

Anthropogenic disturbance shapes plant-herbivore network structure in Brazilian savannas: contrasting holometabolous and hemimetabolous insects

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Abstract

Ontogenetic development shapes how insect herbivores interact with host plants, yet its role in structuring plant–herbivore networks across human-disturbed landscapes remains poorly understood. We investigated how network topology differs between holometabolous and hemimetabolous immatures insects along an anthropogenic disturbance gradient encompassing urban, rural, and wildland remnants of Neotropical savannas in Brazil. We sampled immature herbivorous insects and their host plants across 16 sites using beating trays during two seasons (dry and wet) and constructed quantitative bipartite networks for each insect group per environment. Network descriptors (connectance, modularity, and specialization) were compared against null models. Corroborating our expectations, holometabolous insects consistently exhibited high specialization across all environments, along with low modularity and high connectance in urban areas, reflecting the functional decoupling between larval and adult stages. In contrast, hemimetabolous insects showed highly modular and lowly connected networks in all environments, and low specialization in urban areas. Both groups responded to the disturbance gradient, suggesting that environmental context interacts with developmental mode in shaping network structure. These findings highlight that ontogenetic traits and habitat disturbance interact to shape the organization of plant–herbivore interactions in Neotropical savannas.

Introduction

Interactions between herbivorous insects and plants structure key processes in terrestrial ecosystems, influencing population dynamics, community composition, and the maintenance of biological diversity (Agrawal and Maron 2022). Beyond mediating energy and matter fluxes, herbivory acts as a selective force capable of shaping plant defenses and induced responses, with implications for habitat stability and functioning (Howe and Jander 2008; Schowalter 2012). These interactions contribute to ecological stability and functional balance, particularly in biodiverse and dynamic ecosystems such as the Brazilian Cerrado (Del-Claro and Torezan-Silingardi 2009). Representing a significant portion of Neotropical biodiversity, plant-herbivore interactions are shaped by environmental factors, making them sensitive to land-use change and climate change.

Different insect groups show contrasting responses to human-induced habitat modification (Araújo et al. 2015), and this variation is closely associated with ontogenetic development. Herbivorous insects can be grouped into two major developmental types with distinct implications for plant interactions (Gullan and Cranston 2017; Chapman 2013). Hemimetabolous insects undergo gradual development, with nymphal stages morphologically similar to adults and, in general, maintain consistent feeding habits throughout their life cycle (Gullan and Cranston 2017; Chapman 2013). In contrast, holometabolous insects undergo complete metamorphosis, with morphologically distinct larvae and adults that frequently exploit different food resources and occupy distinct ecological niches, potentially reducing intraspecific competition (Grimaldi and Engel 2005; Pierce and Berry 2011). These differences directly influence patterns of plant resource use, responses to environmental disturbance, and ecosystem function (Yang 2001).

Ontogenetic distinction also helps explain differential responses of insects to anthropogenic disturbance. For example, immature insects tend to be more sensitive to habitat modification, due to limited mobility, greater dietary specificity, and restriction to specific microhabitats (Pierce and Berry 2011; Silveira and Araújo 2021). In turn, adult insects generally exhibit greater resilience associated with dispersal capacity and the ability to exploit diverse food resources (Ali and Agrawal 2012; García-Robledo and Horvitz 2012). These differences between life stages tend to be more pronounced in holometabolous insects, in which immatures are often highly specialized while adults show greater generalization, generating potential indirect effects on trophic networks (Pierce and Berry 2011). On the other hand, hemimetabolous insects tend to show greater similarity between developmental stages and higher tolerance to gradual environmental changes. Consequently, holometabolous species may respond more sensitively to acute habitat alterations while hemimetabolous communities may better reflect cumulative effects of long-term change (Didham et al. 2020).

