



Original article

Ants have a negative rather than a positive effect on extrafloral nectaried *Crotalaria pallida* performance

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ABSTRACT

Crotalaria pallida (Fabaceae) is a pantropical plant with extrafloral nectaries (EFNs) near the reproductive structures. EFN-visiting ants attack and remove arctiid moth *Utetheisa ornatrix* larvae, the main pre-dispersal seed predator, but the impact of ants on *C. pallida* fitness is unknown. To assess this impact, we controlled ant presence on plants and evaluated the reproductive output of *C. pallida* with and without ants. Predatory wasps also visit EFNs, prey upon *U. ornatrix* larvae, and may be driven out by ants during EFN feeding. Does this agonistic interaction affect the multitrophic interaction outcome? We found it difficult to evaluate the effect of both visitors because cages excluding wasps affect plant growth and do not allow *U. ornatrix* oviposition. Therefore, we verified whether ant presence inhibited wasp EFN visitation and predicted that (1) if ants confer a benefit for *C. pallida*, any negative effect of ants on wasps would be negligible for the plant because ants would be the best guardians, and (2) if ants are poor guardians, they would negatively affect wasps and negatively impact the fitness of *C. pallida*. Surprisingly, we found that the number of seeds/pods significantly increased, ca. 4.7 times, after ant removal. Additionally, we unexpectedly verified that controls showed a higher percentage of herbivore bored pods than ant-excluded plants. We found that wasps spent less time visiting EFNs patrolled by ants (ca. 299 s less). These results support our second prediction and suggest that the outcome of multitrophic interactions may vary with natural enemy actors.

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1. Introduction

Rewards offered by extrafloral nectaries (EFNs) may shape multitrophic interactions among plant producers, predatory or parasitoid arthropods and herbivorous insects. EFNs are not directly involved in pollination (Díaz-Castelazo et al., 2005) and are assumed to protect plant attracting natural enemies of insect herbivores, such as ants (Rico-Gray and Oliveira, 2007, and references therein), predatory and parasitoid wasps (Cuautle and Rico-Gray, 2003; Pemberton and Lee, 1996; Mathews et al., 2011), mites (Pemberton, 1993), and spiders (Romero and Koricheva, 2011, and references therein). The protective role of ants is well established but not universal, and the outcomes may vary. Although many studies have questioned the role of visiting ant on herbivores (Rico-Gray and Oliveira, 2007), few studies have focused on the variation of plant protection outcomes when other non-ant natural enemies and ants participate in this mutualistic system. Cuautle and Rico-

Gray (2003) showed that EFN-visiting wasps and ants act separately to exert a positive effect that decreases herbivory levels of larvae of the nymphalid butterfly *Euptoieta hegesia* on *Turnera ulmifolia* (Turneraceae) and increases the number of unripe fruit; acting together, however, wasps and ants did not produce an additive effect.

In addition, different natural enemies visiting EFN resources may lead to another intriguing question: Does the presence of one potential natural enemy impair plant protection due to interference with another, more efficient enemy? Ants visiting EFNs are known to have the capacity to interfere with other natural enemy actions during competitive interactions or intraguild predation (Rosenheim et al., 1995). Mathews et al. (2011) found that ants visiting the EFNs of *Prunus persica* (Rosaceae) antagonized egg parasitoids (*Trichogramma minutum*, Hymenoptera: Trichogrammatidae) of the oriental fruit moth *Grapholita molesta* (Tortricidae), thereby decreasing the egg parasitism. However, the ants were crucial in reducing *G. molesta* density in both larval and pupal stages.

The interaction between EFN-visiting ants and non-ant predators emerged when we studied the role of ants visiting EFNs in

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Crotalaria pallida (Fabaceae). Our research group demonstrated that ants visiting the EFNs (e.g., *Camponotus blandus* and *Ectatomma quadridens*) attacked, removed and sometimes killed larvae of the specialist arctiid moth *Utetheisa ornatrix*, the main pre-dispersal seed predator, which bores unripe pods to eat the seeds within (Ferro et al., 2006; Guimarães et al., 2006). Although these larvae sequester defensive pyrrolizidine alkaloids from the leaves and seeds of *C. pallida*, the ant behaviors were not influenced by these chemicals (Ferro et al., 2006). However, nothing is known about the impact of ants visiting EFNs of *C. pallida*. From the plant perspective, does ant herbivore removal imply a positive outcome, such as an increase in seed set for dispersal? We next addressed the following question: By removing herbivores, can ants increase the probability that *C. pallida* will leave seeds? Our assessment compared some estimates of *C. pallida* performance when ants were present and when they were artificially excluded. If ants positively affect *C. pallida*, we predict a greater number of bored pods in the absence of ants and a decreased number of seeds produced.

Nevertheless, we observed predatory wasps (e.g., *Polybia* and *Polistes* wasps) visiting EFNs and preying upon *U. ornatrix* larvae. Thus, we hypothesized that wasps may exert an additional high predator pressure on this species, similar to the effect that Stamp and Bowers (1988) found in many other lepidopteran species. We observed that ants occasionally drove the wasps out during simultaneous EFN visits. How does this agonistic interaction between EFN-visitors affect the indirect plant defense against the *U. ornatrix* borer? A factorial experimental design to evaluate both the individual and interactive effects of ants and wasps on the fitness of *C. pallida* is very difficult to assess because cages that exclude wasps affect plant performance (e.g., leaf growth) (J.R. Trigo, pers. obs.) and do not allow oviposition by *U. ornatrix*. Cages would not affect pollination because *C. pallida* is self-compatible and autogamously sets fruits (Almeida, 1986). Therefore, we used an indirect approach to assess the above effects. We examined the effect of ants on predatory wasp visits to the EFNs of *C. pallida* and correlated visits with the impact of the ants on *C. pallida* fitness in light of two predictions. (1) As predicted above, if ants confer a benefit for *C. pallida*, any effect of ants on wasps would be negligible to the plant because the ants would be better guardians than the wasps. (2) Nonetheless, if ants are less effective guardians than wasps, a negative effect of ants on wasps would negatively impact *C. pallida* fitness when ants are present.

