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Effects of biodiversity dimensions (phylogenetic, functional, and taxonomic) of frugivorous bats on the structure of ecological networks

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ABSTRACT

Introduction: Mutualistic interactions between bats and plants can be organized into complex networks and analyzed using various metrics that have revealed the existence of interaction patterns among different networks. These patterns are shaped by the diversity of attributes, evolutionary history, and ecological processes within a community.

Objective: To assess the influence of taxonomic, functional, and phylogenetic diversity on the structure of 12 plant-bat mutualistic networks.

Methods: We constructed 12 plant-bat networks interactions and applied Pearson correlation analyses between diversity indices and network-level metrics. Nestedness, interaction strength asymmetry, specialization asymmetry, specialization, and modularity were used as the network metrics.

Results: Our analysis showed that the network structure varied with diversity dimensions. Taxonomic indices revealed low Shannon diversity but high equitability. Functional and phylogenetic diversities were low. Higher species richness reduced nestedness, whereas stronger functional evenness increased interaction asymmetry. Sampling completeness was low (53.4 %), and correlations indicated that modular networks might support higher diversity.

Conclusion: Taxonomic and functional diversity have a greater influence on network architecture, with the former specifically influencing the formation of modules and specialization, and the latter influencing network asymmetry. This result suggests that diversity indices may affect the interaction network properties in different ways.

Key words: functional traits; modularity; mutualism; nestedness; phylogeny.



RESUMEN

Efectos de las dimensiones de la biodiversidad (filogenética, funcional y taxonómica) de los murciélagos frugívoros en la estructura de las redes ecológicas

Introducción: Las interacciones mutualistas entre murciélagos y plantas se estructuran en redes ecológicas complejas cuya arquitectura puede evaluarse mediante métricas estructurales. Estos patrones están determinados por la diversidad de rasgos, la historia evolutiva y los procesos ecológicos que estructuran las comunidades.

Objetivo: Evaluar como las dimensiones taxonómica, funcional y filogenética de la diversidad influyen en la estructura de 12 redes mutualistas planta-murciélago.

Métodos: Construimos 12 redes de interacción planta-murciélago y analizamos la relación entre los índices de diversidad y las métricas estructurales mediante correlaciones de Pearson. Se utilizaron el anidamiento, la asimetría en la fuerza de interacción, la asimetría en la especialización, la especialización y la modularidad como métricas de red.

Resultados: La estructura de las redes varió según las dimensiones de la diversidad. Aunque la diversidad taxonómica presentó valores bajos del índice de Shannon, mostró alta equitatividad. La diversidad funcional y filogenética fue baja. La riqueza de especies se asoció negativamente con el anidamiento, mientras que una mayor equitatividad funcional se relacionó con un incremento en la asimetría de interacción. La cobertura de muestreo fue baja (53.4 %), y las correlaciones indicaron que las redes modulares podrían sustentar una mayor diversidad.

Conclusión: La diversidad taxonómica y funcional tienen una mayor influencia en la arquitectura de la red. La diversidad taxonómica influye específicamente en la formación de módulos y la especialización, mientras que la diversidad funcional en la asimetría de la red. Estos hallazgos sugieren que los índices de diversidad podrían afectar las propiedades de las redes de interacción planta-murciélago.

Palabras clave: rasgos funcionales; modularidad; mutualismo; anidamiento; filogenia.

INTRODUCTION

Mutualistic interactions form the basis of many ecological processes and are responsible for shaping and sustaining terrestrial biodiversity (Xi et al., 2020). These interactions can be analyzed in the context in community level using statistical tools derived from complex network theory (Gaiarsa & Guimarães, 2019; Schlautmann et al., 2021). Description of different types of mutualistic systems worldwide have led to the emergence of non-random structural patterns of interaction (Lewinsohn et al., 2006). These patterns are influenced by factors such as sampling effort (Blüthgen et al., 2007; Costa et al., 2016; Delmas et al., 2019), biological traits (Olesen et al., 2011; Vázquez et al., 2009), phylogenetic signals (Faith, 2013; Minoarivelo & Hui, 2016), and species abundance (Vázquez & Aizen, 2004; Laurindo et al., 2020).

