

## Mutualism exploitation: predatory drosophilid larvae sugar-trap ants and jeopardize facultative ant-plant mutualism

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**Abstract.** An open question in the evolutionary ecology of ant-plant facultative mutualism is how other members of the associated community can affect the interaction to a point where reciprocal benefits are disrupted. While visiting *Qualea grandiflora* shrubs to collect sugary rewards at extrafloral nectaries, tropical savanna ants deter herbivores and reduce leaf damage. Here we show that larvae of the fly *Rhinoleucophenga myrmecophaga*, which develop on extrafloral nectaries, lure potentially mutualistic, nectar-feeding ants and prey on them. Foraging ants spend less time on fly-infested foliage. Field experiments showed that predation (or the threat of predation) on ants by fly larvae produces cascading effects through three trophic levels, resulting in fewer protective ants on leaves, increased numbers of chewing herbivores, and greater leaf damage. These results reveal an undocumented mode of mutualism exploitation by an opportunistic predator at a plant-provided food source, jeopardizing ant-derived protection services to the plant. Our study documents a rather unusual case of predation of adult ants by a dipteran species and demonstrates a top-down trophic cascade within a generalized ant-plant mutualism.

**Key words:** ants; *Drosophilidae*; extrafloral nectaries; indirect effects; insect herbivory; multitrophic interaction; mutualism disruption; top-down effects; trophic cascade; tropical savanna.

### INTRODUCTION

Mutualism is a beneficial pairwise interaction, the outcomes and effects of which are largely determined by the occurrence and actions of other species and other trophic levels (Boucher et al. 1982, Stanton 2003). Variation in the abundance of an associated species can affect the outcomes of mutualisms to a point where benefits no longer exist to one or both partners (Bronstein and Barbosa 2002). Exploiter species use services or resources inherent to a mutualistic interaction but provide no benefit in return (Bronstein 2001, Yu 2001). A main question about mutualisms is how their disruption by exploiters affects the community in which the mutualistic partners are inserted. Investigation of such exploiting species helps to explain the evolution and maintenance of mutualism, as well as its indirect effects on the associated community. Here we report on a newly discovered *Drosophilidae* species whose carnivorous larvae grow on

extrafloral nectaries of a tropical plant species and prey on nectar-feeding ants. Our field study demonstrates that predation on protective mutualistic ants cascades through three trophic levels, resulting in the disruption of reciprocal ant-plant benefits. This rare case of predation of adult ants by a dipteran species is unique by generating a top-down trophic cascade within a generalized ant-plant mutualism.

Ants (Formicidae) and flowering plants have crossed evolutionary paths for at least 100 million years (Wilson and Hölldobler 2005), and a variety of facultative and obligate ant-plant mutualisms have been studied in many types of terrestrial ecosystems (Rico-Gray and Oliveira 2007). Facultative ant-plant protective mutualisms are usually mediated by the offer of plant-derived food that attracts aggressive ants, which in turn deter herbivores and thus reduce the damage they inflict on the plant (Heil and McKey 2003). Plant-derived food resources may consist of nutritious food bodies (rich in lipids and protein) or sugar-rich secretions produced by extrafloral nectaries (Fig. 1a). Such food rewards, however, attract not only aggressive mutualistic ants but also many other organisms that visit the plant to complement their diets, such as nonprotective ants, bees, and spiders (Nahas

