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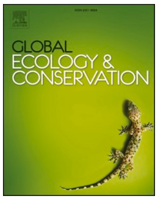

Original research article

Human-induced habitat modification affects the structure of insect communities and the topology of plant-herbivore networks in Brazilian Neotropical savannas

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ABSTRACT

Human-induced habitat modification can alter various aspects of biological diversity, such as interspecific interactions that form ecological networks. In this study, we investigated how species diversity and the interaction structure of plant-herbivore networks differs between wild, rural and urban fragments of Brazilian savannas. We tested the hypothesis that habitat modification leads to a proportionally greater loss of specialized species and interactions, reducing the diversity of herbivorous insect species, increasing network connectance, and decreasing network modularity. The study was conducted in 2018 and 2019 across 16 savanna fragments located in the Neotropical savannas of Brazil, spanning a gradient of habitat disturbance including wild, rural, and urban areas. In total, we sampled 312 insect species, 94 plant species, and 503 interspecific interactions in 16 plant-herbivore networks. Using a model selection procedure, we found that the conservation status of savanna (wild, rural and urban fragments) was present in all the best-selected models. Our results show that urban and rural areas had a lower proportion of host plants with herbivores, lower insect abundance, and lower richness of herbivorous insects compared to wild areas. In addition to changes in species richness, we also observed that urban areas exhibited more connected, more robust and less modular networks compared to wild areas, supporting our expectations. These findings indicate that the intensification of human-induced habitat modification along the urbanization gradient leads to species loss and generalization of plant-herbivore networks in Neotropical savannas.

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1. Introduction

Human-induced habitat conversion is a major driver of biodiversity change, promoting the extinction of native species while facilitating the spread of invasive species, both plant and animal (Sandor et al., 2022; Araújo et al., 2024a; Proesmans et al., 2024). These modifications in the species composition of ecological communities disrupt long-established interspecific ecological interactions and foster novel interactions, particularly through the establishment of non-native species (Tylianakis et al., 2010; Araújo et al., 2024a). Consequently, habitat modification can modify not only the composition but also the structure and dynamics of interspecific interactions (Araújo et al., 2015; Staniczenko et al., 2017; Morrison et al., 2020). Interspecific interactions can form complex ecological networks that may be simplified in the face of anthropogenic disturbances (Tylianakis et al., 2010). Therefore, understanding and preserving the integrity of ecological networks is essential for mitigating the adverse effects of habitat conversion and ensuring the sustainability of natural ecosystems.

The ecological network approach facilitates the analysis of complex structural patterns across multiple species (Pires, 2017; Tylianakis and Morris, 2017; Delmas et al., 2019). In the context of human-induced habitat modifications, this approach has been widely used to explore changes in community structure and ecosystem functioning (Staniczenko et al., 2017; Moreira et al., 2018; Neff et al., 2021; López-Flores et al., 2024). Conceptual models have illustrated how the loss of biotic interactions—especially under structured interaction loss scenarios—can lead to cascading effects in network robustness and potentially affect community stability (Morrison et al., 2020). Changes in interaction networks can impact community functionality and ecosystem services (Valiente-Banuet et al., 2014; López-Flores et al., 2024), thereby accelerating the current biodiversity crisis (Sandor et al., 2022). In this context, focusing on ecological networks enables assessing changes in ecological communities even when changes in species richness are not detected.

In terrestrial ecosystems, the suppression of the natural vegetation and their replacement by introduced species are two important negative effects of habitat conversion (Foley, 2005). Consequently, interactions between plants and their herbivores are directly affected (Rossetti et al., 2019; Silveira and Araújo, 2021), with potential consequences on ecological processes and functions (Rossetti et al., 2019). For example, there is evidence that habitat modification can alter the structure of plant-herbivore networks (Pinho et al., 2017; Miles et al., 2019; Neff et al., 2021) and it is expected that these effects can accelerate the loss of those more specialized interactions (Vázquez and Simberloff, 2002; Araújo et al., 2015). In addition, since generalist species can easily switch their food resource in response to disturbances, their populations can be favored when compared to cooccurring specialists.

