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Habitat type outweighs urban proximity in shaping cavity-nesting hymenopteran communities

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Research Article

Keywords: Beta diversity, cavity-nesting Hymenoptera, ecological networks, species turnover, organic agriculture.

Posted Date: November 2nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10437357/v1

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Additional Declarations: No competing interests reported.

Abstract

Habitat type and land-use change are key drivers of biodiversity patterns, influencing species composition and ecological interactions in human-modified landscapes. We investigated the relative effects of habitat type, comparing forest fragments and organic crops, and urban proximity on cavity-nesting hymenopteran communities and their natural enemies. We recorded 846 nests and 2,366 individuals, comprising 12 host species, 16 natural enemy species, and 42 trophic interactions. Habitat type significantly influenced community structure, whereas urban proximity showed no consistent effect across response variables. Abundance was higher in crop habitats, but species richness did not differ between environments. Community composition differed markedly between habitats and was mainly driven by species turnover, indicating the presence of distinct species pools rather than nested subsets of the same community. Interaction dissimilarity was moderate and primarily explained by rewiring among shared species. Crop networks showed higher nestedness than expected under null models, whereas modularity was similar between habitats. These results indicate that local habitat characteristics are more consistent drivers of cavity-nesting hymenopteran communities than urban proximity, and that biodiversity responses in human-modified landscapes are better explained by species turnover and interaction reorganization than by species loss alone.

Introduction

Over recent decades, global biodiversity has undergone a drastic decline driven by the intensification of human activities, which is consistently recognized as the primary driver of accelerated species extinctions (Brooks et al. 1999; Robinson & Sutherland, 2002; Pimm et al. 2014; IPBES 2019). In this context, the increasing necessity of urban environments have promoted landscape fragmentation and disrupted spatial connectivity (Fahrig 2003; Grimm et al. 2008; Cunningham et al. 2025). This process associated with land-use intensification have promoted the replacement of old-growth species by disturbance-adapted ones, leading to biotic homogenization and reducing regional diversity (Evans et al. 2006; Tabarelli et al. 2012; Dirzo et al. 2014; Hou et al. 2023; Gonçalves-Souza et al. 2025). Moreover, urbanization can also alter microclimatic conditions, such as increasing temperatures, which can modify phenological patterns and disrupt species interactions, mainly in those more sensitive organisms, such as solitary cavity-nesting hymenopterans (Walther et al. 2002; Cheela et al. 2021).

Solitary wasps and bees that nest in preexisting cavities (i.e., cavity-nesting hymenopterans) have been widely used as bioindicators in studies on environmental changes on community structure and interaction networks (Staab et al. 2018; Deus et al. 2022; Klates et al. 2025; dos Santos et al. 2026). This suitability in shown changes is promoted by their small body size, high species richness, trophic complexity, and their importance for ecosystem functioning (Tscharntke, Gathmann & Steffan-Dewenter 1998; Klein et al. 2007; Tylianakis et al. 2007). Moreover, these species are commonly parasitized by two groups of natural enemies: parasitoids and kleptoparasitoids (Staab et al. 2018). Parasitoids develop by feeding on host larvae, whereas kleptoparasitoids exploit the food provisions stored within the brood cells (Veddeler et al. 2010). Thus, trap-nests allow the simultaneous assessment of host communities

and their associated natural enemies, providing an effective system to investigate how urbanization and land use affects both community structure and their ecological interactions (LaSalle & Gauld 1993; Iantas et al. 2017; Nether et al. 2019, Deus et al. 2022).

The effects of urbanization on cavity-nesting hymenopterans, however, may be context-dependent, varying according to taxonomic group, spatial scale, and the intensity of urbanization, although richness often declines in highly urbanized environments (Rocha-Filho et al. 2020; Xie et al. 2022). However, urbanization does not act in isolation, and local habitat characteristics may also shape hymenopteran communities. For cavity-nesting bees and wasps, fine-scale habitat features, including vegetation structure and nesting-substrate availability, can influence species richness, abundance, and community composition (Loyola & Martins 2008). More broadly, studies along urban gradients have shown that local habitat conditions may outweigh landscape-scale urbanization effects in shaping pollinator abundance and diversity (Williams & Winfree 2013).

Furthermore, local variation in habitat structure, such as forest and non-forest environments, and land-use systems, including conventional and organic agriculture, may strongly influence species responses (Tscharntke et al. 2005; Tylianakis et al. 2007; Carrié et al. 2022; Deus et al. 2022; Alves et al. 2024). Such differences may cascade through ecological networks, affecting trophic interactions and the strength and stability of species relationships, altering community responses between urban effects and habitat requirements (Pimm 1991; Tylianakis et al. 2007; Queiros et al. 2025).

Understanding the threats posed by urbanization and the intensification of land use on cavity-nesting hymenopterans may be particularly important facing their contribution to important ecosystem services they provide (Staab et al. 2018). Bees pollinate a wide range of native and cultivated plant species (Ashman et al. 2004; Klein et al. 2007), from which they obtain the resources required for their development, while, wasps are efficient predators and parasitoids of various arthropod species, being used as biological control in many crop fields (Staab et al. 2018, Deus et al. 2022). Thus, both regulation services may suffer with current landscape change due to urban growth and agriculture intensification, which may be even high in regions where the intensity of such altercation is high such as the Atlantic forest domain, one of the world's 35 biodiversity hotspots (Myers 1988; Conservation International 2015; Vancine et al. 2024).

