Ants often interact aggressively for resources (e.g. nest sites and food) with members of their own or another species. In these competitive interactions, dominant ant species exert a strong influence on ant species coexistence and plant-associated arthropod community structure. However, few studies have experimentally manipulated the relative abundance of dominant ant species on plants, preventing a mechanistic understanding of the effects of ant competitive interactions on ant community structure as well as on their interactions with other insects, particularly mutualistic hemipterans. In this study, we performed a field experiment in a tropical dry forest in Brazil to investigate the effects of two dominant ant species (*Camponotus crassus* and *Cephalotes pusillus*) on the structure ant communities and the abundance of the ant-tended hemipteran *Enchenopa brasiliensis* in *Solanum lycocarpum* plants. For this, we identified and quantified all ant species foraging on plants and estimated the number of egg masses, nymphs and adults of the mutualistic hemipteran before and after experimentally removing nests of both two dominant ant species. Our results showed that removal of *C. pusillus* nests significantly changed ant community structure, whereas removal of *C. crassus* nests did not. We also found that nest removal of both dominant ant species had significant effects on hemipteran abundance. In particular, plants generally hosted more hemipteran eggs, nymphs and adults after (vs before) nest removal of both dominant ant species. Overall, this study demonstrates that dominant ant species can play a pivotal role in structuring ant communities and the interactions between ants and honeydew-producing hemipteran insects.

**Keywords:** ant assemblages, Brazilian cerrado, *Camponotus crassus*, *Cephalotes pusillus*, *Enchenopa brasiliensis*, honeydew, *Solanum lycocarpum*
**Introduction**

Ants are the most numerous insects globally and are also a highly diverse group comprising more than 12,500 known species (Lach et al. 2010). Because most ant species are omnivorous and occupy a wide range of ecological niches (e.g., nesting sites, foraging areas: Rico-Gray and Oliveira 2007, Lach et al. 2010), they often compete over food, shelter or both with members of their own or another species (Davidson et al. 2003, Camarota et al. 2016, Ribeiro et al. 2019). In these competitive interactions, some ant species use agonistic and/or territorial behavior to alter foraging patterns, resource use and abundance of other non-dominant ant species (Savolainen and Vepsäläinen 1988, Blüthgen et al. 2004, Palmer et al. 2010, Arnan et al. 2011, Mottl et al. 2021).

According to ant mosaic theory, dominant ant species (i.e., both numeric and behavioral dominance) are mutually exclusive in their territories (Leston 1973). Dominant ant species often exploit very important amounts of resources (e.g., nectar rewards) and only coexist with submissive and/or opportunistic ant species (Room 1971, Leston 1973, 1978, Savolainen and Vepsäläinen 1988, Arnan et al. 2011). Therefore, dominant ant species are thought to play a key role in structuring local ant communities and species composition by aggressively displacing competitors (Andersen 1992, Arnan et al. 2011, Camarota et al. 2020, Mottl et al. 2021). For instance, in boreal regions dominant ant species are able to divert food resources away from subdominant competitors (Savolainen and Vepsäläinen 1988). In Mediterranean ecosystems, dominant ant species usually forage at favourable climatic conditions and reduce their heat mortality risk while subdominant species are forced to forage at close to lethal climatic conditions (Cros et al. 1997). In tropical ecosystems, dominant ant species have easier access to food resources than subdominant species (Díaz-Castelazo et al. 2004, Røsumek et al. 2009).