The Brazilian Cerrado, the larger and more diverse Neotropical savanna ecosystem, is currently one of the terrestrial biomes most affected by human-induced habitat modification (Colli et al., 2020; Françoso et al., 2020). Recent estimates indicate that more than 50 % of the original coverage of Neotropical savannas has already been converted into other types of landscapes, mainly due to agriculture, livestock farming, and urbanization (Colli et al., 2020). As a result, the remaining savanna fragments are often isolated amidst non-natural matrices of monocultures, planted pastures, or cities (Freitas et al., 2020). These changes in land use and alterations in the landscape can affect the diversity of plant and insect species, as well as the organization of their interactions within the vegetation fragments (Araújo et al., 2024b). For example, recent studies have demonstrated that plant communities in Neotropical savannas significantly differ in plant composition between urban, peri-urban, and rural areas (Freitas et al., 2020), and that the diversity of herbivorous insects and the topology of plant-galling networks are altered in urban fragments (Araújo et al., 2024b). In contrast, exophagous herbivorous insects—despite their functional importance and taxonomic diversity—remain poorly studied in the context of interaction network structure and land-use gradients in Neotropical savannas.

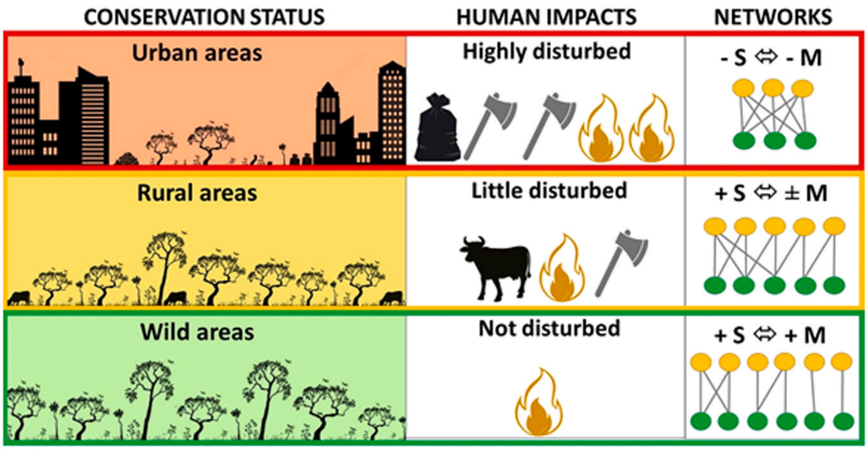

Fig. 1. Conceptual model illustrating expected patterns in plant-herbivore interaction networks in relation to conservation status and intensity of human impacts in neotropical savannas. Urban fragments have more frequent and intense human impacts, such as cutting, pollution and fire, resulting in lower species richness and lower specialization of networks. At the other opposite of the gradient, wild areas located within permanent conservation units are characterized by having little or no anthropogenic impact (where only natural or anthropogenic fire is present). High species richness (S) and greater Modularity (M) of plant-herbivore networks are expected for these areas.

This study aimed to evaluate the effects of different types of habitats (wild, rural and urban fragments), on the diversity of exophagous herbivorous insects and on the structure of plant-insect interaction networks in Brazilian savanna areas. We hypothesize that habitat disturbance alters both the diversity of herbivore communities and the topology of plant–herbivore interaction networks (Fig. 1). Specifically, we expect that urban and rural fragments will show reduced herbivore species richness, abundance, and proportion of plant species hosting herbivores, compared to wild fragments, which are expected to retain higher insect diversity. To describe changes in network topology along the disturbance gradient, we used connectance (i.e., the number of realized interactions in relation to the potential total number), modularity (i.e., the formation of interaction clusters where species are densely connected among themselves and weakly connected with others), and robustness (i.e., resistance of an ecological network to species loss). Given the greater vulnerability of specialized species to disturbance, we expect higher network connectance and robustness in urban fragments—driven by the dominance of generalist species—compared to rural and wild areas. Finally, we predict a decline in network modularity along the disturbance gradient, with urban networks showing reduced levels of modularity.

2. Materials and methods

2.1. Study areas

The study was conducted in neotropical savanna (cerrado *sensu stricto*) areas in the municipalities of Montes Claros, Joaquim Felício, Buenópolis, and Bonito de Minas, located in the northern region of the state of Minas Gerais, Brazil (Fig. 2a). Neotropical savannas in the Brazilian Cerrado are characterized by the presence of a grassy herbaceous layer and a shrubby and arboreal layer, featuring low, inclined, tortuous trees, with irregular and twisted branches that often show evidence of burns (Ribeiro and Walter, 2008). The climate of the region is tropical savanna, predominantly classified as *Aw* according to the Köppen classification, with well-defined dry and rainy seasons. Annual precipitation and temperature range between 900 and 1200 mm and 21° to 24°C per year, respectively (Silveira and Araújo, 2021).

