



## Territory and trophic cascading effects of the ant *Azteca chartifex* (Hymenoptera: Formicidae) in a tropical canopy

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### Abstract

Consumer pressure on species interactions is considered one of the major forces in organizing ecological communities. Dominant ants are commonly reported to be efficient predators and, by constantly patrolling their territories, can regulate prey / enemy population sizes and distribution. However, cascading effects involving dominant ants in tropical forest canopy are poorly understood, especially when taking a multitrophic approach. Here, we evaluated the trophic cascading effect caused by the arboreal ant species *Azteca chartifex* FOREL, 1896 on coexisting arthropods (other predators and chewing herbivores) and leaf herbivory levels in a tropical forest canopy associated with the dominant tree species *Byrsonima sericea* (Malpighiaceae). We investigated the effects of the presence of *A. chartifex* on: i) arthropod diversity (species richness, abundance, and composition) and ii) host plant herbivory levels. We sampled 68 trees, half of which had no records of *A. chartifex* patrolling their crowns while the other half has constantly been patrolled by this ant species for about two decades. The presence of *A. chartifex* corresponded to lower species richness and abundance of other predators, and reduced chewing herbivores abundance. Our findings suggest that *A. chartifex* may be capable of modifying the arthropod species composition and have important top-down effects on the community structure of arthropods in *B. sericea*, though manipulative experiments are needed to test this hypothesis. Our results help to understand how top-down cascading effects influence the community structure of forest canopies. We also added some important implications on how canopy communities are assembled and maintained over time.

**Key words:** Arthropods, multitrophic systems, top-down effect, trophic cascade.

Received 8 October 2021; revision received 6 May 2022; accepted 20 May 2022

Subject Editor: Christina Kwapich

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## Introduction

In most trophic interactions, predation is one of the most important forces driving population dynamics and community structure and promoting species diversity in natural ecosystems (ROMERO & KORICHEVA 2011, GARVEY & WHILES 2016). PAINE (1966) was the first to experimentally demonstrate how predation maintains community diversity by controlling competitors and herbivores. Trophic interactions such as predation trigger cascading effects by causing indirect effects across the food web, that is, effects that change abundance or biomass in more than one inferior trophic level (PAINE 1980, POLIS & al. 2000). Since then, studies have highlighted the influence of predator species in community structure using species of different trophic levels, such as predatory ants (VANDERMEER & al. 2010).

Known for their efficient predation ability, ant species are considered excellent models to understand community assembly (DEJEAN & al. 2018) via cascading effects on lower trophic levels (SANDERS & PLATNER 2007, MOREIRA & al. 2012). Through constant patrolling of their host plants, dominant ants (i.e., characterized by dominance behavior, with inter- and intraspecific confrontations to defend resources and territory, and by having populous colonies; DAVIDSON 1998) are able to reduce species richness and species composition, mostly involving potential competitors (such as spiders, ladybugs, and other ants) and herbivorous insects, thereby modulating the distribution of other organisms and reducing leaf damage in plants (NOVOTNY & al. 1999, ROSUMEK & al. 2009, TRAGER & al. 2010, VANDERMEER & al. 2010, NAHAS & al. 2012, LOURENÇO & al. 2015, SCHMITT & al. 2020). Additionally, some dominant ant species are skilled at building large nests for the main colony, which are connected by a network of small bivouac nests and sometimes related to polydomy (DAVIDSON 1998), as in the genus *Azteca*. Such a complex housing system of the dominant ants facilitates their movement along the tree branches and allows a broad territory defense. Consequently, greater arthropod species richness is found in sites not occupied by dominant ants, avoiding direct confrontation (thus, an enemy-free space sensu RIBEIRO & al. 2013, LOURENÇO & al. 2015). However, detailed studies delving further than a description of the effect of dominant ants on arthropod diversity in canopies are relatively rare (YANOVIK & KASPARI 2000, DO ESPÍRITO SANTO & al. 2012, RIBEIRO & al. 2013).

Dominant ant species are able to alter species connection patterns in ecological networks as they are competitively superior in monopolizing resources and preventing access by other arthropods (DÍAZ-CASTELAZO & al. 2013). In addition, dominant ant species are extremely abundant, which favors high recruitment rates and well-established territories, resulting in a great number of interactions with their host plants and other arthropods (DÁTILLO & al. 2013, 2014, COSTA & al. 2016). Thus, the territory of dominant ants can also alter the community structure among other arthropods and host plants. For example, the dominant genus *Azteca* is well known for participating as a

mutualist in several neotropical systems, promoting biotic defense (DEJEAN & al. 2009, OLIVEIRA & al. 2015) and improved reproductive success (PRINGLE 2014) for their host plants. Additionally, we may expect that dominant ants are also able to change the functional structure of the arthropod species present in their territory, restricting or favoring the activity of these arthropods in the environment.

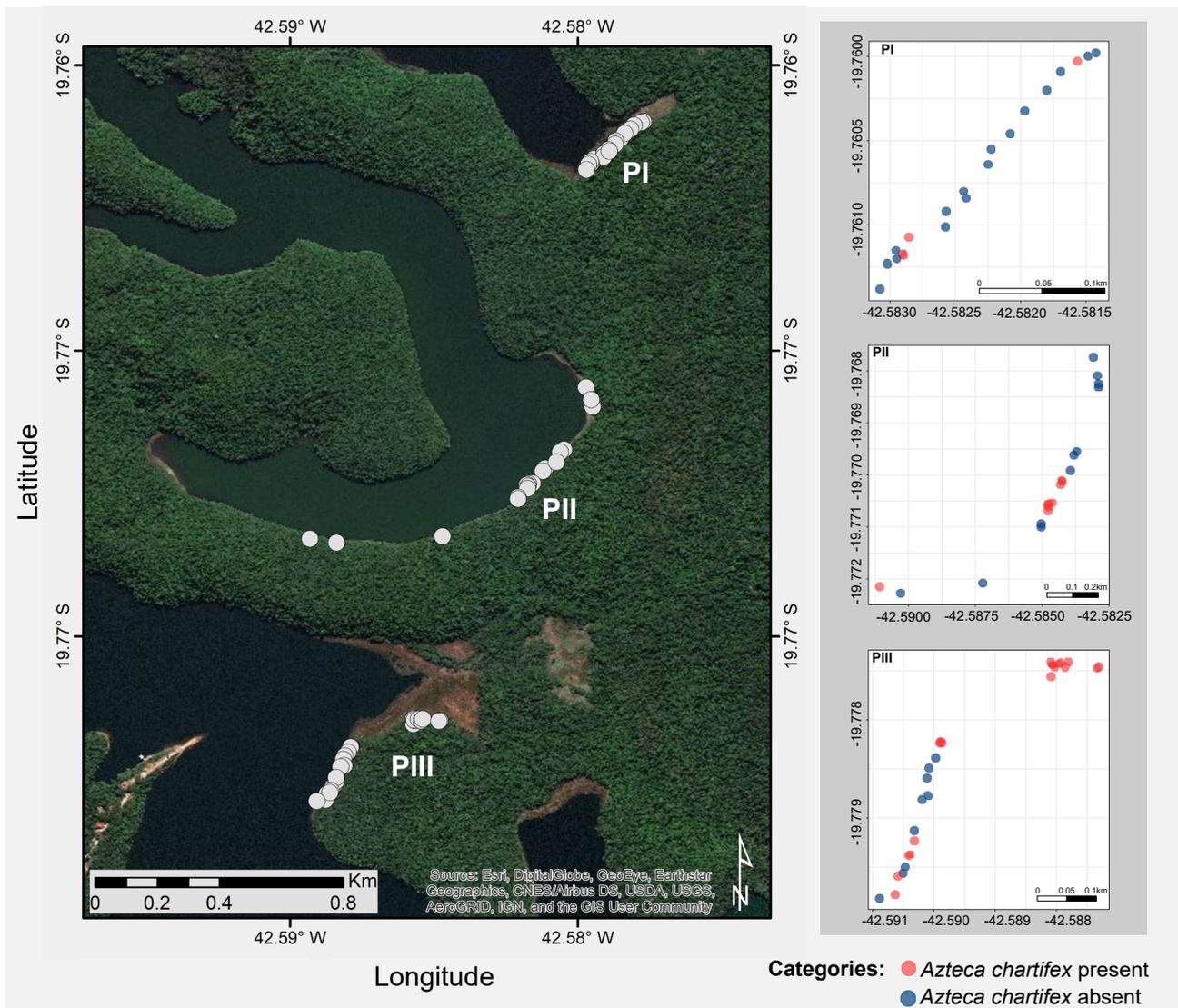
Among well-known dominant ant species, *Azteca chartifex* FOREL, 1896 (Formicidae: Dolichoderinae) stands out for its territorial and dominant behavior (LONGINO 2007). The territory of *A. chartifex* is dominated by many workers who patrol the territory by monopolizing resources and removing competitors (LONGINO 2007). The genus *Azteca* is well known due to the symbiosis of these ants with trees of the genus *Cecropia* being one of the most successful relationships of mutualism in the Neotropics (DAVIDSON & McKEY 1993). This tree provides shelter and food for *Azteca*, which in turn protects the plant against herbivory and vines (RICO-GRAY & OLIVEIRA 2007). Therefore, *A. chartifex* might be a suitable model to investigate the effect of a dominant arboreal ant species on other species assemblies, especially in multitrophic systems, considering its potential to protect tree species.