Ecological networks provide a powerful framework for understanding how these ontogenetic and functional differences are reflected in community organization and responses to environmental disturbance. Networks represent species as nodes and their interactions as links, enabling the analysis of the complexity of biological interactions (Jordán 2009; Delmas et al. 2019). This approach has been widely applied to plant-herbivore networks, helping to elucidate how patterns of specialization, and stability are shaped by plant-insect interactions (Lewinsohn et al. 2006; Oliveira et al. 2020). Network structure can be assessed along a continuum between two organizational extremes: generalist networks, in which interactions are broadly distributed across many species pairs, and specialist networks, in which interactions are concentrated among specific partners (Blüthgen et al. 2006; Delmas et al. 2019). The position of a network along this continuum reflects the ecological and evolutionary constraints that shape species interactions, including resource availability, habitat filtering, and the biological traits of the interacting organisms (Lewinsohn et al. 2006; Tylanakis and Morris 2017). Holometabolous insects, whose larval and adult stages impose functionally distinct demands on host plants, are expected to generate more specialized and compartmentalized networks compared to hemimetabolous insects, whose developmental continuity may allow for broader and more overlapping interactions across the life cycle (Yang 2001; Grimaldi and Engel 2005). These contrasting developmental constraints therefore represent a biologically meaningful axis along which network specialization is predicted to vary, with direct implications for how each group responds to environmental disturbance (Pierce and Berry, 2011; Didham et al. 2020).

In the Brazilian Cerrado, the influence of human activities on ecological network structure has been recently studied, with evidence consistently pointing to contrasting patterns between human-influenced and wildland environments (Silveira and Araújo 2021; Freitas et al. 2025). In highly disturbed environments, such as urban remnants, network simplification is promoted by reducing habitat heterogeneity and host plant diversity, eroding interaction specialization and favoring generalist species that persist under high environmental stress (Silveira & Araújo, 2021; Araújo et al. 2024; Miles et al. 2019). On the other hand, less anthropogenically disturbed environments may sustain more diverse and structured interaction networks, although substantial variation can occur among protected areas

depending on local habitat conditions and vegetation structure (Silveira and Araújo 2021; Freitas et al, 2025). However, recent studies have treated herbivorous insects as a single functional unit, without accounting for ontogenetic developmental mode as a potential mediator of network responses to disturbance.

Because immature herbivorous insects are generally more host-specific, less mobile, and more dependent on local microhabitat conditions than adults, interaction networks based on immature stages may provide a particularly sensitive framework for detecting structural responses to anthropogenic disturbance in plant–herbivore systems. Accordingly, the present study focuses exclusively on immature herbivorous insects, including larvae of holometabolous taxa and nymphs of hemimetabolous taxa. Our study investigates how plant-herbivore network structure responds to landscapes under different levels of human impact encompassing urban, rural, and wildland areas in the Brazilian Cerrado. The structure of plant-herbivore networks was characterized using different structural descriptors (connectance, specialization, and modularity). Based on previous studies indicating that anthropogenic disturbance is associated with network simplification and generalization in Neotropical savannas (Silveira and Araújo 2021; Araújo et al. 2024; Freitas et al. 2025), we hypothesize that: (1) holometabolous insects will exhibit more specialized and modular networks compared to hemimetabolous insects, reflecting the functional decoupling between larval and adult stages and the associated constraints on host-plant use; and (2) both groups will respond to the disturbance gradient, but holometabolous networks will show greater sensitivity to environmental change, while hemimetabolous networks will exhibit more variable structural responses associated with environmental context.

Materials and methods

Study area

This study was conducted in areas of Neotropical savannas (*cerrado sensu stricto*) in the northern region of the state of Minas Gerais, Brazil (Fig. 1). The vegetation of the Neotropical savanna is dominated by sclerophyllous plants occurring in nutrient-poor soils with limited water availability (Ribeiro and Walter 2008). The regional climate is tropical dry (Aw in the Köppen classification), characterized by well-defined rainfall seasons, a mean annual temperature of 24.2°C, and annual precipitation of 1,000 mm (Alvares et al. 2014).

Table 1
Species richness of herbivorous insects (morphospecies) and host plants recorded in quantitative bipartite plant–herbivore networks across four environment types (urban, rural, PEVP, and PESC) in *cerrado sensu stricto* areas of northern Minas Gerais, Brazil, stratified by insect developmental mode (hemimetabolous and holometabolous).

Networks	Status	Insect richness	Plant richness
Hemimetabolous	Urban	24	35
	Rural	26	44
	Wild PEVP	22	30
	Wild PESC	47	98
Holometabolous	Urban	2	3
	Rural	5	6
	Wild PEVP	7	9
	Wild PESC	36	50

We sampled plants and immature insects across three environment types: urban, rural, and wildland areas. Urban fragments are located in an urban matrix in Montes Claros city and are subject to more frequent and intense anthropogenic impacts, such as vegetation cutting, paved roads with heavy traffic, waste disposal areas, pollution, and fire, resulting in lower plant species richness and reduced structural complexity of the remaining vegetation (Freitas et al. 2025). Rural sites are located in zones of moderate land use with ongoing human activities, including unpaved roads, and livestock farming. On the other hand, wildland sites are located within protected areas with preserved vegetation and minimal human interference, being *Parque Estadual da Serra do Cabral* (PESC) and *Parque Estadual Veredas do Peruvaçu* (PEVP). We sampled three urban sites, three rural sites, four in the wildland sites of PESC and three in the wildland sites of PEVP, totaling 16 sampled sites (Fig. 1).