The Brazilian Atlantic Forest is recognized to maintain species populations from the Late Quaternary to the present, acting as important ecological refugia (Carnaval et al. 2009). Despite this long-term history structuring communities through natural processes such as habitat requirements and biotic interactions patterns, the current rates of landscape depauperation imposes urgent studies to understand how species and their interactions can persist in this constant changing world (Theodorou 2020; Vancine et al. 2024; Queiros et al. 2025). In this context, different approaches have been proposed to promote more sustainable practices aimed at reducing the impacts of urbanization on species occurrence and encouraging low-impact land use, such as improving organic agriculture practices, which may enhance

ecosystem services and human well-being (Sandhu et al. 2010; Bloom & Crowder 2016; Rocha-Filho et al. 2020; Theodorou et al. 2020).

However, despite these advances, it remains unclear how multiple environmental drivers, particularly urbanization and habitat structure, may differentially influence community structure and interaction patterns. Thus, the aim of this study was to assess the relative contribution of local habitat differences and spatial gradients of urbanization on abundance, species richness, community composition, and interaction structure of cavity-nesting hymenopteran communities. We hypothesized that both urban proximity and habitat type would influence cavity-nesting hymenopteran communities and their associated host–natural enemy interactions, but that their effects would occur through different ecological pathways. Specifically, we expected urban proximity to affect community structure by imposing landscape-level filters, whereas habitat type would influence local species composition and interaction patterns by altering nesting opportunities, resource availability, and host–enemy encounter rates.

Material and methods

Study area

This study was conducted in southern Brazil, in the municipalities of União da Vitória, in the state of Paraná, and Porto União, in the state of Santa Catarina. According to the updated Köppen-Geiger climate classification (Peel et al. 2007), the climate in this region is humid subtropical mesothermal (Cfb), characterized by mild summers and cold winters with frequent frosts, and a mean annual temperature of approximately 23°C. The studied areas present an average monthly precipitation of around 140 mm, with rainfall well distributed throughout the year (Hort 1990). The soils of the region are predominantly quartzose, porous, and permeable, with feldspathic composition, as well as other characteristics such as reddish coloration, clayey texture, good drainage, and high organic matter content (Maack 2002).

The municipality of União da Vitória is located in the extreme southern region of the state of Paraná and lies predominantly within the Third Paraná Plateau. It is part of the Middle Iguaçu Microregion, bordering the state of Santa Catarina, and is limited by the Serra da Esperança, with average elevations ranging from 700 to 900 m (Maack 2002). Continuously adjacent to União da Vitória, the municipality of Porto União is situated in the northern region of the state of Santa Catarina, with relief belonging to the Canoinhas Plateau, located in the northern portion of the Western Plateau. This subregion is predominantly composed of sedimentary rocks, presenting undulating relief and average elevations of approximately 800 to 900 m (Santa Catarina 1984).

The vegetation formation of these municipalities corresponds to the Montane Mixed Ombrophilous Forest, and the phytogeographic landscape is inserted within the Middle Iguaçu microregion. This formation is represented by subtropical forests characterized by the presence of *Araucaria angustifolia* (Bertol.) Steud., as well as traditional *faxinal* systems and floodplain areas (Klein 1980).

To sampling bees, wasps, and their natural enemies, private rural properties containing patches of Mixed Ombrophilous Forest (n = 4) and organic crops (n = 8) were selected, including vineyards (*Vitis vinifera* L.) and strawberry crops (*Fragaria × ananassa* Duchesne). Due to their structural similarity regarding organic management practices and surrounding environment structure, agricultural crops were considered as a single habitat category. Distances between sampled areas were always greater than 1 km based on foraging distance of species (Gathmann & Tscharntke (2002) (Fig. 1). After site selection, we quantified the distance of each sampling site to the nearest urban area and used this variable to represent a gradient of urban proximity.

Sampling design

Data were collected using trap-nests consisting of wooden blocks (120 × 35 × 25 mm) longitudinally split and containing an internal cavity 80 mm deep, with entrance diameters of 5, 7, 10, and 13 mm. Trap-nests were grouped into blocks of 16 units, with four nests of each diameter randomly arranged at each sampling point (Fig. 2). Each sampling point was mounted on a wooden stake at a height of 1.5 m above the ground, following adaptations of the design proposed by Buschini (2006). In each study area, six sampling points were installed, spaced at least 30 m apart from each other.

Samplings were conducted every two weeks from August 2011 to July 2012. At each sampling event, occupied and completed trap-nests were removed and replaced with empty nests of the same diameter. The occupied nests were transported to the laboratory and maintained until adult emergence. After the emergence of wasps, bees, and their natural enemies, individuals were counted and identified. The abundance was computed and the number of individuals emerged from the nests and the interaction between hosts (wasps and bees) and their natural enemies was recorded qualitatively, indicating that a host species *i* was parasitized by the natural enemy *j*.

For measuring the distance for the nearest urban area we used the land classification provided by the MapBiomas project, which provides a mapping and classification of land use for the whole Brazilian territory, on a scale of 1:5000 and pixels of 30 m X 30 m (Souza et al. 2020). We used collection nine, with a classification specific for the year when the collections were made.