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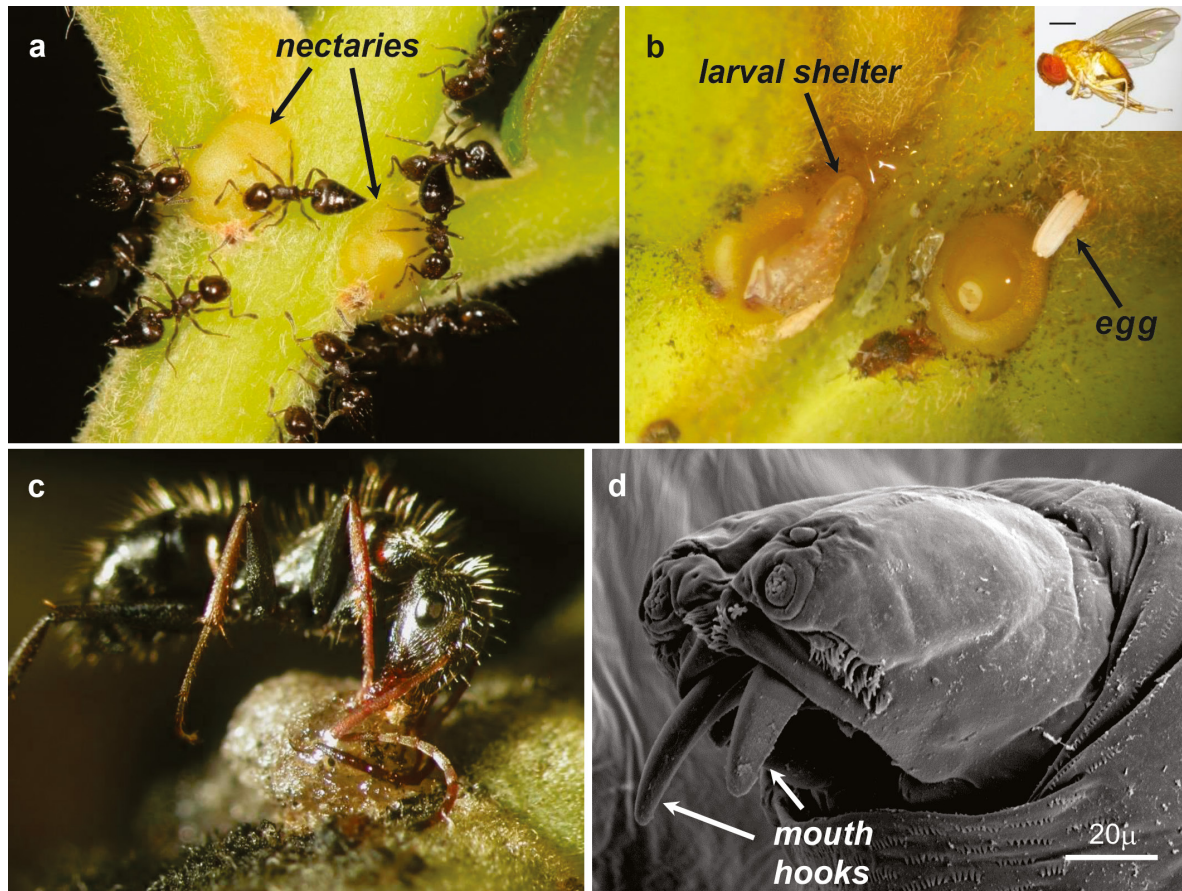


FIG. 1. Interaction between predatory larvae of *Rhinoleucophenga myrmecophaga* and nectar-feeding ants on *Qualea grandiflora*. (a) Workers of *Crematogaster* sp. gathering around a pair of extrafloral nectaries (EFNs). (b) Shelter of a first- (or early second-) instar larva and egg of *R. myrmecophaga* on top of EFNs. Inset photograph: adult fly; scale bar = 0.5 mm. (c) Worker of *Camponotus blandus* trapped at EFN; the ant will be sucked empty by the predatory larva (hidden in shelter). (d) Scanning electron micrograph of a third-instar larva of *R. myrmecophaga* showing mouth hooks used to strike at the ants' cuticle. See also Video S1.

et al. 2012, Koptur 2005, Sendoya et al. 2009). Although these opportunistic feeders can be regarded as mutualism exploiters, in most cases they do not cause direct harm to either the plant or mutualistic ants (Bronstein 2001, but see Gaume and McKay 1999).

Protective mutualisms between ants and plants are often considered as examples of trophic cascade, in which the negative effect of ants on herbivores results in positive indirect effect on the plants (Schmitz et al. 2004). Thus, the presence of an ant-preying exploiter may drastically affect the balance of the trophic cascade, to a point where it could cause the collapse of the mutualism. For instance, in the obligate mutualism between ant inhabitants and *Piper* plants (Piperaceae), ant-preying beetles end up negatively affecting ant-defended plants by decreasing the numbers of protective ants on foliage and indirectly causing increased herbivory (Dyer and Letourneau 1999). Among mutualism exploiters, those causing the death of one of the mutualistic partners are expected to have greater negative effects on the stability of the interaction compared to non-lethal exploiters (Bronstein

2001, Yu 2001). Disruption of mutualism through ant-predation, however, has never been shown in a facultative, generalized ant-plant mutualism.

