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The Habitat Affects the Ecological Interactions between *Azteca* Forel (Hymenoptera: Formicidae) and *Cecropia* Loefl. (Urticaceae Juss.)

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Abstract

In order to understand the effects of human impacts on structure and functioning of tropical forests, we should consider studies on animal-plant interactions such as ant-plant mutualistic interactions.We investigated the mutualistic interactions between ants (*Azteca* genera) and *Cecropia* plants in habitats of secondary forest and pasture used as cattle fields. We tested for the following hyphothesis: *(i) Cecropia* from pasture are more susceptible to foliar herbivory than the *Cecropia* from the forest, and *(ii)* the defense promoted by ants of *Azteca* genus is less efficient in the pasture when compared to the forested areas. We selected four areas inserted in Atlantic rain forest domain surrounded by secondary forest and by cattle pastures. The herbivory was more intense in the pasture than in the secondary forest. The presence of *Azteca* species diminished foliar herbivory only in the forested areas, where we observed a significant increase in herbivory after the removal of *A. alfari* colony. We argue that the greater herbivory in pasture occurs probably due the lack of other plant resource, being *Cecropia paschystachya* Trécul and *C. glaziovii* Snethl., isolated in a "sea of grass" without connection with other tree vegetation, opposite scenario observed in forested habitats. The defense of *Azteca* only in the secondary forest, leading us to suppose that: 1) not even the your aggressive behavior is able to reduce the intense herbivory in the pasture; 2) the your behavioral pattern in forest is not the same in deforested environments and / or 3) mutualism may be undergoing changes due to abiotic effects on pasture.

Introduction

The genus *Cecropia* Loefl. (1758) represents an important and abundant group of pioneering plants (Berg et al., 2005) with a characteristic morphological aspect (Vasconcelos & Casimiro, 1997; Sposito & Santos, 2001), which presents a large number of species structurally adapted to shelter ants with which establishes mutualistic relations (Janzen, 1969). Ants nest within their trunks (Harada & Benson, 1988) and feed on a glycogen-rich substance produced by the Müllerian bodies located at the base of leaf petioles (Yu & Davidson, 1997). These species, known as myrmecophytes, are commonly colonized by ants of the genus *Azteca* Forel, which presents up to five species occupying the same plant (Longino, 1991).

This mutualistic relation can act as an environment of biotic defense against herbivory (Longino, 1989; Berg et al., 2005; Davidson, 2005) and in natural environment, *Cecropia* occupied by ants suffers less herbivorous attacks than those not occupied (Jolivet, 1990). This is an extremely important event, especially if we consider the high herbivory rates of *Cecropia* (12 to 18% according to Coley, 1983) that are considered significantly higher than those presented for other myrmecophytes (4 to 12% according to Frederickson, 2005).

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Despite ant protection against herbivory, a classic study by Janzen (1969) shows that it is so common to find *Cecropia* plants occupied by ants with foliage devoured by insects, as it is common to find unoccupied and healthy plants. It evidencing that the intensity and / or quality of the mutualistic relationship can be extremely variable between habitats or plants. Moreover, it perhaps a punctual condition, responds for momentary differences of these relations. The myrmecophytes, in fact, can vary between the different species of plans and between populations of the same species along one gradient (Longino, 1989; Berg et al., 2005). Thus, studies of the ecological relationships between herbivores and plants of wide geographic distribution such as *Cecropia* (from Mexico to the South of Brazil according to Berg et al., 2005) can elucidate some gaps in the insect-plant evolution process. This knowledge becomes especially important in a scenario of constant anthropic aggression and expansion of the agricultural frontier, the main cause of deforestation and conversion of primary forests to secondary habitats (Geist & Lambin, 2002; Sanchez-Azofeifa & Portillo-Quintero, 2011).

