Neotrop Entomol (2018) 47:750–756
https://doi.org/10.1007/s13744-018-0616-5

ECOLOGY, BEHAVIOR AND BIONOMICS

Ants Associated with *Turnera subulata* (Turneraceae): Elaiosome Attraction, Seed Dispersion and Germination

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Keywords

Myrmecochory, plant-ant, context-dependent, symbiosis

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Edited by Marcelo N Rossi – UNIFESP

Received 8 February 2018 and accepted 11 June 2018

Abstract

Symbiosis between plants and ants include examples in which the plant provides shelter and/or food for ants that, in turn, act in the defense or in the dispersion of seeds from the host plant. Although traditionally referred as mutualistic, the results of these interactions may vary with the ecological context in which patterns are involved. A range of species have facultative association with *Turnera subulata* (Turneraceae). Here, using behavioral bioassays, we investigated the effects of the most frequent ant species associated with *T. subulata* (*Brachymyrmex* sp.1, *Camponotus blandus* (Smith), *Dorymyrmex* sp.1, *Crematogaster obscurata* Emery, and *Solenopsis invicta* Buren) in the dispersion of plant host seeds and in the number of seedlings around the associated ant nests. We also evaluated the effects of these ant species in the germination of *T. subulata* seeds, in the consumption of elaiosome, and in the attractiveness to elaiosome odor. Our results showed that the ant species associated with *T. subulata* presented variation in the attraction by the odor and in the rate of consumption of the elaiosomes. However, none of the ant species studied contributed significantly to the increase of seed germination and seedling growth. Our results suggest that the consumption of the elaiosome by ant species is not a determinant factor to the success of germination of *T. subulata*. However, such species could contribute indirectly to seed germination by carrying seeds to sites more fertile to germination. In general, our results help to elucidate the results of ecological interactions involving ants and plants.

Introduction

Interactions among species can interfere in ecological patterns and process (Bøhn & Amundsen 2004), playing an important role in the dynamics and structuring of communities. Since ecological interactions are complex and dynamic, their results can be variable in the time and space (Pires & Del-Claro 2014), according to the balance between costs and benefits for the species involved. Symbiosis between plants and ants, traditionally referred as mutualistic, is among the most studied ecological interactions (Rico-Gray & Oliveira 2007). These interactions include examples in which the plant provides shelter (e.g., domes) and/or food (e.g., extrafloral nectaries [EFNs] or elaiosome) for the ants that, in turn, act in the defense (Janzen 1966) or in the dispersion of seeds from the host plant (myrmecochory) (Inouye & Taylor 1979).

Ants are considered the largest group of invertebrate seed dispersers (Folgarait 1998; Beattie & Hughes 2002). Some plant species have their seed covered by elaiosome—appendix rich in proteins and lipids—that are usually attractive for some species of ants due to its important nutritional complement for the ant's diets (Gammans *et al* 2005; Fischer *et al* 2008). The elaiosome is frequently transported to the nest because they are preferred mainly for feeding larvae (Fischer *et al* 2005). This behavior can contribute to the increase of the productivity of the ant colonies and to the success of seed germination in the soil of the nest, which are rich in nutrients. In addition, the success of germination due the dispersion of seeds by ants may also occur due to other indirect benefits, for example, colonization of new habitats (Whitney 2002), decreased intraspecific competition between seedlings (Gibson 1993; Bronstein *et al* 2006), and the seed predation by animals (O'Dowd & Hay 1980; Tanaka *et al* 2015), as well as the protection against abiotic stress (e.g., fire) (Christian & Stanton 2004). The positive role of ants in the success of seed germination has been observed mainly in nutrient-poor soils (Leal *et al* 2007). On a larger scale, the dispersion of seeds by ants can influence the patterns of spatial distribution of plant populations (Gómez *et al* 2005).

Like other plant-ant interactions, myrmecochory has also been reported as strongly context-dependent (Giladi 2006; Pfeiffer *et al* 2010; Chlumský *et al* 2012). In some cases, ant species associated with host plant may behave as cheaters, removing the elaiosome from the seed without carrying out the dispersion. Similarly, some host plants may release substances that induce dispersion behavior without nutritionally rewarding the associated ants (Turner & Frederickson 2013).