At the community level, ants frequently engage in concurrent associations with diverse partners, leading to outcomes that extend beyond the predictability of pairwise interactions alone (Savage and Rudgers 2013, Stefani et al. 2015). The ultimate results are instead regulated by a collective influence, where multiple species directly or indirectly impact one another (Grinath et al. 2012, Lange and Del-Claro 2014), like in the case of honeydew-producing hemipteran insects (Blüthgen et al. 2000, 2004, Campos and Camacho 2014, Fagundes et al. 2016). In nature, ants protect hemipterans from predators and parasitoids, as well as improve the hygiene of hemipteran colonies by removing sick and dead colony members, in exchange for carbohydrate-rich honeydew (Stryský and Eubanks 2007). Indeed, honeydew-producing hemipterans thrive in groups consisting of adults and offspring, primarily restricted to meristems and plant reproductive structures (Del-Claro 2004, Blüthgen et al. 2006). These insects create localized patches of a consistent food source, continuously generating honeydew, and their population is influenced by ant tending behaviour (Delabie 2001, Del-Claro 2004, Devegili et al. 2020). For instance, the number of ant-tended hemipterans tends to be higher in plants patrolled by dominant ant species because such ants commonly exhibit an aggressive behaviour and effectively expel hemipteran natural enemies from plants (Devegili et al. 2020). Differences in the quality, quantity and availability of honeydew might be reflected in the amount and diversity of ant species interacting with trophobiont hemipterans (Blüthgen et al. 2000, Del-Claro 2004). Competitively superior ants could monopolize the most limited, nutritious and energetic sources of honeydew and allow the coexistence of only a few other submissive ant species (Blüthgen and Fiedler 2004, Fagundes et al. 2012, Campos and Camacho 2014). This is critical to understanding the effect of dominant ant species on dominated ones, as it may drive the ant–plant–hemipteran network structure and regulate mutualistic outcomes (Chamberlain et al. 2010, Lange et al. 2013, Lange and Del-Claro 2014). Consequently, territorial ant species with superior abilities to protect constant supplies of renewable resources would likely establish more enduring interactions with honeydew producing hemipterans (Fagundes et al. 2016, Devegili et al. 2020). Dominant ant species are thus thought to dramatically determine the abundance of these insects (Del-Claro and Oliveira 2000, Vilela and Del-Claro 2018, Devegili et al. 2020). However, recent studies have demonstrated that the effects of dominant ant species on honeydew producing hemipterans are context-dependent because such effects strongly depend on ant aggressiveness, feeding behaviour, ant social organization, distance between foraging areas and ant nest, resource availability and quality, and ant recruitment capacity (Fagundes et al. 2016, Vilela and Del-Claro 2018, Anjos et al. 2022). Dominant ants with the highest recruitment and territoriality compose the main core of interacting species in ant–plant–hemipteran ecological networks and interacted with the most species at frequencies higher than expected by their abundance (Dáttilo et al. 2014a,b). To comprehend the impact of dominant ants on subjugated ones may be a crucial step to a better understanding of how these interactions impact the diversity of associated systems.

Despite good evidence about the role of dominant ant species in altering the behaviour and population dynamics of other species, few studies have experimentally manipulated the relative abundance of dominant ant species on plants (Gibb and Hochuli 2004, Gibb and Johansson 2011), preventing a mechanistic understanding of role of dominant ants in structuring ant communities and on ant-tended hemipteran insects. In this study, we performed a field experiment in a tropical dry forest in Brazil to investigate the effects of two dominant ant species (Camponotus crassus and Cephalotes pusillus) on ant community structure and abundance of the ant-tended hemipteran Enchenopa brasiliensis in Solanum lycocarpum plants. For this, we identified and quantified all ant species foraging on plants and estimated the number of egg masses, nymphs and adults of the mutualistic hemipteran before and after removing nests of the two dominant ant species. In doing so, our study builds toward a better understanding of the role of interspecific competitive interactions of ant communities in structuring plant-associated insect communities.
Material and methods

Study area

This study was carried out in a transitional area from cerrado sensu stricto to open areas in the Private Natural Heritage Reserve of Clube de Caça e Pesca Itororó de Uberlândia, Uberlândia, Brazil (18°58′30.6″S, 48°17′27.0″W). The study area had ~230 ha of cerrado sensu stricto vegetation (Oliveira and Marquis 2002). Open areas consisted of shrubs and small trees, whereas more enclosed areas consisted of trees reaching up to 15 m in height (Del-Claro et al. 2019). The climate is markedly seasonal with the rainy season from October to March, and the dry season from April to September. The annual mean temperature varies from 18 to 28°C and the rainfall from 800 to 2000 mm (Calixto et al. 2021a, b).

