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Ants offset bottom-up control of spiders in Amazonian savanna trees

Pedro A.C.L. Pequeno [a,*], Ciro Campos [b], Reinaldo Imbrozio Barbosa [c]

[a] *Programa de Pós-graduação em Recursos Naturais, Universidade Federal de Roraima, Boa Vista, Roraima, Brazil*
[b] *Instituto Socioambiental, Boa Vista, Roraima, Brazil*
[c] *Instituto Nacional de Pesquisas da Amazônia, Núcleo de Pesquisas de Roraima, Boa Vista, Roraima, Brazil*

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ABSTRACT

Community trophic structure is shaped by concurrent bottom-up (resources) and top-down effects (predators), but the extent to which they interact remains uncertain. The Exploitation Ecosystems Hypothesis predicts that predators should offset increases in herbivore abundance with plant productivity, which is supported by data. However, the extent to which interactions within trophic levels (e.g. competition, intraguild predation) have similar effects is less clear. Ants and spiders are abundant in vegetation and consume similar arthropod prey (occasionally each other) and plant exudates, with ants generally showing competitive dominance over spiders. We tested whether ants could shape the trophic structure of tree-dwelling macroarthropod communities by offsetting increases in spider abundance with insect prey. We performed three surveys of the macroarthropod community of 97 trees from two sites in the savanna of Northern Amazonia. Together, ants and spiders represented 74% of the sampled individuals per tree. Insect prey abundance increased with tree crown volume and crown flower cover, consistent with bottom-up limitation. Likewise, both ants and spiders increased with insect prey abundance, with ant abundance also varying with tree species, suggesting reliance on both animal and plant resources. However, as predicted, the positive relationship between spider abundance and insect prey abundance disappeared as ant abundance increased. Our results suggest that agonistic interactions within trophic levels can strongly shape community structure and size by modifying bottom-up effects as much as interactions across trophic levels.

1. Introduction

Community trophic structure is shaped by opposing ecological interactions. On the one hand, predator exclusion tends to increase herbivore prey abundance, a so-called “top-down effect” (Estes et al., 2011; Terborgh, 2015) that may prevent herbivores from consuming all plant biomass (Hairston et al., 1960). On the other hand, animals are often limited by resource quantity and/or quality to some degree, so-called “bottom-up effects” (Polis, 1999; White, 2008, 2019). Positive correlations between abundances of plants, herbivores and predators are suggestive of bottom-up limitation and occur even when top-down control is indicated by predator exclusion (Rosumek et al., 2009; Szefer et al., 2022) or measured predation rates (Mollot et al., 2012; Richards and Coley, 2007). However, the extent to which these effects interact remains uncertain (Hunter and Price, 1992; Oksanen and Oksanen, 2000; Polis, 1999; Wilkinson and Sherratt, 2016).

The Exploitation Ecosystems Hypothesis predicts how top-down and bottom-up effects should interact in controlling the abundance of trophic levels, assuming each trophic level behaves as a functional unit or “single exploitative population” (Oksanen, 1992; Oksanen et al., 1981; Oksanen and Oksanen, 2000). Herbivore prey abundance should increase with plant productivity, but only where predators are absent; otherwise, it should be unresponsive to productivity. This is because predators can consume increments in prey abundance prompted by resource surplus, but also because prey tend to avoid predators and reduce foraging in their presence (Mestre et al., 2020; Oksanen, 1992; Verdolin, 2006). This “ecology of fear” could limit the efficiency of energy transfer from lower to higher trophic levels (Zanette and Clinchy, 2019). Equivalently, from a top-down perspective, herbivore prey abundance should decrease with predator abundance, but only where productivity is high; otherwise, both prey and predators should be limited to low abundance by low productivity (Oksanen et al., 1981; Richards and Coley, 2007; Wilkinson and Sherratt, 2016). Indeed, vertebrate herbivore abundance increases with primary productivity across continents, but only where canid predators are rare (Letnic and Ripple, 2017; Ripple and Beschta, 2012), and insect herbivore biomass

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* Corresponding author.
E-mail address: pacolipe@gmail.com (P.A.C.L. Pequeno).

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increased with plant biomass in temperate grasslands, but only where spider abundance was low (Welti et al., 2020). However, it is unclear whether this effect generalizes across trophic levels (e.g. parasitoids attacking predators) (Polis et al., 1998) or within them (e.g. competition and/or intraguild predation) (Polis, 1999; Wilkinson and Sherratt, 2016).