Plants of the genus *Turnera* L. (Turneraceae) are recognized for interactions with ants. These plants are shrub and are distributed from the Southern USA to Argentina (Prata *et al* 2013). The *T. subulata* species occurs throughout the Brazilian northeast (Arbo 2005), in natural and anthropic areas. *Turnera subulata* present at the base of their leaves a pair of EFN and have seeds covered by elaiosome (Arbo 2013). Recently, 21 species of ants were observed in facultative associations with *T. subulata* (Cruz *et al* 2018), in which the five most frequent species were *Brachymyrmex* sp.1 Mayr (Formicidae: Formicinae), *Camponotus blandus* (Smith) (Formicidae: Formicinae), *Crematogaster obscurata* Emery (Formicidae: Myrmicinae), *Dorymyrmex* sp.1 Mayr (Formicidae: Dolichoderinae), and *Solenopsis invicta* Buren (Formicidae: Myrmicinae). The association with these ants contributes to increase *T. subulata* reproduction (Cruz *et al* submitted) and to decrease the herbivory in the host plant (Cruz *et al* 2018). However, the relative contribution of these ant species to the germination of *T. subulata* seeds, as well as the attractiveness and consumption of elaiosome by the ants associated with *T. subulata*, has not been studied.

In the present study, we investigated the effects of the most frequent ant species associated with *T. subulata* (i.e., *Brachymyrmex* sp.1, *Ca. blandus*, *Dorymyrmex* sp.1, *Cr. obscurata*, and *S. invicta*) in the dispersion of plant host seeds and in the number of seedlings around the associated ant nests. We also evaluated the effects of these ant species in the germination of *T. subulata* seeds, in the consumption of elaiosome, and in the attractiveness to elaiosome odor. The results of this study may be useful for comprehending the cost-benefit dynamics that determine the results of ecological interactions, as well as for the comprehension of community structure.

Material and Methods

Ants species associated with T. subulata

In the present study, we evaluated the behavior of the five most frequent ant species associated with *T. subulata* in the same site that our study was conducted (Universidade Federal de Sergipe, São Cristóvão-SE [10°55′35″S, 37°6′14″ W], Brazil) according to Cruz *et al* (2018). The most frequent species were *Brachymyrmex* sp.1, *Ca. blandus*, *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta.*

For laboratory bioassays, workers of each species were collected directly in nests at Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil. Workers were kept in an incubator chamber (B.O.D.) until the performance of bioassays. The species were identified using specific taxonomic keys.

Effect of plant-associated species in the seed dispersion

The direct effect of plant-associated species in the dispersion of *T. subulata* seeds was evaluated under natural conditions (field). For this, 10 mature seeds of *T. subulata* were deposited, for 10 min, at 3 cm of nests ($N = 3$) of each ant species tested (*Brachymyrmex* sp.1, *Ca. blandus*, *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta*). During the 10 min, we measure the (i) time spent by ants to arrive to each seed and (ii) behaviors triggered by ants when they arrived in the seeds. The behaviors were classified as follows: (1) consumption without dispersion, (2) dispersion to the nest, and (3) dispersion to another site.

For each ant nest, eight repetitions were performed interspersed every 1 h, totaling 80 seeds per nest.

Effect of associated ant nests in T. subulata plants

The indirect effect of plant-associated species in the *T. subulata* plants was evaluated under natural conditions by measuring the number of seedlings around the nests of each ant species. In each nest, a transect (5 m) was established in the cardinal points and the number of *T. subulata* seedlings was counted in each meter. The mean of *T. subulata* seedlings in the cardinal points was used in the statistical analysis.

For each ant species, three repetitions were performed, totaling 15 nests.

Effect of plant-associated species in the seed germination and seedling growth

The direct effect of plant-associated species in the seed germination and seedling growth of *T. subulata* was evaluated under laboratory conditions. For this, mature seeds of *T. subulata* were submitted to eight different treatments: (i) intact seed (IS; control); (ii) elaiosome removed by ants (ERA—being a distinct treatment for each of the four ant species [*Brachymyrmex* sp.1, *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta*]; (iii) elaiosome manually removed (EMR); (iv) scarification with hot water (SW); and (v) manual scarification (SM).