In this scenario, forest loss favors insect herbivory by undermining the bottom-up control and by improving the conditions required for herbivores proliferation (Morante-Filho et al., 2016). In this context, the present study investigated *Azteca*-*Cecropia* mutualistic interactions in secondary forest and pasture habitats. In particular, we try to answer the following question: What is the relationship between different habitat types and herbivory in ant-plant mutualistic systems? This question was based on the assumption that vegetational diversity can decrease or increase the likelihood of damage to a focal plant (Tahvanainen & Root, 1972; Letourneau et al., 2011; Kim, 2017) so we predict that more simplified and/or homogeneous environments, such as pastures, offer less resources and may lead to a higher feeding pressure of herbivores on *Cecropia* plants compared to forests. In this sense, we formulate the following hypotheses: *(i) Cecropia* plants established in pasture habitats present more foliar herbivory than plants established in the secondary forest, and *(ii)* the defense against herbivory performed by *Azteca* is less efficient in *Cecropia* plants of pasture than in secondary forest plants.

Material and Methods

Study area

The study was carried out from January to June of 2016, in four areas located along the highways margins of the municipalities of Jequié and Ubatã, state of Bahia, Brazil. We selected the areas of secondary forest (area 1: 14°00’55.9”S, 39°55’53.6”W; area 2: 13°59’11.2”S, 39°56’20.1”W) and two pasture areas (area 1:14°11’45.7”S, 39°37’43.0”W; area 2: 14°12’38.3”S 39°34’43.6”W). According to the surrounding vegetation, all areas were immersed in Ombrophilous Atlantic Forest.

Experimental design and determination of Cecropia and Azteca species

We established a minimum distance of one kilometer between the four sample areas, to ensure data independence, and in each area, we randomly chose 20 plants (totaling 80 plants). In each area, we determined the minimum distance of 5 meters between the selected plants, in order to ensure the aerial isolation of the colonies located in each plant, in which we performed morphological measures (plant height, CAP - Circumference at breast height and total number of leaves) to homogenize the samples.

For the determination of the species of *Cecropia*, we collected samples of leaves and reproductive material for the preparation of exsiccates that were identified by the specialists: Dr. André Luiz Gaglioti and Dr. Sergio Romaniuc Neto of the Instituto de Botânica, São Paulo, Brazil (registration number: SP 489810/SP 489811- *C. pachystachya* and SP 489812/ SP 489813- *C. glaziovii*).

Specimens of Formicidae colonizer (*Azteca* spp.) collected manually at the entrance of the nest (Prostoma) were identified by Dr. Jacques Hubert Charles Delabie, at CEPEC/CEPLAC Laboratory of Myrmecology in Ilhéus, Bahia, Brazil, where they are deposited (registration number: 5823).

Determination of herbivory levels and leaf damage

In order to determine the herbivory rates of the plants, we selected, in each area, ten *Cecropia* plants (treatment) that were submitted to the experimental removal (*in situ)* of the colonies of *Azteca*, and ten plants of *Cecropia* (control) with the presence of colonies of *Azteca*.

In each plant, we selected three leaves in an initial state of development, which we individually marked with the use of plastic clamps. Leaf shoots were under the same conditions/position in the branch, indicating a similar age. We monitored the selected plants weekly, and at the end of 45 days, we removed the leaves marked for the determination of the foliar area that suffered herbivory.

In order to determine the total area of leaf damage by herbivory by plants, we adopted the average area (cm^2) of leaf consumed in each individual of *Cecropia* (treatment and control). To measure the area of leaf damage, we removed the marked leaves and submitted them individually to digitalization by photographic method for image generation with a resolution of 15MP (standardized with scaling, tripod and Canon 50d camera). We used ImageJ Software version 1.49s (Wayne Rasband - National Institutes of Health, USA) to measure the leaf damaged area in the images.

To describe the patterns of damage, we adopted the categories described in Delunardo et al. (2010), as: marginal cut; Simple drilling; Sequential perforation, following rib; scraping and leaves totally consumed (removed).