Plants provide habitat for abundant and diverse arthropod communities, forming ecosystems whose higher trophic levels are often shared by ants and spiders (Helms et al., 2021; Sanders and Platner, 2007). These groups are generalist predators, competing for insect prey and occasionally preying on each other (intraguild predation), but also using plant exudates (e.g. nectar) and, in the case of some ants, insect exudates (e.g. hemipterans and lepidopteran larvae) (Lange et al., 2021; Mody and Linsenmair, 2004; Nahas et al., 2012). Both ants and spiders can decrease insect herbivore abundance and herbivory rates, thus having indirect, positive effects on plant fitness, although they may also repel pollinators (Nahas et al., 2012; Rosumek et al., 2009; Stefani et al., 2015). Yet, ants are typically superior competitors over spiders given traits such as group foraging and territoriality, possibly decreasing spider predation rate on insect prey (Buckley, 1990) and spider abundance (Lange et al., 2021; Mody and Linsenmair, 2004; Nahas et al., 2012), or changing spider community composition (Izzo and Vasconcelos, 2005; Sanders and Platner, 2007; Schuldt and Staab, 2015). Based on the Exploitation Ecosystems Hypothesis, we reasoned that agonistic interactions between generalist predators such as ants and spiders may offset their response to shared prey. For instance, in an ant-plant mutualism, ant presence suppressed the increase of spider abundance with host plant size (Izzo and Vasconcelos, 2005). However, it is unclear whether this response reflected prey availability, and to what extent such interference of ants on spiders generalizes beyond specialized systems such as myrmecophytes.

Much of what is known about the trophic dynamics of plant-dwelling macroarthropod communities is based on tropical plants with extrafloral nectaries, many of which occur in the largest Neotropical savanna, the Brazilian Cerrado (2,045,000 km^2; (Calixto et al., 2018; Oliveira and Freitas, 2004). However, in Northern Amazonia lies another continuous savanna region (68,145 km^2) – the largest within the Amazon rainforest – covering parts of Guyana and Venezuela but mostly Brazil, where it is locally known as “Lavrado” (Barbosa and Campos, 2011). This region has a significantly different floristic composition compared to other Neotropical savannas, with only three species accounting for up to 70% of tree individuals and over 80% of aboveground plant biomass: *Curatella americana* (Dilleniaceae), *Byrsonima crassifolia* and *Byrsonima coccolobifolia* (Malpighiaceae) (Barbosa et al., 2007). *Byrsonima* spp. produce floral lipids rather than nectar, the former having two-to-four-times higher energy content (Vinson et al., 1997). However, the extent to which the abundances of macroarthropods inhabiting these trees reflects plant traits or biotic interactions between each other is unclear.

In this study, we investigated the interaction between top-down and bottom-up effects in macroarthropod communities inhabiting the dominant tree species in the Lavrado. We examined the relationships among the abundances of ants, spiders, insect prey and plant traits across 97 trees surveyed three times from two sites in Northern Brazilian Amazonia. We tested the following hypotheses: (1) herbivore insect prey should be limited by plant resources, thereby increasing in abundance with habitat size (tree crown volume) and floral resources (relative flower cover) and possibly varying among tree species due to differences in resource quality and/or quantity offered by host trees; (2) ants should be limited by both plant and animal resources given their generalist niche, thereby responding to plant traits similarly to insect prey but also increasing in abundance with insect prey abundance; (3) like ants, spider should also be limited by both plant and animal resources, and thus should respond to plant traits and insect prey similarly. However, competitive dominance of ants over spiders predicts that increasing ant abundance should weaken the increase of spider abundance with insect prey abundance.

2. Methods

2.1. Study site

The study was performed in two sites of Long-Term Ecological Research under supervision of the Brazilian Program for Biodiversity Research (PPBio), near the city of Boa Vista, capital of Roraima state. The sites were: Cauamé Campus, located in the Federal University of Roraima (2.8676 N/−60.7223 W – 80 m a.s.l.), and Água Boa Experimental Field, located in the Brazilian Agricultural Research Corporation (2.6586 N/−60.8594 W – 79 m a.s.l.) (Supplementary Information, Fig. S1). Both sites have permanent plots (10 × 250 m) that follow terrain contour lines to minimize natural variation in altitude within plots, which reduces environmental variation within them as much of it is related to altitude in Amazonia (Magnusson et al., 2005). The sites are representative of general landscape of the Lavrado: mosaics of grassy and woody savanna with low density of trees (Barbosa et al., 2012). Average annual rainfall is 1600–1700 mm (Barni et al., 2020). Both sites undergo hydric stress during the dry season (December to March), related to higher sunlight, temperature and recurrent fires (Barbosa and Fearnside, 2005).