Plants bearing extrafloral nectaries (EFNs) are abundant in the Brazilian "cerrado" savanna, where ant-plant-herbivore interactions are ubiquitous due to continuous ant attendance to these sugar-rich liquid rewards on foliage (Oliveira and Freitas 2004). *Qualea grandiflora* (Vochysiaceae) is a typical cerrado plant well-endowed with EFNs that are visited day and night by numerous nectar-gathering ants (Fig. 1a). Previous experimental work has shown that aggressiveness by visiting ants can deter potential herbivores and reduce herbivory levels to leaves of *Q. grandiflora* (Oliveira et al. 1987, Costa et al. 1992).

A newly discovered dipteran species, *Rhinoleucophenga myrmecophaga* (Drosophilidae), has been reported to oviposit on the EFNs of *Q. grandiflora*, on which larval development occurs (Vidal and Vilela 2015, Fig. 1b). Although the larvae construct a sticky shelter on top of the plant's glandular tissue, occupied EFNs are not

entirely obstructed and continue to secrete nectar and attract ants. Indeed, field observations revealed that dipteran larvae take advantage of persistent nectar secretion to feed on lured insects that end up trapped in their sticky shelter (Fig. 1c; Video S1). Predatory dipteran larvae remain in the shelter while feeding on trapped ants and use their mouth hooks (Fig. 1d) to strike at the exoskeleton of the victim, which is sucked empty.

This complex set of interactions is ecologically meaningful, because predatory dipteran larvae directly exploit both sides of what has been identified as a one-way consumer-resource mutualism (Holland et al. 2005): the consumer species (ants) benefit from liquid food produced by the resource species (*Q. grandiflora*), which in return benefits from reduced herbivory resulting from ant protection (Oliveira et al. 1987, Costa et al. 1992). This raises the question of whether mutualism exploitation by ant-preying *R. myrmecophaga* larvae can negatively affect ant protective services to the host plant, thereby jeopardizing this facultative ant-plant mutualism.

Here we report on a series of experiments in Brazilian cerrado designed to address the following questions: (1) Does the presence of *R. myrmecophaga* larvae reduce ant foraging constancy on foliage of *Q. grandiflora*, and decrease potential deterrent effects of ants on simulated herbivores? (2) If so, do plant branches that host dipteran larvae have decreased numbers of ants and, consequently, increased herbivore numbers? (3) Does the presence of ant-preying larvae generate a cascading effect resulting in increased herbivore damage on the plant?

## MATERIALS AND METHODS

### *Study area and organisms*

Field work was undertaken from March 2011 to February 2013 in an area of cerrado savanna at Itirapina (22°15' S, 47°49' W), state of São Paulo, southeastern Brazil. The vegetation consists of a dense scrub of trees and shrubs, which corresponds to the cerrado *sensu stricto* (Oliveira-Filho and Ratter 2002). The climate of the region is characterized by a dry/cold season from May to September and a rainy/warm season from November to March. *Qualea grandiflora* is a main representative of the cerrado flora, growing as shrubs and trees (0.5–10 m) at high densities in cerrado areas in southeastern Brazil (Oliveira et al. 1987). Plants have paired EFNs along the stem, next to the insertion of leaves (Fig. 1a), and are continuously visited by many ant species in the study area, several of which belong to the genus *Camponotus*. *Camponotus* ants are the most frequent visitors to EFNs on cerrado foliage and tend to behave aggressively towards herbivores on foliage (Sendoya et al. 2009, Sendoya and Oliveira 2015). Previous field experiments have shown that aggressiveness by visiting ants can deter potential herbivores and reduce leaf damage to *Q. grandiflora* (Oliveira et al. 1987, Costa et al. 1992).

### *Larval infestation and prey items of Rhinoleucophenga myrmecophaga*

Infestation levels by *R. myrmecophaga* on *Q. grandiflora* were evaluated on 40 plants (0.5–3.0 m tall) along eight transects (50 m from one another). On each tagged plant, we counted the number of larvae found on EFNs, and their location along the infested branch (apex/middle/base). Surveys were carried out in both hot/wet season (December 2009) and cold/dry season (July 2010). Given that *R. myrmecophaga* larvae suck empty their prey, the remaining exoskeletons of captured insects allowed us to identify to the generic level a good range of prey items ( $n = 78$ ) found on tagged plants.