Data sampling

We established five 100 m² plots (10 × 10 m) per site, totaling 80 plots. Plots were spaced at least 20 m apart and located at least 30 m from fragment edges. Within each plot, we inventoried and individually tagged all living trees and shrubs with a circumference at breast height (CBH ≥ 15 cm), recording species identity, CBH, and total height. Plant identification was performed in the field, and unidentified specimens were collected for subsequent identification following standard herbarium techniques. Taxonomic classification followed APG IV (2016), Flora Brasil (2020), and The Plant List (2013).

Herbivorous insects were sampled during two seasons, dry (July–September) and wet (October–December), in 2018 and 2019, across urban, rural, and wildland environments. Sampling across seasons was conducted to better characterize herbivore assemblages, given that seasonality may influence

species occurrence and abundance. In each plot, we selected three branches per tagged plant and performed 30 beating samples (10 per branch) using a modified beating tray. Collected specimens were preserved in 70% ethanol and subsequently transported to the laboratory for sorting and identification. Insects were sorted into morphospecies and classified according to developmental mode (hemimetabolous or holometabolous). Only immature herbivorous insects were used for network construction, including larvae of holometabolous taxa and nymphs of hemimetabolous taxa.

Data analyses

Because some environment-specific sites contained relatively low numbers of species and interactions, particularly for holometabolous insects in urban and rural environments, networks were analyzed at the environment level rather than at the individual site level. This approach allowed the construction of ecologically interpretable quantitative interaction networks while minimizing excessive matrix sparsity and the instability of topological metrics associated with extremely small networks (Dormann et al. 2009; Delmas et al. 2019). Accordingly, our analyses focus on broad structural tendencies along the disturbance gradient rather than on formal statistical comparisons among independently replicated networks. Thus, quantitative bipartite plant–herbivore networks were constructed for each environment type (urban, rural, PESC and PEVP), resulting in two networks per environment: one for hemimetabolous insects and one for holometabolous insects. Networks were organized as bipartite matrices, with host plants and herbivorous insects representing the two trophic levels.

Network structure was characterized using three topological descriptors: connectance, modularity, and specialization. Connectance (C) was calculated as the ratio of observed interactions to the total number of possible interactions in each network (Dormann et al. 2009). Bipartite modularity was estimated using the Q index (Barber 2007), with module detection performed by the DIRTLPAbw+ algorithm (Beckett 2016). Network-level specialization was assessed using the H2 index, ranging from 0 (fully generalist) to 1 (fully specialized) (Blüthgen et al. 2006). All metrics were calculated from quantitative interaction matrices.

Because some network descriptors (e.g., connectance and modularity) may be influenced by matrix size and interaction frequency, observed values were interpreted in association with null model expectations rather than in isolation. This procedure reduces the influence of differences in network size and allows the evaluation of whether observed topological patterns deviate from randomized interaction structures with similar marginal totals. Thus, to assess the significance of each structural descriptor, we employed null models based on the *r2dtable* algorithm (Dormann et al. 2009), with 999 permutations. For each descriptor, null model outputs are reported as mean $\pm$ standard deviation (SD), and statistical significance was assessed based on the probability that the observed value falls within the null distribution. All networks and descriptors were computed using the *bipartite* package (Dormann et al. 2021) in R (version 3.4.4; R Development Core Team 2024).

Results

A total of 275 immature herbivorous insects were recorded, distributed across 143 morphospecies and 64 host plant species. Hemimetabolous insects were the most abundant group, comprising 207 individuals across 97 morphospecies, with Hemiptera as the dominant order ($n = 167$). Holometabolous insects represented 68 individuals distributed across 46 morphospecies, with Lepidoptera as the dominant order ($n = 60$). Among families, Geometridae (Lepidoptera) was the most abundant family for holometabolous insects ($n = 28$), while Cicadellidae (Hemiptera) dominated among hemimetabolous insects ($n = 79$). Species and plant richness per network are summarized in Table 1.