Here, we evaluated the trophic cascading effect of the ant *Azteca chartifex* on coexisting arthropods (other predators and chewing herbivores) and leaf herbivory levels in a forest canopy dominated by *Byrsonima sericea* DC (Malpighiaceae) tree. Due to the dominant behavior and high patrolling activity of *A. chartifex* (see LONGINO 2007, BACCARO & al. 2015, ADAMS 2016), we formulated two hypotheses: i) The presence of *A. chartifex* reduces species richness and abundance and changes the composition of co-existing arthropod predators (including ants) and chewing herbivores in *B. sericea* crowns, and ii) the presence of *A. chartifex* restricts the occurrence of chewing herbivores and consequently decreases *B. sericea* herbivory levels. Hence, if our predictions are true, we may start paving the way to understand the potential of *A. chartifex* as a mutualistic partner for *B. sericea*.

## Materials and methods

### Study area

The study was conducted in the Rio Doce State Park (hereafter PERD, relating to the Portuguese acronym) (19° 48' - 19° 29' S and 42° 38' - 42° 28' W), Minas Gerais State, southeastern Brazil. The climatic regime of the region is tropical seasonal (Aw) according to the Köppen's classification (ALVARES & al. 2013). The climatic seasons are well defined, with the dry period between May - September and rainy season between October - April. Average precipitation is around 1500 mm per year (ALVARES & al. 2013). The PERD covers an area of approximately 36,000 ha of semideciduous Atlantic Forest, varying from 200 to 500 m above sea level, and is part of the largest natural Neotropical lake system. Approximately 11% of the area of the park is covered by its 42 lakes, which are the same



**Fig. 1:** *Byrsonima sericea* tree populations (PI, PII, and PIII) and sampling design distributed across the studied populations located at three distinct forest-lake ecotones in Rio Doce State Park, Brazil. Colors represent the arrangement of two categories: i) *Azteca chartifex* present (red circle) and ii) *A. chartifex* absent (blue circle).

age and have an intimate, though evolutionarily young, history with the forest (FONSECA-SILVA & al. 2015, 2019). These lakes evolved on the very same soil and, thus, provide quite a similar background for the three population patches studied here (FONSECA-SILVA & al. 2015, 2019). Inside these patches, the trees are in lines with distance of a few meters from each other. The lake system inside the park supports very particular ecotonal areas that are characterized by natural transitions of forest-lake, where the trees grow branches bent towards the water as they seek light. This results in what has been called “brought low canopy”, which is, strictly speaking, a typical canopy habitat resting close to the ground, on the ecotone shore, or over the lakes (LOURENÇO & al. 2019). The PERD is an International Long-Term Ecological Research site (ILTER) whose tree-arthropod system has been investigated since 1999 (CAMPOS & al. 2006a, b, COELHO & RIBEIRO 2006, RIBEIRO & al. 2008).

### Study system

*Byrsonima sericea* is a dominant and pioneer tree species that defines most of ecotone vegetation in the PERD, forming a long-lived and complex canopy architecture (BARBOSA 2014). In these ecotones, *B. sericea* crowns are structured by branches growing vertically as well as by branches and foliage bent towards the lakes, positioned at the same height as the understory (Fig. S1, as digital supplementary material to this article, at the journal’s web pages). Flowering and fruiting of *B. sericea* occurs between the second fortnight of October and the end of April (TEIXEIRA & MACHADO 2000). According to the assessments carried out here, *B. sericea* trees studied in the PERD had a mean density of 550.58 leaves per sample ( $\pm 28.9$  standard error, SE), mean height of 5.68 m ( $\pm 0.13$  SE), and mean diameter at breast height of 59 cm ( $\pm 3$  SE).

*Azteca chartifex* was identified using the key of BACCARO & al. (2015) and subsequent assistance by Rodrigo

**Tab. 1:** Number of trees sampled over two years from *Byrsonima sericea* populations (PI, PII, and PIII) with *Azteca chartifex* present or absent.

Year	<i>Azteca chartifex</i>	<i>Byrsonima sericea</i> populations			
		PI	PII	PIII	Total of individuals
2016	present	4	9	19	32
	absent	16	11	9	36
	total	20	20	28	68
2017	present	1	5	10	16
	absent	9	5	4	18
	total	10	10	14	34

Feitosa from Universidade Federal do Paraná and Museu Nacional de São Paulo. *Azteca chartifex* is a polydomic species (i.e., multiple nests per colony) from a strictly Neotropical group of arboreal ants (LONGINO 2007) and builds its nests using cellulose and processed fibers, which protects the colony that may contain thousands of individuals (WHEELER 1986, BACCARO & al. 2015). This ant species preys upon living insects (HÖLLDOBLER & WILSON 1990) that cause damage to the plant and has a potential mutualistic association with *Byrsonima sericea* trees, wherein the ant establishes its main nest on the principal tree trunk and numerous smaller satellite nests along the secondary branches of surrounding *B. sericea* individuals (Fig. S1). In the PERD, it was observed that when *A. chartifex* is present, *B. sericea* trees within its territory were constantly patrolled by a large number of *A. chartifex* workers. For instance, an average of 23 satellite nests were counted per tree in a radius of 8 m around the main nest.