Despite the recognized influence of sampling, there is still no comprehensive understanding of its potential biases. The choice of sampling method significantly affects

interpretations of network structure and species roles (Costa et al., 2016; Vitorino et al., 2022), often blurring the distinction between biological patterns and sampling artifacts (Costa et al., 2016). Taxonomic biases, particularly the underrepresentation of less detectable groups, can distort species-level metrics, such as centrality and interaction frequency (Acevedo-Quintero et al., 2020).

Biological traits (i.e., morphological, physiological, and behavioral characteristics) fundamentally constrain potential species interactions (Bascompte & Jordano, 2013; Olesen et al., 2011; Stang et al., 2009). These traits collectively determine functional diversity, which reflects their range and ecological importance, rather than species identity (Tilman, 2001). Many ecologically relevant traits show phylogenetic conservation (Blomberg et al., 2003), although the phylogenetic effects on mutualistic networks are generally modest (Rezende et al., 2007; Vázquez et al., 2009). Both functional and phylogenetic diversity have been associated with structural features

of interaction networks, often correlating with modularity, nestedness, and interaction asymmetry (Maruyama et al., 2018).

Neotropical bat-fruit networks exemplify how these processes unfold in diverse ecological systems. These networks typically involve species with high functional and phylogenetic diversity (Kunz et al., 2011; Farneda et al., 2020) and are structured by a combination of species abundance and trait complementarity. Abundant bat species tend to interact with more partners (Chamberlain & Holland, 2009; Laurindo et al., 2020), while phylogenetic signal strength in these networks can vary geographically -often increasing with annual precipitation, likely due to stronger niche partitioning in resource-rich environments (Corro et al., 2021). Bats play a central role in these interactions, visiting over 700 plant species as pollinators and seed dispersers (Bredt et al., 2012).

Previous studies have described bat-plant mutualistic networks as highly modular and specialized, with a few species concentrating on most interactions and shaping the overall network architecture (Laurindo et al., 2019; Laurindo et al., 2020). However, anthropogenic changes such as deforestation and habitat fragmentation can reduce bat diversity, especially functional diversity, thereby compromising the stability and resilience of these ecological networks (García-Morales et al., 2016; Farneda et al., 2020).

Although considerable attention has been given to how diversity shapes network structure, the reverse also occurs network organization may influence community dynamics and the maintenance of diversity. For example, modularity can enhance stability by containing perturbations within compartments whereas nestedness may promote species coexistence by enabling rare species to interact with generalists (Bastolla et al., 2009). Thus, assessing the relationship between diversity and network metrics (such as modularity and nestedness) can provide insights into the potential resilience and functionality of mutualistic systems under environmental change. Based on the central role of functional traits in mediating species

interactions, we hypothesize that functional diversity will be the main driver of network structure, with a stronger influence than either taxonomic or phylogenetic diversity. We predict that networks with higher functional diversity will exhibit higher modularity and nestedness, as a greater range of traits would lead to more specialized compartments of interaction and a more structured pattern of interactions. In this study, we evaluated how multiple dimensions of diversity (taxonomic, functional, and phylogenetic) influence the structure of mutualistic networks of frugivorous bats in a highly fragmented region.

MATERIALS AND METHODS

Study area: The study was carried out in the Alto São Francisco Karst province, also known as Arcos, Pains, and Doresópolis Karst, Brazil (Fig. 1) (Menegasse et al., 2002). The climate of the region, according to the Köppen classification system, is of the Cwa type, that is, a subtropical climate with dry and mild winters and humid and hot summers (Alvares et al., 2013). The average annual temperature is approximately 20 °C, with a minimum mean in the coldest month of 12 °C and a maximum mean in the hottest month of 30 °C, and an average annual rainfall of approximately 1 500 mm (Nimer, 1989). The study region is located in the Cerrado domain, coinciding with the inland boundaries of the Atlantic Forest. The native vegetation in this region is highly uncharacterized, having been largely replaced by pastures and plantations (Sano et al., 2010). For methodological details, see the supplementary material (SM 1).