For the establishment of ERA treatment, two seeds were placed in a Petri dish (60 × 15 mm), containing a piece of cotton with water and 10 ant individuals of the same species. The Petri dishes were kept in B.O.D. (27°C and a photoperiod of 12 h) for 24 h. For the ERM treatment, the removal of elaiosome was carried out using a stereomicroscope, where each elaiosome was removed with entomological forceps, avoiding any type of damage to the seeds. For SW, seeds were placed in 5-ml glass pots filled with water at 80°C. The seeds were removed from water after 1 h. For the SM treatment, elaiosomes were removed and three parallel cuts (at the ends and in the middle of the seeds) were made using a stylet using a stereomicroscope.

For each treatment, seeds were deposited in polystyrene seeding separated by cells (two seeds/cell) with a substrate consisting of a mixture of sand and earthworm humus (50:50). Seeds were irrigated daily with 5 ml of water per cell. Daily evaluations were made for 30 days to measure (i) the time spent for seedling emergence and (ii) the final height of the seedlings.

The experimental design was performed in a completely randomized block. In all treatments, mature seeds were used from 50 individuals of *T. subulata*. For each treatment, five different plants were used being 10 repetitions per plant, totaling 50 repetitions per treatment. Each repetition consisted of two seeds, totaling 800 seeds.

Elaiosome consumption by plant-associated species

The elaiosome consumption by ant species associated with *T. subulata* was evaluated under laboratory conditions. Initially, two mature seeds of *T. subulata* were weighted in a precision balance and placed in a Petri dish (5.5 cm in diameter) with 10 ant individuals and a piece of cotton with water (2 ml). The Petri dishes were kept in the B.O.D. under controlled temperature (± 25°C) for 24 h. Subsequently, the seeds of each Petri dish were weighed and the difference between initial and final seed weight (mg) was used as a surrogate of the consumption of elaiosome by plant-associated species.

For each species tested, 50 repetitions were performed, totaling 200 repetitions (seeds).

Attractiveness of plant-associated species to elaiosome extract

Elaiosome extracts were prepared from mature seeds of *T. subulata* plants ($N = 5$) obtained in July 2015, at the same sites of the collection of ant species. The elaiosomes were removed from the seeds with sterilized entomological forceps, weighed on a precision balance, and immersed in 100 µl of *n*-hexane (99% P.A./ACS; Neon Comercial Ltda.®, São Paulo-SP, Brazil) for 24 h at 4°C. Then, elaiosomes were removed from the extract, and 100 µl more of *n*-hexane was added. For calculation of the concentration of elaiosome extracts, the final volume of hexane after extraction was divided by the weight of the elaiosomes. The extracts were kept in a freezer at − 18°C until the performance of bioassays.

The response of associated ants to elaiosome extracts was verified with behavioral bioassays under laboratory conditions. Initially, we performed a bioassay to obtain a response threshold of the ants to the concentrations of the elaiosome extracts (see details in SM01). Then, the main bioassays were performed using, for each species of ants tested, the concentration of elaiosome extract that triggered the attraction behavior (see Tab SM01).

The main bioassay consisted in a choice test between elaiosome extract and control (hexane). The bioassays were performed in a Petri dish covered with filter paper; the diameter of the Petri dish varied proportionally to the size of the individuals of each ant species (*Brachymyrmex* sp.1 5.5 cm; *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta* 9 cm). In the center of each Petri dish, a plastic camera (with two openings) was inserted where an ant was conditioned (*Brachymyrmex* sp.1 3.0 cm; *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta* 4.0 cm). The treatments were applied on two pieces of filter paper (0.5 cm) positioned on opposite sides of a Petri dish, using a Hamilton® syringe. The concentrations of the elaiosome extract applied for each ant species were as follows: 0.007 mg/µl for *Brachymyrmex* sp.1; and 0.01 mg/µl for *Cr. obscurata*, *Dorymyrmex* sp.1, and *S. invicta* (see SM01). The individuals from *Ca. blandus* did not respond to any of the concentrations tested and were not tested in the main bioassays (see more details in SM01).