2.2. Field sampling

We sampled 97 trees (*C. americana* = 35, *B. crassifolia* = 34, *B. coccolobifolia* = 28) across 16 permanent terrestrial plots split between the two sites, with 9 plots in Cauamé and 7 plots in Água Boa (Supplementary Information, Fig. S1) (Souza et al., 2006a, 2006b). Sampling occurred during daylight and was repeated in three seasons: dry (December 2005), dry-to-wet transition (April 2006) and wet-to-dry transition (September 2006), resulting in 291 measurements of individual trees. Trees were sampled using a beating method: branches were involved using an entomological net (1.8 m × 1.2 m, 0.5 mm mesh size) and beaten for 30 s, so that macroarthropods fell into a collector bag at the bottom of the net (30 cm × 30 cm). For trees shorter than 1 m, the whole individual was involved with a single net, whereas for taller trees two branches were sampled using one net for each branch and beating them simultaneously. This method avoided loss of individuals by wind or flight. After daily collections, collector bags were kept at −4 °C for 1 h, after which macroarthropods were sorted and identified to the level of orders. All individuals were sorted according to three groups: ants (Hymenoptera), spiders (Araneae) and putative insect prey (all remaining individuals, including Hemiptera, Orthoptera, Coleoptera, Dictyoptera and other minor insect orders). Except for caterpillars and adult Lepidopterans, all individuals were conserved in alcohol 70% (Almeida et al., 2003). Tree crown volume was estimated for each tree using a metric tape, assuming a cylinder shape. Crown flower cover was estimated visually as the proportion of the crown volume containing flowers, based on five ordinal classes (no flowers, 1–25%, 26–50%, 51–75% and >75%). Voucher specimens were deposited in the Entomological Collection at the National Institute for Amazonian Research (INPA), Manaus, Brazil. All macroarthropod and tree data are available online (Souza et al., 2006a, 2006b).

2.3. Statistical analysis

We used Linear Mixed-effects Models to test for the predicted relationships among macroarthropod groups and plant traits at the level of individual trees. The 97 trees sampled three times generated 291 observations, but due to missing values for some variables, only 277 observations were used. Three models were created, each having the abundance of one of the three groups as response variable (i.e. insect prey, spiders and ants). The identities of sites, plots and individual trees were used as nested random factors to account for spatial autocorrelation among nearby trees and repeated counts on the same tree. All models included as predictors tree crown volume (m^3), relative flower cover (ordinal variable with five levels), season (ordinal variable with three levels), tree species (*C. americana*, *B. crassifolia* and *B. coccolobifolia*) and tree sampled volume (m^3) to account for variation in sampling effort. Further, the ant and spider models included insect prey abundance as a further predictor, and the spider model included an interaction between insect prey abundance and ant abundance, as hypothesized. All numeric variables were log-transformed to account for heteroscedasticity and non-linearity. Models were estimated through maximum likelihood, and their predictive power was measured by the marginal R^2 (i.e. variation explained by predictors only) and conditional R^2 (i.e. variation explained by predictors plus random factors). Partial residual plots were used to visualize statistically supported responses to predictors while keeping remaining predictors constant (Breheny and Burchett, 2017). All analyses were performed in R 4.1.1 (R Core Team, 2021).

3. Results

We collected 5787 individual macroarthropods across the 97 trees split between the two sampling sites over the three sampling campaigns. Tree-dwelling macroarthropod communities were numerically dominated by ants (Hymenoptera) and spiders (Araneae), which represented 74% of all sampled individuals per tree (Supplementary Information, Fig. S2). The Linear Mixed-effects Models showed that insect prey, ants and spiders responded each to some of the investigated predictors, although predictors differed between groups. First, insect prey abundance increased with both tree crown volume and flower cover (Table 1, Fig. 1). Further, ant abundance increased with insect prey abundance, and also changed among tree species in the order: *B. coccolobifolia* < *B. crassifolia* < *C. americana* (Table 1, Fig. 2). Lastly, spider abundance increased over the study period, while also reflecting an interaction between insect prey abundance and ant abundance: spiders increased in abundance with increasing insect prey, but only where ant abundance was relatively low (Table 1, Fig. 3). Overall, the strength of relationships increased in the order insect prey < spiders < ants, as indicated by the proportion of variation explained by models (Table 1).