### *Experiment 1: effect of Rhinoleucophenga myrmecophaga infestation on ant foraging constancy and ant deterrent potential*

Potential effects of ant-preying dipterans on ant constancy and ant-induced herbivore deterrence on leaves were investigated in March 2011 on 20 *Q. grandiflora* shrubs (0.5–2.0 m tall). In each shrub, we selected a pair of neighboring branches, which were randomly assigned as control or treatment. Branches in a pair were chosen based on the following criteria: they had the same height within the plant crown (upper third), had similar numbers of leaves (12–16), and had functional EFNs. All experimental branches had dipteran larvae, and for each pair we randomly assigned one branch as control and the other as treatment branch (larvae removed). We were not able to do the opposite (i.e., include larvae in control branches) because larval shelters are very delicate and any major disturbance could cause larval death. Control branches were infested by 2nd or 3rd instar larvae ( $2.7 \pm 0.9$  larvae per branch; mean  $\pm$  SD;  $n = 20$ ). Removal of larval shelters from treatment branches apparently did not damage the nectary tissue or nectar production, and ant visitation to EFNs continued after larval removal. Branches not involved in the experiment were removed or isolated with Tanglefoot® resin (Grand Rapids, MI, USA) to prevent ant access. Aggression of visiting ants toward potential herbivores was evaluated by using live termite workers of *Nasutitermes* sp. (Termitidae) as simulated herbivores on experimental branches. Termites are commonly seen on *Q. grandiflora* (Lima-Ribeiro et al. 2006) and have already been used as live baits to assess ant aggressiveness on this plant species (Oliveira et al. 1987). One termite was glued by the dorsum (agitated legs upwards) on the basal third of each of two apical leaves of either branch in a pair ( $n = 40$  termites in each branch class). The fast-drying adhesive (Colapel® plastic glue, Brazil) had no detectable effect on ant behavior (Oliveira et al. 1987, Oliveira 1997). Once all termites were distributed on a branch pair, we waited 30 s before recording data on ant activity. We then recorded the amount of time each experimental branch was occupied by ant foragers within a 10-min period, and at the same time the number of live termites attacked by



ants on the apical leaves in either branch category. Trials were performed intermittently, during sunny days, between 09.00 and 16.00 h.

*Experiment 2: effect of *Rhinoleucophenga myrmecophaga* infestation on ant and herbivore numbers and on herbivory*

Potential cascading effects from ant predation by *R. myrmecophaga* larvae were experimentally investigated from November 2012 to February 2013. We tagged 33 shrubs (0.5–2.0 m tall) in early November, when dipteran eggs and larvae begin to appear on the EFNs of *Q. grandiflora* (Fig. 1b). In each shrub, we selected a pair of experimental branches in the same categories and under the same procedure as described previously: one dipteran-occupied branch (control;  $2.8 \pm 1.1$  larvae per branch;  $n = 33$ ) and one dipteran-free branch (treatment). Because the experiment was set early in the rainy season, we regularly checked and removed new eggs and early-instar larvae from treatment branches. Branches not involved in the experiment were removed or isolated with Tanglefoot® resin to prevent ant access. To increase the chance that experimental plants would be visited by potentially mutualistic ants, we selected shrubs whose EFNs were attended mainly by *Camponotus* ants, which are aggressive and deter herbivores on leaves of *Qualea* (Oliveira et al. 1987, Nahas et al. 2012). Once the experimental branches were established, all arthropods were removed from the foliage of selected plants (except for *R. myrmecophaga* larvae on control branches). We allowed 2 weeks before taking data on experimental branches. We recorded the number and identity of arthropods on control and treatment branches at intervals of 1–2 weeks over 2 months, from 01 December 2012 to 03 February 2013. Records included visiting ants and other arthropods; the latter were categorized as chewing or sucking herbivores, or predators (mostly spiders). Our censuses lasted 10 min per plant and we carried them out during diurnal (09.00–12.00 h, 14.00–17.00 h) and nocturnal sessions (20.00–24.00 h). The leaf area consumed by herbivores was measured in experimental branches at 30-d intervals from November 2012 to February 2013. By the time control and treatment branches were established (early November), most leaves were still very young and leaf area (treatment =  $355.52 \pm 175.87$  cm<sup>2</sup>, control =  $388.99 \pm 208.12$  cm<sup>2</sup>;  $Z_{24,1} = 1.2$ ,  $P = 0.2301$ ) and herbivore damage (treatment =  $3.92 \pm 4.31$  cm<sup>2</sup>, control =  $3.63 \pm 3.69$  cm<sup>2</sup>;  $Z_{24,1} = 0.973$ ,  $P = 0.3304$ ) did not differ between experimental branches. Leaf area lost to herbivory was calculated by photographing leaves with a Nikon D5100® digital camera and using ImageJ® software (Rasband 1997–2012).