The choice of each ant was recorded, considering the maximum time of 300 s. Individuals who did not choose in this time were considered as "no response." For each repetition, the Petri dish and the ant individual tested were replaced. All bioassays were performed in July 2016. For each species tested, 10 repetitions *per* nest ($N = 3$) were performed, totaling 30 repetitions per ant species/bioassay.

Statistical analyses

All analyses were performed in R software (R Development Core Team 2016) using generalized linear models (GLM), followed by residual analysis to verify the suitability of distributions and the tested models. In all models, the differences among ant species were verified by contrast analysis (Crawley 2012), in which ant species that did not present significant differences among themselves ($P > 0.05$) were grouped.

To analyze whether there is a variation of the behaviors performed by each ant species in relation to seeds in the field, the data were submitted to ANODEV under Normal error distribution. To analyze the attractiveness of the ants by *T. subulata* seeds in the field, the mean time spent by ants to arrive in 50% of the seeds was estimated using survival analysis with Weibull distribution ("survival" package). The censor traditionally used in survival analysis corresponded to the seed visited by ants (1) or not (0). Similar analysis was performed to analyze the contribution of ants on the germination of *T. subulata* seeds under different treatments (*x-var*). In this case, the censor in the survival analysis corresponded to the germination (1) or not (0) of one of the two seeds of each repetition. The effect of treatments on plant growth was tested using ANODEV under Normal error distribution.

To analyze the effect of ant species (*x-var*) in the consumption of elaiosomes (*y-var*; mg intake), the data were submitted to analysis of deviance (ANODEV) under Normal error distribution.

The attractiveness of elaiosome extract was analyzed using Chi-square test (χ^2), independently for each ant species.

Results

Effect of plant-associated species in the seed dispersion

The mean proportion of seeds visited over the time was significantly affected by ant species ($\chi^2 = 1396.5$, d.f. = 1194, $P > 0.001$). Individuals of *S. invicta*, followed by *Dorymyrmex* sp.1, *Cr. obscurata*, and *Brachymyrmex* sp.1, visited the *T. subulata* seeds faster than workers of *Ca. blandus*, which showed a lower percentage of seeds visited (Fig 1).

In relation to the behavior after arriving in the *T. subulata* seeds, workers of *Dorymyrmex* sp.1 and *S. invicta* presented a higher proportion of dispersion of seeds to the nest ($P = 0.001$). However, *Cr. obscurata* showed the higher proportion of seed consumption without dispersion. The individuals of *Brachymyrmex* sp.1 and *Ca. blandus* showed a very low proportion of seed visitation (Fig 1) and did not show any behavior.

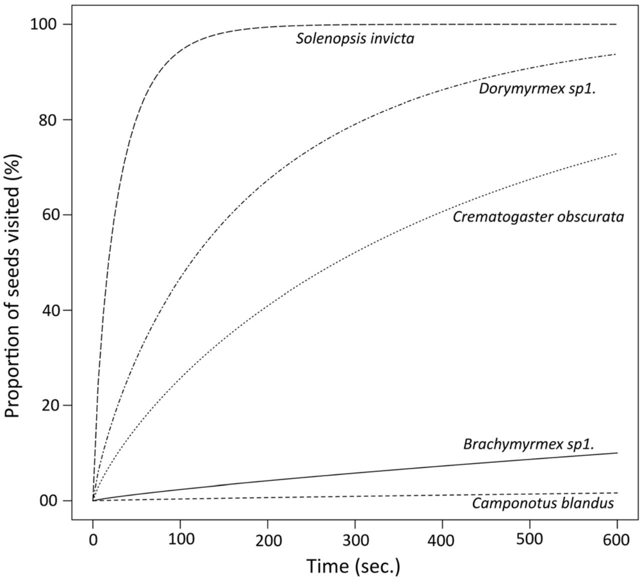

Fig 1 Proportion of *Turnera subulata* seeds visited by different ant-associated species (*Brachymyrmex* sp.1, *Dorymyrmex* sp.1, *Crematogaster obscurata*, *Solenopsis invicta*, and *Camponotus blandus*) over time in a field experiment. Each curve is significantly different from each other.

