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Coexistence of Aphid Predators in Cacao Plants: Does Ant-aphid Mutualism Play a Role?

EN Silva[1] and I Perfecto[2]

1 - Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil.
2 - University of Michigan, Ann Arbor, Michigan, USA.

Corresponding author

Evandro N. Silva
Univ. Estadual de Feira de Santana
Depto. de Ciências Biológicas
Av. Transnordestina s/n
Feira de Santana, BA
44036-900 Brazil
E-Mail: evandro@uefs.br

Abstract

Mutualism between ants and hemipterans that produce honeydew has important implications for biological control because hemipterans defended against predators can reach economic injury levels. We tested the hypothesis that ant-aphid mutualism can mediate competition and promote the coexistence of aphid natural enemies. A quadrate in the field measuring 30 x 30 meters (10 plants in 10 rows = 100 plants) was established in a cacao plantation and a whole quadrate survey was carried out in vegetative shoot flushings from the trunk. The number of ants and predators, the identity of ant and natural enemy species and colony occupancy by ants were recorded. Spatial association indexes were used to evaluate the degree of overlap in ant-ant and ant-predator spatial distributions. The ant *Crematogaster victima* F. Smith was selected for a test on differences in its attack behavior against larvae of the syrphid *Ocyptamus antiphates* (Walker) and a species of ladybird beetle (Coleoptera: Coccinelidae). Five species of ants were found tending aphids more frequently and their level of spatial association was slightly negative with remarkable mutual exclusion from aphid colonies. Two of them, *Cr. victima* and *Cr. erecta* Mayr, were potential defendants of aphids and were selected to study their spatial association with the distribution of natural enemies. It was found that spatial association between ants and aphid predators is slightly positive. The results suggest that the occurrence of attack behavior of *Cr. victima* against syrphids, but not against coccinellids, can increase coexistence of predators by generating independent spatial distribution.

Introduction

Arboreal foraging ants are the most abundant group of arthropods in the canopy of trees in forests and structurally complex managed ecosystems in the tropics (Adis et al., 1984; Perfecto et al., 1997). A well known characteristic of ant communities in natural forests and in tree-based cropping systems is the existence of a three-dimensional mosaic determining the spatial distribution of ant species (Majer, 1972; Leston, 1973; Majer & Camer-Pesci, 1991; Armbrecht et al., 2001). This mosaic is comprised of a group of dominant species which are territorial and tend to have mutually exclusive distribution patterns, a sub-dominant group with species that have high number of individuals but do not hold large territories and non-dominants which occur in between or are tolerated within the territories of dominant species (Majer et al., 1994; Dejean et al., 2003).

The spatial distribution of ants in a three-dimensional mosaic has important implications for biological control of insect pests in agroforestry systems (Perfecto & Castiñeiras, 1998; Dejean et al., 2003; Philpott & Armbrecht, 2006). In Africa, dominant arboreal ants have been effective against defoliator insects in cacao and coconut plantations (Majer 1976a, b; Bigger, 1993). In Bahia, Brazil, Majer & Delabie (1993) also found ants to be potential biological control agents of cacao pests. Nevertheless, ant mosaics are essentially structured by the interaction of ants with hemipterans that produce honeydew as energy source (Floren & Lisenmeir, 2000; Delabie, 2001; Vandermeer et al., 2008) and hence along with effective biological control of other herbivores it is also desirable that hemipterans protected by ants do not cause economic loss. Perfecto and Castiñeiras (1998) highlight two situations in which this goal can be achieved in cacao plantations. First, when the hemipterans protected by ants are not significant

pests of the crop and, second, when hemipterans are pests but a much more noxious pest is effectively controlled by ants attracted by hemipteran honeydew.