*Statistical analyses*

All analyses were performed in R 2.15.2 environment (R Core Team 2012). To compare the infestation levels in the summer and winter and on each region of the

branches, we used chi-square test. Ant foraging constancy on the two types of experimental branches was compared using a paired Student *t*-test. The number of live termite baits attacked by ants on each branch category was analyzed with a G-test with Yates's correction. We employed generalized linear mixed models (GLMMs) to investigate the abundance of arthropods and leaf damage on experimental branches through time. We included the experimental branches nested within each plant over time fitted as the random terms, and the type of experimental branch (occupied or not by dipteran larvae) fitted as the fixed term. For each model of arthropod abundance, we tested for Poisson, binomial or negative binomial distributions since the data did not follow a normal distribution and were all count data (Crawley 2007). We fitted the models involving chewing herbivore and predator abundances as response variables by using Poisson error distribution. In the models with ant and sucking herbivore abundances as response variables, we used negative binomial distribution. To analyze herbivore damage on experimental branches, we used GLMM with Gamma error distribution. For this model we used the total leaf area removed by herbivores in each branch category as our response variable. Herbivore damage was evaluated as the sum of the leaf area removed by chewing herbivores for all leaves of each branch category since their establishment early November. Since herbivory levels were initially the same in control and treatment branches (see above), initial leaf damage was not included in the analyses. Potential damage by sucking herbivores was not apparent and thus was not measured. We tested for overdispersion in each model by dividing the residual deviance by the residual degrees of freedom, and found that none of our models were overdispersed.

## RESULTS

*Infestation pattern and insect prey of *Rhinoleucophenga myrmecophaga* larvae*

The frequency of *R. myrmecophaga* infestation on *Q. grandiflora* in the study area varies from 45% (dry season) to 85% (rainy season) of the shrubs sampled. In the rainy season, plants hosted  $4.80 \pm 4.48$  fly larvae (mean  $\pm$  SD;  $n = 40$  plants) and  $1.60 \pm 1.13$  larvae per infested branch ( $n = 86$  branches). On average, plants had 33.8% of active nectaries occupied by dipteran larvae. Apical and middle branch portions (young and adult leaves) tended to have increased numbers of active EFNs compared to basal branch portions (old leaves), and dipteran infestation decreased accordingly from young (58%) to adult (40%) and old foliage (2%) ( $\chi^2 = 67.58$ ;  $P < 0.001$ ;  $df = 2$ ;  $n = 134$  larvae from 40 plants).

The vast majority of captured prey (94%) consists of nectar-feeding ants; flies, wasps and beetles account each for 1–4% of all records ( $n = 78$ ). Predatory dipteran larvae remain in the shelter while feeding on trapped ants and use mouth hooks to strike at the exoskeleton of the victim,