Sampling of bat fauna: Bat sampling was conducted six field expeditions between February 2020 and April 2021, across 12 sampling sites. Individuals were captured during the following months: February, March, April, May, August, October, and November 2020; and February and April 2021. At each site, six mist nets of 12 x 2.5 m were set up and remained open for six hours after sundown; totaling 1 080 m²h

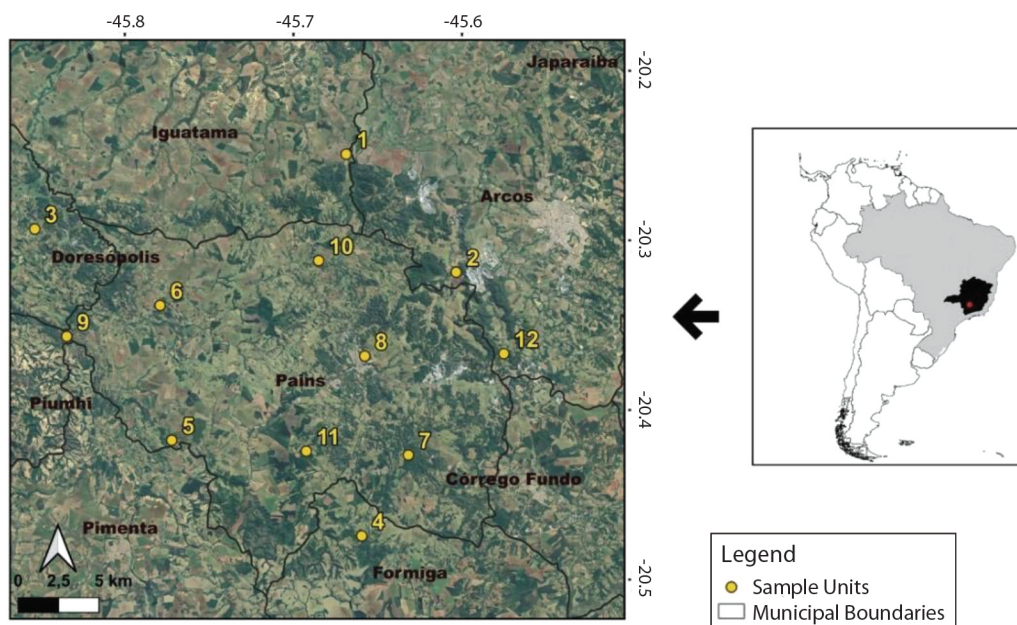


Fig. 1. Sampling units (points) where data collection were obtained for the analysis of interaction networks, in the Alto São Francisco Karst, Brazil (Arcos-Pains-Doresópolis region). The area has a subtropical climate (Cwa) and Cerrado vegetation, with fragmented native cover. Municipal boundaries and a 5 km scale are shown.

for each site and an overall total of 19 960 m²h. Captured bats were placed individually in cotton bags for 60 min to allow for fecal sample collection. Bat species identification was based on Díaz et al. (2021). All handling procedures followed the recommendation of Sikes and el Animal Care and Use Committee of the American Society of Mammalogists (2016). This study was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), license 74010-1, and Animal Bioethics Council of Universidade Federal de Lavras (UFLA), protocol 002/2020. For more details on sampling procedure see Genelhú et al. (2022) and Genelhú et al. (2023).

