

Original Article

Host-natural enemy communities in a changing world: The impact of forest loss on cavity-nesting Hymenoptera and their natural enemies

Comunidades hospedeiras de inimigos naturais em um mundo em mudança: O impacto da perda de florestas nos Hymenoptera que nidificam em cavidades e seus inimigos naturais

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Abstract

Cavity-nesting bees and wasps provide important ecosystem services for humans. This study aimed to understand how the replacement of forests with non-forest habitats affects the structure and interaction network of cavity-nesting bees, wasps, and their natural enemies. From 1,536 trap-nests distributed across 48 sites, we collected a total of 541 built nests, from which 1,420 hosts and 254 natural enemies emerged. We found no significant differences in species abundance, richness, or diversity between forest and matrix environments. However, abundance evenness was higher in forests. Interestingly, host species composition differed between forests and matrix areas, while natural enemy composition remained similar. Similarly, network metrics did not differ significantly between the two environments. Despite this apparent resistance of cavity-nesting hymenopteran communities to forest loss, many species are highly specialized in utilizing wooded areas and are not adapted to other environments. As a result, we risk losing not only specific and rare species but also their unique ecological functions. We emphasize the need to include these forest-dependent species in more conservation plans, as most remain poorly studied, from basic aspects of their natural history to applied research on their ecological functions and economic relevance. Future studies should also investigate the potential unseen effects of host composition shifts and the increased dominance of certain species in matrix areas on biodiversity patterns. This could provide clearer insights for improving conservation and management strategies.

Keywords: interactions, wasps, cavity-nesting bees.

Resumo

Abelhas e vespas que nidificam em cavidades fornecem importantes serviços ecossistêmicos para os humanos. Este estudo teve como objetivo entender como a substituição de florestas por habitats não florestais afeta a estrutura e a rede de interação de abelhas, vespas e seus inimigos naturais que nidificam em cavidades. De 1.536 ninhos-armadilha distribuídos em 48 locais, coletamos um total de 541 ninhos construídos, dos quais emergiram 1.420 hospedeiros e 254 inimigos naturais. Não encontramos diferenças significativas na abundância, riqueza ou diversidade de espécies entre os ambientes florestais e matriciais. No entanto, a uniformidade da abundância foi maior nas florestas. Curiosamente, a composição das espécies hospedeiras diferiu entre florestas e áreas matriciais, enquanto a composição dos inimigos naturais permaneceu semelhante. As métricas de rede também não diferiram significativamente entre os dois ambientes. Apesar dessa aparente resistência das comunidades de himenópteros que nidificam em cavidades à perda florestal, muitas espécies são altamente especializadas na utilização de áreas florestais e não são adaptadas a outros ambientes. Como resultado, corremos o risco de perder não apenas espécies específicas e raras, mas também suas funções ecológicas únicas. Enfatizamos a necessidade de incluir essas espécies dependentes de florestas em mais planos de conservação, pois a maioria continua mal estudada, desde aspectos básicos de sua história natural até pesquisas aplicadas sobre suas funções ecológicas e relevância econômica. Estudos futuros também devem investigar os potenciais efeitos invisíveis das mudanças na composição do hospedeiro e o aumento da dominância de certas espécies em áreas de matriz sobre os padrões de biodiversidade. Isso pode fornecer insights mais claros para melhorar as estratégias de conservação e gestão.

Palavras-chave: interações, vespas, abelhas solitárias.

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1. Introduction

Species have evolved in relatively stable environments or in habitats with predictable seasonality for hundreds or thousands of years (Tonkin et al., 2017). However, global warming and habitat loss have led to accelerated climate and environmental changes in the last few decades affecting species persistence in different, and frequently unexpected ways (Fjeldsaå and Lovett, 1997). For example, the negative effects of habitat loss on communities can largely vary, reducing biodiversity of 13% up to 75% worldwide (Haddad et al., 2015). In general, habitat loss has intensified selective pressures, which increase the homogenization of communities due to the higher proportion of generalist species (Didham, 2010; Martinson and Fagan, 2014). Consequently, species with more restricted requirements are isolated in forest patches immersed in anthropic matrices (Haddad et al., 2015). This growing biodiversity crisis needs to be studied in depth and fully understood, to provide the best ways to conserve and manage species, mainly those more sensitive to habitat loss, such as forest specialists' ones. Thus, an approach comparing community structure and their species networks between native forest patches and adjacent matrices may provide valuable information for this scientific endeavor (Tylianakis et al., 2007; Magrath et al., 2014; Nether et al., 2019).

Forest fragmentation can affect species within a community differently, leading to changes in community structure, interspecific interactions, and ecological functions (Tschardt et al., 2002), mainly because all species are linked in networks of mutualistic and antagonistic interaction and the effect of habitat loss can propagate throughout this network (Tylianakis et al., 2010). Native forests provide important resources that increase species persistence, such as nests, food, and shelter (Morato and Martins, 2006). The amount and heterogeneity of these resources are important drivers of community structure and may influence species interactions (Moura et al., 2019). Observations indicate that forest habitats and crop monocultures can differently influence species interactions and change host-natural enemy network properties (Tylianakis et al., 2007; Staab et al., 2016). Differences in land management, even of a particular habitat type, can generate differences in the structure of host-natural enemy networks, where more-natural systems tend to have networks with higher complexity and evenness of interactions (Tylianakis and Binzer, 2014).