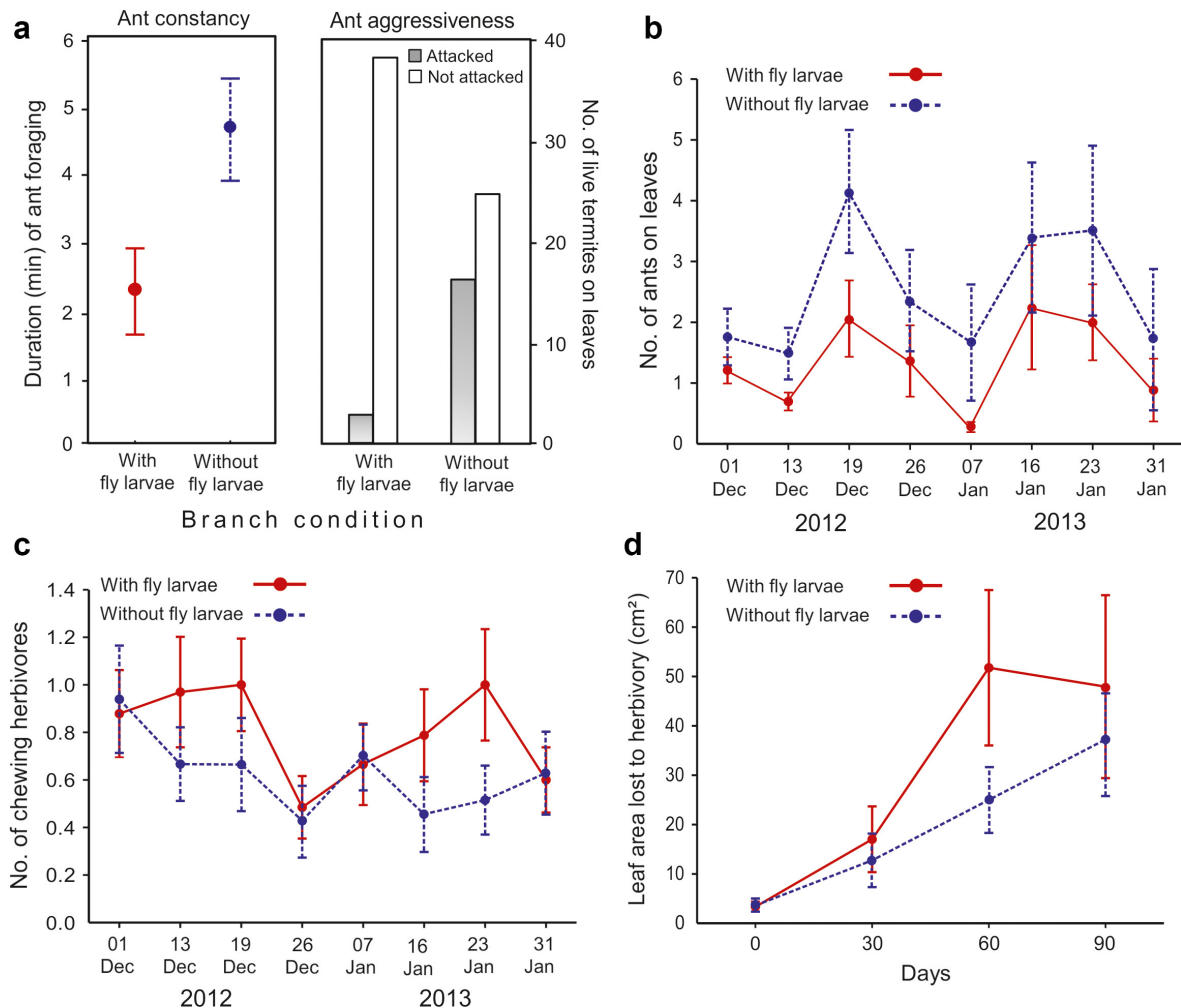


FIG. 2. Direct and indirect effects of *Rhinoleucophenga myrmecophaga* infestation on ant and herbivore numbers, and herbivory levels on *Qualea grandiflora* shrubs. (a) Left: Ant foraging constancy on paired experimental branches, with or without ant-preying fly larvae. Values are means  $\pm$  1 SE ( $n$  = 20 plants with paired branches). Right: Aggressiveness by ant foragers as expressed by attacks to live termites on leaves of either type of branch ( $n$  = 40 termites in each category; 2 termites per branch). (b) Number of ant foragers and (c) of chewing herbivores through time on paired experimental branches. (d) Leaf damage by chewing herbivores on paired experimental branches along 3 months, from November 2012 to February 2013. Values are means  $\pm$  1 SE ( $n$  = 33 plants).

which is sucked empty (Fig. 1d). Ants from 10 genera were recorded to fall prey to dipteran larvae in the field (Video S1); the most common were *Brachymyrmex* (27% of all prey items), *Camponotus* (26%), *Crematogaster* (10%) and *Wasmannia* (9%) ( $n$  = 78 prey items).