Statistical analysis

To assess which independent variable (urban proximity or habitat type) influences abundance and richness of cavity-nesting hymenopterans we used Generalized Linear Models (GLMs). This type of model allows for a better adjustment according to the data distribution (Dobson 2002; da Silva et al. 2022). To test the abundance of individuals we fitted a Negative Binomial Generalized Linear Model which avoided the overdispersion of data, using the function *glm.nb()* from the MASS package (Venables & Ripley 2002). The overdispersion checking was fitted using the function *check_overdispersion()* from the performance package (Lüdecke et al. 2021), which did not detect dispersion (dispersion ratio = 1.201, p value = 0.52). To fit the richness of species we used a simple GLM, with a Poisson error

distribution and a log link function, using the function *glm()*, from the stats package (R Core Team 2025), which also had no overdispersion (dispersion ratio = 0.588, p-value = 0.808). For both model approaches we normalized urban proximity using log10.

To analyse how the urban proximity and habitat type would change species composition we used Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA). The dissimilarity distance matrix was measured using the function *vegdist()*, and the PERMANOVA using the function *adonis2()*, both from the vegan package, and with Bray-Curtis distance, since we had abundance data from each sampling point (Oksanen et al. 2026). For PERMANOVA we used 999 permutations. Moreover, we also measured the petitioned beta diversity into turnover (species replacement, measured as Simpson pair-wise dissimilarity) and nestedness (species loss, measured as the nestedness-fraction of Sorensen pair-wise dissimilarity) (Baselga 2010). We used the *beta.pair()* function, from the betapart package (Baselga et al. 2023). To confirm the patterns achieved in the PERMANOVA analysis, we used Mantel test, using the distance matrix from the partitioned beta diversity analysis as response variable and a matrix of distance of urban proximity (Euclidian distance) and habitat type (binary matrix) as explanatory variables, using the function *mantel()*, from the vegan package (Oksanen et al. 2026).

To compare abundance and richness between forest and organic crops, we used a Mann-Whitney test, using the function *wilcox.test()*, from the stats package (R Core Team 2025). To compare community composition among habitats, we performed a non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity, with two dimensions (k = 2) and a maximum of 100 random starts (trymax = 100), using the *metaMDS()* function, from the vegan package (Oksanen et al. 2026). Ellipses representing 95% confidence intervals were fitted to the ordination.

To compare interaction composition, we built a network to each environment (forest and organic crop), using the function *graph_from_biadjacency_matrix()*, from the igraph package (Csárdi & Nepusz 2006). We then used the function *network_betadiversity()*, from the betalink package (Poisot et al. 2012), which returns the pairwise beta-diversity components between habitats, separating the components into: S: total network beta diversity; OS: differences due to species replacement between networks; WN: changes in interaction patterns among shared species between networks; and ST: dissimilarity due to loss or gain of interactions caused by species turnover (Poisot et al. 2012).

To test the difference between environments regarding the network architecture, we used an approach based on null model analysis. Firstly, we used the null model *mgen*, which generates new binary matrices from the real network, fixing the connectance (Vázquez et al. 2009). We generate 1000 matrices using the function *nullmodel()* from the package bipartite (Dormann et al. 2009). As a proxy for network architecture, we quantified nestedness using the NODF, which quantifies nestedness architecture of interaction networks based on overlap and decreasing fill of columns and browns of the binary matrix (Almeida-Neto et al. 2008). This metric evaluates the extent to which interactions in a bipartite network are organized in a nested pattern, where species with fewer interactions (specialists) tend to interact with subsets of the partners of more connected species (generalists) (Almeida-Neto et al. 2008). The

final NODF value is scaled from 0 (no nestedness) to 100 (perfect nestedness) (Almeida-Neto et al. 2008). This approach is less sensitive to matrix size and fill than earlier metrics, and is widely used in the analysis of ecological interaction networks (Almeida-Neto et al. 2008). We estimated a null-based 95% confidence interval based on the 2.5th and 97.5th percentiles of the null distribution to evaluate whether observed values deviated from random expectations.

We also computed modularity as a proxy for network architecture. This metric measures the extent to which a network is subdivided into modules (i.e., groups of species more densely connected among themselves than with the rest of the network) (Newman 2006). We used the function *modularity()* from the package igraph, which uses the resolution parameter γ that weights the random null model (Clauset et al. 2004; Csárdi et al. 2006). This metric ranges from 0 (non-modular) to 1 (completely modular) (Csárdi et al. 2006).

Results

We sampled 846 built nests, of which 2,366 individuals emerged. Regarding host species, we sampled 2,024 individuals, four species of bees from the families Apidae and Megachilidae, and eight species of wasps, from the families Vespidae, Crabronidae, and Pompilidae. Natural enemies represented 342 individuals, belonging to 16 species, which were distributed among Hymenoptera families Chrysididae, Apidae, Mutillidae, Ichneumonidae, and Trigonalidae, and Bombyliidae from Diptera order. In total, 42 interactions were observed between 12 host species and 16 natural enemy species.

Host communities differed between forest fragments and crop habitats, with each environment harboring distinct species and ecological roles. Forest habitats were mainly characterized by wasp hosts such as *Trypoxylon lactitarse* Saussure, 1867 and *Pachodynerus guadulpensis* Saussure, 1853. In contrast, crop habitats included host species typically associated with more open and managed environments, such as *Centris tarsata* Smith, 1874, *Auplopus subaurarius* Dreisbach, 1963, and *Isodontia costipennis* Spinola, 1851. Notably, crop areas also exhibited a higher number of host species without observed parasitism.