2. Materials and methods

2.1. Study site and organisms

We conducted this study in an abandoned field in an urban area in the Campinas municipality of southeast Brazil (22°44'46''S, 47°03'11''W). The vegetation cover is a pasture dominated by *Brachiaria* sp. (Poaceae), and three species of *Crotalaria* are present, namely, *C. lanceolata*, *C. pallida* and *C. incana*. These species are used as hosts by *U. ornatrix*, and *C. pallida* is the most abundant (Ferro, 2001; Ferro et al., 2006; Guimarães et al., 2006).

The smooth rattlebox *C. pallida* Ait. (Fabaceae: Papilionoideae: Crotalariaeae) is a pantropical annual shrub. The natural distribution of this species is obscured by widespread cultivation as a green manure and fodder crop (Polhill, 1982). In Brazil, the species occurs alongside pastures, roadsides, old fields, and forest edges (Lorenzi, 2000). *C. pallida* produces from one to dozens of racemes, each with 30–50 flower buds, flowers or pod fruits with a dozen seeds, and the same individual may simultaneously have racemes with flower buds, flowers, and pods that may be either unripe or ripe. This plant bears racemes throughout the year, and pod production peaks in the wet season (Ferro, 2001). *C. pallida* presents EFNs located at the

base of the pedicel (Díaz-Castelazo et al., 2005; Melo et al., 2010). The EFNs remain active from early flower development to the formation of ripe pods, and the ants continuously patrol the flowers and pods, visiting them and throwing out the *U. ornatrix* larvae that are external to the pods (Ferro et al., 2006; Guimarães et al., 2006).

Utetheisa ornatrix L. (Lepidoptera: Arctiidae) is a New World species (Da Costa, 2010), and the larvae are primarily found inside the unripe pods of several alkaloid-containing *Crotalaria* species (Ferro et al., 2006; Guimarães Jr. et al., 2006; Conner, 2009; Cogni, 2010; J.R. Trigo, pers. obs.). The eggs are laid in clusters on the leaves. The 1st–2nd instar larvae may feed on the leaf apex, but they are also found to bore into very young and soft unripe pods (J.R. Trigo, pers. obs.); from the 3rd instar onwards, larvae are predominately found in the unripe pods. By feeding on the seeds in the pods, the larvae are protected against predation (Ferro et al., 2006). Flowers and flower buds are also occasionally consumed (Ferro, 2001). Larvae sequester pyrrolizidine alkaloids (PAs) primarily from unripe seeds, and these alkaloids have been shown to provide protection against predators, except for some ant species (Ferro et al., 2006; Guimarães et al., 2006), during various life stages of this arctiid species (see Trigo, 2011). To our knowledge, no data have been gathered to analyze the role of PAs in protecting the larvae against predatory wasps. However, our observations indicate that wasps prey upon *U. ornatrix* larvae and other unpalatable caterpillars (e.g., the danaine butterfly *Danaus erippus*), suggesting that this type of predator is not affected by these toxic preys.

2.2. The impact of ants visiting the EFN on growth, reproduction and seed herbivory in *C. pallida*

We sampled 500 *C. pallida* seeds from different individuals in the study area. We germinated the seeds in 30 L pots (100 pots with five seeds each) in the above location in July 2005. Three months after planting, we kept the tallest seedling from each pot for the experiments and discarded the remaining four. No germination occurred in 42 of the pots. We began the experiments when the plants flowered, ca. 4 months after planting (October 2005), and ended the experiments when the last plant died (February 2006). We placed the potted plants randomly in a 20 × 10 m area, with all pots placed 1.5 m apart. We watered all plants daily. We submitted the plants to two treatments (29 plants each, randomly assigned using a coin toss) to examine the impact of ant visits to the EFN on growth, reproduction and seed herbivory in *C. pallida*. We excluded the ants in one treatment by applying Tanglefoot™ resin on an adhesive tape placed around the base of the stem at 10 cm above the ground. We did not apply Tanglefoot™ directly on the stem because preliminary experiments showed that this resin negatively affects the plant. The second treatment (control) used adhesive tape instead of Tanglefoot™. The tape did not affect negatively the plant. One week after the experiment commenced, three ant-excluded plants died, leaving 29 control and 26 ant-excluded plants that we followed during the experiment.

In both treatments, we recorded the number of leaves on a monthly basis and the numbers of flowers, ripe pods, seeds into ripe pods, as well as the percentage of perforated ripe pods (as a measure of seed herbivory) on a weekly basis. The monthly record did not underestimate the leaf biomass measure because leaves live for a long time; senescence generally occurs only when the last pod set is mature. To avoid an overestimation of the number of flowers, we marked the last flower counted on the stalk and counted the flowers from this point during the observation made in the following week. The ripe pods were harvested every week. The weekly measures did not underestimate the number of flowers and ripe pods because flowers and ripe pods lasted longer than a week. We recorded the seed weight at the end of the experiment, as

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