A total of 16 natural vegetation fragments located in regions with different land use types were sampled (Fig. 2a): (i) four in urban areas in Montes Claros, susceptible to various anthropogenic actions such as air and noise pollution, litter, fire, and vegetation disturbance, considered areas with intense land use; (ii) five rural areas located > 10 km away from urban habitats with occasional human interference and fires; (iii) seven fully preserved areas of Neotropical savannas, including four in the Serra do Cabral State Park (Buenópolis and Joaquim Felício), and three in the Veredas do Peruaçu State Park (Bonito de Minas), two full-protection conservation units located > 100 km away from urban habitats. The selection of sampling areas was based on a stratified design along a land-use gradient (wild, rural, and urban), but the specific sites within each category were chosen based on accessibility, safety, and the presence of cerrado *sensu stricto* vegetation.

2.2. Sampling of plant species

Five 100 m^2 (10 m × 10 m) plots were randomly allocated in each area, totaling 80 plots across the 16 sampling areas. In each plot, all living woody plants (shrubs and trees) with a diameter at breast height (DBH) $\geq$ 15 cm were inventoried and marked with numbered plastic bands. Plant species were identified to the species level in the field whenever possible. Identifications were confirmed using specialized literature and expert consultation when needed, and nomenclature was verified using the Flora e Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>) and The Plant List (<http://www.theplantlist.org/>) databases. From the field-collected data, the species richness and abundance of plants per area were calculated based on the number of species and individuals observed in the plots, respectively. All five plots in each area were sampled twice, once during the dry season and once during the rainy season in order to obtain sample completeness.

2.3. Sampling of insect herbivores

Insects present on the plants were collected using the beating method with a beating sheet on three branches per plant (Silveira and Araújo, 2021). Herbivore collections took place in 2018 and 2019, with nine areas sampled at 2018 (five rural areas and four urban areas, all located of Montes Claros municipality) and seven areas sampled at 2019 (four areas at Serra do Cabral State Park and three areas at Veredas do Peruaçu State Park). Subsequently, the insects falling onto the beating sheet were captured using entomological forceps, preserved in 70 % alcohol, and placed in containers labeled with information regarding the area, plot, and plant from which they were collected. In the laboratory, the insects were identified to the lowest taxonomic level possible and sorted into morphospecies. All guilds of exophagous herbivorous insects (chewers, suckers, and scrapers) were considered. The identified insect and plant species were used to construct interaction networks.

2.4. Network topology analyses

Quantitative plant-herbivore interaction networks, based on the abundance of herbivorous species per plant species, were constructed for each study area. For each area, data from the five 10 × 10 m plots and two seasonal sampling campaigns (dry and rainy) were pooled to construct a single interaction matrix and derive network metrics. From the collected data, the species richness and abundance of insects in each network were quantified. Additionally, in each network, the proportion of host plant species exhibiting herbivores was determined with reference to the total number of plant species recorded in the respective area. Networks were also

