



Plant-herbivore networks composed by adult and immature insects have distinct responses to habitat modification in Brazilian savannas

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Abstract

Human-induced habitat modification can affect species interactions and ecological networks composed of specialized species may be more susceptible to these effects. Immature and adult insect herbivores have different mobility and specificity levels related to their host plants, which can affect their tolerance to anthropic disturbances. In the present study, we compared the structure of plant-herbivore networks composed of adult and immature insects in 16 Neotropical savanna sites under different land-use intensification levels. We compared insect species richness, insect abundance, connectance, specialization, generality, vulnerability, modularity, and nestedness in plant-immature insect and plant-adult insect networks occurring in preserved and non-preserved areas. In total we sampled 328 individuals of 98 species of host plants and 557 individuals of 310 species of insect herbivores (275 individuals of 143 species of immature insects and 479 individuals of 196 species of adult insects). Although the richness of insect species did not differ between the networks, plant-immature insect networks had a lower insect abundance, generality and nestedness than networks of adult insects. On the other hand, connectance was lower for networks of adults than for networks of immature insects. Our results also show that the effects of habitat modification are more pronounced for immature insects than for adults, as network connectance increases and network vulnerability decreases between preserved habitats and disturbed habitats. Our findings support previous warnings that habitat modification can alter plant–herbivore interactions, and advance the understanding of how these effects can be different for assemblages composed of adult and immature insects.

Implications for insect conservation Our results indicate more consistent effects of habitat modification on immature insect interactions, which showed more specialized networks in preserved environments. Thus, our results contribute to the understanding of how plant–insect interactions are structured in highly disturbed environments, such as Neotropical savannas.

Keywords Anthropization · Cerrado · Ecological networks · Habitat conservation · Plant–animal interactions

Introduction

Land-use intensification through human activities generates environmental changes, such as loss, fragmentation, and pollution of natural habitats (Tylianakis and Morris 2017). These changes can strongly affect biological communities, altering the species richness in the communities,

and influencing the structure of ecological networks formed by species interactions (Araújo et al. 2015a, 2016; Moreira et al. 2018). The complex network approach for the study of interactions has achieved promising advances in understanding interspecific interactions (Poisot et al. 2016; Tylianakis and Morris 2017; Landi et al. 2018; Delmas et al. 2019) and how land-use intensification affects them (Araújo et al. 2015b; 2016, Tylianakis and Morris 2017). Studies on the effect of land-use intensification on ecological networks are essential, as they have significant ecological and evolutionary implications for biodiversity, through the understanding of changes, dynamics, and functioning of natural ecosystems (Tylianakis et al. 2010; Moreira et al. 2018). Interactions between insect herbivores and plants constitute a large proportion of Neotropical biodiversity, and their ecological and

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evolutionary importance has aroused the interest of many researchers in last years (review in López-Carretero et al. 2018a).

Recent studies indicate that habitat modification through land-use intensification can alter different properties of the network structure (Tylianakis and Morris 2017), reducing the host range of herbivores characterized by highly specialized eating habits (Araújo et al. 2015b). In preserved environments, plant-herbivore networks tend to have highly specialized interactions (Castagneyrol et al. 2014), with most insect species consuming only a small part of the available host plant species (Jaenike 1990; Morais et al. 2011). In contrast, as land use intensifies, the average food specialization of herbivorous insects is expected to decrease, as general herbivores tend to persist longer than specialist herbivores (With and Pavuk 2011; Kaartinen and Roslin 2011).

Topological patterns in plant-herbivore networks may differ according to their life-form (e.g., endophages and exophages) (Araújo et al. 2015b) and insect guild (e.g., gallers, suckers, and chewers) (Oliveira et al. 2020). Therefore, the level of specialization and intimacy in the association with host species can be a determining factor in plant-insect interactions (Pires and Guimarães 2013; Araújo et al. 2015b). In this context, insect metamorphosis can also influence the specialization in plant-herbivore interactions, as the holometabolous or hemimetabolous life cycle allows immature and adult stages to occupy different food niches (Yang 2001). Previous studies indicate that interactions between phytophages and their host plants may differ between immature and adult stages of insect development (Novotny and Basset 2005). However, we are not aware of any study addressing these differences from the perspective of ecological networks, or land-use intensification.

In holometabolous insects, the functions of growth, reproduction, and dispersion are segregated between life stages (Pierce and Berry 2011). Larvae are specialized in feeding and growth, whereas, adults prioritize colonizing suitable habitats for reproduction (Pierce and Berry 2011). Larval stages usually have limited mobility due to the absence of wings, feeding on the host plants selected by their parents (Agosta and Klemens 2009), but adults can actively move between different host plants (García-Robledo and Horvitz 2012). In hemimetabolous insects, the differences between juveniles (nymphs) and adults are not as pronounced as in holometabolous ones (Truman and Riddiford 1999), but there may still be differences in the degree of association between insects and plants due to the lower mobility of nymphs.