### Experimental design

To assess whether *Azteca chartifex* influences arthropod diversity, in March 2016, 68 individuals of *Byrsonima sericea* were arbitrarily selected and divided into two categories (Tab. 1): i) *Azteca chartifex* present (n = 32) – trees that were naturally colonized by this ant; and ii) *A. chartifex* absent (n = 36) – trees that, according to the records of the present research group, had no *A. chartifex* nests for at least a decade (CAMPOS & al. 2006a, b, COELHO & RIBEIRO 2006). Trees from three independent populations of *B. sericea* located in ecotones of three distinct lakes were sampled, separated by hills high enough to prevent dispersion and covered with denser forest than that in the ecotone, thus without *B. sericea* individuals, as this is a typical lowland tree. Each population was arranged into the following categories: population I (PI): *A. chartifex* present (n = 4) and *A. chartifex* absent (n = 16); population II (PII): *A. chartifex* present (n = 9) and *A. chartifex* absent (n = 11); and population III (PIII): *A. chartifex* present (n = 19) and *A. chartifex* absent (n = 9) (Fig. 1).

In March 2017, half of the previously studied plants were resampled (Tab. 1). Thirty-four individuals of *Byrsonima sericea* were randomly selected and sampled (16 trees with *Azteca chartifex* and 18 without *A. chartifex*) distributed within each population, following the cate-

gories arrangement: PI: *A. chartifex* present (n = 1) and *A. chartifex* absent (n = 9); PII: *A. chartifex* present (n = 5) and *A. chartifex* absent (n = 5), and PIII: *A. chartifex* present (n = 10) and *A. chartifex* absent (n = 4). Only half of the same plants were sampled because the other 34 individuals of *B. sericea* were used for an experiment parallel to this work (SOARES & al. 2022).

### Arthropod sampling and herbivory estimation

Arthropods and leaves from *Byrsonima sericea* crowns were sampled with the aid of an aluminum ladder (max. 5 m high) and basic climbing security gear. Arthropods were collected via beating technique using entomological adapted umbrellas (RIBEIRO & al. 2005) by performing 10 beats on at least three randomly selected branches, a suitable method to show the community of arthropods associated with trees (CAMPOS & al. 2006b, NEVES & al. 2013, 2014). Arthropods were identified with taxonomic keys and the aid of revisions (ARNETT & al. 2002, BACCARO & al. 2015, ANZALDO 2017), as well as the assistance of experienced taxonomists (Rodrigo Feitosa from Universidade Federal do Paraná and Museu Nacional de São Paulo, Adalberto José dos Santos from Universidade Federal de Minas Gerais, and Germano H. Rosado Neto from Universidade Federal do Paraná). In this study, only adult arthropods were considered (except for Lepidoptera caterpillars that were included), which were classified into predators and chewing herbivores. Vouchers were deposited at the Laboratório de Ecologia do Adoecimento & Florestas, Instituto de Ciências Biológicas, Universidade Federal de Ouro Preto, Minas Gerais, Brazil. Permits for the field studies were issued by the state authority (Instituto Estadual de Florestas – IEF) and national authority (Sistema de Autorização e Informação em Biodiversidade / Instituto Chico Mendes de Conservação da Biodiversidade – SISBIO / ICMBio).

The leaves were collected to estimate herbivory level with the guidance of wire-framed cubes (dimensions of a cube = 30 cm on each side) positioned at three distinct locations inside the tree crowns (adapted from SHAW & al. 2006, RIBEIRO & BASSET 2007) (Fig. S2), defined first by the safety of access while still being a blind specific location to avoid visual bias. Sampling locations were positioned at a maximum possible distance from each other

while climbing the tree and represented contrasting parts of the crown (closer to the top and two opposite sides); this methodology guarantees a random leaf sampling that avoids bias from choosing leaves with higher levels of herbivory, which has commonly been documented in herbivory studies (KOZLOV & al. 2015). In order to better represent the tree herbivory, the cube was positioned using a ladder and climbing devices and three different branches were sampled inside the crowns, randomly positioned by coordinates and prior visual contact. All the leaves that were inside the cube were collected, resulting in a final volume of 0.081 m<sup>3</sup> per tree. The leaves were digitalized and analyzed in ImageJ software (version 1.50i) (SCHNEIDER & al. 2012). The proportion of leaf area removed was calculated via ImageJ software using the following formula: removed area \* 100 / total area of each leaf, and then averaged per plant. Subsequently, herbivory levels were quantified by measuring the proportion of foliar damage from the sum of the leaf area removed from each leaf in relation to the total leaf area.

### Data analysis

For each individual of *Byrsonima sericea* studied (n = 68 in 2016 and n = 34 in 2017), the following were quantified: i) species richness, abundance, and composition of coexisting arthropods, including other predators (i.e., spiders, some beetles, mantis, and other ants, excluding *Azteca chartifex* as it was the factor to be tested) and the chewing herbivores (the orders: Coleoptera, except the families Carabidae, Coccinellidae, and Staphylinidae; Lepidoptera; and Orthoptera; Tab.S1); and ii) herbivory levels. A model including the richness and absolute abundance of ant species was built, showing ant foraging mosaic distribution in each of the populations studied and how *A. chartifex* affects the distribution of other ants.

Generalized Linear Mixed Model (BATES & al. 2015) (GLMM, “glmer” function for the data with lme4 package in R software version 4.0.0; R CORE TEAM 2020) was used to test the effect of *Azteca chartifex* on coexisting arthropod diversity, using the presence / absence of *A. chartifex* as explanatory variable and species richness and abundance of coexisting arthropods (other predators and chewing herbivores) as response variables. Additionally, the effect of *A. chartifex* on the herbivory level was tested by using the presence / absence of *A. chartifex* as the explanatory variable and the proportion of leaf area removed by chewing herbivores as the response variable. In these models, the treatments presence / absence of *A. chartifex* were fitted as an explanatory variable of fixed effects and populations (I, II, and III) were treated as explanatory variable of random effects in order to control variance into the intercepts. All the data are difficult to combine into single analyses because of uneven sampling between years; therefore, the data were considered as two separate sets (2016 and 2017). Appropriate families were selected based on the data distribution. Significance of variables in the models was verified by contrasting the predictive models with a null model, and models were selected when

there was a difference in the explanatory power compared with the null model ( $\alpha < 0.05$ ). Lastly, data-distribution adequacy was tested by residual analysis (ZUUR & al. 2009).

A multivariate analysis with Generalized Linear Models (GLMs) was used to test the influence of presence / absence of *Azteca chartifex* on species composition of other predators and chewing herbivores. This analysis was carried out in R software (version 4.0.0) (R CORE TEAM 2020) using the “manyglm” function in the “mvabund” package (WANG & al. 2012). This analysis fits a GLM via resampling for each sampled species using species abundances (WANG & al. 2012), and allows for multiple species testing and resampled p-values to detect significance where the null-hypothesis ( $H_0$ ) considers *A. chartifex* to have no effect on the species composition of other predators and chewing herbivores. A negative binomial distribution was used and model assumptions were evaluated by examining plots of residuals (WANG & al. 2012). The “anova.manyglm” function in “mvabund” was used to test for significant effects of *A. chartifex* on species composition of other predators and chewing herbivores. Subsequently, Non-metric Multidimensional Scaling (NMDS) was used, using abundance data and Bray-Curtis dissimilarity index, to visually summarize species composition.