Overall, interactions between ants, hemipterans, other herbivores, other predators and the crop are complex and have to be evaluated, at least qualitatively, in order to develop effective and sustainable pest management programs (Perfecto & Castiñeiras, 1998). One aspect of these interactions that requires attention both for theoretical comprehension of predator-prey dynamics and applied biological control is the ability of ants to defend tended hemipterans from the attack of predators. It can be hypothesized that ants that tend aphids are prone to defend them from predators and parasitoids and, by doing so, they can also determine spatial distribution of natural enemies and effectiveness of biological control. An empirical example in a natural ecosystem (Brazilian Savanna – the so called Cerrado) showed that spiders, parasitoid wasps and syrphid larvae had a reduction in their density when colonies of the treehopper *Guayaquila xiphias* (Membracidae) were tended by ants that attacked these natural enemies (Del-Claro & Oliveira, 2000). Another example in support for this hypothesis was found by Michaud and Browning (1999) whom observed that the imported fire ant *Solenopsis invicta* Buren was ubiquitous and the most common species in attendance of the brown citrus aphid *Toxoptera citricida* (Kirkaldi) in citrus groves in Puerto Rico. In this study, the observed frequency of larvae of syrphid flies and coccinellid beetles in colonies of *T. citricida* was lower than what would be expected by chance, indicating an impact of *S. invicta* in the distribution of natural enemies of *T. citricida*.

In traditional coffee farms in southern Mexico, the mutualism between the ant *Azteca instabilis* F. Smith and the green scale *Coccus viridis* (Green), offers protection against the adult coccinellid *Azya orbigera* Mulsant, thus driving the distribution pattern of *C. viridis* (Vandermeer & Perfecto, 2006; Vandermeer et al., 2010).

Toxoptera aurantii (Boyer de Fonscolombe) is an aphid that develops colonies in patchy and short-lived leaf flushes of cacao. Species of predators belonging to the families Syrphidae and Coccinellidae and the order Neuroptera have been recorded in different regions of the world (Entwistle, 1972; Kauffman 1973; Firempong & Kumar, 1975; Cortez-Madrigal, 1996). These records indicate that the guild of *T. aurantii* predators consists of four to seven species from local to regional scales, respectively. The predators are very effective in reducing aphid populations even in low densities because they attack aphid colonies when aphid density is still low (E. N. Silva, unpublished data). Furthermore, there is a good synchronization of predator and prey colonization, predators are able to reach optimum prey consumption at higher prey densities and there is a complementary action of the different predator species (Firempong & Kumar, 1975). This phenomenon of complementary effects was also observed by Nahas et al. (2012) regarding herbivory reduction as an effect

of multiple predators.

Up to date, there is no detailed study on the interaction between ants and predators of *T. aurantii*. Our study aimed to investigate the degree of spatial association between ants and natural enemies of *T. aurantii* in a cacao plantation as well as the attack behavior of the ant *Cr. victima* against two predaceous species. We tested the hypothesis that ant-aphid mutualism determines the spatial association and coexistence of predators of *T. aurantii*.

Material and Methods

Spatial Association

On March of 2006 a survey was carried out in an experimental area of the Cacao Research Center, in Ilhéus, Bahia, Brazil (14º47'45''S - 39º11'21''W). A whole quadrate survey was conducted to quantify populations of *T. auranti*, its predators and mutualistic ants. The quadrate consisted of 100 cacao plants, in an array of 10 rows with 10 consecutive plants (an area of 30 x 30 m). Aphids and natural enemies were counted once only in vegetative shoot flushings arising from the tree trunk up to 1.5 m height. All colonies present in the chupons flushing from the trunks were included in the survey. The survey was carried out once. In each observed colony the presence or absence, species identity and number of ants, larvae of hoverflies, ladybird beetles and lacewings were recorded.

Attack behavior of ants against two predators

During a survey of specimens of *T. aurantii* and its predators for species identification it was noticed that aphid colonies tended by the ants *Cr. erecta* and *Cr. victima* (E. N. Silva personal observation) seemed to have less syrphid larvae than colonies not tended by the ants. These two ant species were seen attacking Syrphidae larvae after encounters in the colonies. On the other hand, no attack of ants against larvae of coccinellids was observed. A behavioral experiment was set up in the field in order to test for differences in the frequencies of attack and removal of larvae of the syrphidae *Ocyptamus antiphates* (Walker) and a unidentified species of ladybird beetle (Coccinellidae) by workers of *Cr. victima*. This species was the one chosen for experimentation because it was numerically easier to find them tending aphids, making replication possible in our study.