Hemimetabolous networks

Across all environments, hemimetabolous networks showed low connectance and high specialization and modularity relative to null model expectations (Table 2). In urban environments, connectance was significantly lower than expected by chance ($C = 0.071$; null: 0.988), while specialization ($H2 = 0.443$; null: 0.137) and modularity ($M = 0.688$; null: 0.540) were significantly higher (Fig. 2). In rural environments, the same directional pattern was observed, with connectance remaining low ($C = 0.079$) and both specialization ($H2 = 0.888$) and modularity ($M = 0.811$) significantly exceeding null expectations. In PEVP, connectance was low ($C = 0.066$), and lower than expected by chance, and specialization ($H2 = 0.739$) and modularity ($M = 0.756$) were significantly higher than null expectations. Similarly, in PESC the connectance was low ($C = 0.066$), while specialization ($H2 = 0.633$) and modularity ($M = 0.764$) were high, both significantly different than null expectations (Table 2).

Table 2

Observed and null model values (mean $\pm$ SD) of three topological descriptors (connectance, specialization, and modularity) for quantitative bipartite plant–herbivore networks across four environment types (urban, rural, PEVP, and PESC) in *cerrado sensu stricto* areas of northern Minas Gerais, Brazil. Networks are stratified by insect developmental mode (hemimetabolous and holometabolous). Statistical significance is indicated by p-values derived from null model permutations.

Networks	Status	Topological descriptor	Observed value	Null value	Null SD	P-value
Hemimetabolous	Urban	Connectance	0.071	0.406	0.574	< 0.05
	Urban	Specialization	0.443	0.137	0.069	< 0.05
	Urban	Modularity	0.688	0.540	0.028	< 0.05
	Rural	Connectance	0.079	0.374	0.314	< 0.05
	Rural	Specialization	0.888	0.199	0.065	< 0.05
	Rural	Modularity	0.811	0.592	0.028	< 0.05
	Wild PESC	Connectance	0.066	0.301	0.137	< 0.05
	Wild PESC	Specialization	0.633	0.070	0.041	< 0.05
	Wild PESC	Modularity	0.764	0.491	0.017	< 0.05
	Wild PEVP	Connectance	0.066	0.570	0.335	< 0.05
	Wild PEVP	Specialization	0.739	0.135	0.036	< 0.05
	Wild PEVP	Modularity	0.756	0.493	0.020	< 0.05
Holometabolous	Urban	Connectance	0.500	0.610	0.079	< 0.05
	Urban	Specialization	1.000	0.326	0.469	< 0.05
	Urban	Modularity	0.500	0.330	0.116	< 0.05
	Rural	Connectance	0.200	0.181	0.133	< 0.05
	Rural	Specialization	1.000	0.111	0.168	< 0.05
	Rural	Modularity	0.800	0.518	0.069	< 0.05
	Wild PESC	Connectance	0.110	0.109	0.002	< 0.05
	Wild PESC	Specialization	0.963	0.097	0.084	< 0.05

Networks	Status	Topological descriptor	Observed value	Null value	Null SD	P-value
	Wild PESC	Modularity	0.850	0.620	0.034	< 0.05
	Wild PEVP	Connectance	0.061	0.352	0.150	< 0.05
	Wild PEVP	Specialization	0.830	0.080	0.045	< 0.05
	Wild PEVP	Modularity	0.872	0.590	0.023	< 0.05

Holometabolous networks

Holometabolous networks showed high specialization and modularity and low connectance compared to null models (Table 2). In urban environments, connectance was significantly lower than null expectations ($C = 0.500$; null: 0.610), while specialization ($H2 = 1.000$) and modularity ($M = 0.500$) were significantly higher than expected (Fig. 2). In rural environments, connectance was significantly lower than expected ($C = 0.200$; null: 0.315), and both specialization ($H2 = 1.000$) and modularity ($M = 0.800$) remained significantly elevated. In wildland environments, holometabolous networks maintained low connectance (PEVP: $C = 0.200$; PESC: $C = 0.098$) and high specialization ($H2 = 0.830$ and 0.963 , respectively) and modularity ($M = 0.864$ and 0.855 , respectively), all significantly exceeding null model expectations.