Experiments of removal and elimination of colonies

In order to verify the influence of mutualism on herbivory, we removed ant nests using a contact insecticide (DIMY DDVP, Dimy Prod. Jard. Ltda. Cajamar, SP, Brazil Reg. MS 33994.0004 / 001-2, formerly Dimmyt , Serv-San). We applied it abundantly with a syringe in each prosthesis of the plant by the prostome, until the visual verification of the internodes filling, with the transhipment during the application. We carried out the removal of the colonies in ten plants (treatment) and left ten plants intact (control), without removal in all areas.

We monitored the treatment plants weekly, to avoid recolonization and whenever the presence of *Azteca* was detected, the insecticide was reapplied. The insecticide applied is non-residual and action by direct contact with insect, not affecting the action of herbivores in the plants with colonies removed (Izzo & Vasconcelos, 2002).

Data analysis

We used the Mann-Whitney test to evaluate differences in herbivory levels between plants of both habitats (secondary forest and pasture).

We evaluated the effects of mutualism on herbivory levels by means of Analysis of Variance (Two-way ANOVA) using habitat (secondary forest and pasture) and ant colony (present or excluded) in the model, as explanatory variables.

We used Shapiro-Wilk (ZAR, 1996) to test the assumptions of normality and residual homogeneity of variance. The analyses were performed in the statistical program Systat - version 12.0 (2007) and in all the tests, we adopted the level of significance of $p < 0.05$.

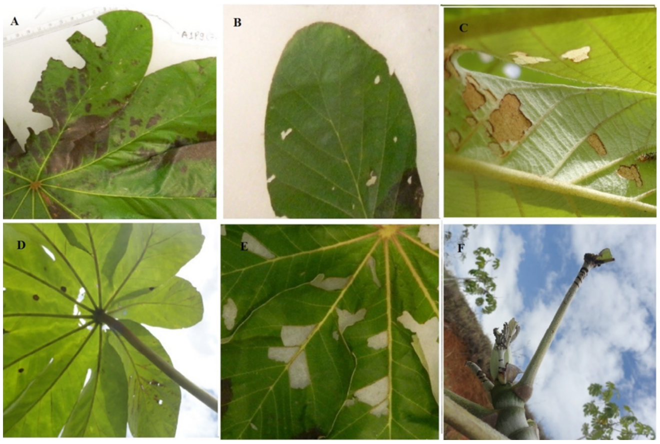


Fig 1. Patterns of leaf damage caused by herbivory in *Cecropia*, following the classification adopted by Delunardo et al. (2010); A) marginal cut; B) drilling; C) scraping; D) sequential perforations; E) in the direction of the rib; F) total removal of the limbus. These standards were registered from February to June 2016 in secondary forest and pasture (Mata Atlântica domain), Bahia, Brazil.

Results

Patterns of foliar damage by herbivory found in leaves of Cecropia

In the secondary forest, simple drilling (Fig 1B) was the predominant foliar damage, while in the pasture, simple drilling (Fig 1B) and marginal cutting (Fig 1A) occurred similarly. In general, the pattern of sequential drilling (Fig 1D) was more pronounced in the pasture (25%), when compared to the secondary forest (2.5%). A complete leaf removal (Fig 1F) was registered only on pasture.

Establishment and characterization of Cecropia and its mutual association with Azteca ants in habitats of secondary forest and pasture

Two species of *Cecropia* are established in the studied areas: *Cecropia pachystachya* Trécul (1847) and *C. glaziovii* Snethl. (1923), being the first one more frequent in both habitats (pasture: 92% and secondary forest: 78%).

Two species of *Azteca* ants were associated with *Cecropia* plants: *Azteca alfari* Emery, 1893 and *A. ovaticeps* Forel, 1904. The *Azteca alfari* species had the highest occurrence frequency in *Cecropia pachystachya*, in both habitats in a similar proportion (pasture: 63.2.% and secondary forest: 60%).