Regarding cavity-nesting Hymenoptera communities, the effects of habitat loss and changes in land use do not follow a consistent pattern. For instance, high heterogeneity and availability of cavities found in forests may hamper the ability of generalist natural enemies to locate many hosts (Kruess and Tschardt, 1994; Steckel et al., 2014), thus benefiting the persistence of specialized natural enemies and increasing species richness in forest habitats compared to crop plantations (Sperber et al., 2004). On the other hand, anthropogenic matrices usually comprise crop monocultures and pastures in which only a few species can exploit available resources (Tylianakis et al., 2007). Although the number of studies that evaluated

the effects of habitat loss and changes in land use on communities of cavity-nesting insects or their natural enemies has increased in the last few years (Ebeling et al., 2012; Matos et al., 2013; Rocha-Filho et al., 2017), only a few studies have investigated community structure and network properties of both host and natural enemies' communities in the same areas (Tylianakis et al., 2007; Nether et al., 2019). In Ecuador, 48 networks involving cavity-nesting bees and wasps and their parasitoids across a land-use intensity gradient were compared and in the most intensive systems, the networks had highly uneven interaction strengths, dominated by one or two interactions (Tylianakis et al., 2007). These changes to the patterns of interactions were not driven simply by changes in species diversity, but also by the spatial arrangement of different habitats, their proximity to one another, and the distance between patches of a single habitat. Thus, in simpler environments compared to forests, generalist natural enemies may be benefited instead of specialists because they have a higher trophic niche range and may have lower physical or structural impediments to find their hosts (Sperber et al., 2004; Laliberté and Tylianakis, 2010). In this scenario, the antagonistic network in matrices may consist of few species which are more connected (Hagen et al., 2012).

We studied the effect of forest loss habitats on the community structure and interaction network of cavity-nesting bees, wasps, and their natural enemies in one of the most threatened biomes of South America, the Atlantic Forest, in which 97% of native habitat patches have presented less than 50 ha and only 23% of remaining forest cover (Vancine et al., 2024). A substantial portion of this biome is now an archipelago of small islands of vegetation embedded into a matrix of degraded areas, pasture, agriculture, forestry and urban areas (Joly et al., 2014). In this biome, bees are responsible for pollinating more than 80% of their plants, and the wasps are predators and parasitoids, playing an important role in the biological control of other species (LaSalle and Gauld, 1993). To measure the species' richness and abundance of bees and wasps simultaneously we used trap-nests that provide a standardized nesting resource and allow for the analysis of parasitism by natural enemies (Tschardt et al., 1998). We hypothesized that the replacement of natural forest areas with anthropogenic matrices affects the diversity and interaction among cavity-nesting wasps and bees and their natural enemies. We predict that forest habitats will present (1) the highest host and natural enemy diversity (abundance and richness) and (2) more specialized interactions. We also evaluated if host and natural enemy communities are affected by temperature and humidity between habitats.

2. Material and Methods

2.1. Study area

We conducted the data collection from August 2018 to August 2019 in four forest fragments and four matrix areas (without forest, see nest section) located at the

Guarapuava city, Paraná, Brazil (Figure 1). According to Köppen classification, the climate of the region can be described as Cfb (wet subtropical mesothermic) without a dry season, with cold summers and moderate winters (Peel et al., 2007). The average annual rainfall is 1961 mm, and the average annual temperature is around 22°C, ranging from 6.8 to 36.0 °C (Diniz and Buschini, 2016).

2.2. Data collection

We built trap-nests for wasp and bee species using wood (*Araucaria angustifolia*) measuring 25 × 20 × 120 mm, which were longitudinally drilled to a depth of 80 mm with three apertures, containing 5, 7, 10, and 13 mm in diameter. We also built trap-nests with bamboo segments of different diameters (ranging from 4 mm to 16 mm) and lengths (ranging from 80 mm to 190 mm). In addition, wood and bamboo nests were sewed in half, lengthwise. We used adhesive tape to hold pieces together, allowing the examination of the cavities when opened.

We carried out samples in four forest fragments, with similar vegetation types, and four adjacent matrices to these forests, which were mainly comprised by pastures with cattle, sheep, or cultivation areas with corn and soy monocultures (Figure 1). In each area, we had six sample stations, in which we installed 32 trap-nests, 16 wooden trap-nests (four of each diameter described above) and 16 bamboo ones (variate diameters). In summary, we built 48 sampling stations and installed 1,536 trap-nests. The nests were 1.5 m above ground and were inspected in intervals of 15 days. When a nest was occupied, we collected it and immediately replaced it with an empty trap-nest of the same diameter. We also measured the local temperature

(°C) and relative humidity (%RH) using a thermometer/hygrometer with an external probe (Simpla TH02; at accuracy ±1°C/ ±5% RH).

2.3. Statistical analysis

In this study, we estimated abundance as the number of emerging individuals, because some nests usually present more than one brood cell, and natural enemies may emerge from some cells but not from others. To evaluate factors potentially driving the abundance of hosts and natural enemies, we performed a two-step analysis. In the first step, we calculated distance-based Moran's eigenvector maps (dbMEM; Legendre and Gauthier, 2014) from the coordinates of each sampling station. We estimated Euclidian geographic distance matrices for each data set using the "dist" function from the "vegan" package (Oksanen et al., 2013). We then calculated the dbMEM eigenvalues using these matrices, which are proportional to Moran's I coefficient of spatial correlation, using the "dbmem" function from the "adespatial" package (Dray et al., 2020). Therefore, the dbMEM can be used to control or test for spatial autocorrelation (Legendre and Legendre, 2012).