## Results

### General results

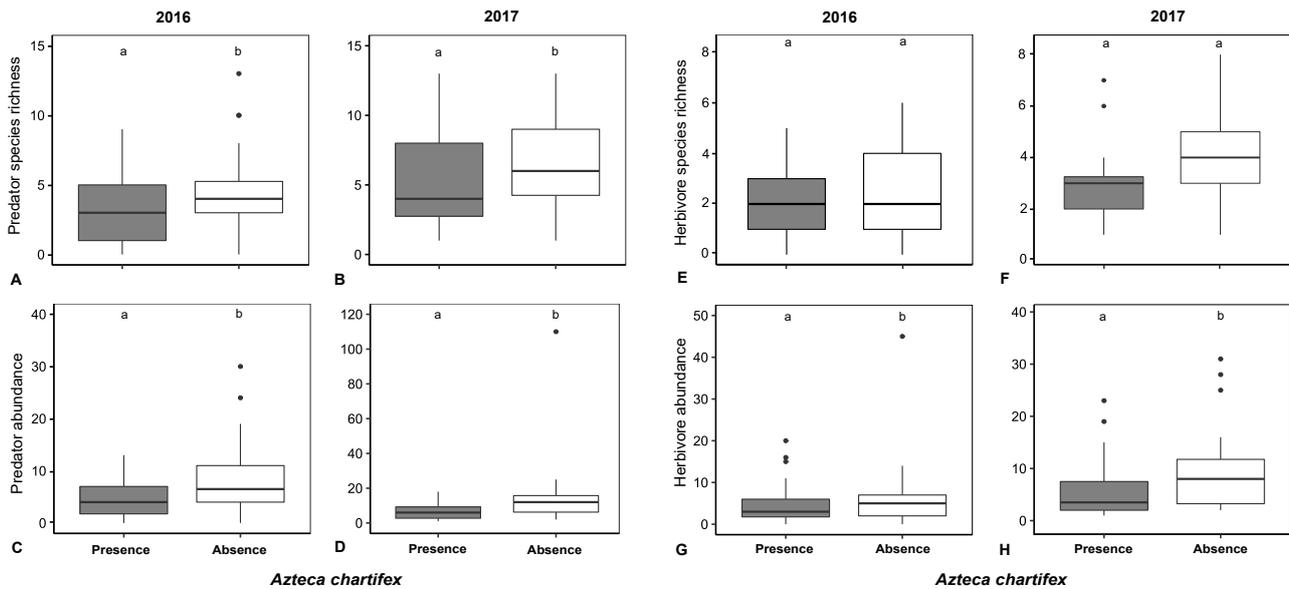
Over two years, we captured a total of 7775 arthropod individuals, with predators and chewing herbivores totaling 5257 individuals (67.6% of total community) distributed in 154 morphospecies (115 predators and 39 chewing herbivore species; Tab.S1). Predator species were mainly represented by spiders (56%), followed by ants (30%), beetles (10%), grasshoppers (2%), and mantis and pseudoscorpions (1% each). Chewing herbivore species were mainly represented by beetles (85%), followed by grasshoppers and crickets (10% total), and caterpillars (5%).

We also observed an ant mosaic distribution in the ecotones, with *Azteca chartifex* corresponding to the absence of non-dominant ants in the territory (Fig. 2). *Azteca chartifex* had a minimum overlap with the next dominant and abundant species, *Crematogaster* sp.1, which occurred in 89% of the trees not occupied by *A. chartifex*. In Figure 2, we can see that in PI, where there was lower patrolling activity of *A. chartifex* (n = 184), there was higher *Crematogaster* sp.1 abundance (n = 80). Conversely, subordinate ant species, such as *Cephalotes minutus* and *Camponotus sanctaefidei*, occurred with 63% and 52% of overlap with *A. chartifex* territory, respectively, thus shown to be tolerated by this ant.

### Effects of *Azteca chartifex* on *Byrsonima sericea* arthropod species richness, abundance, and composition

In both years of sampling, we found that *Byrsonima sericea* trees with presence of *Azteca chartifex* corresponded to lower predator species richness (2016: 7% and





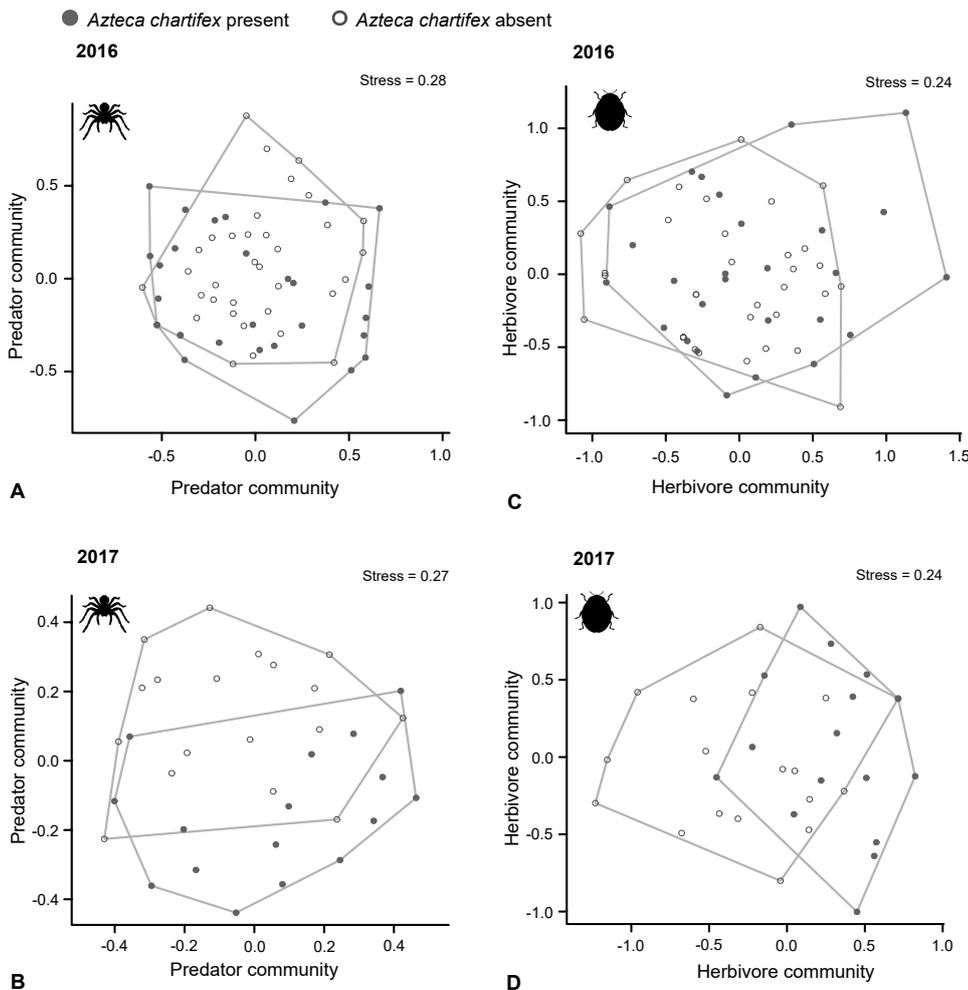
**Fig. 3:** *Azteca chartifex* presence / absence effects on coexisting arthropods of *Byrsonima sericea* canopy in two sample years (2016 and 2017). The effects of *A. chartifex* presence (grey boxplot) and *A. chartifex* absence (white boxplot) on: A) and B) predator species richness, C) and D) predator abundance, E) and F) herbivore species richness, and G) and H) herbivore abundance. In order to represent such models, coefficients have been re-estimated keeping only the significant terms in the model. Lines represent the first and fourth quartiles, boxes represent the second and third quartiles, and lines within the box represent the median. Points outside of the boxplot represent atypical data, while different letters above boxplots indicate significant differences ( $\alpha < 0.05$ ).