Study species

*Solanum lycocarpum* is a woody shrub commonly found in open areas of the cerrado with environmental disturbances, reaching 1–3 m in height (Fig. 1A). This species has hollow trunks, continuous flowering, a berry like fruit, absence of extraloral nectaries, and is usually infested by the sap-sucking hemipteran *E. brasiliensis* (Fig. 1D–E). This hemipteran is absent or in low abundance on *S. lycocarpum* plants between the months of December and August, and exhibits high abundance between September and November (Stefani and Del-Claro 2000) (Supporting information). Because this hemipteran insect produces honeydew, it is commonly tended by different ant species such as *C. pusillus* (Fig. 1B) and *C. crassus* (Fig. 1C). *Camponotus crassus* (worker size: 5–10 mm) is indigenous to many forested parts of the Neotropics (e.g. Argentina, Brazil, Colombia, Paraguay and Peru). This ant species nests in ground, often building several small satellite nests (Lange et al. 2019). The distribution of nests is aggregate, with density of 450 nests ha⁻¹ and average distance of ca 4 m between nests (Lange et al. 2019). Workers forage for up to 150 min out of the nest, covering a route of up to 9 m from the entrance of the nest (Lange et al. 2019). On the other hand, *C. pusillus* (worker size: 3–7 mm) is sympatric with *C. crassus* throughout most of its distribution range. This ant species nests in sticks, dry branches or hollow trunks of many tree species, including *S. lycocarpum* (Powell 2008). Mature colonies have only one queen and 170 workers and 25 soldiers (Byk and Del-Claro 2011). Foraging trails extend from trees with nests to trees with food sources, covering a route of up to 8 m from the entrance of the nest (Powell 2008). Because they occur at large proportions in plants, both ant species are usually classified as numerically dominant species in the cerrado (Powell 2008, Lange and Del-Claro 2014, Fagundes et al. 2017, Camarota et al. 2020, Calixto et al. 2021a). These species do not coexist in abundance on the same *S. lycocarpum* individual plants when aggregations of *E. brasiliensis* are present (Costa-Silva unpubl.).

Experimental design

On 9 October 2017, we selected 20 adult *S. lycocarpum* plants with similar phenological status (1–2 m tall, 50% young leaves and 50% adult leaves) and a minimum distance of 15 m from each other. We selected this distance to avoid plant clones. Ten of the selected plants were dominated by *C. crassus*, and the other 10 plants were dominated by *C. pusillus*. All plant individuals had aggregations of the ant-tended hemipteran *E. brasiliensis*. Immediately after selecting experimental plants (‘before ant nest removal’ hereafter), we identified and counted all ants on each plant, and estimated the total number of eggs, nymphs, and adults of the ant-tended hemipteran *E. brasiliensis*. For this, we carried out observations for 30 min on each plant from 8:00 to 12:00 h because it was the time of the day with highest activity for both ant species (Lange and Del-Claro 2014, Lange et al. 2017, 2019).

On 16 October 2017, we removed nests of *C. crassus* and *C. pusillus* on experimental plants (‘after ant nest removal’ hereafter). In the case of *C. crassus*, we excavated 10 ground nests (the most distant nest was 5 m away from the focal plant) and transferred them 200 m away from their original location. Before the excavation of *C. crassus* nests, we monitored individuals of this species that foraged on host plants and their nests to verify satellite nests. To ensure that dominant ants were not from the same colony, we checked that the queen and/or chambers with immatures (eggs, larva and pupae) were also removed. Chambers with immature nests are usually associated with the presence of the queen (Lange et al. 2019). In the case of *C. pusillus*, we pulled out *S. lycocarpum* branches with *C. pusillus* nests and deposited these branches 200 m away from their original location. For both nest removal treatments, we also manually removed all ants present on the plants. During three consecutive weeks after removing the nests of both dominant ant species (27 October, 3 November, 11 November), we carried out observations for 30 min on each plant to identify and count all ant species and estimate the total number of eggs, nymphs and adults of the ant-tended hemipteran *E. brasiliensis*.