In the present study, we compared the structure of plant-herbivore networks composed of adult and immature insects in Neotropical savanna areas under different land-use intensification levels. We characterized networks using the richness and abundance of insects and the topological measures of interactions (connectance, specialization, generality,

vulnerability, modularity, and nestedness). We hypothesize that the species diversity and the network structural parameters differ between insect development stages and between environments at different conservation levels. We expect that: (i) immature insect networks will be more specialized (e.g., less connected, more modular, and less nested) than adult insect networks; (ii) anthropized environments will have less diverse and specialized networks (e.g., more connected, less modular, and more nested) than preserved environments; and (iii) plant-immature insect networks will be more sensitive to habitat modification than plant-adult insect networks.

Materials and methods

Study areas

The present study was carried out in Neotropical savanna areas (*cerrado sensu stricto*) in northern Minas Gerais State, Brazil (Fig. 1). The vegetation in Neotropical savanna is dominated by sclerophyllous plants that occur in poor soils, where the availability of water and mineral nutrients in the soil is limited (Ribeiro and Walter 2008). The regional climate is dry tropical (Aw in the Köppen system), characterized by well-defined rainfall periods, an average temperature of 24.2 °C, and an annual rainfall of 1000 mm (Alvares et al. 2014). We sampled 16 savanna remnants, located in preserved and anthropized landscapes (Fig. 1). Preserved areas were characterized by pristine vegetation with no or extremely low human interference, distributed in full-protection conservation areas (Serra do Cabral State Park and Veredas do Peruáçu State Park). We sampled seven sites in preserved areas and nine sites in non-preserved ones. The anthropized areas (non-preserved) were located outside conservation areas in vegetation remnants within landscapes with intensive human land use. These areas were located in urban and peri-urban zones, in the vicinity of paved roads, garbage dumps, selective logging areas, with the presence of domestic animals and livestock.

Plant and insect sampling

We established five 100-m² plots (10×10 m) for plant sampling, totaling 80 plots in 16 areas. Plots showed a minimum 20-m distance from each other and at least 30 m from the fragment edge. In each plot, we inventoried and marked with numbered plastic clamps all live tree-shrub individuals with CBH (circumference at breast height, i.e., 1.30 m from the ground) ≥ 15 cm. We recorded the species, the CBH, and the total height of all marked plants. We measured the CBH with a measuring tape and estimated the height visually.

Species identification occurred in situ, but unidentified samples were collected for later identification and treated

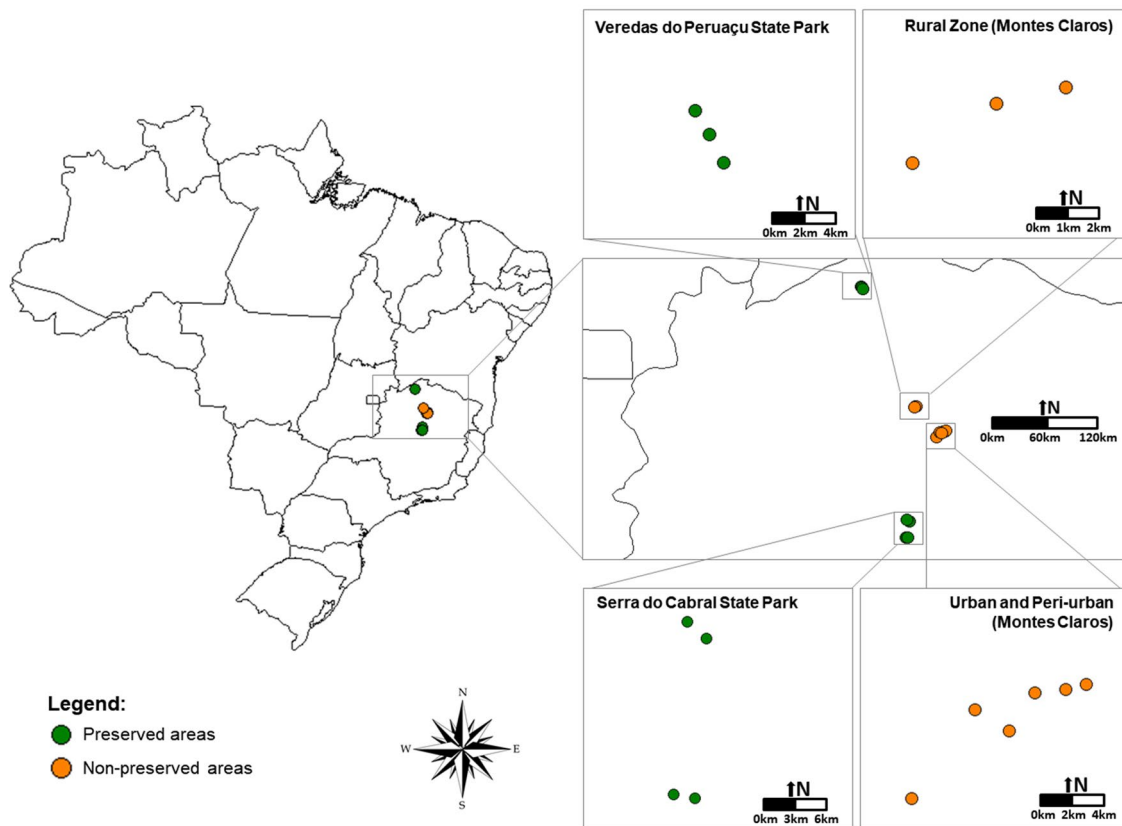


Fig. 1 Location of the 16 Neotropical savanna sites sampled in the Northern region of Minas Gerais, Brazil. Green circles represent preserved areas located in full-protection conservation areas (Serra do Cabral State Park and Veredas do Peruáçu State Park) and orange circles represent non-preserved areas located outside conservation areas in vegetation remnants urban, peri-urban, and rural zones. (Color figure online)

