received roughly 30,000 *L. humile* visits per day, which is in line with numbers reported from invaded Californian vineyards (Daane et al. 2006). Sugar consumption remained stable over the three sampling dates. This is a promising result, as it suggests that ants did not lose interest in feeders over time and continuously forage on sugar. It is known that *L. humile* has a strong preference for sugar throughout the entire year, although the sugar content of their diet can vary depending on the nutritional needs of the colony (Rust et al. 2000; Abril et al. 2007). While sugar feeders can be attractive to other ants, *L. humile* was the only ant observed on the feeders, which can be explained by probably due to the dominance of this species which readily outcompetes other ants (Holway et al. 2002; Human and Gordon 1996).

Two recent publications evaluated the provision of artificial sugar sources to attract ants as plant biological control agents in apple and pear orchards (Offenberg et al. 2019; Schifani et al. 2020). Both studies found that the attracted ants were able to control non-hemipteran herbivory by lepidopteran larvae. Our results are following these studies, but the implications of our study are limited to potted vine plants that did not produce grapes. Future experiments should be carried out in commercial vineyards over the whole growing season and might also evaluate ant-mediated plant defense against other common herbivore grapevine pests (e.g., Lepidoptera, Diptera).

Several studies evidenced *L. humile*'s capacity to protect plants from non-hemipteran herbivores. In California, the exclusion of *L. humile* increased non-hemipteran herbivory on

Vicia spp. (Koptur 1979), as well as herbivore-related mortality of the shrub *Baccharis halimifolia* (Altfeld and Stiling 2009). Way et al. (1999) showed that *L. humile*'s predation of pine processionary moth (*Thaumetopoea pityocampa*) larvae lowered defoliation to negligible levels in stands of pine trees. Conversely, it has been reported that *L. humile* did not reduce the abundance of *Orthotomicus erosus* in pines, probably due to the difficulty of removing these large beetles from the trees (Henin and Paiva 2004). Some studies report contrasting results whereby plant protection by *L. humile* went along with negative impacts on pollinators (Ludka et al. 2015), severe hemipteran outbreaks (Nygard et al. 2008), hemipteran outbreaks and increased pollination (Stanley et al. 2013), and no effects on natural enemies (Anjos et al. 2021).

Previous studies focused on *L. humile*'s disservices only and reported aggression against natural enemies of pest hemipterans (with their consequential increase) and/or pollinator decline (Blancafort and Gómez 2005; Lach 2007; Mgocheki and Addison 2009). Grapevine is wind-pollinated, but hemipteran outbreaks are of great concern in viticulture. Generally, studies recommend *L. humile* control via toxic baits or pheromones to interrupt the ants' mutualism with vineyard mealybugs (Mgocheki and Addison 2009; Nelson and Daane 2008; Phillips and Sherk 1991; Westermann et al. 2016). These control measures effectively kill or exclude *L. humile* from vines; however, they also eliminate its potential plant protection services. Alternatively, supplementation of artificial carbohydrate sources, such as sugar feeders, can distract ants from protecting hemipterans, leaving them exposed to natural enemies (Nagy et al. 2015; Wäckers et al. 2017). While the success of this method depends on the specific ant-hemipteran combination (Del-Claro and Oliveira 1993; Offenberg et al. 2019), sugar feeders placed in Spanish vineyards inhabited by *Lasius grandis* (Forel), *Pheidole pallidula* (Nylander) and *Plagiolepis schmitzii* (Forel) ants lowered the abundance of the vine mealybug *Planococcus ficus* (Signoret), Hemiptera, Pseudococcidae, up to 72% (Beltrà et al. 2017). Similarly, predation and parasitoidism of vineyard and citrus mealybugs augmented when sugar solution was offered to disrupt ant-mealybug mutualisms (Parrilli et al. 2021; Pérez-Rodríguez et al. 2021). Sugar supplementation can also produce diet shifts, by which ants start preying on their hemipteran partners (Offenberg 2001). The present study did not include mealybugs, and it is unclear how sugar feeders influence the mutualism between *L. humile* and *P. ficus*, which is a common pest in Cafayate. As this mutualism is of special interest for grape growers, future studies should investigate whether sugar supplementation could play a dual role in pest control by attracting ants for plant defense, while also interrupting their mutualistic relation with mealybugs.

Possibly, sugar feeders might increase *L. humile* abundance in the area over time. We suggest monitoring the ant's abundance. If ant numbers reach undesired levels, some sugar feeders could be supplemented with toxic compounds, e.g., boric acid (Klotz et al. 1998, 2000), to limit ant numbers while maintaining their biocontrol services.