To choose the best dbMEM(s) to include in each model, we conducted generalized linear mixed models (GLMM) with negative binomial error distribution for host abundance and GLMM with Gamma error distribution with log link function for natural enemy abundance, using the "glmer" function from the "lme4" package (Bates et al., 2015) and the "glmer.nb" function from the "MASS" package (Venables and Ripley, 2002), respectively. We compared alternative models, as well as the null model, using Akaike

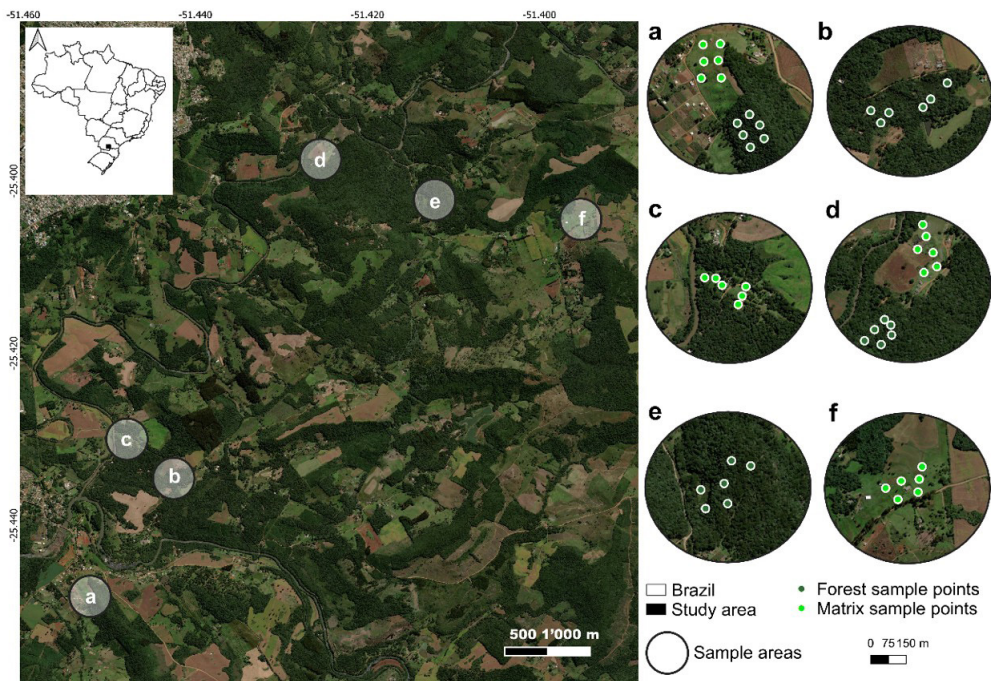


Figure 1. Samples areas of cavity-nesting hymenopterans and their associated natural enemies. Red dots: natural forest areas; Yellow dots: matrix (areas without forest, encompassing grassland, pastures with cattle, sheep, or cultivation areas with corn and soy monocultures).

Information Criterion corrected for small samples, AICc (Burnham and Anderson, 2002), in the “dredge” function from the “MuMIn” package (Barton, 2019). We considered models within a range of 2.0 AICc from the model with the smallest AICc to represent the best fits. We then chose the dbMEM(s) found in the model with the lowest number of predictors and the highest weight (ω_i), because the addition of new dbMEM in the alternative models do not increase the explanatory power of the variation observed in the data (Burnham and Anderson, 2002). We provided the complete tables of model comparisons in Tables S1 and S2 (see Supplementary Material).

In the second step, we tested which factors may drive host and natural enemy abundance using GLMM. We included the best dbMEM(s) selected in the first step, habitat type (forest and matrix), temperature, and relative humidity as fixed predictors, and the identity of host or natural enemy as a random variable in its corresponding model. We obtained χ^2 and P-values using the “Anova” function from the “car” package (Fox and Weisberg, 2019).

We compared the richness of host and natural enemies (response variable) that emerged from trap-nests collected in the forest fragments and matrices using the chi-square test (χ^2). We calculated P-values from the χ^2 -distribution built using Monte Carlo simulations of our data (2,000 replicates) with a continuity correction (Hope, 1968). We considered insect abundance in these analyses. We used the ‘chisq.test’ function from R base packages (R Core Team, 2024).

We also tested the difference between total diversity indexes aggregating hosts and natural enemies using a *t* test. The diversity indices used were: Abundance (sum of number of hosts and natural enemies); richness (sum of number of species of hosts and natural enemies); Shannon Diversity, which compares the richness and the abundance distribution among species; and finally the Pileous evenness index, which tests the distribution of abundance of species between the forest and matrix.