according to conventional techniques of herborization. The classification of species into families followed the angiosperm phylogeny group IV (APG IV 2016), and the identification of the botanical material collected was carried out by consulting the specific literature and, when necessary, a specialist. The species nomenclature and the abbreviations of the respective authors followed Flora Brasil 2020 *online* databases (<http://floradobrasil.jbrj.gov.br>) and The Plant List (<http://www.theplantlist.org/>).

We carried out collections of herbivorous insects on two occasions, once during the dry season (July to September) and the other during the rainy season (October to December) of 2018 and 2019. The collections took place in both seasons for a better characterization of herbivore assemblages as seasonality can influence the occurrence of some species (Silva et al. 2011). In each plot, we selected three branches of each marked plant, which received ten strikes. We used the tapping method to collect all the insects present, with a modified tapping cloth (Oliveira et al. 2020). The collected specimens were stored in 70% alcohol, in containers duly identified with information on the area, plot, and plant from

which they were collected. Later, they were sent to the laboratory for screening and identification of insects.

The insects were separated into morphospecies using external morphological characteristics and identified to the lowest possible taxonomic level. They were also separated according to their development stage (adult or immature). Adults were identified using the taxonomic keys of Triplehorn and Johnson (2011), whereas, immatures were identified following Costa et al. (2006). Adults and nymphs were assembled in entomological boxes and individually cataloged, whereas the larval forms were cataloged and placed in Eppendorfs with 70% alcohol for conservation. We selected only insect taxa known to be phytophagous for the construction of interaction networks, following information available in the literature (e.g., Carrano-Moreira 2015).

Measurements of the plant-herbivore network structure

For the construction of interaction networks, we created quantitative adjacency matrices from the collected