Effect of associated ant nests in T. subulata plants

The mean number of *T. subulata* seedling was significantly affected by the distance from the nest of plant-associated species ($F_{1,73} = 26.79$, $P < 0.001$) and by species identity ($F_{4,69} = 4.81$, $P = 0.001$). In general, the mean number of seedling decreases with the distance of ant nests. However, nests of *Dorymyrmex* sp.1 and *S. invicta* showed a higher number of seedlings around the nest, followed by nests of *Cr. obscurata* and nests of *Brachymyrmex* sp.1 and *Ca. blandus* (Fig 2).

Effect of plant-associated species in the seed germination and seedling growth

The mean time spent for seed germination ($\chi^2 = 12.11$, d.f. = 391, $P = 0.09$) and the height of seedlings ($F_{7,190} = 1.07$, $P = 0.37$) were not significantly affected by treatments and ant species.

Elaiosome consumption by plant-associated species

The elaiosome consumption by associated ants showed significant variation among studied species ($F_{1,38} = 6577$, $P = 0.014$). Although the elaiosome was consumed by all species, none of them consumed the elaiosome totally. Workers of *Brachymyrmex* sp.1, *Cr. obscurata*, and *Dorymyrmex* sp.1

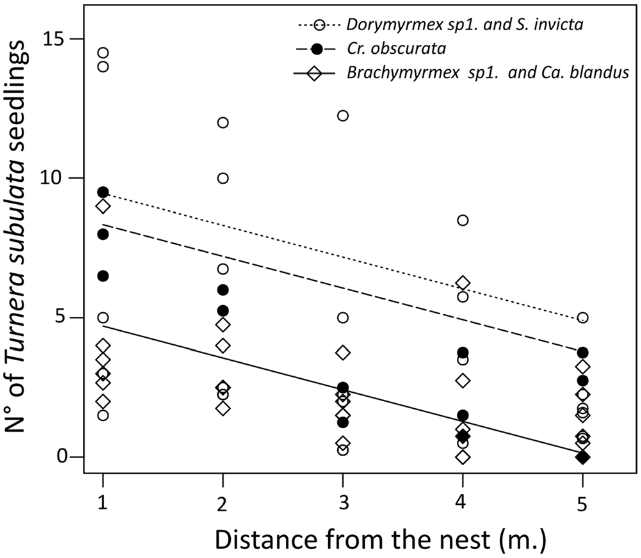

Fig 2 Number of *Turnera subulata* seedlings depending on the distance from the nest (m) and identity of ant associated species (*Brachymyrmex* sp.1, *Dorymyrmex* sp.1, *Crematogaster obscurata*, *Solenopsis invicta*, and *Camponotus blandus*). Each curve is significantly different from each other (see "Results" section for details).

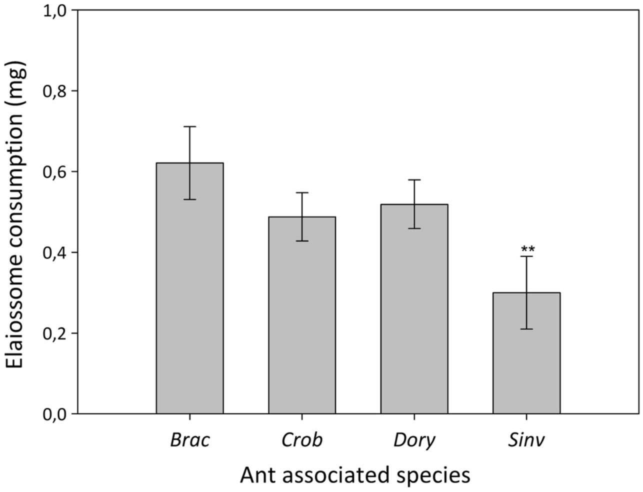

Fig 3 Elaiosome consumption (mg) of *Turnera subulata* seeds by different ant-associated species. *Brac*, *Brachymyrmex* sp.1; *Crob*, *Crematogaster obscurata*; *Dory*, *Dorymyrmex* sp.1; *Sinv*, *Solenopsis invicta*. **Significant differences among treatments ($P < 0.05$).

consumed, on average, a greater amount of elaiosome when compared to individuals of *S. invicta* (Fig 3).