Discussion

This study investigated whether holometabolous and hemimetabolous immature insects generate structurally distinct plant–herbivore networks along an anthropogenic disturbance gradient in the Brazilian Cerrado. Our results supported the initial prediction with holometabolous insects consistently exhibiting high specialization across all environments. Holometabolous networks also showed low modularity and high connectance in urban environments, a pattern coherent with the larval life history (Grimaldi and Engel 2005; Yang 2001; Truman 2019) and consistent with the expectation that this group responds more strongly to anthropogenic disturbance. However, hemimetabolous insects, did not conform to the expected pattern of more generalist networks – instead showing similarly high modularity and low connectance throughout the disturbance gradient, suggesting that factors beyond developmental mode shape interaction structure in this group (Didham et al, 2020; Tylianakis and Morris 2017). Additionally, networks of hemimetabolous insects had low specialization in urban environments. Together, these results indicate that while ontogenetic developmental mode influences network organization, environmental context and habitat filtering impose additional constraints on realized interactions, modulating the structural responses of both groups across human-influenced landscapes.

The consistently high specialization observed in holometabolous networks across all environments suggests that developmental mode appears to impose relatively consistent structural constraints on plant–herbivore network organization (Kemp et al. 2017). Holometabolous insects maintained elevated specialization (> 0.830) values regardless of habitat condition, from highly disturbed urban remnants to well-preserved wildland areas. This pattern is consistent with the expectation that insect larvae are highly specific in their use of host plants, as previously demonstrated for caterpillars in tropical ecosystems (Dyer et al. 2007; Homem-de-Carvalho et al. 2025). Similarly, modularity values were consistently high (> 0.800) across all environments, with the exception of urban areas, where a slightly lower value was recorded ($M = 0.500$). These results align with the hypothesis that networks of holometabolous insects and host plants are highly sensitive to habitat changes (Pierce and Berry 2011; Didham et al. 2020).

Hemimetabolous insects, however, did not conform to the expected pattern of generalist, highly connected networks. Despite the developmental continuity between nymphal and adult stages, which theoretically allows for broader and more overlapping host-plant use (Gullan and Cranston 2017; Chapman 2013), hemimetabolous networks exhibited high modularity (> 0.688) and low connectance (< 0.100) across all environments, and low specialization in urban areas. This pattern suggests that factors beyond ontogenetic mode are shaping interaction structure in this group. The low specialization observed in urban hemimetabolous networks may reflect the dominance of a few generalist morphospecies, particularly within Cicadellidae, that persist under high environmental stress and exploit a broader range of host plants when specialist competitors are filtered out (Valiente-Banuet et al. 2015; Tylianakis and Morris 2017).

When comparing network structure (i.e. absolute values) across groups, specialization emerges as the descriptor that most consistently differentiates holometabolous from hemimetabolous networks. Holometabolous networks reached high specialization values in all environments, whereas hemimetabolous networks showed considerably lower and more variable specialization, particularly in urban areas ($H2 = 0.443$). These results suggest that, contrary to expectations, hemimetabolous networks exhibit greater variation in interaction specialization across urban and wildland environments than holometabolous networks. On the other hand, modularity was broadly similar between groups across most environments, though holometabolous networks showed a notably lower value in urban areas ($M = 0.500$) — the only environment where this descriptor diverged markedly between groups. This pattern suggests that while both groups tend to organize interactions into discrete modules (Yang 2001), holometabolous insects show a notable reduction in compartmentalization in urban environments, likely reflecting the narrower range of available host-plant resources that characterizes highly disturbed habitats.

Connectance, in turn, showed contrasting responses between holometabolous and hemimetabolous networks along the disturbance gradient. In holometabolous networks, connectance was highest in urban environments, and decreased progressively toward wildland areas. This pattern suggests that as habitat quality improves and host-plant diversity increases, holometabolous insects become increasingly

selective, concentrating interactions among a smaller proportion of available species pairs (Araújo et al. 2024). However, some caution is warranted when interpreting connectance in holometabolous networks from urban and rural environments, as these assemblages were represented by relatively small interaction matrices, which may increase the sensitivity of topological descriptors to small changes in species composition and interaction frequency. In contrast, hemimetabolous networks maintained consistently low connectance across all environments, indicating that interaction organization in this group is characterized by relatively limited overlap among realized associations regardless of disturbance level. Even in wildland environments, where plant richness and habitat complexity were greater, hemimetabolous networks remained highly modular and specialized, suggesting that increased environmental heterogeneity does not necessarily promote generalized interaction patterns (Freitas et al. 2023). Overall, the observed differences in connectance reinforce that interaction structure varies not only along the disturbance gradient but also according to the developmental and ecological characteristics of each insect group.