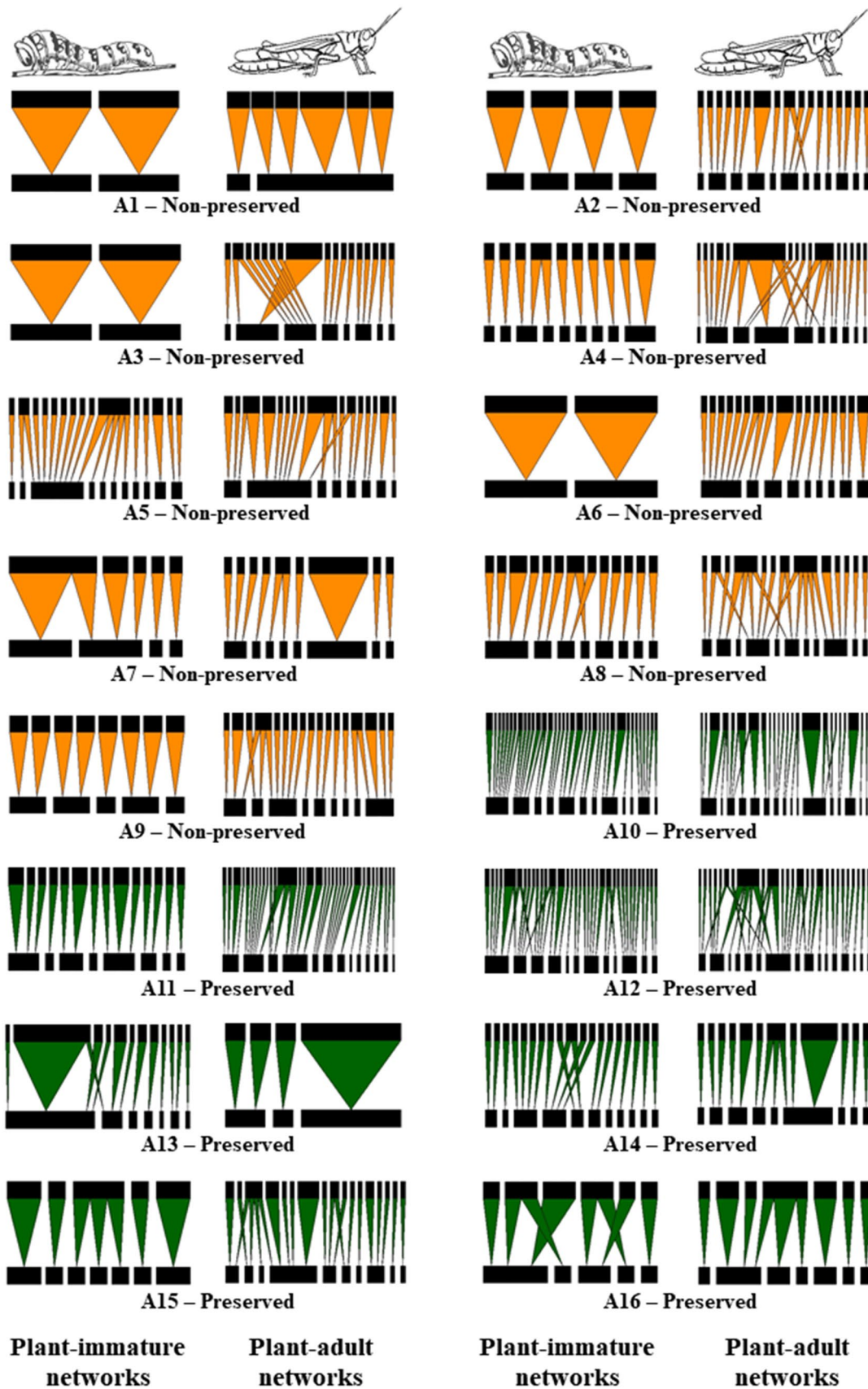


Fig. 2 Plant–herbivore quantitative networks constructed for immature and adult herbivorous insects in preserved (green) and non-preserved areas (orange) of Neotropical savannas in Brazil. Upper black bars represent insect species; lower black bars represent plant species, green lines indicate the interactions in the preserved areas, and orange lines indicates the interactions in the non-preserved areas. The width of the lines represents the number of interactions. (Color figure online)

interaction data. We quantified plant–herbivore interactions according to the abundance of herbivores per plant species. We built networks for adult and immature insects from each area. In this way, we obtained 16 networks of each type. Each network was characterized according to plant species richness, herbivore species richness, and ecological descriptors of plant–insect interactions.

We used the topological descriptors connectance (C), specialization (H2), generality (G), vulnerability (V), modularity (M), and nestedness (NODF) to describe the network structure. Connectance refers to the proportion of interactions performed in relation to the total possible relationships within the network (Landi et al. 2018; Delmas et al. 2019). Connectance is an inverse measure of specialization, i.e., the smaller the connectance, the more specialized the network (Araújo et al. 2015b). Specialization was measured using the index H2, which is a quantitative measure of specialization at the network level and ranges from 0 (total generalization) to 1 (total specialization) (Blüthgen et al. 2006). Generality is the mean effective number of plant species per insect species, whereas vulnerability is the mean number of insect species per plant species, both weighted by their marginal totals (abundance sums) (Dormann et al. 2021).

Modularity is a measure of the occurrence of groups of species (i.e., modules) within the network that interact strongly with each other and little with other groups (Olesen et al. 2007), i.e., the more modular, the more specialized the network will be. We computed the bipartite modularity index Q (Barber 2007) using the DIRTLPawb+ algorithm to detect network modules (Beckett 2016). Nestedness describes to which extent interaction partners of one species have a subset of interaction partners of another species (Bascompte et al. 2003; Dehling 2018). We calculated nestedness using the NODF metric based on overlap and decreasing fill (Almeida-Neto et al. 2008). All networks and descriptors were calculated using the Bipartite package (Dormann et al. 2021) in software R (version 3.4.4).

Statistical analysis

We used generalized linear mixed-effect models (GLMMs) to test the effects of development stage (immature vs. adult) and habitat conservation status (preserved vs. non-preserved) on the variables of network structure (connectance, generality, vulnerability, specialization, modularity, and nestedness)

and insect diversity (insect richness and abundance). In each model, the collection area was used as a random effect variable in order to control for possible intrinsic differences between areas that may affect the diversity and structure of plant–insect interactions. For the models in which insect species richness, insect abundance and network connectance were the variable responses, we used plant species richness as an additional explanatory variable, in order to control the effect of this variable on the diversity and connectivity of the insects (Araújo et al. 2015b). All explanatory variables were included in the GLMMs as fixed effect variables. All models were checked for the distribution of residuals, and appropriate error distributions were used. All analyses were performed in the R program version 3.6.1 (R Development Core Team 2020).

Results

The plant–herbivore interaction networks (Fig. 2) were represented by 328 plants, distributed in 98 species, and 33 families (Supplementary Material 1). Fabaceae was the most important family, with 23 species and 158 individuals, followed by Vochysiaceae, with ten species and 109 individuals, and Anacardiaceae, with three species and 73 individuals. Insects showed 557 individuals, ascribed to 310 morphospecies. Immature insects represented 275 individuals and 143 morphospecies distributed in five orders (Coleoptera, Hemiptera, Lepidoptera, Orthoptera, and Thysanoptera), whereas adults represented 479 individuals distributed in 196 morphospecies also in five orders (Coleoptera, Hemiptera, Orthoptera, Phasmatodea, and Thysanoptera). Hemiptera was the most abundant order regarding immature insects, with 167 specimens, and Cicadellidae was the most representative family, with 79 individuals and 33 morphospecies. Regarding adult insects, Coleoptera was the most abundant order, with 244 specimens, and Curculionidae was the most important family, with 135 individuals and 42 morphospecies. Of the 310 insect morphospecies recorded, 28 were recorded both in immature and adult stages, 115 were exclusively immatures and 167 were exclusively adults.