Forest fragments harbored several natural enemy species not recorded in crop areas, including *Ipsiura myops* (Buysson, 1904), *Neochrysis bubba* Kimsey, 1985, and *Pleurochrysis* sp., primarily associated with wasp hosts such as *T. lactitarse* and *P. guadulpensis*. Conversely, crop habitats supported a distinct natural enemies community, with exclusive species such as *Mesocheira bicolor* (Fabricius, 1804), *Orthogonalys* sp., *Caenochrysis parvula* (Fabricius, 1804), and *Xystromutilla bucki* Suárez, 1960, and exhibited a high diversity of interactions involving *Anthrax aquilus* Marston, 1970, which interacted with seven host species.

The abundance of cavity-nesting hymenopterans communities was significantly affected by habitat type, while the distance to the nearest urban center has no significant relationship (Table 1). The higher influence of habitat type on the cavity-nesting community resulted in higher abundance in organic crops ($W = 1$, *p value* = 0.008) and no difference in species richness ($W = 18.5$, *p value* = 0.729) (Table 1).

Furthermore, despite the PERMANOVA model showing a significant effect of urban proximity on species composition, the partitioned beta diversity into turnover and nestedness was not associated with urban distances (Table 2). Moreover, there was a remarkable difference in species composition between habitats (Fig. 3). The partitioned beta diversity between habitats was more explained by turnover than a nestedness pattern (*beta.sim* = 0.76, *beta.sne* = 0.06, *beta.sor* = 0.83) (Table 2). Finally, interaction beta diversity between forest and crop habitats was moderate (S = 0.51) and largely driven by interaction rewiring among shared species (WN = 0.83). Differences between habitats were more explained by a replacement of interactions (OS = 0.5) rather than loss of interactions (ST = 0.33).

Table 1
Generalized Linear model with a Negative Binomial and Poisson distribution comparing the effect of urban proximity and habitat type on abundance and richness of cavity nesting hymenopteran communities. Bold values are significant (p-value < 0.05).

Explanatory variable	**Response variable**	**Estimate Std.**	**Error**	**z value**	**R 2**	**p-value**
(Intercept)		2.621	1.099	2.385		**0.017**
Urban center	Abundance	0.328	0.285	1.150	0.59	0.250
Habitat (forest - organic crop)		0.477	0.137	3.478		**0.001**
(Intercept)		1.091	2.081	0.524		0.600
Urban center	Richness	0.232	0.540	0.430	0.05	0.668
Habitat (forest - organic crop)		-0.104	0.244	-0.428		0.669

Table 2
Effect of urban proximity and habitat type on species composition of cavity-nesting hymenopteran community. a) PERMANOVA model, b) Mantel test using the partitioned beta diversity. Bold values are significant (p value < 0.05).

a) Model	**Variables**	**Df**	**SumOfSqs**	**R2**	**F**	**p value**
	Model	**1**	**0.23186**	**0.22433**	**2.8921**	**0.049**
Beta diversity ~	Residual	10	0.80171	0.77567	0.59	
Urban center proximity	Total	11	1.03356	1		
Beta diversity ~	Model	1	0.55818	0.54005		
Habitat (forest - organic crop)	Residual	10	0.47538	0.45995	11.742	**0.002**
	Total	11	1.03356	1		
b) Beta-diversity component	90%	95%	97.50%	Mantel r	Permutations	p-value
Turnover	0.263	0.351	0.468	0.061	999	0.310
Nestedness	0.236	0.290	0.344	-0.018	999	0.504
Total beta diversity	0.229	0.313	0.403	0.068	999	0.276
Turnover	0.194	0.289	0.388	0.736	999	**0.004**
Nestedness	0.156	0.288	0.356	-0.326	999	0.404
Total beta diversity	0.168	0.258	0.362	0.749	999	**0.003**

The architecture of networks measured through the NODF was outside of the explanation of the null model only in the crop lands. The null model distribution (95% confidence interval) in croplands ranged from 17.29 (2.5%) to 41.65 (97.5%), whereas the observed network value was 60.16, exceeding the upper bound of the null model expectation. In contrast, in forest habitats, the null model ranged from 12.39 (2.5%) to 45.73 (97.5%), and the observed value (40.11) fell within this interval (Fig. 4, Fig. 5). Regarding the modularity architecture, both environments (crops and forests) showed similar values, with croplands presenting a modularity of 0.35 and forest 0.35.

Discussion

Our results indicate that proximity to urban areas exerted a limited and non-directional influence on cavity-nesting hymenopteran communities. Despite being a central driver in many ecological contexts, urban distance did not significantly structure species richness, community composition, or interaction networks in our system. This weak effect is consistent with previous studies suggesting that the impact of urbanization on insect communities is often scale-dependent and may not impose strong

environmental filters at local scales (McDonnell & Hahs 2008). Additionally, studies have shown that urbanization effects may become more evident when assessed across multiple spatial scales, and that contemporary insect communities in urban landscapes may already be shaped by long-term filtering processes that favor tolerant and mobile species, resulting in limited variation along urban gradients (Corcos et al. 2019). Furthermore, the relatively high dispersal capacity of many cavity-nesting hymenopterans may buffer the effects of urban proximity, allowing species to persist across heterogeneous landscapes (Winfree et al. 2011).