As a subsidiary test, we performed another field experiment to estimate aggressiveness of both *C. crassus* and *C. pusillus* ants. On 9 October 2017, we selected another set of 20 plants at the same field site used for the previous experiment. Ten of the selected plants were dominated by *C. crassus*, and the other 10 plants were dominated by *C. pusillus*. Again, all plant individuals had aggregations of the ant-tended hemipteran *E. brasiliensis*. Immediately after selecting the plants, we recorded the number of times each *C. crassus* or *C. pusillus* worker bit or chased non-nestmate ants or other insects (‘agonistic interactions’ hereafter) on plants. Again, we performed these observations for 30 min on each plant from 8:00 to 12:00 h. Because >95% of the agonistic interactions were between ant species, we only included such ant–ant interactions in the statistical analyses.
Figure 1. (A) *Solanum lycocarpum* (Solanaceae; ~ 2 m tall) plants, (B) a *Cephalotes pusillus* (Myrmicinae; ~ 0.6 cm) ant foraging on plant reproductive structures, (C) *Camponotus crassus* (Formicidae; ~ 0.7 cm) ants attending a colony of the hemipteran insect *Enchenopa brasiliensis*; and (D) an adult (~ 0.9 cm) and (E) nymphs (~ 0.6 cm) of the hemipteran insect *E. brasiliensis* feeding on *S. lycocarpum*. 
Statistical analyses

To investigate the effect of dominant ant species on ant community structure, we tested for the effects of ant nest removal treatment (four levels: before ant nest removal, and one, two and three weeks after ant nest removal) on the relative abundance (i.e. percentage) of each ant species, separately for plants dominated by *C. crassus* or *C. pusillus*. For this, we performed non-metric multidimensional scaling (NMDS), and similarity analysis (ANOSIM) with Euclidean distance and 999 permutations including ant nest removal treatment as a fixed factor.

To investigate the effect of dominant ant species on the abundance of the hemipteran insect *E. brasiliensis*, we ran generalized linear mixed models (GLMMs) with a Poisson distribution testing for the effects of ant nest removal treatment (four levels: before ant nest removal, and one, two and three weeks after ant nest removal) on the number of eggs, nymphs and adults of *E. brasiliensis*, separately for plants dominated by *C. crassus* or *C. pusillus*. In all these models, we included the total number of ants in each plant as a covariate to control that changes in hemipteran abundance were attributable to shifts in ant community composition, rather than a reduction in attendant ants. In addition, we also included individual plant as a random factor to account for repeated measures taken from each plant throughout the sampling period (i.e. before and after ant nest removal treatments).

To investigate aggressiveness of both *C. crassus* and *C. pusillus* ants, we ran a generalized linear model (GLM) with a Poisson distribution testing for the effect of the identity of dominant ant species (two levels: *C. crassus* or *C. pusillus*) on the number of agonistic interactions between the dominant ant species and the other species. In this model, we included the total number of ants in each plant as a covariate because antagonistic interactions between ants depend on how many ants are present on the plant.

We performed all analyses using R ver. 4.0.1 ([www.r-project.org](http://www.r-project.org)). We ran NMDS and ANOSIM using the ‘vegan’ package ([Oksanen et al. 2016](https://www.r-project.org)). We implemented GLMMs and GLMs using the `lmer` and `lm` functions, respectively, from the ‘lme4’ package ([Kuznetsova et al. 2017](https://www.r-project.org)). For this GLMMs and GLMs, we reported back-transformed least-square means and standard errors from these models using the `lsmeans` function from the ‘lsmeans’ package ([Lenth 2016](https://www.r-project.org)). In all the above models, if the treatment effect was significant we conducted post hoc comparisons (using the ‘emmeans’ package) to test for pairwise differences between treatments.

![Figure 2](https://example.com/figure2.png) Figure 2. Variation in ant community structure in *S. lycocarpum* (Solanaceae) plants before and one, two and three weeks after removing nests of the dominant ants (A) *Camponotus crassus* and (B) *Cephalotes pusillus*. We performed ANOSIM with 999 permutations and Euclidean distance. The line represents ellipses of covariance with a 95% confidence interval. Different letters indicate significant differences within treatments at $p < 0.05$. 