#### *Predatory dipteran larvae reduce ant foraging constancy and aggressiveness*

Ant-preying *R. myrmecophaga* larvae had a significant negative effect on the time spent by ants (i.e., foraging constancy) on *Q. grandiflora*; visiting ants remained for less than half the time on dipteran-infested compared to dipteran-free branches ( $t_{19,1} = 2.6$ ,  $P = 0.017$ ; Fig. 2a). Decreased ant constancy on foliage resulted in significantly lower numbers of live termite-baits being attacked by ant foragers

on branches infested by ant-preying larvae than on uninfested branches ( $G = 10.5$ ,  $P = 0.0012$ ; Fig. 2a). The ant genera most frequently seen on *Q. grandiflora* shrubs ( $n$  = 20) used in this experiment were *Camponotus* (25% of the plants), *Pseudomyrmex* (15%), *Crematogaster* (10%), *Brachymyrmex* (5%), *Wasmannia* (5%), and *Cephalotes* (5%). Ants in the genus *Camponotus* were responsible for 47% of the termites attacked on *Q. grandiflora* ( $n$  = 19), followed by *Crematogaster* (21%), *Pseudomyrmex* and *Cephalotes* (5% each).

#### *Predatory dipteran larvae facilitate herbivory through reduced ant abundance*

The 3-month experiment using paired branches confirmed that predation on nectar-gathering ants by

*R. myrmecophaga* larvae cascaded through the interaction system. The number of visiting ants through time was significantly lower on dipteran-infested than on dipteran-free branches of *Q. grandiflora* ( $Z_{32,1} = -2.06$ ,  $P = 0.039$ ; Fig. 2b). The negative effect of ant-preying larvae on ant numbers was accompanied by a positive indirect effect on the abundance of chewing herbivores through time ( $Z_{32,1} = 2.07$ ,  $P = 0.039$ ; Fig. 2c), which in turn led to higher levels of leaf damage on dipteran-infested than on uninfested branches of *Q. grandiflora* ( $Z_{30,1} = 2.09$ ,  $P = 0.037$ ; Fig. 2d). A total of 47 ant species were recorded on *Q. grandiflora* shrubs (different plant individuals from previous experiment) during day and night censuses over the 3-month experiment; the ant genera most frequently seen were *Brachymyrmex* (100% of the plants), *Camponotus* (78%), *Pseudomyrmex* (63%), *Crematogaster* (48%), and *Cephalotes* (42%). Of all chewing herbivores recorded ( $n = 341$ ), leaf beetles (27.5%; Coleoptera: Chrysomelidae) and *Compsolechia* caterpillars (18.4%; Lepidoptera: Gelechiidae) were the most commonly seen on experimental *Q. grandiflora* shrubs.

Sucking herbivores ( $Z_{32,1} = 0.11$ ,  $P = 0.92$ ) and predatory arthropods ( $Z_{32,1} = -0.68$ ,  $P = 0.493$ ) were equally abundant through time on the two types of experimental branches (fly-infested/uninfested) of *Q. grandiflora*. Among sucking herbivores ( $n = 2626$ ), we recorded mainly scale insects (51.4%; Hemiptera: Coccoidea; some of which attended by ants) and leafhoppers (20.5%; Hemiptera: Cicadellidae). Spiders (Araneae) represented 92.9% of the predatory arthropods seen on *Q. grandiflora* ( $n = 513$ ).

## DISCUSSION

Here we have shown that the drosophilid *Rhinoleucophenga myrmecophaga* uses the EFNs of *Qualea grandiflora* as sites for larval development to lure nectar-gathering ants and consistently prey on them (Fig. 1b,c). Predation on ants by fly larvae caused cascading effects through three trophic levels, resulting in fewer ant foragers on leaves, increased herbivore numbers, and greater leaf damage (Fig. 2a–d). Mutualistic benefits between ants and *Q. grandiflora* are thus jeopardized by predatory fly larvae.

Ants represent an extremely abundant food resource, but their structural and chemical weapons associated with aggressive behavior (Hölldobler and Wilson 1990) pose problems for capturing adult ants with safety and require morphological and behavioral specializations by the predator (e.g., Oliveira and Sazima 1984). Predation on ant brood, however, is more common and has been registered for a few dipteran families and several other arthropod groups that live asinquilines in ant nests (Hölldobler and Wilson 1990). Our research on *R. myrmecophaga* provides the first report of ant predation among the few carnivorous Drosophilidae (Ashburner 1981, Vijendravarma et al. 2013), and represents a rather unusual case of predation on adult ants among Diptera.