The contrasting structural responses of holometabolous and hemimetabolous networks to anthropogenic disturbance have direct implications for biodiversity monitoring and conservation planning in Neotropical savannas. This pattern is particularly concerning in the Cerrado, a global biodiversity hotspot under intense and ongoing land-use pressure, where the erosion of specialist interactions may undermine ecosystem functions that depend on specific plant–herbivore associations (Del-Claro and Torezan-Silingardi 2019; Freitas et al. 2025). Hemimetabolous networks, by exhibiting greater structural variation along the disturbance gradient, may serve as more sensitive and tractable indicators of habitat integrity in monitoring programs. Together, these results reinforce the importance of disaggregating community-level network analyses by biologically meaningful axes, such as developmental mode, to avoid masking functionally distinct responses that have different implications for conservation (Delmas et al. 2019; Didham et al. 2020).

Some caution is necessary when interpreting absolute differences among environments because certain networks, especially those from urban holometabolous assemblages, were based on relatively few species and interactions. Small quantitative networks are expected to exhibit greater sensitivity in descriptors such as connectance and modularity (Dormann et al. 2009; Delmas et al. 2019). Nevertheless, the recurrent directional patterns observed across descriptors and their consistent deviations from null model expectations support the interpretation that anthropogenic disturbance and developmental mode jointly influence plant–herbivore network organization.

Conclusion

Our results demonstrate that the structure of plant–herbivore networks in the Brazilian Cerrado is shaped by the interplay between insect developmental mode and the degree of anthropogenic habitat modification. Holometabolous immature insects consistently generated specialized networks regardless of environmental context, but showed high connectance and low modularity in urban environments. In contrast, networks of hemimetabolous immature insects showed structural variation along the

disturbance gradient, with lower specialization in urban environments while maintaining relatively low connectance across the disturbance gradient. Contrary to the classical prediction that urbanization always promotes network generalization, holometabolous and hemimetabolous networks varied in distinct topological aspects along urban and wildland environments, suggesting that the structural responses of plant–herbivore networks to disturbance are complex and contingent on the biology of the interacting organisms. These findings highlight the importance of incorporating developmental mode as a biologically meaningful axis in network ecology studies, and caution against interpreting structural stability in disturbed environments as evidence of ecological resilience. More broadly, our results demonstrate that grouping herbivorous insects according to ontogenetic developmental mode can reveal distinct structural responses that may remain obscured when herbivore assemblages are analyzed as a single functional unit.

Declarations

Competing interests

The authors declare no financial or non-financial competing interests.

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Author Contribution

Author Contributions LTS and WSA conceived and designed the study and wrote the main manuscript. LTS and EVDF carried out the fieldwork and data collection. ASO and FVSA contributed to editing the manuscript and proofreading. All authors reviewed and approved the final manuscript.

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Data Availability

Data Availability The datasets generated and analyzed during the current study are not publicly available because they are still being used in the ongoing REDES ANTRÓPICAS project funded by FAPEMIG. The data are available from the corresponding author upon reasonable request.