The collected fecal samples were placed in 1.5 ml plastic microtubes containing 70 % alcohol, duly labeled, and then taken to the laboratory for analysis under a stereomicroscope. The material was identified to the lowest possible taxonomic level with the aid of available literature (Lobova et al., 2009; Lorenzi, 1992; Lorenzi, 1998; Lorenzi, 2009; Bredt et al.,

2012; Kuhlmann, 2018; Lima et al., 2016) (more information in Sampling of chiropterofauna and use of food resource, and SMT 1 in Supplementary Material).

Analysis of interaction networks: We constructed 12 quantitative interaction networks (one per sampling site) where each matrix value represents the number of individual bats of species *j* whose fecal samples contained seeds from plant species *i*. Interaction intensity (I_{ij}) was calculated the count of distinct bat individuals showing evidence of consuming each plant species, using raw counts without standardization. This approach provides two main advantages: first, it directly measures the number of bats involved in each plant interaction, and second, it enables the comparison of interaction patterns both within and across communities (Laurindo et al., 2019). The full interaction matrices are available in the Supplementary Material. To assess the sampling completeness of our networks, we applied the

Chao 1 index (Chao, 1987; Fründ et al., 2016) to estimate the total number of interactions per community. The Chao 1 estimator was calculated using the ‘iNEXT’ package in R software (Hsieh et al., 2016).

We used five metrics to describe the structure of the interaction networks. First, we quantified nestedness using the Weighted Nestedness metric based on Overlap and Decreasing Fill (WNODF) index (Almeida-Neto & Ulrich, 2011), which measures the extent to which the interactions of a species are subsets of those of more generalist species when the interaction matrix is ordered by decreasing numbers of links (Dormann et al., 2008; Almeida-Neto & Ulrich, 2011). Second, we assessed modularity (Q), defined as a tendency for interactions to occur more frequently within modules than between them (Dormann & Strauss, 2014), using the DIRTLPawb+ algorithm (Beckett, 2016). Third, we calculated network-level specialization (H_2), which quantifies the overall selectivity of an entire bipartite network with values ranging from 0 (low selectivity) to 1 (high selectivity) (Blüthgen et al., 2006). And fourth, we measured strength asymmetry (ISA), which assesses whether specialized species tend to interact with generalized species at the opposite trophic level (Blüthgen et al., 2007). Finally, we calculated the specialization asymmetry (SA), which similarly reflects asymmetry, in interaction specialization but are based on species-level specialization patterns (Bascompte & Jordano, 2007). All selected metrics exhibit either moderate sensitivity to sampling completeness and network size (ISA, SA, and Q) or are robust to such biases (H_2 and WNODF) (Fründ et al., 2016).

To estimate the significance of the network metrics, we employed the null model proposed by Vázquez et al. (2007). To control for potential biases arising from differences network size, we applied a *z*-score transformation to each metric. The *z*-score represents the difference between the observed value and the mean value derived from the null models, divided by the standard deviation of those models (Ulrich et al., 2009). Accordingly, the values used in

subsequent statistical analyses were the *z*-score transformed metrics (SMT 2). All network metrics were calculated using the “bipartite” package (Dormann et al., 2008) in R version 4.0.4 (R Core Team, 2021).

Functional traits and phylogeny of bats:

We calculated three functional traits. The first was based on established classifications of bat frugivory in the Neotropical region (Fleming & Kress, 2013; Lobo et al., 2009). Accordingly, we categorized the species within each network into three groups: (1) predominantly insectivorous species that occasionally consume fruits (phyllostomids of the subfamily Phyllostominae and Micronycterinae), (2) predominantly nectarivorous, species that regularly include fruits as secondary food source (subfamilies Glossophaginae and Lonchophyllinae), and (3) fruit-dependent obligate frugivores (subfamilies Carolliinae and Stenodermatinae).

The second functional trait was the body condition index (BCI), expressed in g/mm, and calculated using body mass and forearm length. This index serves as a proxy for individual health, energy reserves, and potential for long-distance dispersal, which may influence a species’ ecological role-particularly in relation to fruit availability and seed dispersal efficiency (Speakman & Racey, 1986).