In contrast, habitat type emerged as the primary factor structuring these communities. Although species richness remained similar between forest and organic crop habitats, abundance, community composition, and interaction networks differed markedly, indicating that habitat-related differences are primarily expressed through compositional and interaction-level reorganization rather than simple species loss. This pattern was mainly driven by species turnover, with a smaller contribution of nestedness, suggesting that forest and crop habitats harbor distinct species assemblages rather than subsets of the same community (Baselga 2010; Socolar et al. 2016). Habitat filtering likely operates through trait-mediated processes that favor species with particular nesting strategies, dispersal capacities, or tolerance to microclimatic variation (Keddy 1992; Kraft et al. 2015). In cavity-nesting hymenopterans, traits such as nesting substrate preference, voltinism, body size, and host specificity may determine persistence under agricultural conditions (Tscharntke et al. 2005; Williams et al. 2010). Thus, the observed turnover may reflect non-random filtering of species and interactions, resulting in functional reorganization even when taxonomic richness remains stable (Tylianakis et al. 2007).

Similar patterns have been reported across different insect groups and habitats, where richness-based metrics remain relatively stable despite substantial shifts in species identity, relative abundance, and biotic interactions (Tscharntke et al. 2005; Tylianakis et al. 2007; Queiros et al. 2025). This pattern suggests that agricultural environments do not represent impoverished subsets of forest communities, but rather support distinct communities shaped by environmental filtering and habitat-specific conditions (Tylianakis et al. 2007; Tscharntke et al. 2012). In addition, the use of organic management practices may contribute to the maintenance of species richness despite habitat conversion, as these systems are known to support higher biodiversity and more complex trophic interactions compared to conventional agriculture (Crowder et al. 2010; Tuck et al. 2014; Alves et al. 2024). This mechanism is consistent with patterns observed for cavity-nesting Hymenoptera in the Brazilian Atlantic Forest (Deus et al. 2022).

At the interaction level, this taxonomic turnover is mirrored by a reorganization of ecological networks. Interaction beta diversity was moderate and driven mainly by the rewiring of interactions among shared species, rather than by interaction loss associated with species exclusion, a pattern widely reported in studies of ecological networks under environmental change (Poisot et al. 2015). This correspondence between species turnover and interaction rewiring highlights a high degree of flexibility in species interactions, indicating that environmental changes can reshape functional community structure without necessarily leading to immediate local extinctions (Valdovinos et al. 2013). Such shifts may have

important ecological and evolutionary consequences by modifying selective pressures, population dynamics, and the stability of ecological networks (Bascompte & Jordano 2007; Tylianakis et al. 2010).

Notably, crop areas also exhibited a higher number of host species without observed parasitism, suggesting that these environments may function as partial enemy-free spaces or reduce encounter rates between hosts and natural enemies. This pattern indicates that habitat type may influence not only which species occur in each environment, but also the probability that potential interactions are realized. In addition, although some host species occurred across habitats, their interaction patterns varied, reinforcing the idea that habitat type shapes host availability, parasitoid access, and interaction opportunities. Consistently, *Trypoxylon opacum* Brèthes, 1913 was parasitized by the highest number of natural enemy species (S = 12), followed by *Pachodynerus guadulpensis* (S = 8) and *Trypoxylon lactitarse* (S = 8), highlighting their central role in structuring host–parasitoid networks.

In addition to changes in species composition and interaction rewiring, network structure metrics provided further insights into how ecological organization differs between habitats. Nestedness patterns differed between environments, with crop networks exhibiting significant nestedness compared to null models, suggesting that interactions are structured by non-random processes, likely driven by environmental filtering and resource distribution. In contrast, forest networks did not differ from null expectations, which may reflect either limited sampling effort, reduced network size, or a genuinely less nested structure in more complex and heterogeneous environments. Such patterns are consistent with previous studies indicating that nestedness can emerge in simplified or disturbed systems where interaction partners are unevenly distributed (Bascompte et al. 2003; Tylianakis et al. 2007).

Conversely, modularity did not differ between habitats, indicating that the compartmentalization of host-parasitoid interactions is maintained across environmental contexts. This suggests that modular structure may represent a relatively stable property of antagonistic networks, potentially contributing to their robustness and stability even under environmental change (Thébault & Fontaine 2010; Tylianakis et al. 2010). High modularity has been associated with increased persistence in ecological networks by limiting the propagation of disturbances across modules (Olesen et al. 2007; Thébault & Fontaine 2010), reinforcing the idea that certain structural properties of interaction networks can be resilient to habitat modification despite shifts in species composition and interaction patterns.

Although our study focused on organic agricultural systems, it is important to contextualize these findings within the broader spectrum of agricultural management. A large body of evidence from non-organic and conventionally managed crops demonstrates that agricultural intensification is typically associated with stronger negative effects on hymenopteran communities, particularly through reduced habitat heterogeneity and increased chemical inputs (Tscharntke et al. 2005). These effects commonly include declines in abundance, shifts in species composition and simplification of ecological networks (Tylianakis et al. 2007; Geiger et al. 2010). In addition, agricultural intensification may also induce sublethal stress responses at the individual level, such as increased fluctuating asymmetry (dos Santos 2026). In this context, the patterns observed in organic crops in our study likely represent a conservative

estimate of community reorganization following habitat conversion, as more intensive management regimes are expected to amplify compositional, interaction-level, and functional changes, beyond those detected under organic practices (Brittain et al. 2010; Tylianakis et al. 2007).