A day before the experiment 20 first instar larvae of *O. antiphates* were collected in the field and kept in the laboratory in petri dishes with abundant food (nymphs of *T. aurantii*). Thus, under food satiation, they would simply set down and not search for prey when put in the presence of aphids in the behavioral trials. Larvae of the Coccinellidae species proved to be more sensitive to manipulation and thus another method was used to manipulate them. It consisted of locating

individual larvae established in aphid colonies in trees where workers of *Cr. victima* were foraging. The ants foraging in the branch to which the colony belonged to were assumed to have previous experience with the individual larvae and were brushed away. Then, ants from neighbor branches (supposedly without previous experience with individual larvae) were allowed to forage in the colony where the coccinellid larvae were present. A five minute count was started whenever a minimum number of three *Cr. victima* workers were foraging in the cacao leaf harboring aphids and one coccinellid larva. The following behaviors were quantified during the five minute counting: 1) events of attack and/or removal of the larva; 2) number of ants at the beginning of trial; and 3) mean time (in seconds) at which first encounter and attack occurred. After the trial, the coccinelid larva was removed with a needle. Then, one larva of *O. antiphates* was placed in the same leaf and trial procedures were carried out as described before.

Species identity

The identity of *O. antiphates* (Walker) larvae was established by observation of color pattern (transparent body and white dorsal fat bodies) (Fig. 1a). The brown lacewing *Nusalala tessellata* Gerstaecker has very conspicuous larvae and hence its identity was easily established in the field (Fig. 1b). One morphospecies of Coccinellidae is still to be identified, but its larva is very conspicuous and, hereafter, it is referred to as Coccinellidae specie (Fig. 1c). Ants were identified in the field up to the generic level and then categorized in morphospecies for observation purposes, following sampling of specimens for identification in the Cacao Research Center. *Ectatomma tuberculatum* (Olivier) was the only species directly identified in the field. Vouchers of the ant biological material are deposited in the Myrmecology Laboratory collection in this research center.

Data Analysis

The spatial association between paired species (ant-ant and ant-predator) was determined by an index of spatial association (the four point correlation coefficient) according to the following equation (Sevenster, 1996):

$$\varphi = ad\text{-}bc/\sqrt{[(a+b)(c+d)(a+c)(b+d)]};$$

where *a*, *b*, *c* and *d* are the number of colonies in the four cells of a standard 2 x 2 absence-presence contingency table for the frequencies of two competing predator species; *a* and *d* refer to cells containing double absences and double presences, respectively. The index value ranges from -1 to +1, representing respectively high negative and positive spatial association between two species.

A linear regression analysis was carried out to test for a significant relationship between the number of ants present in an aphid colony and the time of first attack. A Chi-square test was performed to test whether aphid tending frequencies represented an association between the five most frequent tending ant species and *T. aurantii*. A Fisher's Exact Test was carried out to test for differences in ant attack behavior against two species of predators using the statistical software SPSS for Windows 13.0. A 0.05 significance level was used for statistical inference in these tests.
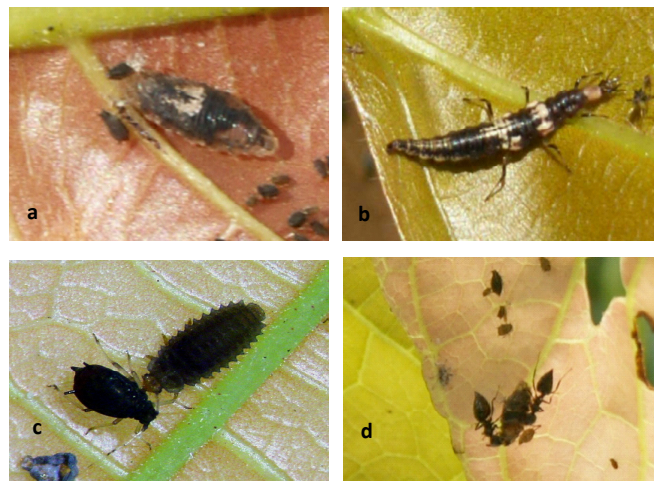

Figure 1. a) Larva of *Ocyptamus antiphates*; b) larva of *Nusalala tessellata*; c) larva of Coccinellidae sp; d) Larva of *Ocyptamus antiphates* attacked by two workers of the ant *C. victima*.