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Figures

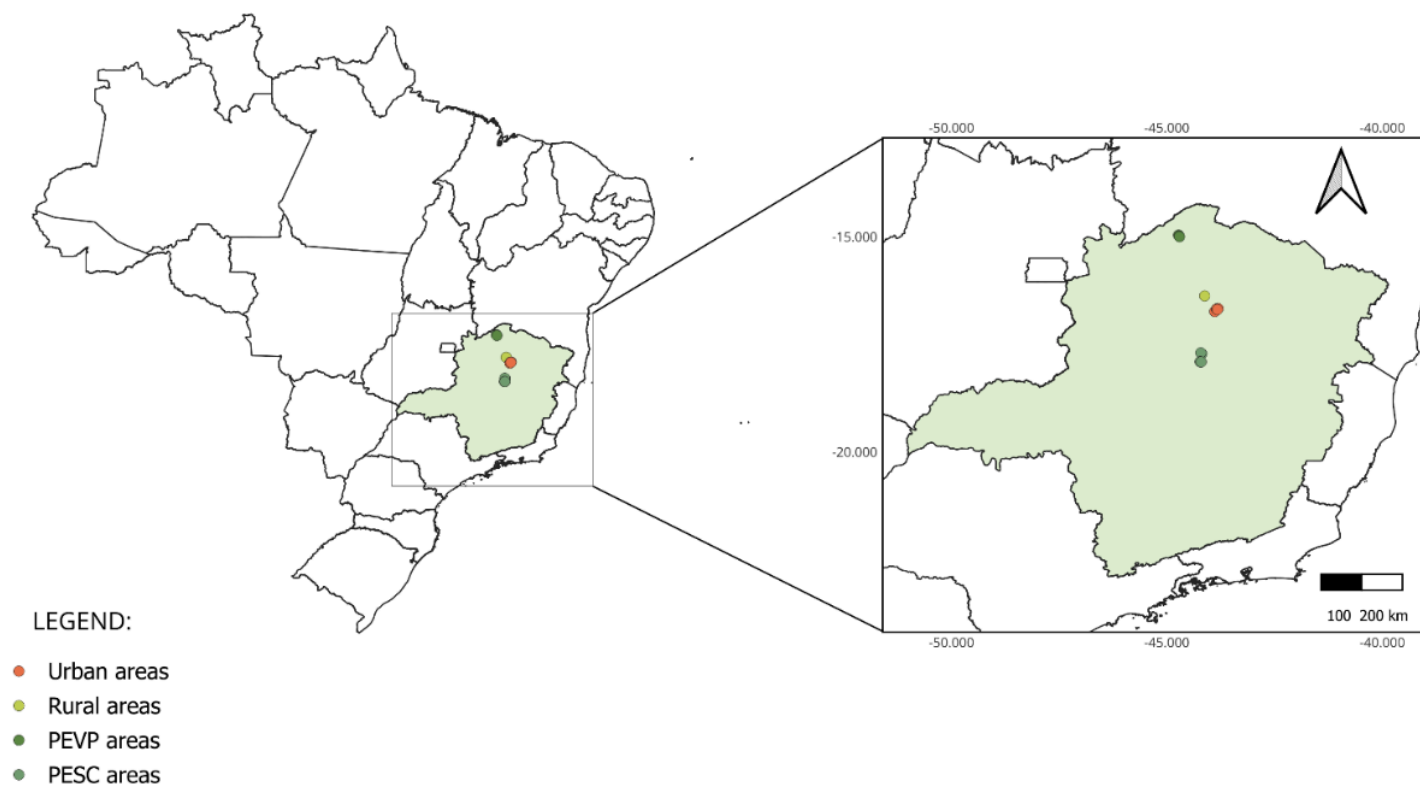


Figure 1

Location of *cerrado sensu stricto* sampling sites across the urban-to-wildland disturbance gradient in the municipality of Montes Claros, Minas Gerais, Brazil. Colors indicate environment type: urban (red), rural (yellow-green), PEVP (olive green), and PESC (dark green). Site codes correspond to those in Table 1.