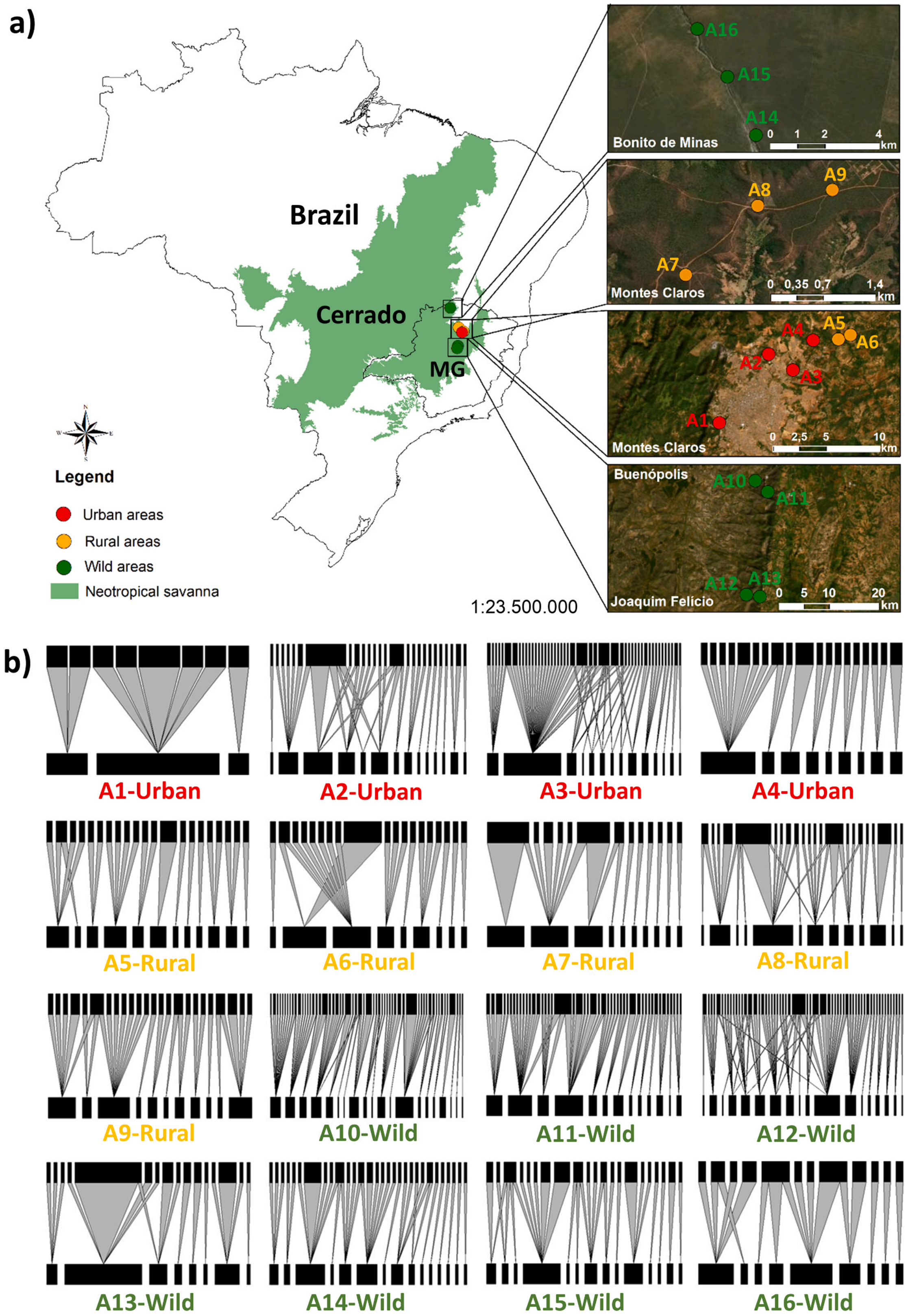

Fig. 2. a) Location of Neotropical savanna areas sampled in the northern region of Minas Gerais, Brazil. Green circles are the wild areas in Serra do Cabral State Park (municipalities of Buenópolis and Joaquim Felício) and Veredas do Peruaçu State Park (municipality of Bonito de Minas). Orange

circles are the rural areas of Montes Claros, and red circles are the urban areas located within the urban zone of Montes Claros. The coverage of the Brazilian Cerrado (Neotropical savanna) is illustrated in green. b) Quantitative plant-herbivore networks of Neotropical savannas with different anthropogenic disturbances. The upper black bars represent insect species, while the lower black bars represent plant species. Gray lines indicate interactions. The width of the lines represents the number of interactions.

characterized using the topological descriptors connectance and modularity. Connectance is the proportion of possible interactions that are realized (i.e., recorded) in a network, interpreted as the mean proportion of host plant species utilized by the herbivores, and the mean proportion of herbivore species observed on the plant species (Araújo et al., 2015). Robustness is a measure of the network's resistance to co-extinctions, often used as an indicator of the network fragility (Dormann et al., 2009). This measure was obtained from the area under the curve formed by the proportion of secondary extinction of herbivore species due to the random removal of plant species (Dormann et al., 2009). Modularity was measured using Beckett (2016) algorithm to assess if potential changes in specialization disrupt preferential interactions among groups of plants and insects. Connectance and modularity are generally negatively correlated indices, both metrics range from 0 to 1, the closer to one the greater the connectance and modularity and the closer to zero, the less connected and less modular the network is. The network descriptors were calcul ated for each network using the *bipartite* package (Dormann et al., 2018) in R software version 4.3.3 (R Core Team, 2023).