Results

Ants surveyed

There were nine species of ants present in 42 out of 211 colonies of aphids observed in 100 plants. The most frequent species were *Cr. erecta*, *Cr. victima*, *E. tuberculatum*, *Dolichoderus bidens* L. and *Pseudomyrmex gracilis* (Fabricius). They were present in 9, 7, 10, 17 and 13 colonies respectively. A Chi-square test (a 5 x 2 contingency table) allowed verifying that these frequencies do not support a hypothesis of association between ant species and *T. aurantii* different from what would occur by chance ($\chi^2 = 5,73$; g.l = 5; P = 0,37). Other less frequent species included *Cephalotes atratus* (L.), *Camponotus fastigatus* Roger, *Camponotus (Myrmaphaenus)* sp. and *Ectatomma brunneum* Smith (Fig. 2).
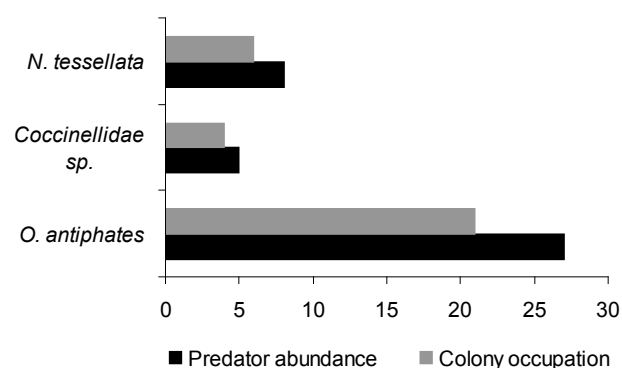

Figure 2. Total number of predators and colony occupation in 211 surveyed colonies of *Toxoptera aurantii*.

Spatial association

All association indexes for pairs of ant species showed slightly negative to neutral values (range = -0.07 to 0), except for the pair *Cr. victima – P. gracilis* which had a slightly positive index (Table 1). This trend towards negative spatial association is remarkably determined by the fact that all ant species pairs, except *Cr. victima – P. gracilis*, never had overlapped distribution even in a single colony. The spatial distribution of ants was very segregated at the colony level. The majority of the colonies of *T. aurantii* were not tended by ants. The number of colonies occupied by ants ranged from a maximum of 17 out of 211 for *D. bidens* to a minimum of 7 out of 211 for *Cr. erecta* (Fig. 3).

The association indexes for the pairs of species *O. antiphates - Cr. erecta* and *O. antiphates – Cr. victima* were slightly positive. Coccinellidae sp. as well as *N. tesellata* had

Table 1 – Indexes of spatial association between ants in 211 colonies of *Toxoptera aurantii* surveyed in a field quadrate in Ilhéus, BA, Brazil.

	Cr. erecta	Cr. victima	E. tuberculatum	D. bidens
Crematogaster erecta				
Crematogaster victima	-0.04			
Ectatomma tuberculatum	-0.04	-0.05		
Dolichoderus bidens	-0.05	-0.06	-0.07	
Pseudomyrmex gracilis	-0.05	0.14	-0.06	0.0

a slightly negative association with *Cr. erecta* and a slightly positive association with *Cr. victima* (Table 2). The spatial association index for the pair of species *O. antiphates* – Coccinellidae sp. was -0.05. The other association indexes were slightly positive (Table 3). Very few aphid colonies had natural enemies present during the survey. The number of colonies with the respective presence of syrphid, ladybird beetle and lacewing larvae were 21, 4 and 7 out of 211. The abundance of predators was also very low (Fig. 3).

Table 2 – Indexes of spatial association between arboreal ants and species of predators of *Toxoptera aurantii* in 211 colonies surveyed a field quadrate in Ilhéus, BA, Brazil.

	Crematogaster erecta	Cr. victima
Ocyptamus antiphates	0.11	0.09
Coccinellidae sp.	-0.03	0.14
Nusalala tessellata	-0.02	0.09

Table 3 – Indexes of spatial association between species of predators of *Toxoptera aurantii* in 211 colonies surveyed a field quadrate in Ilhéus, BA, Brazil.