Hemimetabolous insects

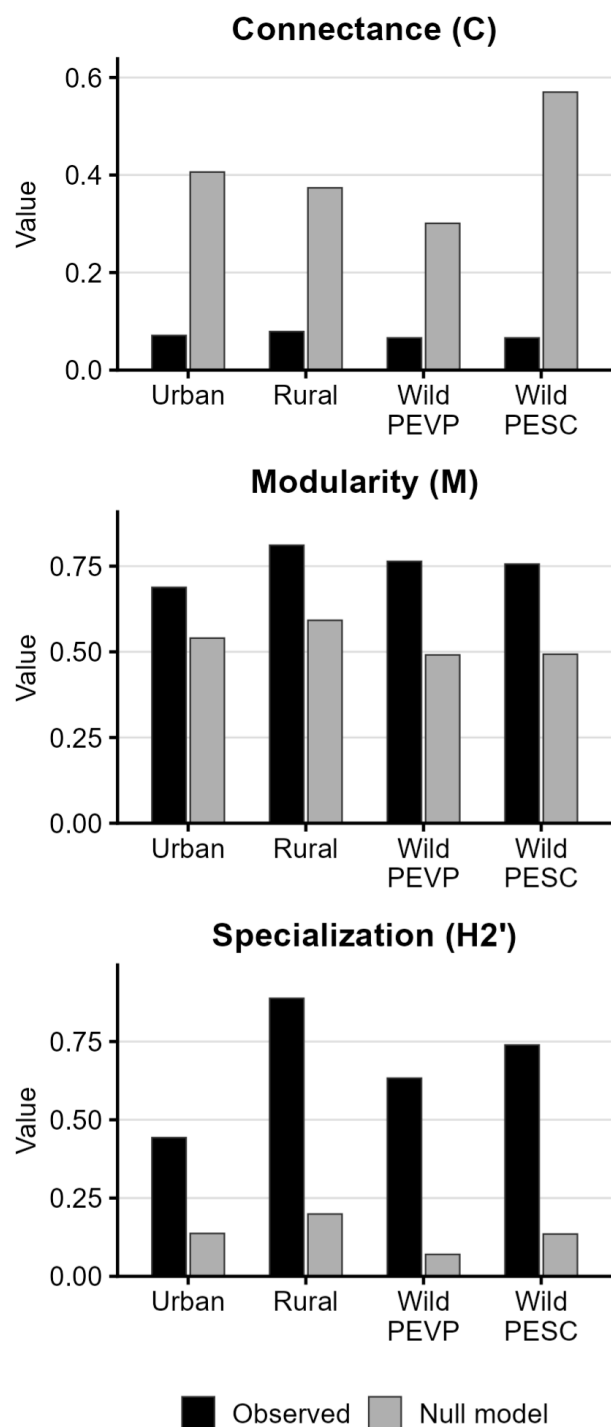


Figure 2

Observed and null model values of three topological descriptors (connectance, modularity, and specialization) for hemimetabolous plant–herbivore interaction networks across four environment types (urban, rural, Wild PEVP, and Wild PESC) in *cerrado sensu stricto* areas of northern Minas Gerais, Brazil. All differences are significant ($p < 0.05$).

Holometabolous insects

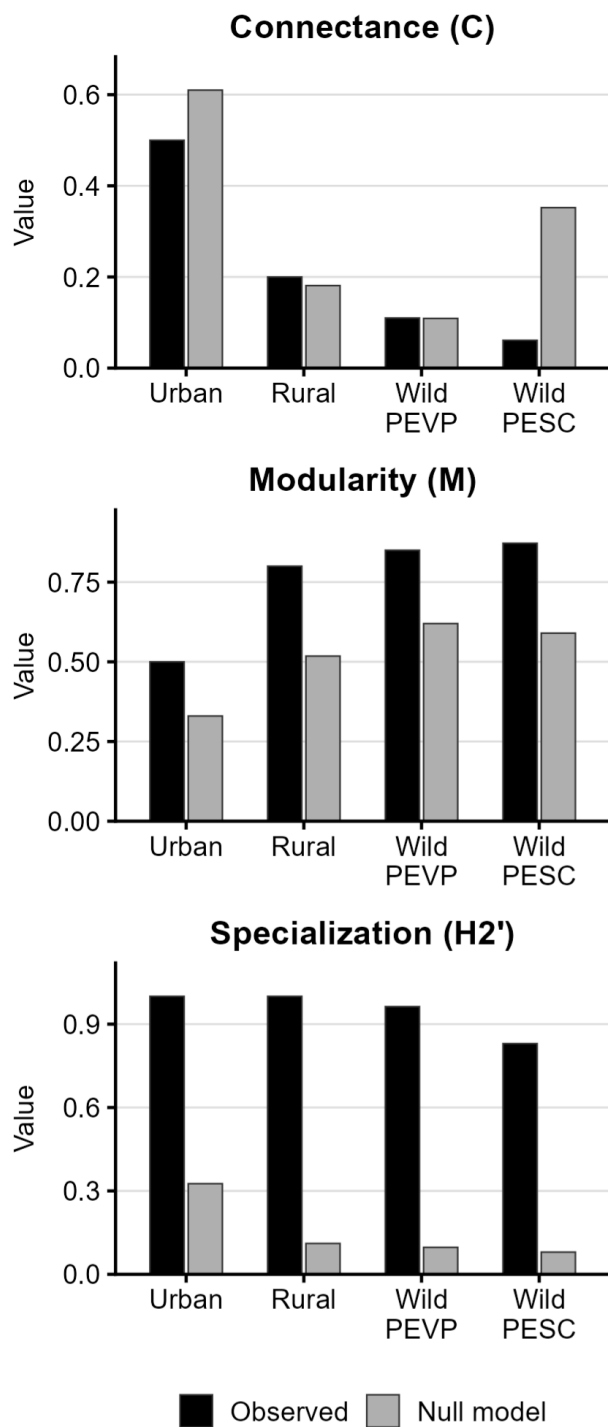


Figure 3

Observed and null model values of three topological descriptors (connectance, modularity, and specialization) for holometabolous plant–herbivore interaction networks across four environment types (urban, rural, Wild PEVP, and Wild PESC) in *cerrado sensu stricto* areas of northern Minas Gerais, Brazil. All differences are significant ($p < 0.05$).