To compare the insect composition of hosts and natural enemies (response variables) between habitat types, i.e., the four forest fragments and four matrices (predictor variable), we conducted two Permutational multivariate analyses of variance (PERMANOVA). We directly calculated statistical differences from Bray-Curtis dissimilarity matrices produced based on insect abundances. We obtained P-values using 999 permutations (Legendre and Anderson, 1999) using the “adonis2” function from the “vegan” package (Oksanen et al., 2013). We also performed a nonmetric multidimensional scaling ordination analysis (NMDS) to visually evaluate differences and similarities in species composition between habitats using the “vegan” package (Oksanen et al., 2013). For methodological reasons, to have more consistence in the statistical analysis, we separated the data according to the year of insect hatching; thus, obtaining eight samples for each habitat type. We built the graphs using the “ggplot2” package (Wickham, 2016). We also evaluated the beta diversity using the “beta.pair” function of the “betapart” package to discover which pattern was acting in the communities. This beta diversity (Sorensen dissimilarity index) can be divided

into two components: turnover (β_{sim}) and nestedness (β_{sne}) (Baselga, 2010).

To test the prediction that the forest fragments have more specialized interactions, we built eight networks for host-natural enemy interactions observed in the four forest fragments and four matrices, aiming to compare the connectance (proportion of observed interaction in the expected interactions), modularity (proportion of species that interact more inside a module than with other modules in the network) (Newman, 2006) and the specialization index, also called “*H2*” (degree of specialization or partitioning among two parties in the network) (Blüthgen et al., 2006). Before computing these network metrics, we measure how good our sampling was in terms of interaction records, using the approach proposed by Jordano (2016). Afterward, we tested if our network had a structure that is being shaped by a biological or environmental condition instead of random characteristics using the null model from Vazquez and Aizen (2003), which creates null networks from the observed one, maintaining the connectance as in the original network. To calculate the network parameters, we used the “network.level” function from the “bipartite” package (Dormann et al., 2009). We compared all network indexes (response variables) among forest fragments and matrices (predictor) using t-tests. We conducted all data analysis in R, version 4.4.2 (R Core Team, 2024).

3. Results

We collected a total of 541 completed nests from which 1,420 hosts and 254 natural enemies emerged. Among the hosts, we found 1,393 wasps and 26 bees. Wasps that emerged were from the Pompilidae (152 individuals), Sphecidae (22), Vespidae (528), and Crabronidae families (694), while bees were from the Apidae (6 individuals) and Megachilidae families (19). Among the natural enemies, individuals from nine families emerged from built nests: Bombyliidae (15), Chalcididae (1), Chrysididae (80), Eulophidae (32), Ichneumonidae (22), Megachilidae (2), Mutillidae (7), and Sarcophagidae (95) (Figure 2). There were 1.4 times more hosts that emerged from trap-nests found in the matrices (817) compared to the nests collected in the forest fragments (603). Similarly, there were 2.9 times more natural enemies that had invaded nests in the matrices (189) than in the forest fragments (65) (Figure 2).

The model containing the 6th dbMEM was the best model for host abundance. In the host abundance model, there was spatial autocorrelation ($\beta_{dbMEM} = 0.24 [0.13 - 0.34]$, $\chi^2 = 9.54$, d.f. = 1, $P = 0.002$), and the host abundance enhanced as the local temperature increased in both forest and matrix areas ($\beta_{temperature} = 0.24 [0.13 - 0.34]$, $\chi^2 = 9.54$, d.f. = 1, $P = 0.002$) (Figure 3). Habitat type and relative humidity were not correlated with host abundance (habitat: $\chi^2 = 0.16$, d.f. = 1, $P = 0.692$; relative humidity: $\chi^2 = 1.582$, d.f. = 1, $P = 0.208$). Concerning the natural enemies' abundance model, the null model was within the best models. Therefore, there was no spatial autocorrelation for natural enemies' data; thus, we did not include any dbMEM in the natural enemy model. No