lower species richness and abundance of other predators and reduced chewing herbivores abundance. In addition, *A. chartifex* may be capable of affecting the community organizational structure of coexisting arthropods (both predators and chewing herbivores), although, the herbivory rate generated by chewing herbivores was not affected by the presence of *A. chartifex*.

Our study suggests that *Azteca chartifex* was efficient in patrolling and defending its territory, reducing the species richness and abundance of coexisting arthropods, resulting in a mosaic distribution following the pattern expected for the interior canopy (MAJER & al. 1994, BLÜTHGEN & STORK 2007, DEJEAN & al. 2007, RIBEIRO & al. 2013). Territorial ants like *A. chartifex* perform ostensible and strategic patrols on their host trees, preventing or discouraging the arrival of other arthropods (OLIVEIRA & FREITAS 2004, FERNANDES & al. 2005, ROSUMEK & al. 2009, LOURENÇO & al. 2015, ZHANG & al. 2015). The detection of the mosaic distribution of *A. chartifex*, a dominant upper canopy ant species in the forest ecotone, shown here supports the hypothesis of LOURENÇO & al. (2019) that the ecotone (brought low canopy) is equivalent to the upper canopy of the forest interior. In fact, we observed that *A. chartifex* generally occurred with many individuals and in aggregate spaces in nearby trees, where coexisting arthropods tended to avoid or were prevented from sharing the same foliage (Fig. 2). Thus, locations associated with less susceptibility to natural enemies (enemy-free spaces) are preferentially selected by herbivorous insects, which seems to be an important cause of spatial distribution patterns of other arthropods in the canopies (JEFFRIES &

LAWTON 1984, RIBEIRO & al. 2013, LOURENÇO & al. 2015). Additionally, we found that the presence of *A. chartifex* corresponded to lower species richness and abundance of other predators (2016: by 7% and 52%, respectively; 2017: by 24% and 64%, respectively), most likely due to the effect of *A. chartifex* on forcing opportunistic and non-dominant predators to leave the territory (e.g., *Crematogaster* sp.1 which in this study was only recorded outside the *A. chartifex* territory; Fig. 2). Likewise, in a study conducted in other tropical regions, the community composition of ants also changed where *Azteca seiceasur* were present (SCHMITT & al. 2020).

We also observed a decrease in the chewing herbivore abundance in locations that correspond to the *Azteca chartifex* territory in both years (by 35% in 2016 and 43% in 2017). More precisely, *A. chartifex* seems to decrease the abundance of important specialist chewing herbivores, such as the beetles *Strabala* sp.1, *Cylindrocopturinus* sp.1, and Entiminae sp.8, which together comprise 69% of all abundance in *A. chartifex* absence. It is known that these chewing herbivore insects are long-term stable species in association with *Byrsonima sericea* (see RIBEIRO & al. 2008), therefore by preventing a large number of these insects from inhabiting the crowns, *A. chartifex* could provide quite significant protection from chewing of the leaves. However, the reduction of specialist chewing herbivore abundance that we saw in *A. chartifex* territory did not reflect a reduction in the herbivory rate. This result is potentially due to the main chewing herbivores, including beetles *Strabala* sp.1 (Alticini tribe), being known for their remarkable jumping abilities, similar to fleas, and using



**Fig. 4:** Non-metric multidimensional scaling ordination based on composition of (A, B) other predators and (C, D) chewing herbivorous insects within treatments (Bray-Curtis dissimilarity). Each point corresponds to species of other predators and chewing herbivores encountered in a single tree. Symbols represent the treatments: *Azteca chartifex* present (circle grey) and *Azteca chartifex* absent (circle white). Outlines encompass all of the points for each treatment.

this behavior to escape from predators or move in the vegetation (FURTH 1988). Consequently, when confronted with *A. chartifex*, it is likely that *Strabala* sp.1 jumps and lands on another leaf, suggesting that the ant does not necessarily prey upon these beetles but may chase them away. Additionally, pioneer trees, such as *B. sericea*, often have short-lived leaves (< 1 year). Especially in open areas / sunny environments, pioneer plants have relatively short leaf longevity, replacing them frequently (KIKUZAWA & LECHOWICZ 2011). As PERD soils are rich in nitrogen (PINTO & al. 2021), resources are more available, and loss of leaf tissue does not seem to be a problem. Thus, the cost of the leaf production should be lower than producing secondary defense compounds (PINTO & al. 2021). This may have caused low herbivory rates due to the low longevity of the leaves, limiting the accumulation of leaf damage.

Connectivity between canopies, which is favored by the presence of lianas, also facilitates both access and escape, thus helping the dispersion of herbivorous insects (CAMPOS

& al. 2006a, MADEIRA & al. 2009). Therefore, the intense patrolling of *Azteca chartifex* that occurs in the studied system, despite being an important behavior, may not result in host plant protection, as some specialist herbivores likely use strategies to escape this defense and continue to feed on the plant, resulting in herbivory rates being unaffected by *A. chartifex*. Likewise, in another study, the authors expected to find a negative effect of the presence of *Azteca sericeasur* on the species richness of other ants (potential predators of possible decomposers), which would result in an increase in leaf litter decomposition. However, they did not detect any effect on species richness of other ants and on decomposition possibly due to a potential behavioral adaptation of non-dominant ants to avoid *A. sericeasur* (walking on soil to avoid encounters) (SCHMITT & al. 2020). In addition, a study carried out with *Azteca alfari* and *Cecropia* trees in Brazilian Amazonia also found no difference between the herbivory rates in territories with removal or presence of *Azteca* (FAVERI &

VASCONCELOS 2004), which reinforces the discussion that some strategies may be used by arthropods to avoid the dominant ants. However, several studies have already demonstrated the effects of the ants' presence in reducing herbivory (ROSUMEK & al. 2009, SANCHEZ & BELLOTA 2015, FAGUNDES & al. 2017), including showing the role of *Azteca* as a mutualistic partner resulting in success for the host plants (DEJEAN & al. 2009, PRINGLE 2014, OLIVEIRA & al. 2015, GOMES & al. 2021).