Results

Ant community structure

We found that removal of *C. pusillus* nests significantly changed ant community structure, whereas removal of *C. crassus* nests did not (Fig. 2A–B). In particular, we found that ant community structure one, two and three weeks after nest removal significantly differed from that before nest removal (Fig. 2B). In plants previously dominated by *C. pusillus*, individuals of *C. pusillus* and *C. crassus* represented 82.72% and 12.8% of all ants before nest removal (Table 1). Three weeks after *C. pusillus* nest removal, individuals of *C. pusillus* and *C. crassus* represented 32.1% and 52.3% of all ants (Table 1). In plants previously dominated by *C. crassus*, individuals of *C. crassus* represented 94.5% of all ants before nest removal (Table 1). Three weeks after *C. crassus* nest removal, individuals of *C. crassus* were still the most abundant, representing 61.2% of all ants (Table 1).

Abundance of ant-tended hemipterans

We found that nest removal of both dominant ant species had significant effects on hemipteran abundance (Table 2A–B). In the case of plants previously dominated by *C. crassus*, plants hosted more hemipteran eggs and nymphs after (versus before) ant nest removal (Fig. 3A–B). In particular, abundance of hemipteran eggs increased gradually after ant nest removal, reaching the maximum three weeks after removal (Fig. 3A). Abundance of hemipteran nymphs also increased gradually after ant nest removal, reaching the maximum two and three weeks after removal (Fig. 3B). We did not find a significant effect of ant nest removal on abundance of adult hemipterans (Table 2A, Fig. 3C).

In the case of plants previously dominated by *C. pusillus*, plants hosted more hemipteran eggs, nymphs and adults after (versus before) ant nest removal (Fig. 3D–F). In particular, abundance of hemipteran eggs and nymphs increased gradually after ant nest removal, reaching the maximum three weeks after removal (Fig. 3D–F). Abundance of hemipteran adults was greater one week (versus two weeks) after ant nest removal, but it did not significantly differ one and three weeks after removal (Fig. 3F).

Ant aggressiveness

We found a significant effect of the identity of the dominant ant species on ant aggressiveness ($\chi^2_{1,33} = 20.90, p < 0.001$). In particular, the number of agonistic interactions between *C. crassus* and other ant species was 67% greater than those observed between *C. pusillus* and other ant species (Fig. 4).

Discussion

Our results showed that removal of *C. pusillus* nests had a significant effect on ant community structure, whereas removal of *C. crassus* nests did not change it. Three weeks after *C. pusillus* nest removal, *C. crassus* became the dominant ant species (52.3%). However, three weeks after *C. crassus* nest removal this same ant species was still the dominant one (61.2%). Following these findings, we can speculate that the level of aggressiveness presented by *C. crassus* (even after a considerable

---

Table 1. Total abundance of ants in *Solanum lycocarpum* plants before and one, two and three weeks after removing nests of the dominant ants *Camponotus crassus* and *Cephalotes pusillus*. We show the relative abundance (%) of each ant species in parentheses.

<table>
<thead>
<tr>
<th>Ants species</th>
<th>Before</th>
<th>1-week after</th>
<th>2-weeks after</th>
<th>3-weeks after</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Camponotus crassus</em></td>
<td>635 (94.5)</td>
<td>403 (78.7)</td>
<td>393 (74)</td>
<td>295 (61.2)</td>
</tr>
<tr>
<td><em>Camponotus crassus</em> sp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Cephalotes pusillus</em></td>
<td>7 (1)</td>
<td>15 (2.9)</td>
<td>8 (1.5)</td>
<td>5 (1)</td>
</tr>
<tr>
<td><em>Ectatomoma brunneum</em></td>
<td>23 (3.5)</td>
<td>86 (16.8)</td>
<td>94 (17.7)</td>
<td>128 (26.5)</td>
</tr>
<tr>
<td><em>Ectatomoma muralculatum</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudomyrmex gracilis</em></td>
<td>5 (0.7)</td>
<td>5 (1)</td>
<td>7 (1.3)</td>
<td>1 (0.2)</td>
</tr>
</tbody>
</table>

Table 2. Results from general linear mixed models testing for the effects of ant nest removal treatment (four levels: before ant nest removal, and one, two and three weeks after ant nest removal) on the number of eggs, nymphs and adults of *E. brasiliensis*, separately for *S. lycocarpum* plants dominated by (A) *Camponotus crassus* or (B) *Camponotus crassus*. We included the total number of ants in each plant as a covariate and individual plant as a random factor. $\chi^2$ values, degrees of freedom of the numerator and denominator and associated significance levels (p-value) are shown. Significant p-values (p < 0.05) are in bold.