*Rhinoleucophenga myrmecophaga* is a generalized ant predator, since at least 15 ant species (10 genera) were trapped by the predatory larvae, roughly in the same frequency as they visited *Q. grandiflora*. Moreover, these predatory larvae have also been observed on EFNs of other species in the study area, such as *Qualea multiflora* and *Bauhinia rufa* (Fabaceae) (Vidal and Vilela 2015). The feeding strategy of *R. myrmecophaga* is peculiar because ant-preying larvae develop at the very location on the host plant where potential prey are mostly seen: the actively ant-visited EFNs of *Q. grandiflora* (Fig. 1a,b). A similar “sit-and-wait” strategy is seen in flower-dwelling spiders that disrupt plant-pollinator mutualisms by preying on visiting pollinators, ultimately decreasing seed production (Suttle 2003).

Although larvae of *R. myrmecophaga* are not active predators (i.e., that search for prey), their presence on *Q. grandiflora* branches is sufficient to decrease ant visitation as well as the ants’ potential to deter chewing herbivores. Branches of *Q. grandiflora* infested by dipteran larvae might have been avoided by ants mainly for two reasons: limited access of ants to the resource (extrafloral nectar) and/or increased predation risk for visiting ants. Although EFNs remain active when occupied by dipteran larvae, the presence of these insects can constrain the direct access of ants to the liquid resource compared to dipteran-free EFNs (Fig. 1a,b). Indeed, removal of nectar reward by an exploiter has already been shown to discourage subsequent visitation by ant mutualists (Gaume and McKey 1999). In addition, ants can decrease or completely stop foraging at risky plant locations, switching their foraging activity to safer places where predation pressure is less severe (Nonacs 1990). As such, the mere presence of ant corpses at EFNs occupied by predatory larvae, or chemical cues released by trapped ants (see Video S1), may signal to visiting ants that dipteran-occupied branches are risky and/or less rewarding.

Although mutualism exploiters can negatively affect the fitness of mutualists, their effect on reciprocal benefits can vary from extremely negative to neutral (Bronstein 2001, Yu 2001). Exploitation of facultative, EFN-mediated ant-plant mutualisms usually results in no major effect on the plant, since the cost of producing extrafloral nectar is low and visitation by mutualistic ants is not ceased (Bronstein 2001, Koptur 2005, but see Rutter and Rausher 2004). Our current study is unique in demonstrating that exploitation of EFNs by the drosophilid *R. myrmecophaga* allows these carnivorous larvae to consistently prey on aggressive visiting ants such as *Camponotus* spp. (Fig. 1c; Sendoya et al. 2009, Sendoya and Oliveira 2015), ultimately resulting in increased herbivore damage. The experimental results and patterns of dipteran infestation suggest a possible negative effect of ant-preying larvae on plant fitness. However, it is necessary to measure how cascading effects at the branch level translates into overall fitness effects at the individual level, both in terms of herbivory and reproductive output.

The interaction involving predatory *R. myrmecophaga* larvae and the facultative mutualism between visiting ants and EFN-bearing *Q. grandiflora* has parallels to the interaction involving ant-preying *Tarsobaenus letourneauae* beetles (Cleridae) and the more specialized mutualism between *Pheidole bicornis* ants and myrmecophytic *Piper cenocladum* shrubs (Piperaceae). In this system too, cascading effects result in increased herbivore damage and ant-preying beetles also consume plant-produced food bodies offered to ant inhabitants (Dyer and Letourneau 1999). These similarities demonstrate that mutualism exploitation through ant predation and consumption of plant-derived food can occur in both specialized (species-specific) and facultative (generalized) ant-plant mutualisms, and in either case can be costly enough to generate cascading effects that disrupt the mutualism. To our knowledge, this rare case of predation of adult ants by a dipteran species is the first demonstration of a top-down trophic cascade within a generalized ant-plant mutualism.

Our study enhances our understanding of the pervasiveness and complexity of ant-plant-herbivore interactions in cerrado savanna. We reveal a peculiar mode of mutualism exploitation by an opportunistic and rather unusual predator, which eventually jeopardizes ant-derived protection services to the plant. Our results are relevant in showing that even in generalized mutualisms, detrimental effects of exploiters can be costly enough to disrupt reciprocal benefits between mutualistic partners. Remarkably, exploitation effects cascaded through the whole interaction system, altering the overall abundance and trophic role of associated ant and herbivore communities.

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