The insect species richness in networks varied from two to 36 species, with an average of $11.68 (\pm 10.99)$ species of immature insects and $17.00 (\pm 10.58)$ species of adults. However, the richness of the insect species did not differ statistically according to development stage or habitat conservation status, or the interaction between these two variables (Table 1). Insect species richness was also not influenced by plant species richness (Table 1). Insect abundance ranged from two to 68 specimens per network, differing significantly between immature (16.62 ± 15.95) and adult insect networks (29.27 ± 20.27) (Fig. 3a) (Table 1). On the

Table 1 Results of the generalized mixed effect linear models (GLMMs) evaluating the effects of habitat preservation status (non-preserved vs. preserved), and insect development stage (adults vs. immatures) on response variables (insect species richness, insect abundance, connectance, specialization, vulnerability, generality, modularity and nestedness) of plant-insect networks

Response variables	Model	Statistical parameters		
Insect species richness	Random effects	Groups	Variance	Std. Dev.
		Area	29.660	5.446
		Residual	61.840	7.864
	Fixed effects	Explanatory variables	Chi-square	p
		Habitat conservation status	0.3109	0.577
		Development stage	3.431	0.063
		Status \times Stage	3.0618	0.080
Insect abundance	Random effects	Plant species richness	3.373	0.066
		Groups	Variance	Std. Dev.
		Area	85.45	9.244
	Fixed effects	Residual	174.62	13.214
		Explanatory variables	Chi-square	p
		Habitat conservation status	1.063	0.093
		Development stage	7.252	0.007
Network connectance	Random effects	Status \times Stage	0.842	0.358
		Plant species richness	1.464	0.226
		Groups	Variance	Std.Dev.
	Fixed effects	Area	0.010	0.103
		Residual	0.008	0.090
		Explanatory variables	Chi-square	p
		Habitat conservation status	0.311	0.576
Network specialization	Random effects	Development stage	5.025	0.024
		Status \times Stage	3.958	0.046
		Plant species richness	2.589	0.107
	Fixed effects	Groups	Variance	Std. Dev.
		Area	0.003	0.057
		Residual	0.092	0.303
		Explanatory variables	Chi-square	p
Network vulnerability	Random effects	Habitat conservation status	0.597	0.440
		Development stage	0.080	0.777
		Status \times Stage	0.117	0.733
	Fixed effects	Groups:	Variance	Std. Dev.
		Area	0.126	0.355
		Residual	1.034	1.017
		Explanatory variables	Chi-square	p
Network generality	Random effects	Habitat conservation status	0.014	0.908
		Development stage	2.518	0.113
		Status \times Stage	3.860	0.049
	Fixed effects	Groups	Variance	Std. Dev.
		Area	0.064	0.252
		Residual	0.174	0.418
		Explanatory variables	Chi-square	p
Network modularity	Random effects	Habitat conservation status	0.009	0.925
		Development stage	3.844	0.049
		Status \times Stage	0.178	0.673
	Random effects	Groups	Variance	Std. Dev.
		Area	0.002	0.048
		Residual	0.019	0.138

Table 1 (continued)

Response variables	Model	Statistical parameters		
Network nestedness	Fixed effects	Explanatory variables	Chi-square	p
		Habitat conservation status	1.347	0.246
		Development stage	0.671	0.413
		Status \times Stage	0.000	0.985
	Random effects	Groups:	Variance	Std. Dev.
		Area	5.398	2.323
		Residual	28.991	5.384
	Fixed effects	Explanatory variables	Chi-square]	p
		Habitat conservation status	0.014	0.906
		Development stage	4.525	0.033
		Status \times Stage	3.117	0.077