Cecropia foliar herbivory in secondary forest and pasture habitats

The average of leaf herbivory per plant was higher in pasture (104.4 cm^2; SD ± 248.4, n = 40) than in the secondary forest (14.05 cm^2; SD ± 20.05; Mann-Whitney = 4647.500; d.f = 1; p = 0.024; n = 40) (Fig 2).

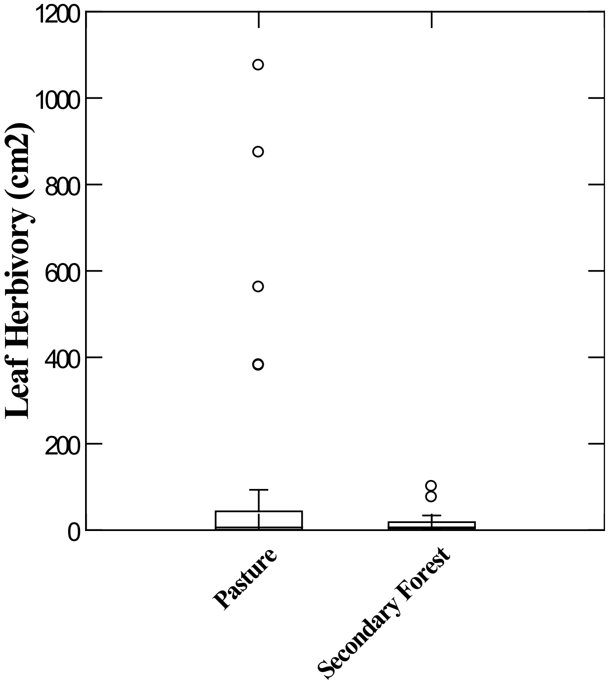
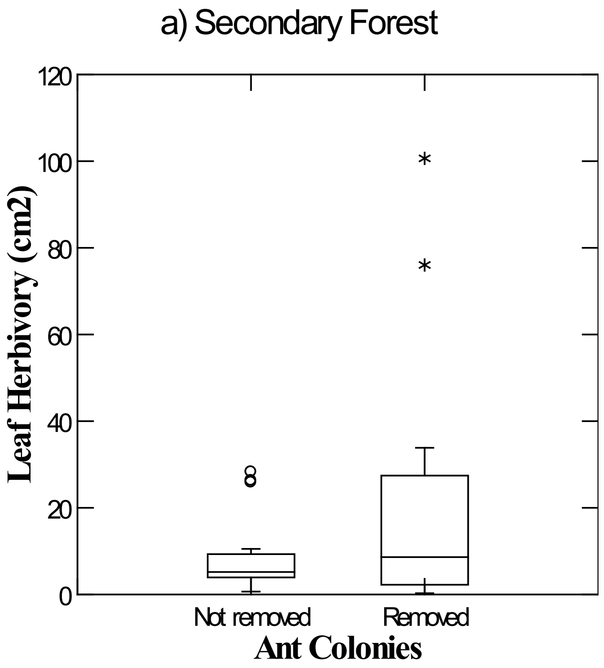


Fig 2. Leaf herbivory (cm^2) in *Cecropia* plants established in the pasture and secondary forest habitat registered during 45 days between February and June 2016in secondary forest and pasture (Mata Atlântica domain), Bahia, Brazil.

In the secondary forest, leaf herbivory was higher in the plants that had the ant colony removed (Treatment) (19.36 cm^2; SD ± 26.4) compared to plants where the colonies were present (Control) (8.74 cm^2; SD ± 8.22; Mann-Whitney = 2158.500; d.f = 1; p =0.005; n = 40) (Fig 3A). There was no difference between the treatment (101.8 cm^2, SD ± 220.5) and control in the pasture (107.3 cm^2, SD ± 283.3, Mann-Whitney = 1667.500; d.f = 1; p=0.411, n = 40) (Fig 3B).