<table>
<thead>
<tr>
<th>Ant nest removal</th>
<th>Ant number</th>
<th>$\chi^2_{1,34}$</th>
<th>p</th>
<th>$\chi^2_{1,34}$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) <em>Camponotus crassus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>252.31</td>
<td>&lt;0.001</td>
<td></td>
<td>190.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nymphs</td>
<td>2498.00</td>
<td>&lt;0.001</td>
<td></td>
<td>26.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Adults</td>
<td>3.38</td>
<td>0.336</td>
<td>13.98</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>(B) <em>Cephalotes pusillus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>305.67</td>
<td>&lt;0.001</td>
<td>16.99</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Nymphs</td>
<td>1330.94</td>
<td>&lt;0.001</td>
<td>0.94</td>
<td>0.332</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>70.54</td>
<td>&lt;0.001</td>
<td>17.64</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>
decrease in their total and relative abundance, Table 1) could result in the inhibition of other ant species. In agreement with this argument, we found that the number of agonistic interactions between C. crassus individuals and other ant species was significantly greater than those observed between C. pusillus individuals and other ant species. Increased aggressiveness of C. crassus compared to C. pusillus has been reported in many plant species growing in the cerrado (Fagundes et al. 2016, Anjos et al. 2017). For instance, in a study including 20 plant species (Fagundes et al. 2016) found that C. crassus ants aggressively interact with more species of ants than C. pusillus. Anjos et al. (2017) found similar results in Bionia coriacea plants. In addition, we found that, after C. crassus nest removal species of the genus Crematogaster drastically increased their relative abundance (26.5%), being the second most abundant species. Crematogaster spp. are very small ants that rarely engages in aggressive interactions with other ants in the cerrado (Del-Claro et al. 1997, Fagundes et al. 2017), and therefore Camponotus ants could maintain high abundances after nest removal because they are more efficient in recruiting workers and establishing dominance over other ant species (Fagundes et al. 2016, 2017, Anjos et al. 2017). Ants compete for resources through a tradeoff between discovery and interference competition (Davidson et al. 2003). When the resource is unpredictable and scarce, like extrafloral nectar, ant species that quickly find and collect resources gain an advantage in discovery competition. Conversely, for predictable and abundant resources, such as honeydew, aggressive and territorial ant species like C. crassus, excel in interference competition. Ant species like C. crassus can break this tradeoff

Figure 3. Abundance of (A, B) egg masses, (C, D) nymphs and (E, F) adults of the hemipteran insect E. brasiliensis in S. lycocarpum plants before and one, two and three weeks after removing nests of the dominant ants C. crassus (left panels) and C. pusillus (right panels). Bars are log back-transformed least-square means ± SE (n = 10). Different letters indicate significant differences within treatments at p < 0.05 based on post hoc tests.
by monopolizing limited resources, allowing them to produce a large number of workers foraging for other resources, making them strong competitors in both discovery and interference (Davidson et al. 2003, Fagundes et al. 2016, 2017).

It is possible that the lack of changes in ant community structure after removal of *C. crassus* nests may have been due to the short-term approach of our study (four weeks from ant nest removal until the last measurements)? For example, Gibb and Hochuli (2004) found that exclusion of the dominant ant species *Iridomyrmex purpureus* over one year had strong effects on ant community structure on sandstone outcrops in the Sydney region, but most changes were observed on ecologically similar ant species. Similarly, Gibb and Johansson (2011) experimentally removed colonies of the dominant ant *Formica aquilonia* over one year in mainland boreal forests in northern Sweden and found drastic changes in ant community structure. However, our study had to be performed at a smaller temporal-scale because ant foraging on *S. lyocarpum* plants is conditioned to the presence of the hemipteran *E. brasiliensis* (this plant species lacks extrafloral nectaries), and the life cycle of this hemipteran insect (eggs, nymphs and adults) encompass from September to November (12 weeks).