The chi-square and p values are the regression coefficients of the general model

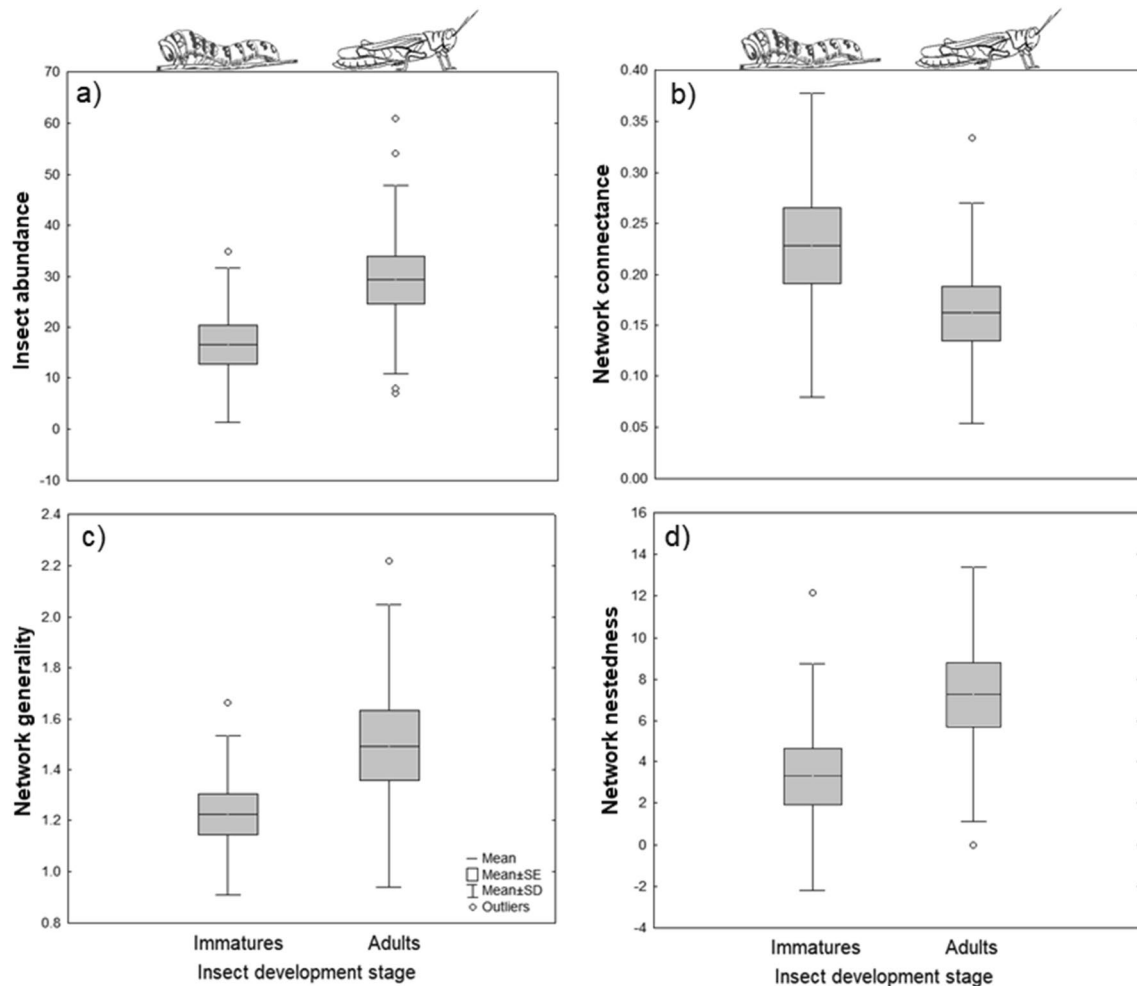


Fig. 3 Comparison of the insect abundance, network connectance, network generality and network nestedness between plant-herbivore networks of immature and adult insects in areas of Neotropical savannas in Brazil

other hand, insect abundance was not influenced by the plant species richness or habitat status or the interaction between status and stage of development (Table 1).

Network connectance varied from 0.07 to 0.50 (0.19 ± 0.13). Contrary what was expected, network connectance was higher for immature insects (0.22 ± 0.11) than for adults (0.16 ± 0.11) (Fig. 3b). Network connectance was also significantly influenced by the statistical interaction between habitat status and development stage (Table 1), because it was only for immature insects that the connectance was lower in preserved habitats than in non-preserved habitats (Fig. 4a). On the other hand, the network connectance was not influenced by plant species richness (Table 1). The network specialization (index H2) ranged from 0.00 to 1.00 (0.62 ± 0.29). By contrast with the connectance, there were no significant effects of the explanatory

variables on the network specialization of the plant–herbivore networks (Table 1).

The network generality differed between development stages, being higher for adults (1.44 ± 0.96) than for immature insects (1.27 ± 1.20) (Fig. 3c), but it was not affected by any other explanatory variable (Table 1). As regards the network vulnerability, the only effect observed was of the interaction between the habitat status and the stage of development (Table 1): for immature insects the vulnerability was higher in preserved habitats, whereas for adults the vulnerability was similar for preserved and non-preserved habitats (Fig. 4b). Average vulnerability was higher for adults (2.67 ± 0.96) than for immature insects (2.11 ± 1.20).

The network modularity ranged from 0.24 to 0.86, with an average of $0.70 (\pm 0.11)$ for immature and $0.66 (\pm 0.15)$ for adult insects, and therefore no significant difference between them (Table 1). Similarly, modularity was not influenced by habitat conservation status or the ecological interaction between habitat status and development stage. Nestedness ranged from 0 to 20 and had higher values for adult insect networks (7.26 ± 5.22) than for immature insect networks (3.29 ± 6.20) (Table 1; Fig. 3d). On the other hand, habitat status (and the interaction between habitat status and development stage) did not affect the nestedness of the networks.

Discussion

Studying the interactions of immature and adult insects on the community scale is very difficult because of the enormous diversity and our low taxonomic knowledge of species in tropical environments (Cagnolo 2018). In the present study, since we used classical taxonomy to differentiate between species and build interaction networks, we were unable to achieve an exact match between the adult and immature morphospecies, with fewer than 10 % of insect species being recorded in both stages. Although it was not possible to use other tools (e.g., DNA barcoding) to identify and compare the species, we believe that there may have been a higher correspondence between the networks of the different stages, as both adult and immature insects were collected in the same sites, at the same time and on the same host plants. However, it is not necessary for our work that the species be the same, as our hypothesis does not depend on the identity of the species: the morphological (e.g., absence of wings) and behavioural (e.g., low mobility) differences between, on the one hand, larvae and nymphs and, on the other, adults are a general rule for Insecta. Moreover, our results show that species richness did not differ between the networks of adult and immature insects. These results indicate a similar number of herbivore species in the