Table 1

Results of linear mixed-effects models relating the abundance of tree-dwelling dominant macroarthropod groups to biotic and abiotic predictors in an Amazonian savanna, Northern Brazil ($n = 277$ observations across 97 trees sampled three times, excluding missing values). Models used individual tree ($n = 97$), sampling plot ($n = 17$) and sampling site ($n = 2$) as nested random factors to account for potential autocorrelation among observations from the same tree/plot/site. R^2_m: marginal R^2, or proportion of variation explained by predictors only; R^2_c: conditional R^2, or proportion of variation explained by predictors plus random factors. Bold numbers indicate statistically supported effects ($P < 0.05$).

Response	R^2_m (R^2_c)	Predictor	*F*	*P*
Log Insect prey	0.07 (0.22)	Sampling effort	0.899	0.346
		Log Crown volume	4.005	**0.048**
		Flower cover	7.400	**0.007**
		Time	0.066	0.796
		Tree species	0.128	0.879
Log Ants	0.37 (0.41)	Sampling effort	2.736	0.099
		Log Crown volume	0.079	0.779
		Flower cover	0.560	0.455
		Time	3.514	0.062
		Tree species	26.013	**<0.0001**
		Log Insect prey	76.015	**<0.0001**
Log Spiders	0.25 (0.25)	Sampling effort	0.058	0.809
		Log Crown volume	0.621	0.432
		Flower cover	0.268	0.605
		Time	4.981	**0.026**
		Tree species	0.829	0.439
		Log Insect prey	13.279	**<0.0001**
		Log Ants	19.680	**<0.0001**
		Log Insect prey: log Ants	13.933	**0.0003**

4. Discussion

4.1. The Exploitation Ecosystems Hypothesis and ant-spider interactions on trees

The Exploitation Ecosystems Hypothesis predicts that increases in herbivore abundance with plant productivity should weaken with increasing predator abundance due to direct consumption of prey surplus and/or foraging costs of predator avoidance (Oksanen, 1992; Oksanen et al., 1981; Zanette and Clinchy, 2019). This has been supported for both vertebrate (Letnic and Ripple, 2017; Ripple and Beschta, 2012) and invertebrate herbivores (Richards and Coley, 2007; Welti et al., 2020). Furthermore, similar patterns have been reported across trophic levels: herbivores weakened the increase of plant biomass with primary productivity at higher latitudes (Oksanen and Oksanen, 2000), and parasitoids appeared to weaken the increase of spider density with insect prey density in desert islands (Polis et al., 1998). Here, we found evidence for bottom-up limitation in insect prey (Fig. 1) and ants (Fig. 2), but in spiders this only occurred when ants were less abundant (Fig. 3), consistent with competitive dominance by the latter. Hence, we suggest that the Exploitation Ecosystems Hypothesis can also apply to groups at the same trophic level (or occupying wide, overlapping trophic niches such as ants and spiders) and which can modify each other's collective response to shared resources (insect prey).

In the following, we discuss our findings with reference to the three specific hypotheses advanced in the Introduction: (1) response of insect prey to plant traits; (2) ant response to plant traits and insect prey; and (3) interference of ants on spider response to insect prey. Then, we highlight (4) the limitations of the study and (5) our main conclusions.

4.2. Response of insect prey to plant traits

The increase in insect prey abundance with tree crown volume and flower cover is consistent with limitation by food resources and/or habitat space. *Curatella americana* and *Byrsonima* spp. are known to be subject to strong insect herbivory in Neotropical savanna, especially on young leaves (Foldats and Rutkis, 1975), and larger tree crowns can offer more food resources and more habitat space and shelter in crevices between branches (Campos et al., 2006). Moreover, *Byrsonima* spp. in particular offer lipid-rich exudate in their flowers (Vinson et al., 1997). Nonetheless, these plant traits accounted for very little variation in insect prey abundance (Table 1). This suggests that, at the scale of individual trees, insect prey abundance may better reflect stochastic ecological processes (e.g. dispersal from neighboring sites and ecological drift) or other, unmeasured environmental factors (see below in *Study limitations*).