	O. antiphates	Coccinellidae sp.
Ocyptamus antiphates		
Coccinellidae sp.	-0.05	
Nusalala tessellata	0.10	0.18

Attack behavior of ants against two predators

Three ants were observed attacking larvae of *O. antiphates* during the plot survey: *Ce. atratus* (one event), *Cr. erecta* (two events) and *Cr. victima* (two events). The ant *Ce. atratus* was foraging on the cacao leaf infested with aphids when encountered and palpated the syrphid larva with the antennae, then grabbed the larva with the jaw and threw it out of the colony. The whole process from encounter to removal lasted about five seconds. The attack behavior of *Cr. erecta* and *Cr. victima* consists of two phases. They were generally tending aphids and when they reached a part of the colony with a larva they palpated the larva with antennae for some time (from a few to 40 seconds) and then inflicted jaw bites and stings on the larva. Most frequently, the larvae were encountered by one ant, but after this ant engaged in the attack other ants came together and the removal effort started. It is appropriate to say that there was a handling stage (after the biting/stinging stage and before removal). The removal stage consisted either of the larva being dropped on the ground or carried out to the ant nest. All three species occurred in less than 10 colonies inside the survey plot but *Cr. victima* was more abundant in other plants outside the survey plot. Therefore, *Cr. victima* was selected for a comparative study of attack behavior against Syrphidae and Coccinellidae larvae. This ant presented a distinct attack behavior when in contact with *O. antiphates* or Coccinellidae sp. The Fisher's Exact test showed that the frequency of attack against *O. antiphates* was higher (9 in 12 trials) than it would be expected by chance (4.5 in 12 trials; n=12; d.f. = 1; p<0.001) while there was never a single event of attack against Coccinelidae sp. Attacks to syrphid larvae consisted either of jaw bites or stings. Regarding events of removal, only syrphid larvae were removed by the ants (3 in 12 trials). Nonetheless, based on the Fisher's Exact test the frequency of removal events was not significantly different (n=12; d.f. = 1; p=0.21) from what would be expected by chance (2 in 12 trials). The lack of significance occurred because some attacked larvae were successful in defending themselves against the attacks. Some syrphid larvae regurgitated a substance over the ants engaged in the attack. After
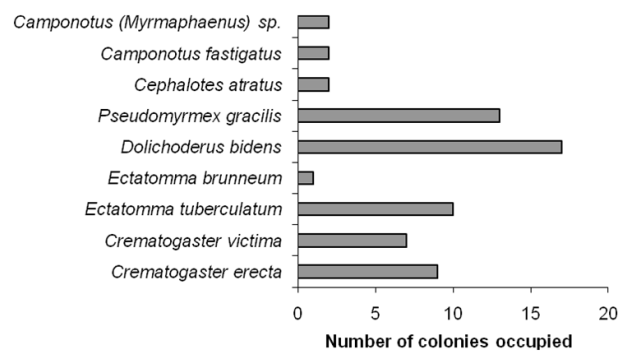

Figure 3. Colony occupation by ants in 211 surveyed colonies of *Toxoptera aurantii*.

the substance was in contact with the ants' tegument they presented a shaking/trembling behavior for a few seconds and then disengaged and failed to proceed towards the removal phase of the attack.

The mean number (±SE) of ants present in the aphid colony during the 300 seconds trial was 6.1±1.70 (n=9). The mean time (±SE) for first attack on a syrphid larva by ants was 121.9±28.02 seconds (n=9). A linear regression analysis did not show a significant relationship between the number of ants present in an aphid colony during the trial and the time of first attack (R^2=0.05; F=0.36; p=0.56). The increase in the number of foraging ants does not increase the probability of a faster attack against syrphid larvae.

Discussion

Although ant-hemipteran mutualisms are prevalent in nature, we were able to find only one other study about ants protecting aphids against predators in cacao agroecosystems in Bahia. Silva (1944) mentioned that the ants *Azteca chartifex* Forel, *D. bidens* and *Solenopsis geminata medusa* Mann. tended and protected *T. aurantii* against natural enemies. In our study three new ant species that protect aphids against predators are recorded. We also provide details on the defensive behavior of *Cr. victima* benefiting from aphids in cacao. It is very conspicuous that the attack of *Cr. victima* is frequent against *O. anthiphates* larvae, but not at all against coccinellids.