The third functional trait used was cranial morphology, based on nine cranial measurements: greater cranial length, greater mandibular length, length of the upper teeth series, length of the lower teeth series, width between molars, width between canines, process width mastoid, mandibular width, and zygomatic length. As these variables are highly correlated, we performed principal component analysis (PCA) to summarize the variation into a single axis (PC1), following Laurindo et al. (2020). These cranial traits were selected because they are indicative of the functional role of bats in relation to feeding strategies. For instance, cranial length and tooth structure can reflect dietary specialization, with species possessing more robust skulls and teeth often being better adapted to consume larger fruits or seeds,



thus influencing the structure of mutualistic networks (Santana et al., 2012). Additionally, the variation in cranial morphology is related to niche differentiation, as different morphologies can impact how bats interact with specific plant species, contributing to the modularity and structure of the networks (Norberg & Rayner, 1987). The data on cranial morphology were obtained from specimens deposited in the Mammal Collection of the Universidade Federal de Lavras (CMUFLA), Brazil, preferably from individuals from regions closer to the study area, to avoid geographic variation (more information in Supplementary Material).

To account for the phylogeny, we used the topology presented by Shi & Rabosky (2015), only with the sampled species. That is, all species that were included in the phylogeny, but that were not in our database, were removed from the original phylogeny. We used the “APE” (Paradis, 2012) and “picante” (Kembel et al., 2010) R packages for the consensus analyses.

Diversity analyses: For each network, we calculated three indices for each diversity dimension: taxonomic, functional, and phylogenetic. For taxonomic diversity we used bat species richness, Shannon index, and Pielou evenness (J') (Pielou, 1967), which together reflect both the number of species and the distribution of interactions among them within each network. For functional diversity, we calculated the functional diversity index (FD), functional uniformity (FEve), and functional dispersion (FDis) (Laliberté & Legendre 2010; Petchey & Gaston, 2002; Mason et al., 2005; Villéger et al., 2008). Regarding which together capture the breadth, regularity, and spread of functional traits within bat communities. For phylogenetic diversity, we used the phylogenetic species variability (PSV), phylogenetic species richness (PSR), and phylogenetic species evenness (PSE) (Helmus et al., 2007; Helmus & Ives, 2012), which assess the evolutionary relationships among species, accounting for both richness and distribution along the phylogeny. Index ranges and interpretations

for all metrics are provided in Supplementary Material (SMT 3).

All diversity analyses were performed using the “vegan” (Oksanen et al., 2020), “FD” (Laliberté et al., 2014) and “picante” packages (Kembel et al., 2010) in R.

Data analysis: To assess how multiple dimensions of diversity (taxonomic, functional, and phylogenetic) affect the structure of mutualistic networks, we first performed diagnostic tests to ensure that the data met the assumptions of parametric analysis. We evaluated the normality of all variables using the Shapiro-Wilk test, and the results indicated that the data were normally distributed ($p > 0.05$ for all variables, SMT 4) (Shapiro and Wilk, 1965). We also tested for spatial autocorrelation in our response variables (network metrics) using the global Moran’s I test. The results confirmed the absence of significant spatial autocorrelation ($p > 0.05$ for all tests; SMF 1, SMT 5), ensuring the statistical independence of our observations. Accordingly, we performed Pearson correlation analyses to evaluate the relationships between network metrics and dimensions of diversity using the `cor.test` function from the “stats” package (R Core Team, 2021). We considered p -values between 0.1 and 0.05 as moderate evidence of effects, while p -values below 0.05 were interpreted as strong evidence of significant effects (Murtaugh, 2014).