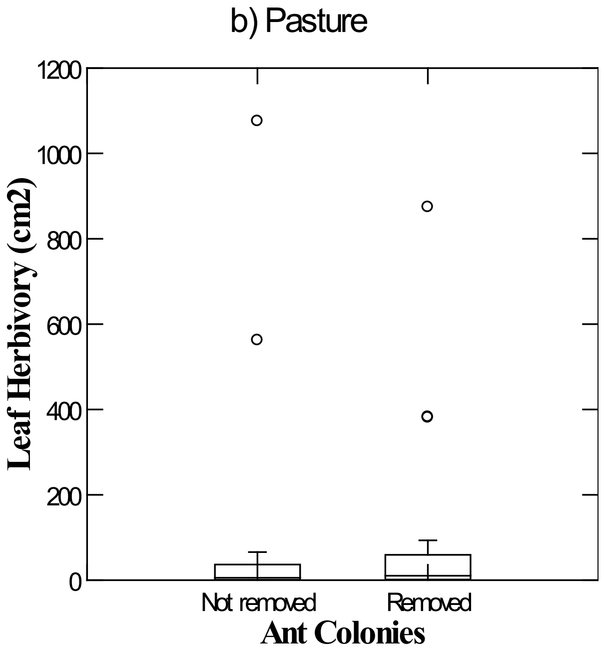


Fig 3. Leaf herbivory (cm2) in *Cecropia* sp. with the removal of colonies of *Azteca* sp. and without removal established in secondary forest habitat (a) and pasture (b). These values refer to a period of 45 days, from the experimental phase of removal of colonies with insecticide treatment plants, between the months of February and June 2016 in secondary forest and pasture (Mata Atlântica domain), Bahia, Brazil.

Influences of Azteca ant colonies on Cecropia leaf herbivory in secondary forest and pasture habitats

In the secondary forest, the *Azteca* ant species influenced the herbivory levels (F = 6.553; df = 1; p=0.015; n = 40) in the host plant. The presence of ant species *Azteca alfari* showed a decrease in foliar herbivory levels in *Cecropia* compared to *A. ovaticeps*. Neither the species of *Cecropia* (F = 3.060; df = 1; p=0.089; n = 40) nor the interaction between *Cecropia* and *Azteca* species (F = 2,523; df = 1; p=0,121; n = 40) explained variations in herbivory in the secondary forest.

In the pasture, where the herbivory was larger in relation to the secondary forest habitat, there was no difference between the treatments, neither the ant species (F = 0.090; df = 1; p=0.766; n = 40), nor the species of (F = 0.227; df = 1; p=0.637; n = 40) or the interaction between these two factors (F = 0.086; df = 1; p=0.771; n = 40) influenced herbivory levels.

Discussion

Foliar Herbivory

As expected, foliar herbivory in *Cecropia* plants established in the pasture was higher than in the secondary forest, probably due to the greater abundance of herbivorous insects present in this habitat. Secondary forest, a forested habitat and visually more heterogeneous than a local pasture with a predominance of grasses, offers a greater supply of resources for herbivorous insects and possibly exerts an herbivory dilution effect (Tahvanainen & Root, 1972; Letourneau et al., 2011; Kim, 2017). Arnold and Asquith (2002) point out that herbivory patterns are sensitive to fragmentation and that they depend on a number of factors, including the plant establishment place.

In addition to high levels of herbivory, when we compare the patterns of foliar damage, between the two habitats, only the pasture presented total leaf removal, the most extreme type of herbivory. This result, according Arnold and Asquith (2002) can indicate various ecological and behavioral changes in abundance, diversity or herbivores composition and variations in their oviposition in this local, when we compared to less degraded environments such as secondary or primary forests.