One possible mechanism causing this difference in the attack behavior of *Cr. victima* against one predator but not against the other is chemical mimicry of aphids by their predators. Lohman *et al.* (2006) studied profiles of cuticular hydrocarbons (CHCs) from the North American woolly alder aphid, *Prociphilus tessellatus* (Hemiptera: Aphididae), their tending ants, and three species of aphid predators: *Feniseca tarquinius* (Lepidoptera: Lycaenidae), *Chrysopa slossonae* (Neuroptera: Chrysopidae) and *Syrphus ribesii* (Diptera: Syrphidae). The results showed that while the CHC profile of each predatory species was distinct, each was chemically more similar to the aphids than to tending ant species. Furthermore, the CHCs of each predator species were a subset of the compounds found in the aphids' profile. Therefore, by producing or acquiring CHC compounds similar to those of aphids the predator Coccinelidae sp. could be mimicking aphids and circumventing ant recognition and aggressiveness. In order to support this hypothesis it is necessary to determine if this coccinelid is a myrmecophile species, since this degree of ant-aphid predator interaction is quite rare. According to Slipinski (2007) cited by Godeau et al. (2009) among the 6,000 species of ladybird beetles, seven are considered to be true myrmecophiles and four are suspected to at least live in association with ants.

In a previous study on the ant mosaic in the canopy of cacao trees carried out in the same locality where this research was conducted, five species of ants were considered dominants: *Azteca instabilis*, *A. chartifex*, *E. tuberculatum*, *Wasmannia auropunctata* (Roger) and *Cr. erecta* (Majer et al., 1994). One of the characteristics they found to determine the ant mosaic was that dominant ants exhibit at least one negative association with another dominant ant and that the 10 sub-dominant ants also exhibit negative association with at least one dominant ant. There was also a tendency to symmetrical exclusion based on ant size with small *A. chartifex* and *Cr. erecta* excluding small ants from their territory and large *E. tuberculatum* excluding large ants.

The results obtained in this study are in accordance with those cited above. The quadrate survey conducted in this study found that two of the species (*Cr. erecta* and *E. tuberculatum*) considered dominants by Majer et al. (1994) were present on aphid colonies. In general, nine out of 10 association indexes for pairs of the five ants considered more frequent were slightly negative. Only one index was slightly positive, reflecting the only case in which double presence of ants was observed (*Cr. victima* and *P. gracilis*) in the survey. *P. gracilis* uses to forage on aphid colonies as individuals and is sometimes attacked by *Cr. victima*. However, *P. gracilis* is a large size ant (ca. 14 mm) while *Cr. victima* is a small size ant (ca. 5 mm). Perhaps this asymmetry in size is more favorable to *P. gracilis* and might be the cause of the common presence of both species in some colonies. Therefore, negative association and body size might be better studied as possible components determining the distribution of ants in aphid colonies.

Whenever *O. anthiphates* larvae were present, ant-predator association indexes were slightly positive. In the case of *N. tesellata* and Coccinellidae sp. association indexes were negative against *Cr. erecta* but positive against *Cr. victima*. Positive indexes for ant-predator spatial distribution should be expected, given the defense capability of syrphid larvae and the absence of attack from ants against Coccinellidae sp. How different the indexes can be depends on how much syrphid larvae can escape ants' attack and on the abundance of Coccinellidae larvae.

In this study, the spatial association with Coccinellidae sp. was slightly positive and did not differ too much from indexes related to *O. anthiphates*. The fact that some syrphid larvae are removed and coccinellid larvae are not, has certainly an effect in the distribution and coexistence of both species. However, the frequency of ants and predators in aphid colonies were too low to draw more emphatic conclusions in this study based on association indexes. Nonetheless, conceptually, we can conclude that the ant-aphid mutualism can mediate the coexistence of these two predators (and others) because the removal of *O. anthiphates* larvae by *Cr. victima* might generate a habitat fraction exclusively occupied by coccinellids, a "competitor free-space".

In the future, carefully planned and well manipulated field and laboratory experiments would prove valuable in answering interesting questions based on this conceptual framework. The ants *Ce. atratus*, *Cr. victima* and *Cr. erecta* vary

in size (large, medium, small, respectively) and so does *O. antiphates* along its ontogenetic development (first to third instar larvae are small, medium and large sized). It would be interesting to test whether the efficiency of ant species in the removal of syrphids and the successful self-defense of syrphids against them depend on the asymmetry of ant-predator size, ant behavior, aggressiveness and agility. These factors were found to be important in mediating ant-hemiptera interactions in a tropical savanna tree (Del-Claro & Oliveira, 2000). Another research approach that deserves attention is the chemical mimicry in the guild of predators of *T. auranti* and its relation with spatial overlap. Finding answers to these questions will certainly shed light on syrphid-coccinellid coexistence in cacao plants mediated by ants.

Acknowledgements

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