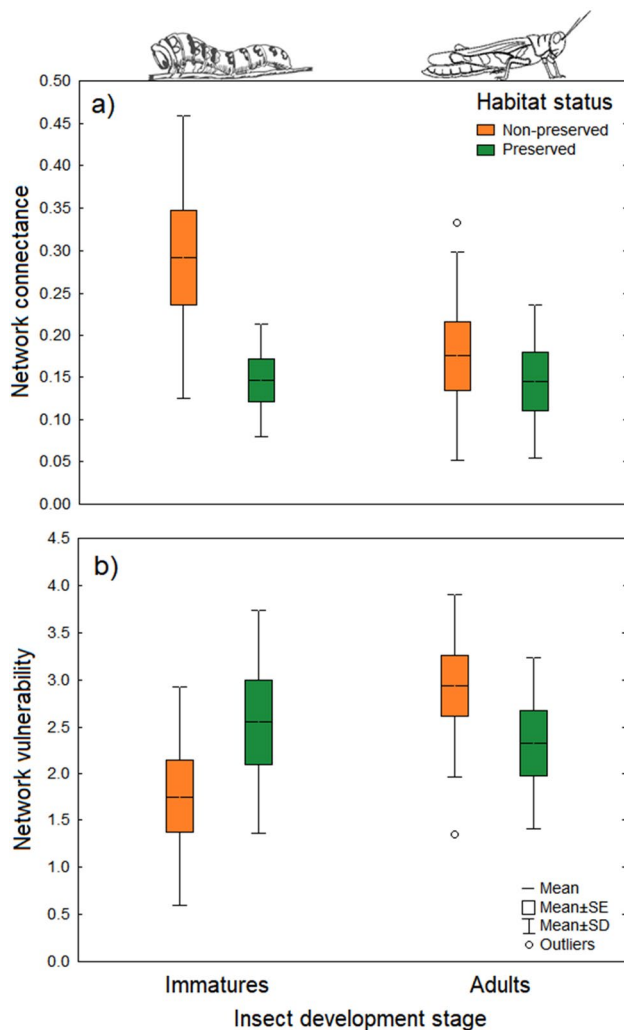


Fig. 4 Effects of habitat conservation status (preserved vs. non-preserved) and insect development stage (immature vs. adult) on the connectance (a) and vulnerability (b) of plant–herbivore networks of Neotropical savannas in Brazil

communities analysed, regardless of the stage of development considered.

We found different structural patterns for the networks composed of adult and immature insects. Our results show that adult insect networks were more abundant, more nested, more generalized and less connected than immature insect networks. Besides, we found that immature insect networks were more sensitive to habitat modification than adult insect networks, confirming our expectations. The networks of plants and immature insects had higher levels of connectance and lower vulnerability in anthropized (i.e., disturbed) habitats, whereas for plant–herbivore networks of adults only the vulnerability differed between habitats, being lower in preserved habitats. As far as we know, this is the first study to investigate patterns in the diversity and structure of plant–herbivore networks of adult and immature insects in Neotropical savannas in the context of intensified land use.

Structure of plant–herbivore networks of adult and immature insects

We recorded a greater abundance of adult herbivorous insects associated with plants. Among the few studies that address this adult–immature comparison, Novotny and Basset (2005) indicate that there are differences in the abundance of insects of different stages because immature insects and adults often have different eating habits. Herbivorous adult insects tend to predominate in tropical vegetation because they are folivorous, whereas their larval stages may be xylophagous, rhizophagous, or endophagous (Basset 2001; Novotny and Basset 2005; Ødegaard 2000). Our findings show a greater abundance of coleopterans, such as curculionids and chrysomelids, among the adult insects. These families are characterized in tropical forests by feeding on roots as larvae and then migrating to the canopy, feeding on leaves as adults (Basset 2001). Thus, many herbivorous adult insects tend to be more visible than immature insects and therefore easier to capture. However, adult insects are winged and tend to have greater mobility than immature ones. In this sense, despite being more visible, the adults are not very easy to capture, especially when the entomological umbrella method is used, as these insects generally disperse very quickly among plants.

Contrary to our expectations, network connectance was higher for networks of immature insects than for networks of adults. As the insect species richness did not differ between the stages of development, we assume that the greater connectance of the immature networks is caused not by sampling effects (e.g., size of the network, which tends to affect connectance, see Araújo et al. 2015b), but by how the insects are distributed among the plant species. We hypothesize that, due to their lower mobility, immature insects tend to

have a higher concentration on a few host plants. As the choice of host plant is made by the mother, on the scale of communities it is likely that the mother will select the most favourable plant species for her offspring (review in Dicke 2000). In the case of neotropical savannas, many plants have a high level of sclerophylly (Allain et al. 1998); some groups of herbivores tend to avoid the harder plants (Neves et al. 2010), and consequently concentrate on those that are less sclerophyllous. Corroborating this idea, we observed that the generality values (i.e., a weighted measure of the distribution of plant species by insect species) were lower for immature networks than for adult networks. This indicates that in immature networks there are, on average, fewer plant species being used by insect species.