Canopy studies have documented that ants can achieve up to 94% of the total arthropod abundance of this forest stratum (DIAL & al. 2006, RICO-GRAY & OLIVEIRA 2007, DEJEAN & al. 2018). Forest canopies provide strong segregation among ant species, evidenced by the fact that territories are almost exclusively occupied by a few dominant species (RIBEIRO & al. 2013, DEJEAN & al. 2015, YUSAH & al. 2018). Territorially dominant ants, such as *Azteca* spp., have complementary spatial distribution and suppress density and activities of hierarchically

inferior species (DEJEAN & al. 2018). Our findings suggest that *Azteca chartifex* territorialism may be capable of changing the arthropod species composition, restricting the occurrence of both predators and herbivores. In this way, we identified that the distribution of organisms in this canopy system seems not to be arbitrary, evidencing a hierarchical structure among arthropods, emphasizing functional dominance of *A. chartifex*. For example, when we assessed the spatial distribution of associated ants, it was possible to detect an *A. chartifex* monodominance where it occurs, even with the presence of other dominant ant species (Fig. 2). In our study, *A. chartifex* had a minimum overlap with other dominant and abundant ant species (*Crematogaster* sp.1) and with subordinate ant species, (*Cephalotes minutus* and *Camponotus sanctaefidei*) demonstrating that *A. chartifex* may be able to restrict or allow the permanence of other species, directing the assembly of canopy arthropods.

In conclusion, *Azteca chartifex* is a dominant species that may be capable of restricting other species with important effects on the community structure of arthropods associated with *Byrsonima sericea*. However, strategies likely used by specialist chewing herbivores result in the ability to bypass the ants' defenses and maintain herbivory rates. Our findings contribute to the current knowledge on how species dominance regulates species coexistence in tropical forests (YANOVIK & KASPARI 2000, DO ESPÍRITO SANTO & al. 2012, RIBEIRO & al. 2013). Further, our results provide strong evidence on the potential of a unique species in prompting cascading effects on complex network of interactions (PAINE 1980, POLIS & al. 2000). The next steps should be to explore the effects of dominant species on host plant reproductive success. This will inform about the potential of those species to modulate disproportional effects on distinct lower trophic levels (PAINE 1980, POLIS & al. 2000). Understanding the cascading effects associated with a dominant species in forest canopies helps to understand how canopy communities are assembled and maintained over time, with further implications on its ecological and evolutionary persistence.

## Acknowledgments

The authors thank Marina Beirão, Graziella F. Monteiro, and Talita Santos for assistance with fieldwork and discussions; the researchers Tatiana G. Cornelissen, Frederico N. Siqueira, Roberth Fagundes, Patrícia A. Moreira, and Marina Beirão for their careful and critical reading of previous versions of this paper; the experienced taxonomists Rodrigo Feitosa from Universidade Federal do Paraná e Museu Nacional – São Paulo, Adalberto José dos Santos from Universidade Federal de Minas Gerais, and Germano H. Rosado Neto from Universidade Federal do Paraná for guidance and confirmation of the species identified. We gratefully acknowledge the staff of the Rio Doce State Park (PERD) for allowing us to work in the park and providing logistical support. We also are grateful to the State Forestry Institute (IEF-MG) and the Chico Mendes Institute of

Biodiversity (ICMBio) for the granting of licenses (SISBIO authorization number 55058-1, IEF authorization 088 / 2016). We also thank Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (478481 / 2013-6) and Minas Gerais Research Foundation - FAPEMIG (APQ-01756-13 and APQ-01184-15) for financial support. GRS thanks for a research scholarship from Brazilian Coordination for the Improvement of Higher Education Personnel – CAPES (1497228 / 2015). GML thanks the research scholarship from CNPQ (155895 / 2014-1) and CAPES (88881.133074 / 2016-01). FVC thanks CAPES for scholarship funding. VDP was granted by CAPES (financial code 001). RIC was granted by FAPEMIG (APQ-01424-15) and SPR by the CNPq (478481 / 2013-6, 304024 / 2015-5, 2024306572 / 2019-2) and FAPEMIG (APQ-01756-13, APQ-01184-15).

## References

- ADAMS, E.S. 2016: Territoriality in ants (Hymenoptera: Formicidae): a review. – *Myrmecological News* 23: 101-118.
- ALVARES, C.A., STAPE, J.L., SENTELHAS, P.C., DE MORAES GONÇALVES, J.L. & SPAROVEK, G. 2013: Köppen's climate classification map for Brazil. – *Meteorologische Zeitschrift* 22: 711-728.
- ANZALDO, S.S. 2017: Review of the genera of Conoderinae (Coleoptera, Curculionidae) from North America, Central America, and the Caribbean. – *ZooKeys* 683: 51-138.
- ARNETT, R.H., THOMAS, M.C., SKELLEY, P.E. & FRANK, J.H. 2002: American beetles, Volume II. – CRC Press, Boca Raton, 881 pp.
- BACCARO, F.B., FEITOSA, R.M., FERNANDEZ, F., FERNANDES, I.O., IZZO, T.J., SOUZA, J.L.P. & SOLAR, R. 2015: Guia para os gêneros de formigas do Brasil. – Editora INPA, Manaus, 388pp.
- BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2015: Fitting linear mixed-effects models using lme4. – *Journal of Statistical Software* 67 (1): 1-48.
- BLÜTHGEN, N. & STORK, N.E. 2007: Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. – *Austral Ecology* 32: 93-104.
- CAMPOS, R.I., SOARES, J., MARTINS, R.P. & RIBEIRO, S.P. 2006a: Effect of habitat structure on ant assemblages (Hymenoptera: Formicidae) associated to two pioneer tree species. – *Sociobiology* 47: 721-727.
- CAMPOS, R.I., VASCONCELOS, H.L., RIBEIRO, S.P., NEVES, F.S. & SOARES, J.P. 2006b: Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. – *Ecography* 29: 442-450.
- COELHO, I.R. & RIBEIRO, S.P. 2006: Environment heterogeneity and seasonal effects in ground-dwelling ant (Hymenoptera: Formicidae) assemblages in the Parque Estadual do Rio Doce, MG, Brazil. – *Neotropical Entomology* 35: 19-29.
- COSTA, F.V., MELLO, M.A.R., BRONSTEIN, J.L., GUERRA, T.J., MUYLAERT, R.L., LEITE, A.C. & NEVES, F.S. 2016: Few ant species play a central role linking different plant resources in a network in rupestrian grasslands. – *Public Library of Science One* 11: art. e0167161.
- DÁTILLO, W., DÍAZ-CASTELAZO, C. & RICO-GRAY, V. 2014: Ant dominance hierarchy determines the nested pattern in ant-plant networks. – *Biological Journal of the Linnean Society* 113: 405-414.
- DÁTILLO, W., GUIMARÃES, P.R. & IZZO, T.J. 2013: Spatial structure of ant-plant mutualistic networks. – *Oikos* 122: 1643-1648.