3. Data analyses

Before performing our analyses, we compared whether the areas sampled in 2018 and 2019 differed in insect diversity and network descriptors using generalized linear models (GLMs). In these models the year was used as an explanatory variable, and the insect species richness, insect abundance, proportion of plants hosting insects (Poisson error distribution), and network descriptors (Gaussian error distribution) were employed as response variables. Based on these analyses, results show no differences between sampling years for herbivore species richness (log) ($F = 1.932$, $p = 0.186$), herbivore abundance (log) ($F = 3.022$, $p = 0.104$), proportion of plant species hosting herbivores ($F = 0.288$, $p = 0.559$), network connectance ($F = 1.579$, $p = 0.229$), network modularity ($F = 1.132$, $p = 0.305$), and network robustness ($F = 0.260$, $p = 0.617$). Because of this, we consider the areas sampled in the two years to be equivalent in our comparisons.

We used generalized linear models (GLMs) and selected the best models from the different explanatory variables using an information-theoretic approach based on Akaike's Information Criterion corrected for small sample sizes (AICc). We used *MuMin* package and the *dredge* function to build the models including different explanatory variable combination (Barton, 2023). All possible combinations of explanatory variables were evaluated using AICc model selection, and the best models (ΔAICc < 2.0) were retained for interpretation.

For AICc model selection procedure, we first constructed full models including conservation status (wild, rural, and urban areas), plant abundance, and plant species richness as explanatory variables to evaluate their effects on herbivore species richness, herbivore abundance, and the proportion of host plant species hosting herbivores. Plant species richness and plant abundance were used as additional explanatory variables in the models to control for potential effects of vegetation structure on the herbivorous insects (Freitas et al., 2023). The full models for network connectance and network modularity include as explanatory variables the conservation status, herbivore species richness, and their interaction as predictors. The natural logarithm of plant abundance, plant species richness, herbivore abundance, and herbivore species richness were calculated in all analyses. The significance of each explanatory variable in the selected best models was assessed using ANOVA, implemented via the *lme4* package (Bates et al., 2015). All analyses were performed in the R software 4.3.3 (R Core Team, 2023).

4. Results

We sampled 755 insects on 546 plants across the 16 areas (Fig. 2b), comprising 503 interspecific interactions between 312 insect species and 94 plant species. The most representative insect orders were Hemiptera (137 species and 23 families), Coleoptera (103 species and 11 families), and Lepidoptera (41 species and 10 families). The abundance of the herbivore species ranged from 1 to 24 individuals, with only 4 % of the species (14 in total) had more than 10 individuals, while 79 % were doubletons (67 species) or singletons (179 species). In our study, the plant families Fabaceae, Vochysiaceae, and Anacardiaceae harbored the greatest richness of herbivorous insects, with 79, 52, and 24 species recorded, respectively. At the species level, *Machaerium acutifolium* (Fabaceae), *Qualea grandiflora* (Vochysiaceae), and *Acosmium dasycarpum* (Fabaceae) supported the highest numbers of herbivorous insect species, hosting 37, 34, and 29 species, respectively.

There was substantial variation in vegetation structure among sites, with the total number of woody plants (DBH $\geq$ 15 cm) per area ranging from 22 to 76 individuals (Table S1). Herbivore abundance ranged from 9 to 118 individuals per site (Table S1). The richness of recorded woody plants varied from 11 to 38 species, while the richness of plants with herbivores varied from 3 to 18 species (Table S1). From these plants, we recorded a total of 8–59 species of herbivores per area (Table S1). The resulting plant-herbivore networks exhibited connectance values ranging from 0.042 to 0.333, modularity values ranging from 0.494 to 0.861, and robustness values ranging from 0.224 to 0.480 (Table S1).

Conservation status was part of all best fit models for all the five response variables, being the only explanatory variable in the best fit model for modularity, and part of the first-best models for all response variables except connectance (Table S2). The best fit models for proportion of plant species with herbivores, herbivore abundance, herbivore richness and network robustness also included plant abundance, plant richness and conservation status (Table 1). On the other hand, the best fit model for connectance included, in addition to conservation status, herbivore richness and the interaction term between conservation status and herbivore richness were included (Table 1). For modularity, the best fit model included only the conservation status (Table 1).

Insect communities from savanna fragments located in urban and rural areas were characterized by lower insect richness (Fig. 3a), and abundance (Fig. 3b), as well as lower proportion of plant species hosting herbivores (Fig. 3c; Table 1); evidencing a depletion of the herbivore insect faunas in human-disturbed areas. We also found positive effects of plant abundance and negative effects of plant richness on the insect species richness, insect abundance and proportion of plant species hosting herbivores (Figure S1; Table 1).