Attractiveness of plant-associated species to elaiosome extract

The mean proportion of individuals choosing between elaiosome extract and control (hexane) differed among associated ant species: *Cr. obscurata* and *S. invicta* showed a higher proportion of individuals choosing the elaiosome extract than hexane (control) ($\chi^2 = 8.33$, $P = 0.003$ [*Cr. obscurata*], $\chi^2 = 5.26$, $P = 0.02$ [*S. invicta*]; Fig 4). On the other hand, individuals of *Brachymyrmex* sp.1 and *Dorymyrmex* sp.1 did not show differences in the mean proportion of individuals choosing between the elaiosome extract and the control (*Brachymyrmex* sp.1 $\chi^2 = 1$, $P = 1$; *Dorymyrmex* sp.1 $\chi^2 = 0.42$, $P = 0.51$; Fig 4).

Discussion

In the present study, we investigated the effects of the most frequent ant species associated with *T. subulata* (*Brachymyrmex* sp.1, *Ca. blandus*, *Dorymyrmex* sp.1, *Cr. obscurata*, and *S. invicta*) in the dispersion of plant host seeds and in the number of seedlings around the associated ant nests. We also evaluated the effects of these ant species in the germination of *T. subulata* seeds, in the consumption of elaiosome, and in the attractiveness to elaiosome odor. In general, our results showed that, under natural condition, associated ant species were attracted to seeds and two of the five associated ant species performed the dispersion behavior of *T. subulata* seeds to their nests (Fig 1), which can be an indirect positive effect once the number of *T. subulata* seedling is higher around nests of these ant species (Fig 2). However, although some species of associated ants were

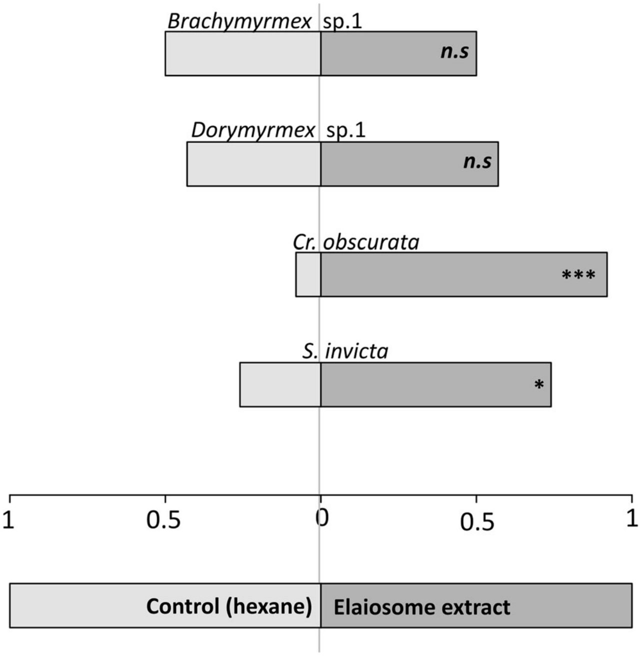

Fig 4 Mean proportion of response of individuals from different ant species (*Brachymyrmex* sp.1, *Dorymyrmex* sp.1, *Crematogaster obscurata*, and *Solenopsis invicta*) to control (hexane) and treatment (elaiosome extract from seeds of *Turnera subulata*). ***$P < 0.001$; *$P < 0.05$; n.s. = nonsignificant.

attracted to elaiosome extracts (Fig 4) and consumed this structure in the laboratory (Fig 3), none of them promoted an increase in seed germination success or seedling growth of *T. subulata*.