- DAVIDSON, D.W. 1998: Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. – *Ecological Entomology* 23: 484-490.
- DAVIDSON, D.W. & MCKEY, D. 1993: The evolutionary ecology of symbiotic ant-plant relationships. – *Journal of Hymenoptera Research* 2: 13-83.
- DE CARVALHO BARBOSA, B. 2014: Arquitetura de ramos, alocação de biomassa e herbivoria em duas espécies arbóreas com diferentes histórias de vida em uma Floresta Tropical Semidecidual. – Master thesis, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil, 1-45 pp.
- DEJEAN, A., CORBARA, B., ORIVEL, J. & LEPONCE, M. 2007: Rainforest canopy ants: the implications of territoriality and predatory behavior. – *Functional Ecosystems and Communities* 1: 105-120.
- DEJEAN, A., GRANGIER, J., LEROY, C. & ORIVEL, J. 2009: Predation and aggressiveness in host plant protection: a generalization using ants from the genus *Azteca*. – *Naturwissenschaften* 96: 57-63.
- DEJEAN, A., ORIVEL, J., LEPONCE, M., COMPIN, A., DELABIE, J.H.C., AZÉMAR, F. & CORBARA, B. 2018: Ant-plant relationships in the canopy of an Amazonian rainforest: the presence of an ant mosaic. – *Biological Journal of the Linnean Society* 125: 344-354.
- DEJEAN, A., RYDER, S., BOLTON, B., COMPIN, A., LEPONCE, M., AZÉMAR, F., CÉRÉGHINO, R., ORIVEL, J. & CORBARA, B. 2015: How territoriality and host-tree taxa determine the structure of ant mosaics. – *The Science of Nature* 102: art. 33.
- DIAL, R.J., ELLWOOD, M.D.F., TURNER, E.C. & FOSTER, W.A. 2006: Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. – *Biotropica* 38: 643-652.
- DÍAZ-CASTELAZO, C., SÁNCHEZ-GALVÁN, I.R., GUIMARÃES, P.R., RAIMUNDO, R.L.G. & RICO-GRAY, V. 2013: Long-term temporal variation in the organization of an ant-plant network. – *Annals of Botany* 111: 1285-1293.
- DO ESPÍRITO SANTO, N.B., RIBEIRO, S.P. & SANTOS LOPES, J.F. 2012: Evidence of competition between two canopy ant species: Is aggressive behavior innate or shaped by a competitive environment? – *Psyche: A Journal of Entomology* 2012: art. 609106.
- FAGUNDES, R., DÁTILLO, W., RIBEIRO, S.P., RICO-GRAY, V., JORDANO, P. & DEL-CLARO, K. 2017: Differences among ant species in plant protection are related to production of extrafloral nectar and degree of leaf herbivory. – *Biological Journal of the Linnean Society* 122: 71-83.
- FAVERI, S.B. & VASCONCELOS, H.L. 2004: The *Azteca-Cecropia* association: Are ants always necessary for their host plants? – *Biotropica* 36: 641-646.
- FERNANDES, G.W., FAGUNDES, M., GRECO, M.K.B., BARBEITOS, M.S. & SANTOS, J.C. 2005: Ants and their effects on an insect herbivore community associated with the inflorescences of *Byrsonima crassifolia* (LINNAEUS) H.B.K. (Malpighiaceae). – *Revista Brasileira de Entomologia* 49: 264-269.
- FONSECA-SILVA, F.M., CARVALHO, M. DE A. & RIBEIRO, S.P. 2015: Caracterização da matéria orgânica particulada dos últimos 10 mil anos a partir de um testemunho do Parque Estadual do Rio Doce, MG, Brasil: implicações paleoambientais. – *Revista Brasileira de Paleontologia* 18: 161-170.
- FONSECA-SILVA, F.M., CARVALHO, M. DE A. & RIBEIRO, S.P. 2019: Palynological evidence of vegetation change during the last 10,000 years in the mid-valley of the Rio Doce, Brazil. – *Acta Botanica Brasilica* 33: 29-38.
- FURTH, D.G. 1988: The jumping apparatus of flea beetles (Alticinae) - the metafemoral spring. In: JOLIVET, P., PETITPIERRE, E. & HSIAO, T.H. (Eds.): *Biology of Chrysomelidae*. – Kluwer Academic Publishers, Dordrecht, pp. 285-297.
- GARVEY, J.E. & WHILES, M.R. 2016: Predation. In: *Trophic ecology*. – CRC Press, Boca Raton, pp. 81-100.
- GOMES, I.J.M.T., SOLAR, R., BLÜTHGEN, N., LUIS VASCONCELOS, H., EDUARDA BASÍLIO SILVA, L., NUNES OLIVEIRA, K., ZACHARIAS MOREIRA, M. & ILDEFONSO CAMPOS, R. 2021: Multiple effects of mutualistic ants improve the performance of a neotropical ant-plant: a long-term study with the *Cecropia-Azteca* system. – *Basic and Applied Ecology* 57: 78-90.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Harvard University Press, Cambridge, 732 pp.
- JEFFRIES, M.J. & LAWTON, J.H. 1984: Enemy free space and the structure of ecological communities. – *Biological Journal of the Linnean Society* 23: 269-286.
- KIKUZAWA, K. & LECHOWICZ, M.J. 2011: *Ecology of leaf longevity*. – Springer Tokyo, Tokyo, 147 pp.
- KOZLOV, M.V., LANTA, V., ZVEREV, V. & ZVEREVA, E.L. 2015: Global patterns in background losses of woody plant foliage to insects. – *Global Ecology and Biogeography* 24: 1126-1135.
- LONGINO, J.T. 2007: A taxonomic review of the genus *Azteca* (Hymenoptera: Formicidae) in Costa Rica and a global revision of the aurita group. – *Zootaxa* 1491: 1-63.
- LOURENÇO, G.M., CAMPOS, R.B.F. & RIBEIRO, S.P. 2015: Spatial distribution of insect guilds in a tropical montane rainforest: effects of canopy structure and numerically dominant ants. – *Arthropod-Plant Interactions* 9: 163-174.
- LOURENÇO, G.M., SOARES, G.R., SANTOS, T.P., DÁTILLO, W., FREITAS, A.V.L. & RIBEIRO, S.P. 2019: Equal but different: Natural ecotones are dissimilar to anthropic edges. – *Public Library of Science One* 14: art. e0213008.
- MADEIRA, B.G., ESPÍRITO-SANTO, M.M., NETO, S.D., NUNES, Y.R.F., ARTURO SÁNCHEZ AZOFEIFA, G., WILSON FERNANDES, G. & QUESADA, M. 2009: Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. – *Plant Ecology* 201: 291-304.
- MAJER, J.D., DELABIE, J.H.C. & SMITH, M.R.B. 1994: Arboreal ant community patterns in Brazilian cocoa farms. – *Biotropica* 26: 73-83.
- MOREIRA, X., MOONEY, K.A., ZAS, R. & SAMPEDRO, L. 2012: Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. – *Proceedings of the Royal Society B: Biological Sciences* 279: 4464-4472.
- NAHAS, L., GONZAGA, M.O. & DEL-CLARO, K. 2012: Emergent impacts of ant and spider interactions: herbivory reduction in a tropical savanna tree. – *Biotropica* 44: 498-505.
- NEVES, F.S., SILVA, J.O., ESPÍRITO-SANTO, M.M. & FERNANDES, G.W. 2014: Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. – *Biotropica* 46: 14-24.
- NEVES, F.S., SPERBER, C.F., CAMPOS, R.I., SOARES, J.P. & RIBEIRO, S.P. 2013: Contrasting effects of sampling scale on insect herbivores distribution in response to canopy structure. – *Revista de Biologia Tropical* 61: 125-137.
- NOVOTNY, V., BASSET, Y., AUGA, J., BOEN, W., DAL, C., DROZD, P., KASBAL, M., ISUA, B., KUTIL, R., MANUMBOR, M. & MOLEM, K. 1999: Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. – *Austral Ecology* 24: 477-483.
- OLIVEIRA, K.N., COLEY, P.D., KURSAR, T.A., KAMINSKI, L.A., MOREIRA, M.Z. & CAMPOS, R.I. 2015: The effect of symbiotic ant colonies on plant growth: a test using an *Azteca-Cecropia* system. – *Public Library of Science One* 10: art. e0120351.