Regarding plant–herbivore network topology, we found higher connectance values in urban fragments compared to wild fragments (Fig. 3d). A negative effect of habitat modification was found on network modularity and robustness (Table 1), with lower values observed in urban areas (Figs. 3e and 3f, respectively). In the model for connectance, we detected a significant interaction between conservation status and herbivore species richness, indicating that the effect of richness on network connectance varied across land-use categories (Table 1).

5. Discussion

This study provides significant insights into how human-induced habitat modification affects the organization of interactions between herbivorous insects and host plants in Neotropical savannas. Our findings show that, in addition to changes in the richness and abundance of insects, the structure of plant-herbivore networks is strongly affected by habitat modification. Our results indicate that plant-herbivore networks in urban fragments are more connected, less modular, and more robust to secondary extinctions compared to networks in wild and rural environments, which support our expectations. These findings suggest that plant-herbivore networks in urban environments have a less specialized structure than in wild environments.

Confirming our expectations, more anthropized environments showed lower diversity and abundance of herbivorous insects, a pattern commonly found in previous studies that observed habitat modifications affecting insect diversity (Öckinger et al., 2012; Araújo et al., 2024b). Both rural and urban environments emerged as habitats marked by low insect diversity, which may be associated with different pressures from matrices on remaining vegetation fragments (such as built-up areas, pastures, and crops). Recurrent wildfires, pollution, and even microclimatic alterations are common in these anthropized fragments, which can affect the diversity and population sizes of herbivores, as well as the prevalence of plants hosting herbivores.

Previous studies indicate that habitat modification alters the structure of trophic networks (Pinho et al., 2017; Neff et al., 2021). Our results corroborate these expectations, as we found that plant-herbivore networks in urban environments were more connected and robust than networks in other habitat types. The high levels of connectance observed in urban areas likely reflect a shift from

Table 1
Effects of variables in the selected model (see Table S2) for each response variable. Selected linear models evaluating the effects of conservation status (natural, rural, and urban), plant variables (abundance and richness, both log-transformed) and interactions between conservation status and plant variables on the following response variables of the plant-herbivore networks: proportion of plant species hosting herbivores, herbivore abundance (log), herbivore richness (log), connectance, modularity and robustness. CS = conservation status; PA: plant abundance (log); PR: plant richness (log); HR: herbivore richness (log).

Response variable of each model	Selected explanatory variables	Estimate	S.E.	t	*P*
Proportion of plant species hosting herbivores	Intercept	1.578	0.064	24.689	< 0.001
	CS_Rural	−0.414	0.108	−3.849	0.003
	CS_Urban	−0.297	0.102	−2.911	0.014
	PA	0.283	0.059	4.804	0.001
	PR	−0.169	0.060	−2.793	0.018
Herbivore abundance (log)	Intercept	1.849	0.082	22.457	< 0.001
	CS_Rural	−0.495	0.139	−3570	0.004
	CS_Urban	−0.411	0.131	−3126	0.010
	PA	0.294	0.076	3866	0.003
	PR	−0.220	0.078	−2833	0.016
Herbivore species richness (log)	Intercept	1.578	0.064	24.689	< 0.001
	CS_Rural	−0.414	0.108	−3.849	0.003
	CS_Urban	−0.297	0.102	−2.911	0.014
	PA	0.283	0.059	4.804	0.001
	PR	−0.169	0.060	−2.793	0.018
Network connectance	Intercept	0.101	0.010	9.778	< 0.001
	CS_Rural	0.001	0.019	0.079	0.939
	CS_Urban	0.031	0.017	1.866	0.092
	HR	−0.037	0.009	−3.933	0.003
	CS_Rural x HR	0.017	0.032	0.537	0.603
	CS_Urban x HR	−0.052	0.015	−3.525	0.005
Network modularity	Intercept	0.743	0.030	24.71	< 0.001
	CS_Rural	0.017	0.047	0.360	0.725
	CS_Urban	−0.140	0.050	−2.815	0.015
Network robustness	Intercept	0.457	0.023	20.069	< 0.001
	CS_Wild	−0.010	0.030	−0.325	0.750
	CS_Urban	−0.092	0.034	−2.691	0.019