4.3. Response of ants to plant traits and insect prey

The increase in ant abundance with insect prey abundance and from *B. coccolobifolia* to *C. americana* suggests that both animal and plant resources are important in limiting ant abundance in those trees. Plant-dwelling ants typically feed on various types of resources, including plant exudates (e.g. flower nectar or lipids, extrafloral nectaries), insect exudates (e.g. aphid honeydew) and arthropod prey (Lange et al., 2021; Mody and Linsenmair, 2004; Nahas et al., 2012). For instance, the abundance of ants also correlated positively with that of sucking insects in Central Brazilian savanna (Kuchenbecker and Fagundes, 2018). Therefore, their increase with insect prey abundance could result both from bottom-up limitation and from mutualistic interactions (e.g. with hemipterans).

However, it should be noted that the causality of this relationship might be reversed, or even go both ways. For instance, experimental exclusion of ants decreased the abundance of phloem-feeding coccids,

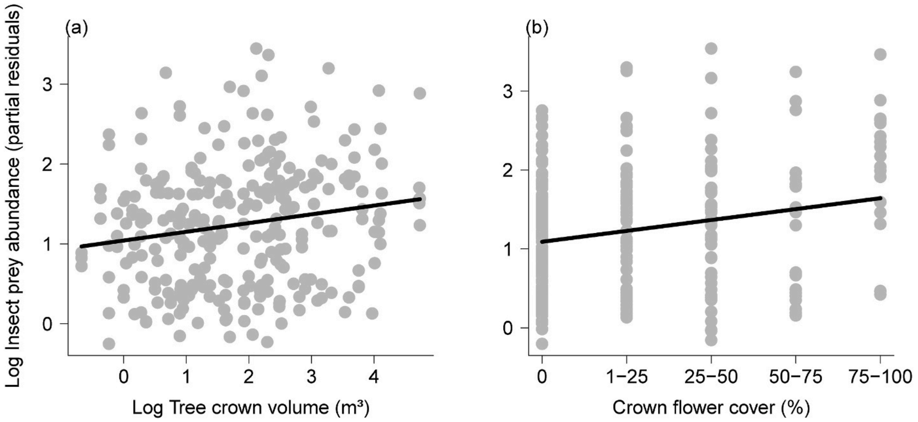

Fig. 1. Response of insect prey abundance to tree canopy volume and canopy flower cover across trees in the savanna of Northern Brazilian Amazonia. Each point represents one tree at a given time (n = 277 observations across 97 trees sampled three times, excluding missing values). Partial residuals represent the variation in the response variable after holding remaining predictors constant. Solid lines indicate statistically supported trends.

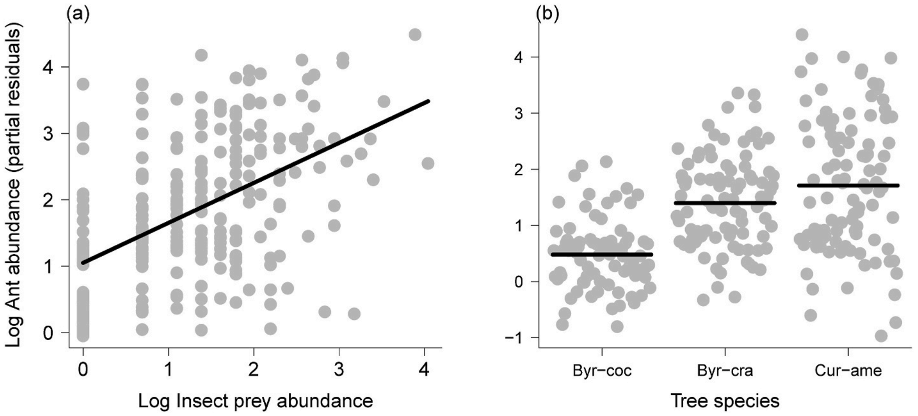

Fig. 2. Response of ant abundance to insect prey abundance and tree species in the savanna of Northern Brazilian Amazonia. Each point represents one tree at a given time (n = 277 observations across 97 trees sampled three times, excluding missing values). Partial residuals represent the variation in the response variable after holding remaining predictors constant. Solid lines indicate statistically supported trends.