4.3 *L. humile*'s effect on *A. bruchi* foraging behavior

Our data shows that one way by which *L. humile* protects vine plants is through the introduced ant's impacts on *A. bruchi* foraging activity and the amount of material transported by it. *Amoimyrmex bruchi* foraging was not simply deviated from vines with *L. humile* to other "undefended" plants, but foraging efficiency (i.e., the number of pieces transported by the ants) was also reduced. Our findings agree with previous studies of this interaction in Cafayate, which suggested a reduction of leafcutter foraging success through aggressive interactions in one-third of all encounters between *L. humile* and *A. striatus*, (Paris 2011). It has been shown previously that *A. striatus* avoids cutting plants occupied by the nectivorous ant *Camponotus blandus* (Folgarait et al. 1994), but the present study is the first to report an impact on foraging activity. Interestingly, in our study, the interaction of *L. humile* with *A. bruchi*'s foraging line occurred independently of colonies' treatment (without sugar feeders). This suggests that this interaction has a degree of fortuitousness and might depend on *L. humile*'s activity in the area rather than on the specific treatment. The observed effects are considerable and might eventually affect *A. bruchi* populations. Possibly, *A. bruchi* could partly compensate for their reduced foraging through mechanisms such as choosing foraging lines and hours leading to the least interaction with *L. humile*. We did not investigate the foraging times of both species in the present study, and there is no literature data on foraging patterns of *A. bruchi*. Foraging times of *L. humile* are temperature dependent (Markin 1970; Rust et al. 2000; Abril et al. 2007). In Cafayate, we observed that both ant species avoid high temperatures around noon. *Linepithema humile* ants usually foraged during the morning, afternoon, and evening, sometimes even at night. Meanwhile, during our experiment, *A. bruchi* was actively foraging during the morning and afternoon, but never at night. We noticed that the foraging hours of both species appear to overlap greatly, although *L. humile*'s hours seemed to be ampler and included the cooler evening temperatures when *A. bruchi* foraging had already ceased. These patterns may change throughout the seasons, which could affect *L. humile*'s plant protection service. Future experiments should explicitly consider the seasonality of both ant's foraging patterns. Yet, the overall negative impact of *L. humile* on native ants has been demonstrated repeatedly (see review Holway et al. 2002). Human and Gordon (1996) showed that native ants that share foraging habitats with *L. humile* avoid invaded areas, where their foraging success is diminished. In Cafayate and other wine-growing areas in Argentina, encounters between leafcutter ants and *L. humile* are limited to

irrigated areas (e.g., vineyards) and their surroundings (Paris 2011; Schulze-Sylvester et al. 2018), while natural areas are too dry for *L. humile*, whose success relies on a certain soil humidity (Holway 1998). However, as local land-use changes progress, new vineyards are planted every year, and *L. humile* is likely to spread (Schulze-Sylvester et al. 2018). Interactions between both ant species are bound to occur more frequently in the future.

4.4 Invasive and native ants as plant defenders

Invasive ants, such as *L. humile*, are often characterized by high abundance, rapid recruitment, aggressive nature, and an attraction to carbohydrate-rich resources (Holway et al. 2002), which can make them successful plant bodyguards in agricultural ecosystems. For example, the red imported fire ant *Solenopsis invicta* (Buren), another invasive ant from Argentina, has been reported multiple times as the main predator of herbivore pests in peanut, soybean, and cotton plantations in the southern USA (Baldwin et al. 2020; Tillman et al. 2009; Vinson 2013). Yet, ant-plant interactions are complex and highly context-dependent, and there is no evidence that invasive ants per se are better plant defenders than native ants (Lach 2003; Lach and Hoffmann 2011; Zhang et al. 2012). The consequences of ant invasions go beyond the ant-herbivore interaction and might eventually negatively impact the entire ecosystem (Holway et al. 2002). We strongly recommend investigating the native ant communities of uninvaded sites with respect to their plant-bodyguard potential against leafcutter ants.

5 Conclusion

In line with our hypotheses, *A. bruchi* leafcutter ants inflict considerable damage on vine plants, while *L. humile* can reduce *A. bruchi* foraging, thus mitigating the impact of herbivory. Previous studies have repeatedly recommended pest control measures against *L. humile* (and other hemipteran-tending ants) to interrupt their mutualism with sap-feeding mealybugs. Yet, while controlling hemipteran-tending ants may improve biological control of mealybugs, it also abates ant-mediated plant defense against herbivores so far largely overlooked. While *L. humile* is an invasive ant that poses threats to natural ecosystems (e.g., arthropod decline in natural ecosystems), it does not directly damage crops, nor harm humans, and its spread abilities to natural ecosystems might be limited in arid regions. We do not argue the importance of preventing and managing ant invasions but call for the abandonment of the focus on this species' origin and its automatic classification as a pest in studies framed in already heavily anthropized ecosystems such as vineyards. These ecosystems are characterized by drastic landscape and land-use alterations, the

introduction of agricultural species, and the loss of biodiversity and ecosystem functions (e.g., natural pest regulation, pollination). Instead, we suggest further investigating the possible use of this ant's services to viticulture in highly modified systems worldwide where this species is already established. Sugar feeders appear to be a simple, inexpensive tool to boost these ecosystem services in two ways: Firstly, sugar feeders promote defense against herbivores, including leafcutter ants. Secondly, they can reduce the negative impact of other pests (e.g., mealybugs) by weakening the ant-hemipteran mutualism. Further research is needed to show if ant-mediated plant defense, including native ant species, could be effective for biological pest control, with the concomitant reduction of pesticide use against leafcutter ants, and vineyard pests in general.

Declarations

Ethics approval   Not applicable.

Consent to participate   Not applicable.

Consent for publication   Not applicable.

Conflict of interest   The authors declare no competing interests.

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