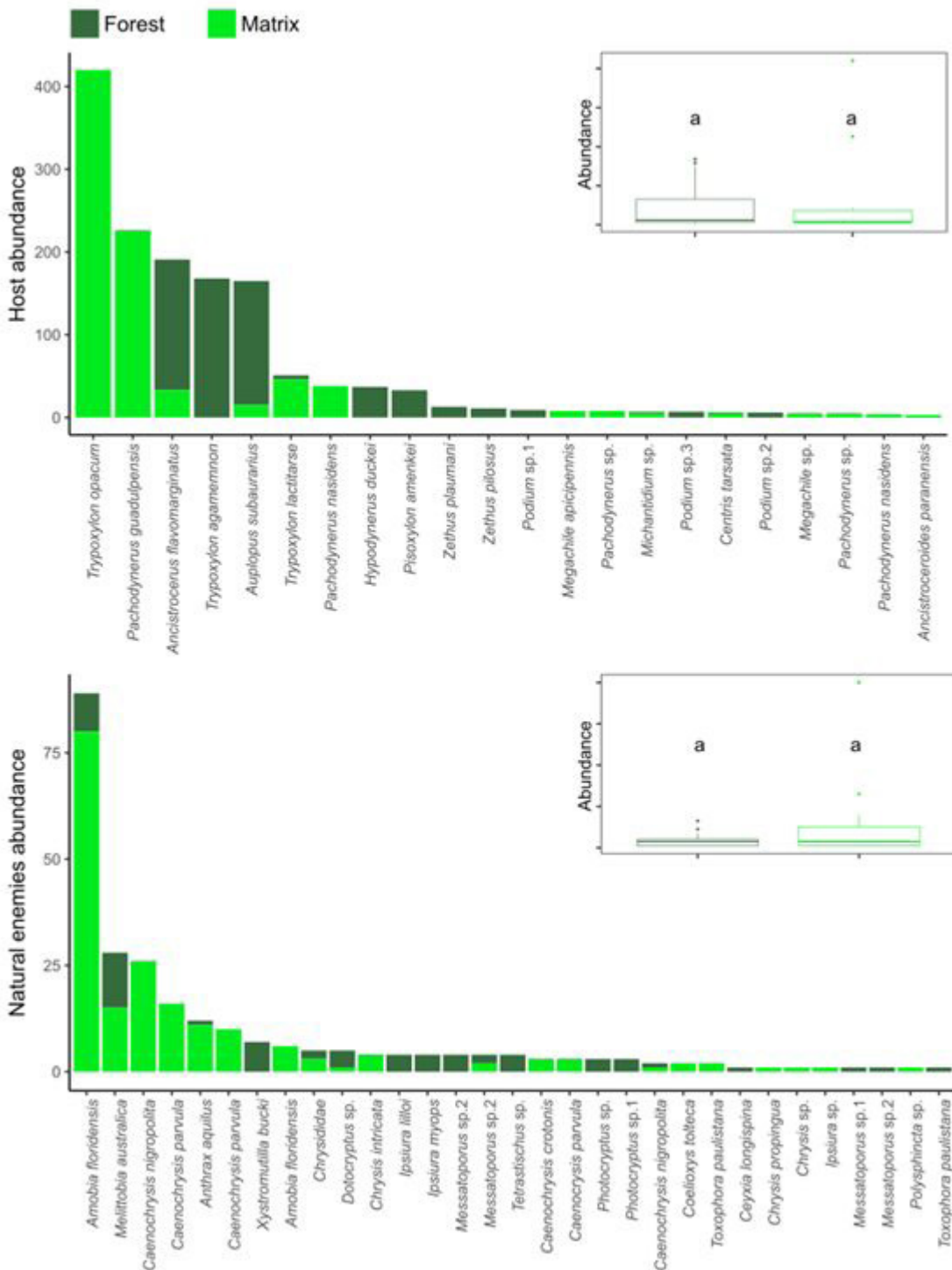


Figure 2. Abundance of host and natural enemy species in the forest (dark green) and matrix (light green) areas. Letters in the boxplot mean significant differences ($p < 0.05$).

factor explained the variation in natural enemy abundance (habitat: $\chi^2 = 0.0007$, d.f. = 1, $P = 0.979$; temperature: $\chi^2 = 0.24$, d.f. = 1, $P = 0.621$; relative humidity: $\chi^2 = 3.17$, d.f. = 1, $P = 0.075$). The most abundant species in the matrix

were *Trypoxylon (Trypargilum) opacum* (Brèthes, 1913) and *Pachodynerus guadulpensis* (Saussure, 1853), while *Auplopus subaurarius* (Dreisbach, 1963) and *Trypoxylon (Trypargilum) agagemmon* (Richards, 1934) were more abundant in the

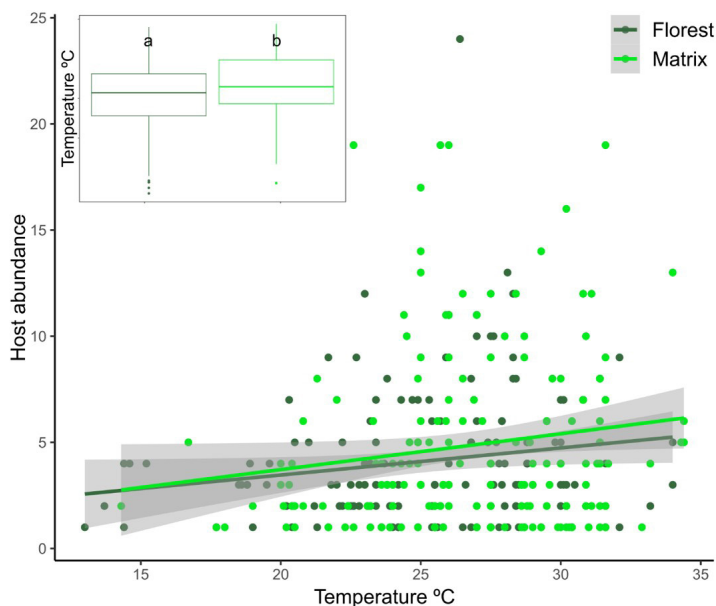


Figure 3. Effect of temperature on host abundance in the forest (dark green) and matrix (light green) areas. Letters in the boxplot mean significant differences ($p < 0.05$).

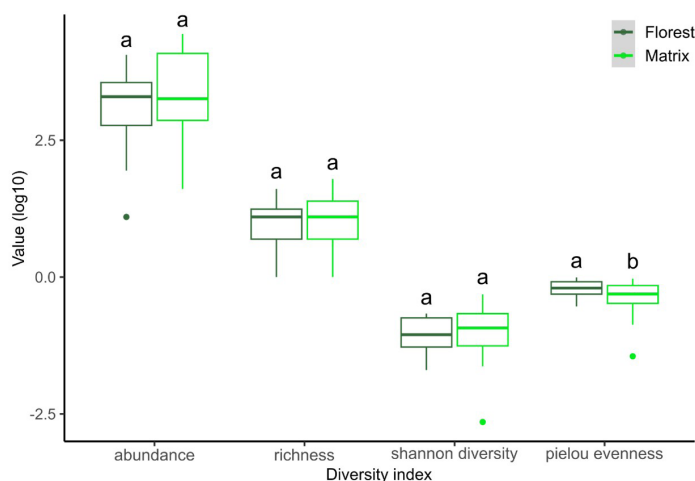


Figure 4. Difference among diversity indexes between forest (dark green) and matrix (light green) areas, accounting for all species (hosts and natural enemies). Letters in the boxplot mean significant differences ($p < 0.05$).

forest. Regarding natural enemies, the most abundant species were found in the matrix (i.e., *Amobia floridensis* (Townsend, 1892), *Caenochrysis nigropolital* (Bischoff, 1910), and *Caenochrysis parvula* (Fabricius, 1804)).