- OLIVEIRA, P.S. & FREITAS, A.V.L. 2004: Ant-plant-herbivore interactions in the neotropical cerrado savanna. – *Naturwissenschaften* 91: 557-570.
- PAINE, R.T. 1966: Food web complexity and species diversity. – *The American Naturalist* 100: 65-75.
- PAINE, R.T. 1980: Food webs: linkage, interaction strength and community infrastructure. – *The Journal of Animal Ecology* 49: 666-685.
- PINTO, V.D., BADIA, C.C.V., SOARES, G.R., DE SOUSA, H.C., CORNELISSEN, T. & RIBEIRO, S.P. 2021: How do soil resources affect herbivory in tropical plants along environmental gradients? A test using contrasting congeneric species. – *Plant Ecology* 222: 1281-1295.
- POLIS, G.A., SEARS, A.L.W., HUXEL, G.R., STRONG, D.R. & MARON, J. 2000: When is a trophic cascade a trophic cascade? – *Trends in Ecology & Evolution* 15: 473-475.
- PRINGLE, E.G. 2014: Harnessing ant defence at fruits reduces bruchid seed predation in a symbiotic ant-plant mutualism. – *Proceedings of the Royal Society B: Biological Sciences* 281: art. 20140474.
- R CORE TEAM 2020: R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria.
- RIBEIRO, S.P. & BASSET, Y. 2007: Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: the importance of leaf sclerophylly. – *Ecography* 30: 663-672.
- RIBEIRO, S.P., BORGES, P.A.V., GASPAS, C., MELO, C., SERRANO, A.R.M., AMARAL, J., AGUIAR, C., ANDRÉ, G. & QUARTAU, J.A. 2005: Canopy insect herbivores in the Azorean Laurisilva forests: key host plant species in a highly generalist insect community. – *Ecography* 28: 315-330.
- RIBEIRO, S.P., ESPÍRITO SANTO, N.B., DELABIE, J.H.C. & MAJER, J.D. 2013: Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy. – *Myrmecological News* 18: 113-120.
- RIBEIRO, S.P., SOARES, J.P., DE CAMPOS, R.I. & MARTINS, R.P. 2008: Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats. – *Zoociências* 10: 237-248.
- RICO-GRAY, V. & OLIVEIRA, P.S. 2007: The ecology and evolution of ant-plant interactions. – University of Chicago Press, Chicago, 346 pp.
- ROMERO, G.Q. & KORICHEVA, J. 2011: Contrasting cascade effects of carnivores on plant fitness: a meta-analysis. – *Journal of Animal Ecology* 80: 696-704.
- ROSUMEK, F.B., SILVEIRA, F.A.O., NEVES, F. DE S., NEWTON, N.P., DINIZ, L., OKI, Y., PEZZINI, F., FERNANDES, G.W. & CORNELISSEN, T. 2009: Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. – *Oecologia* 160: 537-549.
- SANCHEZ, A. & BELLOTA, E. 2015: Protection against herbivory in the mutualism between *Pseudomyrmex dendroicus* (Formicidae) and *Triplaris americana* (Polygonaceae). – *Journal of Hymenoptera Research* 46: 71-83.
- SANDERS, D. & PLATNER, C. 2007: Intraguild interactions between spiders and ants and top-down control in a grassland food web. – *Oecologia* 150: 611-624.
- SCHMITT, L., APONTE-ROLÓN, B. & PERFECTO, I. 2020: Evaluating community effects of a keystone ant, *Azteca sericeasur*, on *Inga micheliana* leaf litter decomposition in a shaded coffee agro-ecosystem. – *Biotropica* 52: 1253-1261.
- SCHNEIDER, C.A., RASBAND, W.S. & ELICEIRI, K.W. 2012: NIH Image to ImageJ: 25 years of image analysis. – *Nature Methods* 9: 671-675.
- SHAW, D.C., ERNEST, K.A., RINKER, H.B. & LOWMAN, M.D. 2006: Stand-level herbivory in an old-growth conifer forest canopy. – *Western North American Naturalist* 66: 473-481.
- SOARES, G.R., ANJOS, D.V., COSTA, F.V., LOURENÇO, G.M., CAMPOS, R.I. & RIBEIRO, S.P. 2022: Positive effects of ants on host trees are critical in years of low reproduction and not influenced by liana presence. – *Basic and Applied Ecology* 63: 93-103.
- TEIXEIRA, L.A.G. & MACHADO, I.C. 2000: Sistema de polinização e reprodução de *Byrsonima sericea* DC (Malpighiaceae). – *Acta Botanica Brasilica* 14: 347-357.
- TRAGER, M.D., BHOTIKA, S., HOSTETLER, J.A., ANDRADE, G.V., RODRIGUEZ-CABAL, M.A., MCKEON, C.S., OSENBURG, C.W. & BOLKER, B.M. 2010: Benefits for plants in ant-plant protective mutualisms: a meta-analysis. – *Public Library of Science* One 5: art. e14308.
- VANDERMEER, J., PERFECTO, I. & PHILPOTT, S. 2010: Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. – *BioScience* 60: 527-537.
- WANG, Y., NAUMANN, U., WRIGHT, S.T. & WARTON, D.I. 2012: Mvabund – an R package for model-based analysis of multivariate abundance data. – *Methods in Ecology and Evolution* 3: 471-474.
- WHEELER, D.E. 1986: Polymorphism and division of labor in *Azteca chartifex laticeps* (Hymenoptera: Formicidae). – *Journal of the Kansas Entomological Society* 59: 542-548.
- YANOVIK, S.P. & KASPARI, M. 2000: Community structure and the habitat templet: ants in the tropical forest canopy and litter. – *Oikos* 89: 259-266.
- YUSAH, K.M., FOSTER, W.A., REYNOLDS, G. & FAYLE, T.M. 2018: Ant mosaics in Bornean primary rain forest high canopy depend on spatial scale, time of day, and sampling method. – *PeerJ* 6: art. e4231.
- ZHANG, S., ZHANG, Y. & MA, K. 2015: The equal effectiveness of different defensive strategies. – *Scientific Reports* 5: art. 13049.
- ZUUR, A.F., IENO, E.N., WALKER, N., SAVELIEV, A.A. & SMITH, G.M. 2009: Mixed effects models and extensions in ecology with R. 1<sup>st</sup> edition. – Springer New York, New York, NY, XXII, 574 pp.