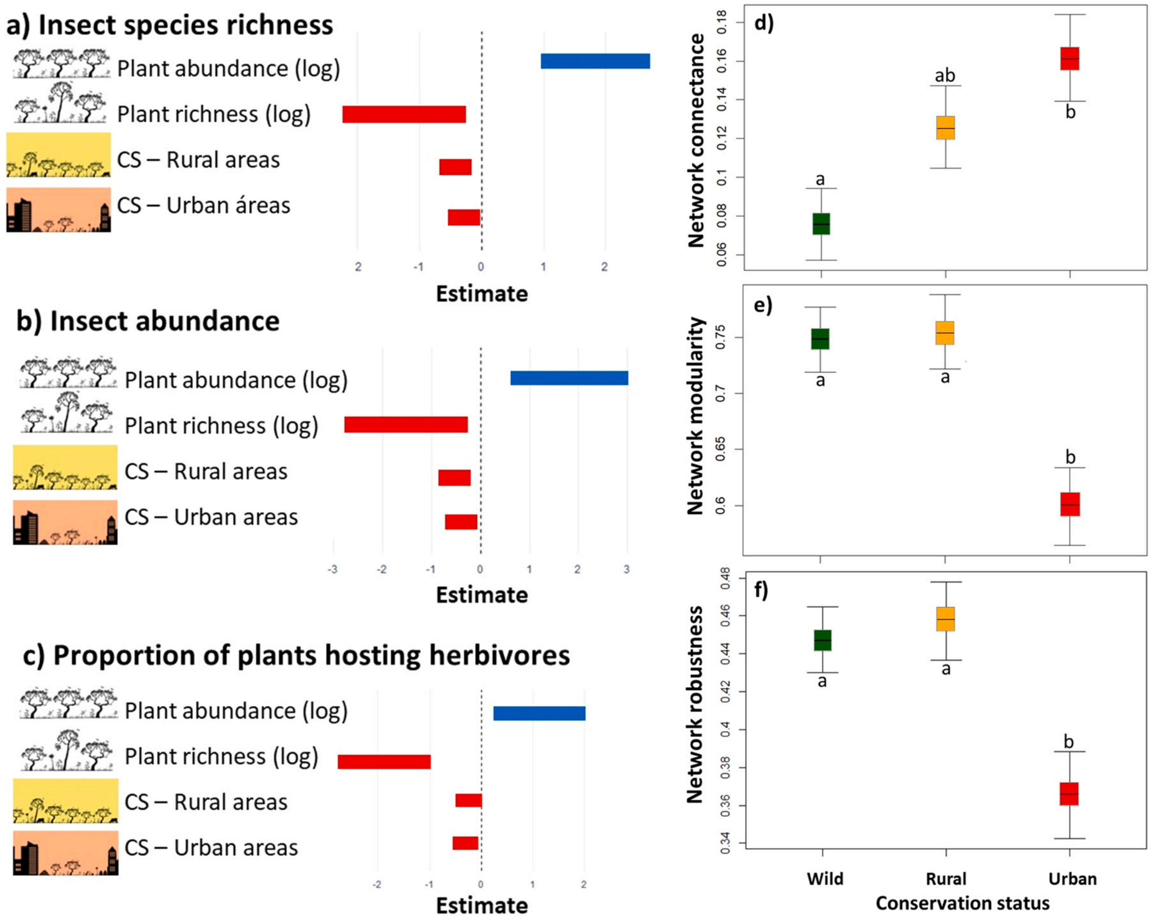

Fig. 3. Effects of variables in the selected model (see Table S2) for each response variable. Comparison of standardized coefficients indicating the effects of variables in the selected model on the a) insect species richness, b) insect abundance, and c) proportion of plant species hosting herbivores. Comparison of d) connectance, e) modularity, and f) robustness of plant-herbivore networks in wild, rural and urban areas. The bars indicate standardized effect sizes, and the different letters denote significant differences ($p < 0.005$).

specialized to generalized interactions, driven by the dominance of generalist herbivores (Pinho et al., 2017). This shift may indicate a breakdown of more selective relationships typical of intact ecosystems (Miles et al., 2019). Moreover, the greater robustness observed in these urban fragments appears to be driven by the dominance of generalist herbivores capable of interacting with multiple host plants, thereby sustaining network structure even under species loss (Neff et al., 2021). However, this structural resilience might conceal a decline in ecological quality, as functional diversity and specificity decrease. These results are in concordance with the idea that anthropogenic changes (e.g., habitat loss, fragmentation, and pollution) lead to structural modifications in the configuration of interaction networks (Araújo et al., 2015), but this was only perceived at extreme levels of impact, as is the case with urban environments. Urbanization is considered a growing threat to biodiversity (Miles et al., 2019), but its effects on ecological interactions can be difficult to predict in ecological communities with higher levels of structural complexity (Srisakrapikoop et al., 2022).