In fact, in degraded environments can occur the exclusion of specialized species and/or low dispersal of some species to the detriment of others (Terborgh et al., 1997; Shahabuddin & Terborgh, 1999). Caterpillar species often seen under *Cecropia* leaves in pasture (personal observation). It is a specialized herbivore and it is considered as one of the main responsible for the high rates of herbivory in the tropics (Basset et al., 2001; Neves et al., 2013). Also in the tropics, the especialized herbivores (monophagous or oligophagous) account for 40-100% of foliar damage whereas the general herbivores play a minimal role (Barone, 1998). Only in the pasture, we saw active nests of leaf-cutting ants near the studied plants. Leaf-cutting ants are prominent herbivores in the neotropics (Cherrett, 1986) and their population increases in disturbed habitats (Rao, 2000).

There are many mechanisms or factores that may direct herbivory patterns in environments. In our study, probably the conversion of forest to pasture has favored herbivory since this event simplifies and homogenizes the habitat. Although it is not a consensus, several studies show, in fact, that the habitat loss and degradation by human impacts increase herbivory levels (Guimarães et al., 2014, Peter et al., 2015; Morante-Filho et al., 2016). This increase, according to Morante-Filho et al. (2016), may occur due to both by increasing in the abundance of herbivores and by simplifying the vegetation structure of habitat. Also for them, that habitat loss increases local pressure of herbivory and reinforces the idea a pervasive threat to biodiversity.

In natural environments, pioneer plants such as *Cecropia*, usually occur as temporary staining of herbivorous insect resources and temporal patterns in local insect abundance can be regulated, for example, by bottom-up (Hunter et al., 1992, Power, 1992). In this sense, besides the conversion of forests to landscapes by human activity cause species destruction (Fahrig 2013), populations loss (Clavel et al. 2011, Tabarelli et al. 2012), it changes ecological interactions such as regulation of herbivore abundance by bottom-up.

Ultimately, besides anthropic disturbances favor the herbivory, according Lôbo et al. (2011), act on the tree flora both evolutionarily, favoring phenotypes adapted to the conditions imposed, and ecologically, exerting effects on populations, communities and ecosystems that can be revealed from a local to a regional scale

Mutualism

Removal of *Azteca* colonies in *Cecropia* plants significantly increased herbivory levels in the secondary forest. In the pasture, there was no difference, confirming the hypothesis that the herbivorous defense exerted by these ants is less efficient in this habitat than in the secondary forest. One of the factors that can explain this result is the similarity of pasture with the hostile environment of forest edges (Murcia, 1995).

Forest boundaries present environmental changes such as increased exposure to wind (which increases tree mortality) and sunlight (which increases the temperature), factors that cause the proliferation of plants that invest in rapid growth (Laurance et al., 2006, 2007). These plant species have little defense against herbivores, which can be abundant in these sites (Coley & Barone, 1996).

In fact, there is a consensus in the literature that the action of herbivores is greater in border environment (Barbosa et al., 2005; Urbas et al., 2007). Although all the individuals of *Cecropia* studied were established at the edge of highways, in a large clearing or linear border, this effect can be enhanced if the plants are as in "islands" surrounded by grasses. Like in pasture habitats. So it is reasonable to assume that mutualistic ants fail to effectively protect plants against herbivores in such a disturbed and modified environment.

The damage caused by herbivores triggers several strategies of physical, chemical and biological defenses in plants (Coley & Barone, 2001; Ohata et al., 2010). Of these, the biological occurs by the presence of other mutualistic organisms attracted to the plant, by the plant itself, by some kind of compensatory resources (Heil & McKey, 2003). In fact, biological defense exerted by ants is considered one of the most effective (Rosumek et al., 2009, Llandres et al., 2011), especially when it comes to the *Cecropia-Azteca* mutualistic association (Janzen, 1969; Davidson, 2005), where all the ants of this genus present highly aggressive behavior (Yu & Davidson, 1997).