Taken together, our findings show that biodiversity responses to habitat modification cannot be captured by species richness alone, as taxonomic stability may mask substantial changes in community composition and interaction structure. Our findings indicate that crop habitats can sustain species richness and maintain complex interaction networks. While proximity to urban areas had a limited effect, habitat type emerged as the dominant driver of both species turnover and interaction rewiring, highlighting the central role of local environmental conditions in shaping ecological organization. These results emphasize that conserving biodiversity in human-modified landscapes requires moving beyond species counts to incorporate the dynamics of species interactions, with habitat heterogeneity and low-impact management playing key roles in maintaining ecological function.

Declarations

Funding

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

Author Contribution

Luana Vieira Carlin dos Santos and Maria Luisa Tunes Buschini contributed to the conceptualization of the study and wrote the main text of the manuscript. Jean Pablo Alves de Deus contributed to the data analysis and statistical procedures. Jucélia Iantas contributed to the field sampling, collection of the specimens, and secondary revision of the manuscript. Maria Luisa Tunes Buschini supervised the study. All authors read and approved the final version of the manuscript.

Acknowledgement

The authors thank the Universidade Estadual do Centro-Oeste (UNICENTRO) for institutional and logistical support. We are especially grateful to the landowners who kindly granted access to their properties and permitted data collection at the study sites.

Data Availability

The data supporting the findings of this study are publicly available in the Zenodo repository under the title Data from: Habitat type outweighs urban proximity in shaping cavity-nesting hymenopteran communities, at https://doi.org/10.5281/zenodo.20430837

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Figures

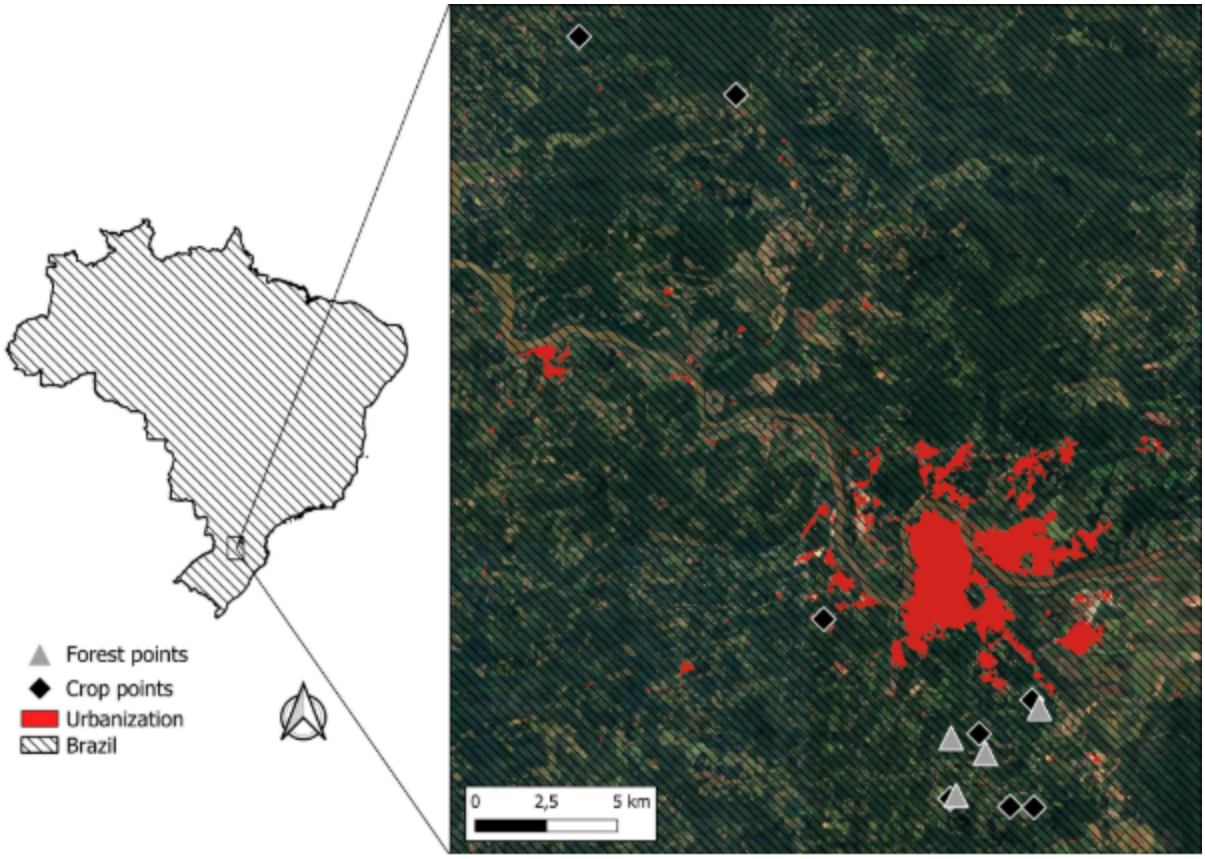


Figure 1

Sampling design of cavity-nesting hymenopteran community located at the south Brazil, within the *Araucaria*Forest photophisiognomy.