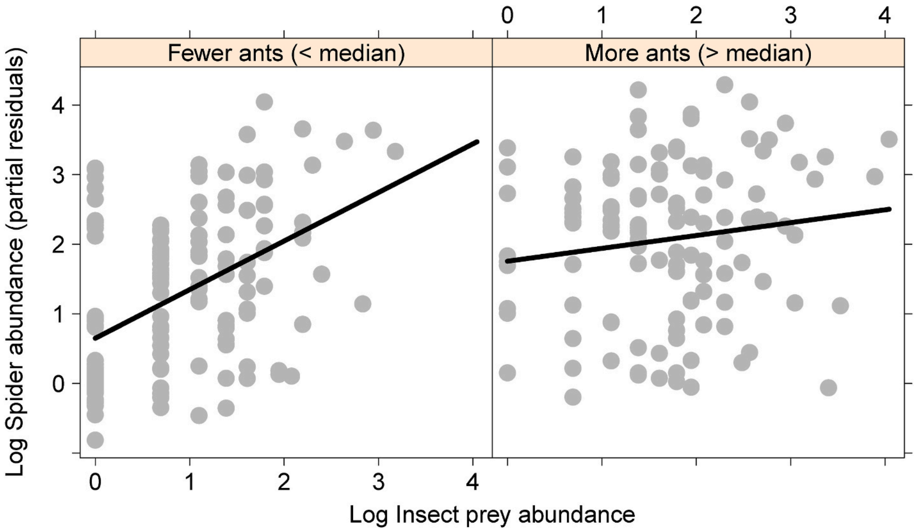

Fig. 3. Response of spider abundance to the interaction between insect prey abundance and ant abundance in the savanna of Northern Brazilian Amazonia. The data were split in two groups (below and above median ant abundance) to facilitate visualization. Each point represents one tree at a given time (n = 277 observations across 97 trees sampled three times, excluding missing values). Partial residuals represent the variation in the response variable after holding remaining predictors constant. Solid lines indicate statistically supported trends.

presumably because ants protect exudate-producing insects from other predators (Sanders and Platner, 2007). Hence, a positive correlation between the abundance of ants and that of other insects, as observed here, might also reflect an effect rather than a response of ants. In fact, ants may simultaneously respond to and affect the abundance of other insects, and the magnitude of each causal direction cannot be easily determined with observational data.

In parallel, the change in average ant abundance between tree species could be driven by differential availability of food resources and/or different structural traits between these tree species, e.g. more nesting sites in the crevices of stems of *C. americana*. Shape, height and crown biomass can change the microclimate and the amount of sunlight available in the crown (Carvalho, 2010), thus affecting the area available for foraging and nesting.

4.4. Interference of ants on spider response to insect prey

Spider abundance increased with insect prey abundance, but this occurred only in trees where ants were less abundant. This contradicts the assumption that ant abundance has a simple, additive effect on spider abundance (Lange et al., 2021; Mody and Linsenmair, 2004; Nahas et al., 2012; Sanders and Platner, 2007). Rather, ants seem to impair the efficiency with which spiders collectively convert insect prey to spider abundance. Plant-dwelling ants and spiders compete for shared animal and plant resource, as indicated by both observation and stable isotope ratios (Helms et al., 2021; Sanders and Platner, 2007), and occasionally prey on each other (Mody and Linsenmair, 2004; Nahas et al., 2012). Nonetheless, the colonial lifestyle of ants correlates with large numbers and aggressive territory defense (Lange et al., 2021). Hence, ants can reduce spider predation rate on insect herbivores (Buckley, 1990), limiting the efficiency with which spiders can benefit from abundant insect prey. Interestingly, in an ant-plant mutualism, experimental removal of ants caused spider abundance to increase with host plant size, but it was unclear whether this increase reflected higher prey availability (Izzo and Vasconcelos, 2005). By including both tree size and insect prey abundance as predictors in our model, we showed that the spider response to insect prey was not confounded by plant size, and that ant interference on spiders' response occurs beyond ant-plant mutualisms.

However, our study is limited in that we lacked finer taxonomic identification and functional data; different ant species could have different effects on spiders, and different spider species could respond differently to ants. Although ant species were not identified, they could be determined to belong to two genera: *Camponotus*, whose species have a generalist diet including plant/aphid exudates and arthropod prey; and *Cephalotes*, whose species are mostly herbivores, occasionally feeding on fungi and animal excreta (Davidson, 2005). Both genera are also dominant tree-dwellers in Central Brazilian savanna, and readily defend newly discovered resources (Camarota et al., 2018). Because *Camponotus* are generally more aggressive, our findings may be mainly driven by this group, either through behavioral avoidance by spiders and/or aggression/predation by ants.