We identified a total of 20 host species in our samples and the richness was equal between forest fragments (12) and the matrices (12), but only four of these species were found in both habitats. Regarding natural enemies, we sampled 24 species, and another group described as 'other Chrysididae' that we consider as a single species in this analysis. The richness also did not differ between forest fragments (16) and matrices (16), while eight species were found in both habitats. We also found no significant

differences between the total species richness ($t = -1.0436$, d.f. = 36.441, $P = 0.3035$) and the Shannon diversity ($t = 0.29$, d.f. = 37.67, $P = 0.765$). On the other hand, the Pielou Evenness index was significantly higher in forest ($\bar{X} = 0.74$) than in matrix ($\bar{X} = 0.55$) areas ($t = 2.02$, d.f. = 41.14, $P = 0.049$) (Figure 4).

The composition of hosts species differed between the forest fragments and matrices ($R^2 = 0.71$, $F_{1,14} = 14.99$, $P = 0.040$) and the partitioning of β -diversity for host species ($\beta_{sor} = 0.68$) showed that the turnover ($\beta_{sim} = 0.66$) accounted for a larger fraction of beta diversity than nestedness ($\beta_{nes} = 0.013$) (Figure 5a). The natural enemy composition in the two habitats was not different ($R^2 =$

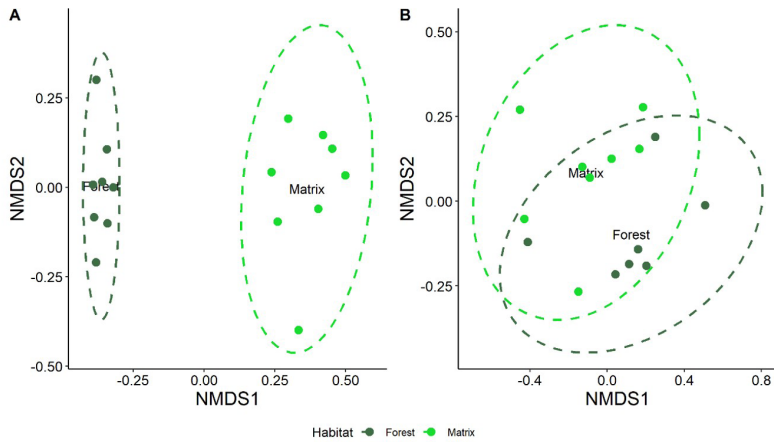


Figure 5. Non-metric multidimensional scaling (NMDS) relationships for (A) host and (B) natural enemy composition from forest fragments (dark green) and matrix (light green). Overlapping among ellipses represents similar species composition, while non-overlapping among ellipses means that habitats housed different species composition.