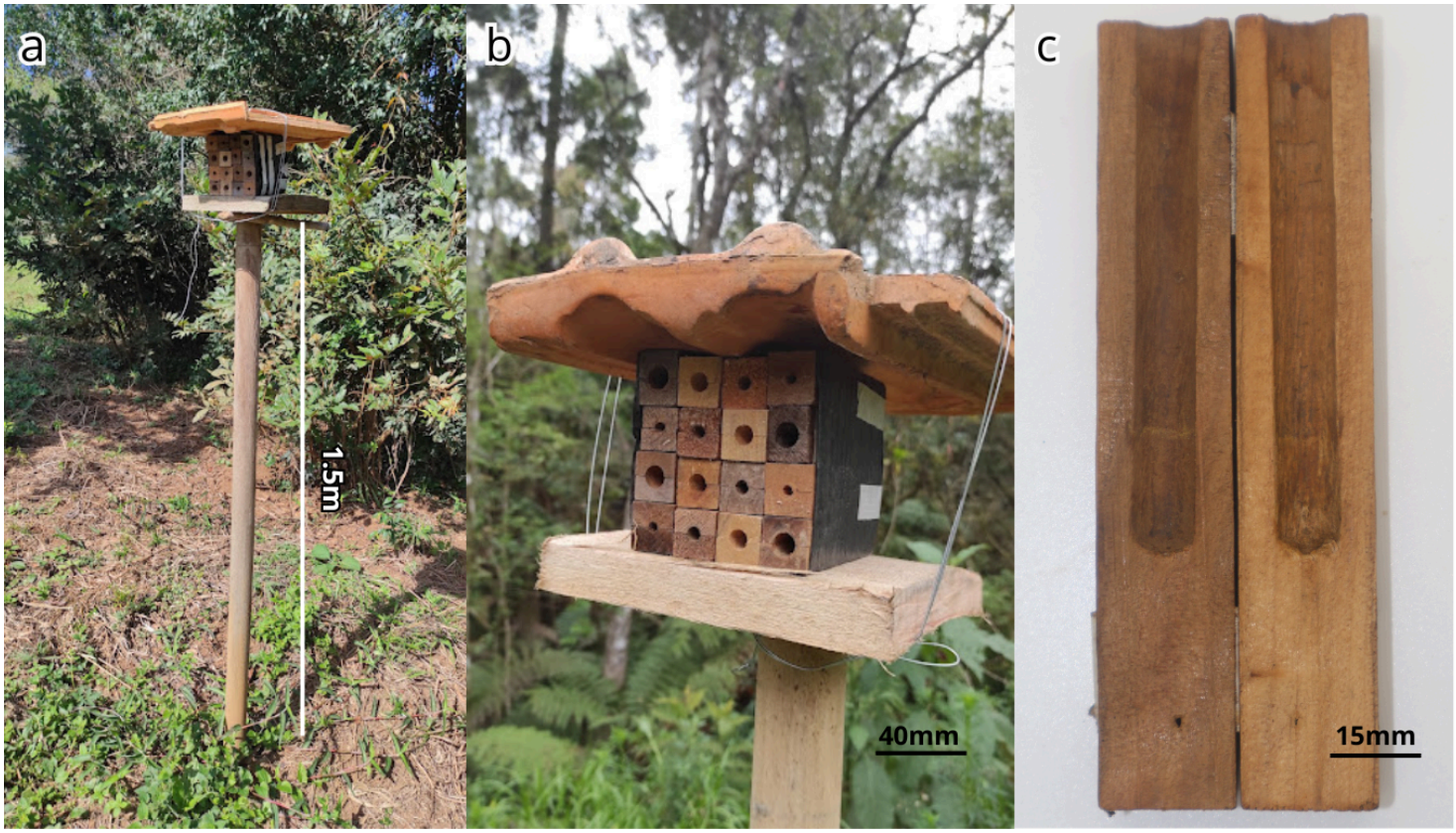


Figure 2

Sampling point with trap-nests fixed in the landscape (a); block of trap-nests (b); trap-nest interior made of wood.