In parallel, the species driving the spider response and their traits are less clear. Behavioral assays indicate that cursorial spiders more readily avoid ant cues, which is presumably an adaptation to higher encounter rates (Mestre et al., 2020). Indeed, cursorial spider species were replaced by web-building species where ants occurred, and more strongly so at higher tree species richness in a subtropical forest (Schuldt and Staab, 2015). This is analogous to the stronger top-down control under higher productivity posited by the Exploitation Ecosystems Hypothesis (Richards and Coley, 2007), albeit driven by a competitor (ants) and affecting cursorial spiders only. In contrast, experimental exclusion of ants increased the abundance of web-building rather than cursorial spiders in both temperate grassland (Sanders and Platner, 2007) and Amazonian rainforest (Izzo and Vasconcelos, 2005), whereas occurrence probability of spiders decreased with ant abundance regardless of species in Central Brazilian savanna (Lange et al., 2021). Furthermore, experimental ant removal can decrease the abundance of specialized ant-feeding spiders (Izzo and Vasconcelos, 2005). Hence, traits other than foraging mode may shape the response of spiders to ants, and both cursorial and web-building species could be involved in the spider response observed here. Conversely, specialized ant-hunting spiders, if present in our study sites, are unlikely to have been negatively affected by ants and may have benefited from more ant prey.

4.5. Study limitations

First, the lack of species and functional identification prevented us from determining whether the observed patterns generalize across species or involve restricted species subsets. Yet, it seems unlikely that higher taxonomic or functional resolution would qualitatively change our conclusions. If the observed patterns are restricted to certain species groups, then discriminating among them would most likely make relationships look even stronger by reducing the noise introduced by mixing species. Secondly, we lacked biomass data. However, it seems reasonable to assume that, for a given group (insect prey, ants or spiders), most variation in biomass among trees is due to variation in number of individuals rather than body size. Therefore, variation in abundance and biomass across trees should be highly correlated and reveal similar patterns, as observed elsewhere (e.g. Sanders and Platner, 2007). Thirdly, we lacked measures of tree nutritional content, which can vary within and between species. Herbivore insect abundance can track the nutritional content of plants, especially of those elements that are typically in short supply to herbivores such as nitrogen (Beltrán and Wunderle, 2013; Prather et al., 2021). Therefore, some of the largely unexplained variation in insect prey abundance may reflect plant nutrient content. Fourthly, we did not consider microarthropods (e.g. oribatid mites and springtails) nor vertebrate animals engaging in trophic interactions with macroarthropods. Microarthropods probably account for very little biomass in these communities, but vertebrate predators such as birds could affect tree-dwelling macroarthropod abundance (Beltrán and Wunderle, 2013).

5. Conclusions

The Exploitation Ecosystems Hypothesis was proposed to explain the trophic structure of communities by assuming that trophic levels function as single exploitative populations. Its main prediction is that herbivore abundance should increase with plant productivity, but only where predators are rare. Despite its simplicity, it has successfully predicted abundance patterns in vertebrates, invertebrates and plants, suggesting it applies across trophic levels. Here, we showed that the strength of resource limitation can also be predicted from asymmetric interactions within trophic levels, such as those between ants and spiders. As these groups are very abundant in trees – often the most abundant macroarthtopods –, their interactions should impact tree arthropod communities by changing not only their trophic structure, but also community size or the total number of individuals in a tree. In turn, community size is expected to affect the relative strength of fundamental ecological processes within trophic levels such as species sorting and ecological drift (Pequeno et al., 2021). Therefore, the Exploitation Ecosystems Hypothesis may provide a link between ecological processes occurring between and within trophic levels, which are typically modelled separately.

Author contributions

RIB and CC conceived the study and its sampling design. Material preparation and data collection were performed by CC. Analysis was performed by PACLP, who also wrote the first draft of the manuscript. All authors commented on previous versions of the manuscript, and read and approved the final manuscript.

Disclosure statements

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated. This study was performed in accordance with institutional and national guidelines. No special approval was required for this type of research.

Declaration of competing interest

We declare that we have no financial interest or relationship related to the subject matter of this manuscript, nor any patents or copyrights relevant to the work in the manuscript, nor anything else that we believe may merit disclosure.

Data availability

All macroarthropod and tree data are available online (Souza et al., 2006a, 2006b).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2023.103955.

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