Our results also showed that nest removal of both dominant ant species had significant effects on the abundance of the hemipteran insect *E. brasiliensis*. Both in plants previously dominated by *C. pusillus* and in plants previously dominated by *C. crassus*, the number of hemipteran eggs, nymphs and adults increased after ant nest removal in comparison with before nest removal. Competitively superior ants have the capacity to monopolize the scarcest, most nutritious, and energetically rich sources like honeydew, leading to the coexistence of only a few submissive ant species (Blüthgen and Fiedler 2004, Fagundes et al. 2012). Understanding the impact of dominant ant species on their subjugated counterparts is crucial, as it can influence the structure of ant–plant–hemipteran relationships and outcomes (Chamberlain et al. 2010, Lange and Del-Claro 2014). As stated before, *C. crassus* was the most abundant species after nest removal of both dominant ant species and the aggressive behaviour of this ant species with insects such as hemipteran predators might explain the increased abundance of hemipterans observed in our study. In this sense, Devegili et al. (2020) found that aphid populations grew faster on *Cardius theoeremi* plants patrolled by the aggressive ant *Dorymyrmex tener* compared to plants patrolled by two less aggressive ants (*Camponotus distinguendus* and *D. richteri*). However, when these authors removed *D. tener* nests, the abundance of aphid natural enemies increased and the density of aphids decreased to levels observed in plants dominated by *C. distinguendus* and *D. richteri* (Devegili et al. 2020). Although we found few agonistic interactions between *C. crassus* and hemipteran enemies, many predators (e.g. spiders, ladybeetles) can detect olfactory and contact chemical cues from ants and consequently avoid plants with ant–hemipteran interactions (Clark et al. 2009, Hayashi et al. 2016).

In interactions between ants and hemipterans, interference competition is notably high (Cushman and Addicott 1989, Fischer et al. 2001), particularly due to the limited nutrient availability provided by honeydew (Blüthgen et al. 2000). Hemipterans serve as constant honeydew sources, influenced by ant tending behaviour, establishing food source availability and interspecific dominance as key factors in ant–plant interactions (Fischer et al. 2001, Del-Claro 2004). This leads to the development of forage fidelity and territority through interference competition (Cushman and Addicott 1989, Fischer et al. 2001). Consequently, such dominance behaviour reduces the number of species coexisting in hemipteran aggregations, even in small ones (Davidson et al. 2003, Fagundes et al. 2013). Overall, this study demonstrates that dominant ant species can play a pivotal role in structuring ant communities and interactions between ants and honeydew-producing hemipteran insects, but such effects were contingent on ant species identity. The logical next step would be to investigate how shifts in ant dominance affect the whole insect herbivore community and plant performance (e.g. growth, reproduction) to decipher what are the consequences of dominant ants for plant fitness.

**Acknowledgements** – We thank Universidade Federal de Uberlandia for provide field work assistance and lab conditions. CCPIU for permit the study in the cerrado reserve. XM thanks to CSIC call LINCGLOBAL.'

**Funding** – Conselho Nacional de Desenvolvimento Científico e Tecnológico 403647/2021-5, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior C01

**Author contributions**

**Vitor M. Costa-Silva:** Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead).

**Eduardo Soares Calixto:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original...
draft (equal); Writing – review and editing (supporting).

**Xoaquín Moreira:** Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (supporting); Methodology (supporting); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

**Kleber Del-Claro:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

**Data availability statement**

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nzs7h44x7 (Costa-Silva et al. 2023).

**Supporting information**

The Supporting information associated with this article is available with the online version.

**References**


Del-Claro, K., Rodriguez-Morales, D., Calixto, E. S., Martins, A. S. and Torezan-Silingardi, H. M. 2019. Ant pollination of...