Our findings of reduced herbivore richness and changes in network topology in urban areas align with previous studies showing that urban intensification can lead to declines in terrestrial arthropod communities (Vergnes et al., 2014), which in turn may disrupt trophic interactions and reduce network complexity (Miles et al., 2019). Consistent with our findings of higher connectance in urban areas, other studies have also reported increased network connectance in anthropogenic environments (Morrison et al., 2020; Araújo et al., 2024b). In particular, Araújo et al. (2024b) found that urbanization enhances the level of connectance among plant–galling herbivorous insects in Brazilian savannas, suggesting that environmental disturbance may promote ecological generalization and increased interaction density, as we also observed for exophagous herbivores.

Currently, it is well accepted that plant-herbivore networks have a highly modular structure (López-Carretero et al., 2018). In the present study, we corroborate this pattern, observing that levels of modularity were moderate to high (> 0.50) in most of the studied networks. However, our findings showed that modularity values were variable in response to urbanization, with urban areas exhibiting significantly less modular networks. Recently, Neff et al. (2021) identified a strong association between high land use intensity and a reduction in the modularity of plant-herbivore networks. Additionally, in forest edge environments, the modularity of networks is lower compared to the interior of forests (Pinho et al., 2017). We have also previously observed lower values of modularity for plant-galling networks in urban savanna areas compared to rural fragments (Araújo et al., 2024b). We hypothesize that because urban environments are more homogeneous in terms of habitat structure and composition, this may result in a more uniform distribution of species and interactions (Miles et al., 2019), which could decrease the distinction between modules in the networks.

Plant diversity and vegetation structure have been shown to affect the diversity of herbivorous insects (Leal et al., 2016; Araújo et al., 2021) and the topology of plant-insect networks (Freitas et al., 2023). In the present study, we observed that plant abundance positively influenced the richness and abundance of herbivorous insects, as well as the proportion of plants hosting herbivores. These results corroborate previous studies suggesting that plant abundance informs how much resources are available to herbivorous insects (Marquis et al., 2002; Shin et al., 2021). On the other hand, plant richness negatively affected all response variables, contrary to our expectation. This result may be related to the characteristics of the herbivore guilds. For example, while specialists usually have a strong positive relationship with plant richness, exophagous herbivores (e.g., chewers and suckers), such as those studied in the present study, may prefer communities with low diversity (Shinohara and Yoshida, 2021, Oliveira et al., 2019, Shin et al., 2021). Although we analyzed networks composed of all exophagous herbivores collectively, different functional guilds may vary in their degree of specialization (Oliveira et al., 2020), host preference, and sensitivity to habitat disturbance, potentially affecting network topology (Araújo and Oliveira, 2021). Therefore, future studies should consider analyzing networks at the level of feeding guilds to disentangle their specific responses to urbanization and better understand how ecological functions are restructured under anthropogenic pressures.

6. Conclusions

Our results show that human-induced habitat modification significantly affects the species richness and the structure of plant-herbivore networks in the Brazilian Cerrado, highlighting urbanization as a key driver of these changes. Beyond the reduced diversity of herbivorous insects in urban environments, we found that networks in urban environments exhibited higher connectance and robustness, and lower modularity along the studied gradient. These findings indicate a generalization in network organization associated with urbanization and corroborate previous findings on how the topology of trophic networks can be altered by the intensification of anthropogenic impacts (Pinho et al., 2017; Miles et al., 2019; Morrison et al., 2020; Neff et al., 2021; Araújo et al., 2024b). Our results also show that rural environments exhibited a topology similar to wild environments, indicating that these ecosystems may be important for maintaining plant-insect networks. Finally, this study is pioneering in assessing the effects of habitat modification and urbanization on plant-herbivore networks in Neotropical savannas considering interactions simultaneously realized by different trophic guilds of exophagous insect herbivores. Future studies could further assess the impacts of urbanization on the roles that species play in structuring ecological networks.

CRediT authorship contribution statement

Araújo Walter: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mário Almeida-Neto:** Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis. **Freitas Érica:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03879.

Data availability

Data will be made available on request.

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