According to Bruna et al. (2004), the aid of alarm pheromones released by the ants at the time of herbivorous attack accelerates the defense response to herbivory. Although herbivory is considered an important factor in the induction of ant recruitment this mechanism varies according to ant species. In our study, only *A. alfari* reduced herbivory levels in secondary forest, while the other species (*A. ovaticeps*) did not show differences with the removal of their colonies. It evidencing that the effectiveness of the defense actually varies between ant species. Different levels of worker aggressiveness may directly relate to nestmate recognition ability, as in myrmecophyte ant, *Pseudomyrmex concolor* (Pacheco & Del-Claro, 2015).

The species *A. alfari* is considered to be the least aggressive of all the *Azteca* inhabitants of *Cecropia* (Longino, 2005). Nevertheless, it has been shown to be more efficient in protecting *Cecropia* plants in the secondary forest, when compared to the congener and sympatric *A. ovaticeps*. On the other hand, for Vasconcelos and Casimiro (1997) *A. alfari* is considered efficient in removing at least some types of herbivorous insects from its host plants. In this way, we need to rethink the mutualism of the *Cecropia-Azteca* system as originally proposed by Longino (1991), in the context of "when" and "where"**.**

Other factors may explain the effectiveness of *A. alfari* in repelling herbivores. Perhaps the simple presence of ant workers may discourage the action of herbivores or your constant vigilance in the host plant. This behavior, which is connected to the production of substances by the host plant, can be related to several factors (e.g.temperature and environmental humidity), which in turn can exert different patterns among ants of the same taxon, as proposed by Yamamoto and Del-Claro (2008). Perhaps this explains the lack of biological defense shown by *A. ovaticeps*.

Based on our findings, we can affirm that the secondary forests can still preserve the mutuality of the *Cecropia-Azteca* system, unlike the pasture, where the presence of the ants did not reveal any difference in the action of the herbivores. So, perhaps the biggest implication for this outcome is the direction which *Cecropia-Azteca* mutualism is taking. Because, in a global scenario of climatic changes with increasingly pronounced dry seasons, it can be assumed that the synergy between deforestation, conversion of forests to simpler habitats and drier climate, can modify the herbivory patterns. It, consequently, modify the efficiency of the *Azteca* defense in mutualism with *Cecropia* in places such as the studied pastures. The maintenance of preserved areas is important not only to protect specific organisms but also to avoid the loss of important mutual associations for the ecological system.

Conclusion and Implications

The biological defense exerted by *Azteca* was effective only for the *Cecropia* plants that occurred in the secondary forest. This leads us to suppose that perhaps even the aggressive behavior of the *Azteca* species is not able to reduce herbivory damage, compared to many herbivores in the pasture environment. Or yet, the pattern of behavior expected by this ant in the forest environment is not the same in deforested environments as is the case of pasture.

Moreover, *Cecropia-Azteca* mutualism may be suffering modifications due to abiotic effects. For example, the production of plant resources (eg, Müllerian bodies) in exchange for protection against herbivores may be insufficient to supply the colonies and maintain an efficient patrol over the plants in the pasture habitat. If this is true, there may also be a change in the size of the colonies in this environment (due to a lower resource supply) being smaller than those in the secondary forest.

In this context, many hypotheses could be tested in the non-forest pasture system *versus* secondary forest, especially considering that the great majority of studies of the *Cecropia-Azteca* relationship have been conducted primarily in primary forests of the Amazon and Central America (Davidson, 2005). In fact, in natural systems, plants usually invest in defenses by reducing the intensity of damage caused by herbivores, consequently by reducing the negative effects of herbivory (Coley & Barone, 2001). But in environments under constant disturbance, such as the studied pasture, is this true? Based on the results of the present study, such research is worthwhile.

Ultimately, it is necessary to consider that the pasture habitat is very different from that in which the association *Cecropia-Azteca* evolved (clearings of forests and riverbank) as punctuated by Fáveri and Vasconcelos (2004). In this environment, the presence of *Azteca*, didn´t decrease the action of herbivores, despite the known positive association of *Cecropia-Azteca* mutualism.

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