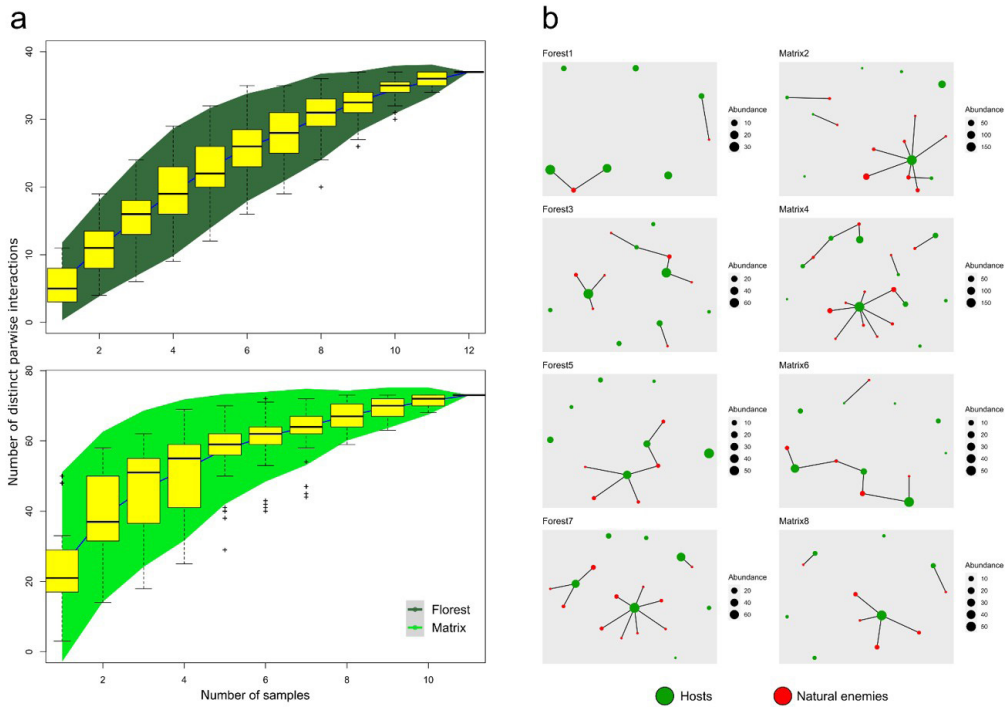


Figure 6. Networks analysis between cavity nesting hymenopterans and their associated natural enemies. a) Interaction accumulation curves over the twelve months of sampling in forest (dark green) and matrix (light green) areas. Box plots overlapping the curve show the distribution of the accumulated interactions in each month. b) Interaction network plot showing the interaction (black line) between hosts (green dots) and natural enemies (red dots). The dot size represents the abundance of each species.

0.34, $F_{1,13} = 3.05$, $P = 0.059$). The beta diversity of natural enemies was smaller ($\beta_{sor} = 0.5$) and the turnover was larger than nestedness ($\beta_{sim} = 0.5$, $\beta_{nes} = 0$) (Figure 5b). We sampled enough interaction in our sample design, as the interaction accumulation curve approached the asymptote (Figure 6a). The null model tests show that

modularity was higher than the expectation of the null network both in the forest and matrix areas. On the other hand, the network specialization of interaction was different from the null model only in the matrix areas, where it was higher. Nevertheless, the network indexes were similar in both the forest fragments and matrices (Table 1, Figure 6b).

Table 1. Mean and standard error of host-natural enemy network parameters in forest fragments and matrices. The *P*-value corresponds to the results of *t*-tests comparing both habitat types.

Measures of network	Forest	Matrix	Pvalue
Connectance	0.43 ± 0.14	0.29 ± 0.05	0.11
Modularity	0.44 ± 0.11 (<i>z</i> _s = 2.28, <i>p</i> = 0.022)	0.48 ± 0.02 (<i>z</i> _s = 6.10, <i>p</i> = <0.001)	0.54
H ²	0.83 ± 0.15 (<i>z</i> _s = 1.24, <i>p</i> = 0.213)	0.72 ± 0.22 (<i>z</i> _s = 6.58, <i>p</i> = <0.001)	0.44

4. Discussion

We did not find a significant difference in abundance, richness and diversity of species between forest and matrix environments. However, the increase in abundance of hosts was positively correlated with higher temperatures, which were higher in matrix areas. Moreover, the greater evenness in abundance was higher in forests, which implies more dominance of some species in matrix areas. This result was clearer after examining each species' abundance separately, where matrix specialists had the greatest abundance. In species that occur in both habitats, their abundance was higher in matrix areas. Interestingly, the composition of hosts species was different between the forest and matrix while the natural enemies were similar. In the same way, the network metrics were not significantly different between both environments.

The high turnover of host species between the forest and matrix may imply different ecological strategies of life. A matrix specialist species, such as those from *Trypoxylon* genus, may be more adapted to living in areas with higher solar radiation, as they are one of the most abundance species among cavity-nesting hymenopterans (Buschini, 2007; Buschini et al., 2006). In our study, *Trypoxylon lactitarse* Saussure, 1867, which is a generalist's habitat species, shows their highest abundance in matrix areas. On the other hand, *T. agamenon*, a forest specialist, shows a lower abundance compared to *T. opacum*, a matrix specialist. This tendency of hosts to present a higher abundance out of the forest could be related to different ecological strategies, such as reproductive patterns and trophic resources. Here we show that the forest had a lower temperature and other studies on the biology of *Trypoxylon* species in this same region show a higher air humidity in forests (Nether et al., 2019; Buschini and Woiski, 2008; Buschini and Woiski, 2006). Higher temperatures and lower air humidity may be used to explain the higher cavity-nesting hymenopteran offspring production (Sobek et al., 2009; Matos et al., 2013). In the same way, the three *Trypoxylon* species collected here also present different hunt strategies, where *T. agamenon* uses walking spiders to feed their brood, while *T. opacum* and *T. agamenon* uses spiders that build bidimensional webs (Buschini et al., 2010a, 2010b; Buschini et al., 2008; Moura et al., 2019). These species can capture only one prey at a time to store in the nest (Moura et al., 2019). One female can store up to 22 spiders per brood cell (Deus' personal information - Supplementary material Figure S1). The process of finishing one nest may take up to 10 days to be completed (Deus et al., 2025, in press). Therefore, the encounter rate between wasps and spiders may have an

influence on the number of offspring per female (Laliberté and Tylianakis, 2010). As forests may have a more complex structure than open areas (number of trees, canopy and understory), the encounter rate of spiders in the forests may be lower compared to the matrix areas. Although we have no information about the encounter rate of spiders, parasitoid wasps have more facilitated to find their hosts more easily in environments with sparse vegetation (Laliberté and Tylianakis, 2010; Deus et al., 2023).

Moreover, as host species can vary different between the two environments, the difference in their abundance may be also linked to the selectiveness of females in the choice of a hole to build a nest. Matrix areas may have less holes than forest ones (Staab et al., 2018; Schüepp et al., 2011), and species adapted to these open environments may be less selective than those from the forest ones. The choice of females must enable the offspring to have access to microclimatic conditions appropriate to the development until adulthood, and the difference in the abundance may be a reflection of this different pattern of hole selection between different species (O'Neill, 2001). As we standardized our samples using the trap nest method, which provide hymenopteran females with the possibility of choosing the hole diameter, as well as the position in relation to the sun (Westerfelt et al., 2015), females from the matrix and forest had the same selection of holes. It may enforce that we are examining different nesting strategies, from different adaptations of varied species.