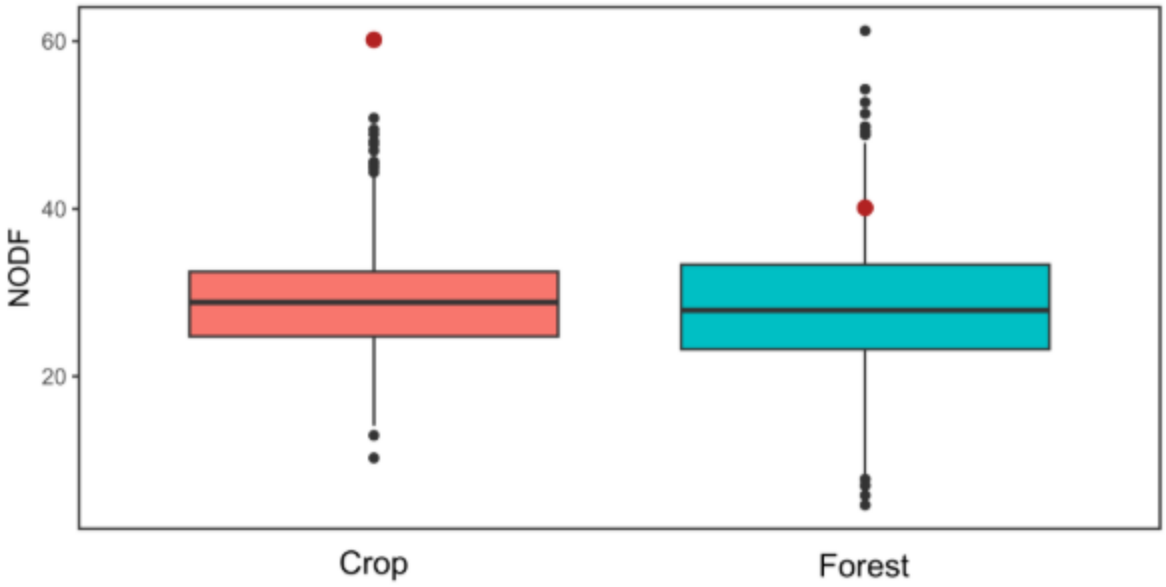


Figure 4

Host-natural enemy network architecture comparison between environments. Boxes are the interquartile range from 25% to 75% of nestedness values from the *mgen* null model type. The horizontal line is the

median and red dots representing the values of nestedness from the real networks.

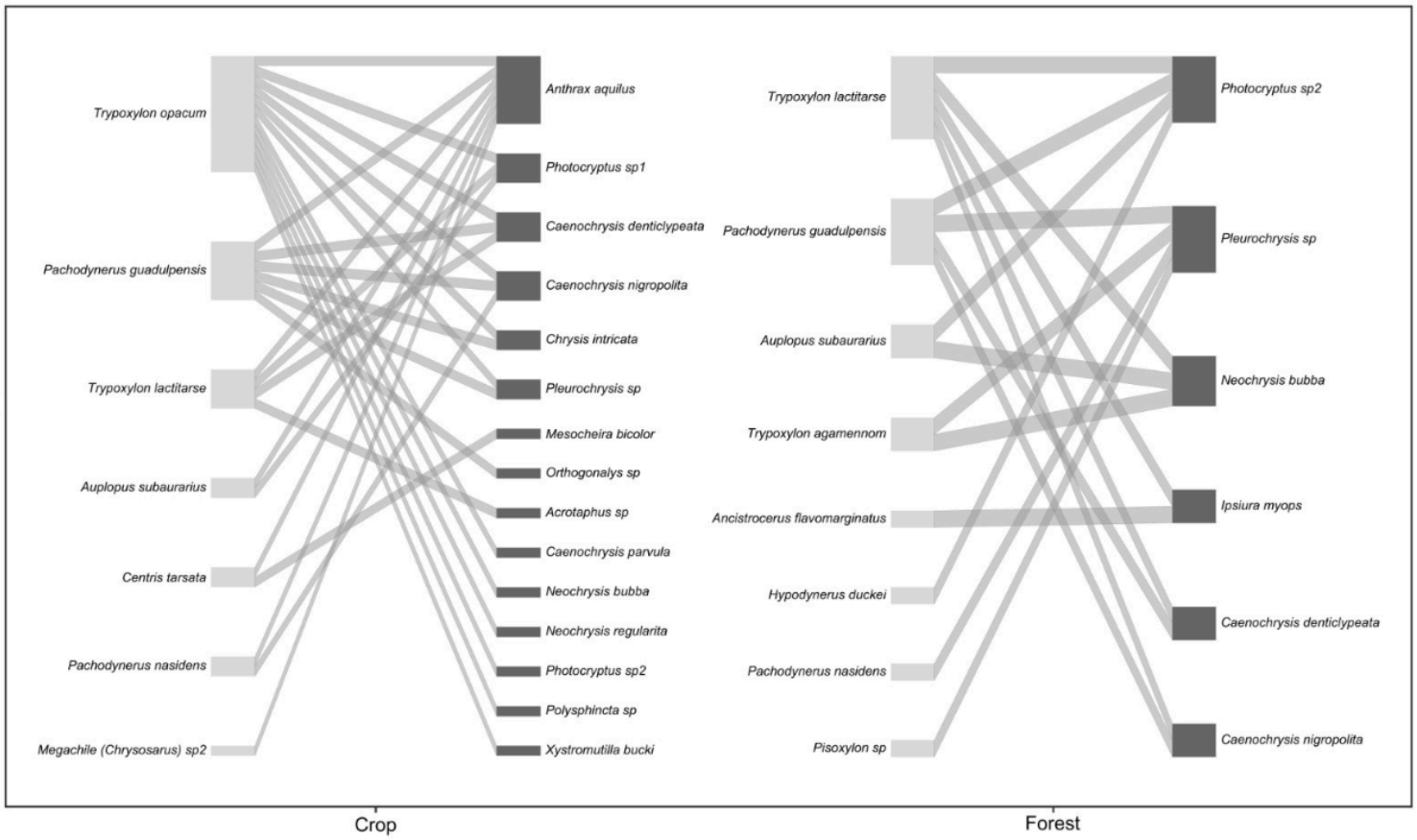


Figure 5

Interaction network between cavity-nesting hymenopterans and natural enemies in crop lands and forested environments. Boxes indicating each species and link are the interaction among them.

Supplementary Files

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