Unlike connectance, network specialization and modularity did not differ between development stages. On average we found relatively high values (> 0.60) of specialization and modularity for both adults and immature insects. This pattern is common in plant–herbivore networks (review in López-Carretero et al. 2018a), and can be caused by high competition between herbivores that restricts the exchange of interaction factors (Villa-Galaviz et al. 2012), and by ecological and evolutionary restrictions on interactions that generate compartments of interacting species within the network (Lewinsohn et al. 2006). Furthermore, modularity is a topological descriptor that tends to be highly correlated with network specialization (Blüthgen 2010; Tylianakis et al. 2007; Olesen et al. 2007). Thus, our results indicate a high degree of specialization and modularity for plant–insect networks independently of the insect group, as has previously been identified for other antagonistic networks (Kemp et al. 2017; Morris et al. 2014). On the other hand, we found higher values of nestedness in adult insect networks than in immature insect networks. The nested organization of adult insect networks likely is due to their higher abundance, as nestedness can be generated by the chance that more abundant species tend to be more connected (Lewinsohn et al. 2006). Therefore, more abundant adult species would be interacting with a large part of the plant community, whereas, in immature insects, these interactions would be more restricted (Lewinsohn et al. 2006).

Conservation status and plant–herbivore networks of adult and immature insects

Our results also showed that plant–immature insect networks were more connected in anthropized environments (i.e., urban and peri-urban areas) than in preserved environments (i.e., reserves). These results suggest that anthropization must be leading to a greater loss of more specialized species and selects generalist species in immature networks. Previous studies have reported that habitat fragmentation can favor the establishment of generalist herbivores,

which increases connectivity and decreases the specialization of plant-herbivore networks (Pinho et al. 2017; Wirth et al. 2008). The low level of connectivity of the immature networks in preserved environments was similar to that observed for adult networks in both preserved and anthropized environments (see Fig. 4a). This pattern suggests that connectance is usually low for the plant-herbivore networks located in the savannas in the study, and that, in the case of adult insects, it remains unchanged even in environments in which anthropic changes occur. This may be related to the high mobility of adults, which allows them to search for preferred hosts in the disturbed landscape and, thus, allows the maintenance of the network structure.

Another observed result is that habitat modification decreases the vulnerability of networks of plants and immature insects, but it seems to have little effect on adult networks. Vulnerability is a weighted measure of the number of insect species per plant species, and can be defined as the degree of host plant specialization (Wang et al. 2020). When considering vulnerability, we found higher values for networks of adults, in both preserved and non-preserved habitats, and for networks of immature insects in preserved habitats. The decrease in the number of insect species per plant species in non-preserved habitats in our study may be a consequence of the change in the composition of plant species in human-modified landscapes (Didham et al. 2007; Kruess and Tscharntke 2000). Recent evidence indicates that habitat disturbance alters the composition of woody plant communities in neotropical savannas, leading to the dominance of species more tolerant to changes in environmental characteristics (Freitas et al. 2020). We believe that homogenization in the plant community can lead to the replacement of key host plant species (e.g., super-hosts) that harbour many insects and interactions (Araújo et al. 2019). Furthermore, previous studies have pointed out that low vulnerability may be a consequence of the loss of species of consumers in human-disturbed environments (Lopez-Carretero et al. 2014; Valladares et al. 2012). Although we did not find any differences in the richness of insect herbivores between preserved and non-preserved habitats, we hypothesize that the loss of some insect species, especially those associated with key host plant species, may be an important factor driving the decrease in vulnerability in disturbed savannas.

Some topological descriptors, such as specialization, modularity and nestedness, did not differ between the preserved and the non-preserved habitats. As previously discussed, high specialization and modularity are very common in plant-herbivore networks, and this can be generated by various ecological and evolutionary restrictions on the realization of trophic interactions (Andreazzi et al. 2020; Landi et al. 2018; Pires and Guimarães 2013). Previous studies have reported how these restrictions on carrying out interactions can generate an invariant pattern for many topological

descriptors, even in contrasting environments (Andreazzi et al. 2018; Kemp et al. 2017; Morris et al. 2014). In the case of nestedness, on the other hand, species abundance is a very important factor, and this did not vary significantly between the preserved and the non-preserved habitats. Thus, our results suggest that some rules of organization of plant-herbivore networks are so strong that they remain even in human-modified landscapes.

Conclusion

Our study explored the topological responses of the plant-herbivore interaction networks to the effects of human-induced habitat modification. Despite the importance of conserving plant-herbivore interactions and associated ecological functions, few studies focused on how land-use intensification through human activities influences the interaction pattern involving immature and adult insects and their host plants. In this context, the present study stands out as the first one to make a systematic comparison of the structure of the interaction network and traditional measures, species abundance, and diversity among immature and adult insects in Neotropical savannas subject to different types of land use. Our results showed differences in specialization between development stages, and point to different effects of conservation status on immature and adult herbivores. We found that plant-herbivore networks of immature insects were more specialized and had more consistent responses to habitat modification, with a more specialized network structure in preserved environments. This result corroborates our expectations, indicating that immature insects are more susceptible to disturbances in natural habitats. Future studies can investigate whether these differences in specialization between development stages are consistent in other types of ecosystems, and contrast whether holometabolous and hemimetabolous life cycles show different response patterns.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval Research complies with current laws in Brazil and all the necessary permits (IEF/ICMBIO) were obtained for the field study.

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