In relation to beta diversity, the turnover was the main explanatory component of this loss, which means that the species are being replaced from forest to non-forest environments (Baselga, 2010). An interesting observation is that, even with this great turnover of species between habitats, it seems that the function may be maintained. Species such as *Ancistrocerus flavomarginatus* (Brèthes, 1906), *Zethus pilosus* Zavattari, 1912, *Zethus plaumanni* Bohart & Stange 1965 and *Hypodynerus duckei* (Bertoni), comb. n., which are lepidoptera larvae hunters that only occur in forests, were replaced by species from *Pachodynerus*, which have the same function. The same occurred to spider hunter wasps, where *T. agamenon*, *Pisoxylon amenkei* Antropov, 1998 and *A. subaurarius* (forest specialists), were replaced by *T. lactitarse* and *T. opacum*. Nevertheless, some functions may also be lost when forests are replaced by matrix areas, as we observed in cockroach hunter wasp, which were recorded only in forest environments. In general, cavity-nesting hymenopterans are positively influenced by the edge between forest and open areas, which may imply that some of these species and their roles may be resistant to habitat loss. However, more importantly is that strict forest specialists that have

unique roles (e.g., cockroach hunters) are very sensitive and are highly threatened by the current state of anthropogenic landscape modifications (Alves et al., 2024).

Unlike hosts, the natural enemy community composition has not changed between habitats. Our results do not corroborate the expectation that higher trophic levels are more sensitive to habitat loss and climate changes (Kruess and Tschamtker, 1994; Thomson and Hoffmann, 2009). The non-change in natural enemies' composition, richness and abundance may mean that these species had enough resources and that they are not specialists in their hosts. The most abundant and generalist natural enemies were *A. floridensis*, *Anthrax aquilus* Marston, 1970, *Melittobia australica* Girault, 1912 and *Tetratichus* sp. We also collected many natural enemies' species from the Chrysididae family. In this group of species, we can find both parasitoids and kleptoparasitoids (Polaszek and Vilhemsen, 2023). In parasitoids, their eggs are oviposited on the last spiders that were deposited in the last brood cells for the host wasp, close to the host egg. The parasitoid larvae emerges first and feeds on the host larvae or the host food (e.g. spiders). On the other hand, regarding kleptoparasitoids their larvae only feed on the host food, causing the host to die of starvation (Polaszek and Vilhemsen, 2023).

Natural enemies of cavity-nesting hymenopteran are very dependent on their hosts to complete their larval development (Staab et al., 2018; Peralta et al., 2015). Therefore, we expected that changes in the host community would directly impact the interaction network between these organisms. Antagonistic interactions are often modular and specialized, which are characteristics inherent to these systems (Krasnov et al., 2012). These properties may provide a higher resilience to extinctions of species, as the perturbation may not spread out along network (Magrath et al., 2014). Some researchers suggest that host-natural enemy interactions are more influenced by the evolutionary history of species and phylogenetic restrictions instead of anthropic actions (Eklöf et al., 2012; Nether et al., 2019). These characteristics may explain why we did not find significant changes in the structure of these interactions, where the connectance, specialization and modularity of network remained stable between the forest and matrix areas.

We need to be cautious when drawing conclusions about the properties of the interaction network, considering that our data is limited. This stability of the networks analyzed here may reflect the presence of the *T. opacum* and *P. guadulpensis* hosts, both only present in matrix and outliers in terms of abundance. These species may serve as hosts for many natural enemies, keeping the connectance and the interaction diversity higher, which act as a buffer to natural enemy species loss (Tylianakis et al., 2010). Similarly, the presence of these highly abundant species may allow interactions to rewire within the network. In other words, natural enemies may alter their interactions when the forest is lost, using these dominant hosts from the matrix as substitutes for their specific forest hosts that have been lost (Borah and Beckman, 2024; Vizentin-Bugoni et al., 2019).

Current changes in climate conditions, agricultural land use, and habitat fragmentation have driven rapid environmental shifts, leading to an increasing number of studies on biodiversity changes caused by these global issues. Here, we found that the replacement of forests with an anthropogenic matrix has the potential to alter the composition of cavity-nesting hymenopterans, putting strict forest specialists and their ecological roles at high risk of extinction. Interestingly, this replacement may also affect ecosystem functioning in terms of species dominance. In matrix areas, we observed highly dominant species that, in some ways, act as buffers against changes in the network but may also influence it in unforeseen ways. Therefore, the next research steps in this field may involve investigating the underlying effects of the presence of dominant matrix species on the interaction network through new analytical approaches.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Species of solitary wasps and bees found in the matrices and forest fragments. The numbers correspond to insect abundance.

Table S2. Interaction of natural enemies and their hosts (cavity nesting hymenopteran) found in forest fragments and anthropogenic matrices.

Figure S1. Spiders recorded from a single brood cell of a *Trypoxylon lactitarse* nest. Collected by Deus, J.P.A.

This material is available as part of the online article from <https://doi.org/10.1590/1519-6984.292217>