In facultative ant-plant interactions, the host plant is usually associated with a distinct composition and abundance of ants over time and space (Heil & Mckey 2003). For *T. subulata*, for example, Cruz *et al* (2018) found 21 ant species and a significant difference in the ant composition throughout the day and sample sites. These variations can result in associations considered context-dependent (Bronstein 1994, Di Gusto *et al* 2001, Chamberland & Holland 2009), which do not always result in a positive balance for both patterns involved.

The direct or indirect contribution of the ants to the seed germination of the host plant initially depends on the attractiveness of the elaiosome. Here, we showed that although most of the ant species studied perceived the signal emitted by elaiosome (responding the concentrations in the pre-test; see SM01), only *Cr. obscurata* and *S. invicta* responded more quickly (Fig SM01) and in a greater proportion than the other species (Fig 4). Factors such as elaiosome size (Hughes & Westoby 1992), its chemical composition, and nutritional aspects (Hughes *et al* 1994) have been a determinant in the attractiveness of the ants to the elaiosome. When the cost of the reward offered by the host plant is greater than the signal emitted in attractiveness, plants could invest more in signal quality than reward, generating a cheating signal (Edwards & Yu 2007, Benitez-Vieyra *et al* 2010). Once attracted by the signal of the elaiosome, the consumption of the elaiosome may be dependent on its reward in relation to the nutritional quantity or quality (Sheridan *et al* 1996). This could explain why *S. invicta*, although responding more quickly to the elaiosome extract, was the ant species that had the lowest rate of consumption among all plant-associated species studied. Similarly, it could be the reason why none of the studied species completely removed the elaiosomes from the *T. subulata* seeds.

The consumption of elaiosome by associated ants can represent a direct benefit for germination of the seeds. During the consumption of the elaiosome, ants can inject salivary substances and promote scarification that optimizes the process of germination (Hughes & Westoby 1992). However, in the present study, the consumption of elaiosome by associated ants did not contribute to the germination and growth success of *T. subulata* seedlings at laboratory conditions. Our results indicate that the direct consumption of elaiosomes by the studied ants is not the factor that could trigger some benefit for the germination in *T. subulata*. However, it should be considered that the positive role of ants in seed germination can be represented by a range of indirect benefits (O'Dowd & Hay 1980, Gibson 1993, Whitney 2002, Christian & Stanton 2004, Bronstein *et al* 2006; Tanaka *et al* 2015). For example, according to the directed dispersal hypothesis, the ants are able to carry seeds in the nest or near the nest, which are nutrient-enriched sites, allowing an increase in the germination of seeds (Giladi 2006). In the present study, two of the five ant species tested performed the seed carrying behavior more times to the nest; this behavior is indicative that *S. invicta* and *Dorymyrmex* sp.1 are the species that most contribute to dispersion, because when they find the seeds, they transport to the nest. In addition, our results showed that the number of *T. subulata* seedlings is higher around the nests of these species (Fig 2). Leal *et al* (2007) also observed an increase in the germination of four plant species from Brazilian Caatinga in soils of the ant nest compared to soils from other sites.

Crematogaster obscurata performed in greater quantity the behavior of consumption of the elaiosome in the site, without dispersing the seed to the nest, acting as an opportunist. This result demonstrates that the role of ants in seed dispersal and germination in *T. subulata* is context-dependent, that is, depending on the ant species associated, the result may be positive or negative for the host plant. In fact, studies have shown that in facultative mutualism, in which the plants are associated with several species of ants, variations of the results are common (Beattie 1985; Passos & Oliveira 2003; Leal *et al* 2014).

It should also be considered that even a possible lack of benefit of the role of the ants in the germination of seeds from *T. subulata* may be compensated by other functions that increase the fitness of the host plant. Previous studies have been shown that ants associated to *T. subulata* reduced herbivory (Cruz *et al* 2018) and increased the reproductive investment of the host plant compared to *T. subulata* plants without ants (Cruz *et al* submitted). The host plant defense is performed mainly by four of the five ant species tested in the present study: *Ca. blandus*, *Cr. obsturata*, *Dorymyrmex* sp.1, and *S. invicta*. In conclusion, our study may be useful for comprehension of the dynamics of facultative interactions involving plant-ants.

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