RESULTS

Network structure and diversity patterns:

Our analysis of 479 fecal samples from 15 phyllostomid bat species revealed that 263 samples (54.9 %) contained seeds, whereas 216 (45.1 %) contained only pulp remains. Among the seed-containing samples, *Carollia perspicillata* ($n = 107$) dispersed seeds from five plant families. *Artibeus planirostris* ($n = 87$) showed preference for Moraceae and Myrtaceae fruits, while *Glossophaga soricina* ($n = 14$) primarily consumed Piperaceae species, and *Sturnira lilium* ($n = 11$) specialized on Cucurbitaceae (SMT 1). Regarding the null models analyses, the metrics SA,

H_2 , and Q exhibited values significantly higher than expected by chance. In contrast, WNODF and ISA showed lower values than predicted by the null models (SMT 2).

The analysis revealed three key patterns: (1) Taxonomic diversity showed low values for the Shannon index (1.22 ± 0.35 , range: 0.74-1.99) and species richness (5.3 ± 1.88 , range: 3-9), but high Pielou's evenness (0.72 ± 0.14 , range: 0.46-0.91), indicating balanced abundance distribution across species; (2) phylogenetic diversity was moderate with PSV values (0.76 ± 0.07 , range: 0.66-0.88) approaching the theoretical maximum of 1, PSR (5.02 ± 1.48 , range: 2.93-8.24), while PSE (0.62 ± 0.13 , range: 0.37-0.82) suggesting some degree of evolutionary clustering; and (3) functional diversity indices exhibited low trait dispersion (FDis: 0.14 ± 0.04 , range: 0.07-0.20) and moderate evenness (FEve: 0.62 ± 0.13 , range: 0.46-0.90), contrasting with relatively high functional diversity (FD: 0.83 ± 0.29 , range: 0.53-1.44). The z -score values for the network metrics and the diversity indices are presented in SMT 3. Sampling completeness across the networks was low ($53.4 \pm 18\%$), ranging from 24.3 to 81.4 %.

Indices of diversity and interaction networks: Pearson's correlation analysis revealed distinct relationships among variables representing different aspects of mutualistic networks structure and functionality (Table 1). A negative correlation was detected between

WNODF and species richness ($r = -0.54$, $p = 0.06$). Although this result did not meet the conventional threshold for statistical significance, the strength and direction of the association suggest that networks with higher species richness tend to exhibit lower levels of nestedness. In contrast, a significant positive correlation was found between ISA and functional evenness (FEve: $r = 0.57$, $p = 0.05$; Fig. 2), indicating that networks with more evenly distributed functional traits among species are associated with greater asymmetry in interaction strengths.

Modularity showed moderate positive correlations with both the Shannon index ($r = 0.52$, $p = 0.07$) and species richness ($r = 0.48$, $p = 0.10$), respectively. Although these relationships were not statistically significant, they suggest that more modular networks may harbor greater taxonomic diversity, possibly due to the subdivisions into modules that reduce intra-network competition and facilitate the coexistence of species with complementary ecological niches. The correlation analysis of H_2 indicated that network specialization was significantly and positively associated with species richness ($r = 0.56$, $p = 0.05$, Fig. 2). Furthermore, a marginally positive association was observed with the Shannon index ($r = 0.54$, $p = 0.07$), suggesting that more specialized networks may be linked with communities exhibiting higher species richness and greater interaction diversity.

Table 1

Comparison of different statistical models showing the relationships between diversity indices and network metrics.

Network metrics	Diversity indices	Corr (r)	t-value	p
WNODF	Richness	-0.54	-2.03	0.06**
ISA	FEve	0.57	2.20	0.05**
Q	Shannon	0.52	1.95	0.07**
Q	Richness	0.48	1.74	0.10**
H_2	Richness	0.55	2.13	0.05**
H_2	Shannon	0.53	2.01	0.07**

WNODF: weighted nestedness, ISA: Interaction Strength Asymmetry, Q = Modularity, H_2 = specialization, Richness: species richness, Shannon: Shannon index, FEve: Functional Evenness, Corr: Correlation coefficients (r). / Correlation coefficients t -values, and p -values are provided for each comparison. / *Strong evidence of significant effects. / **Moderate evidence of effects.

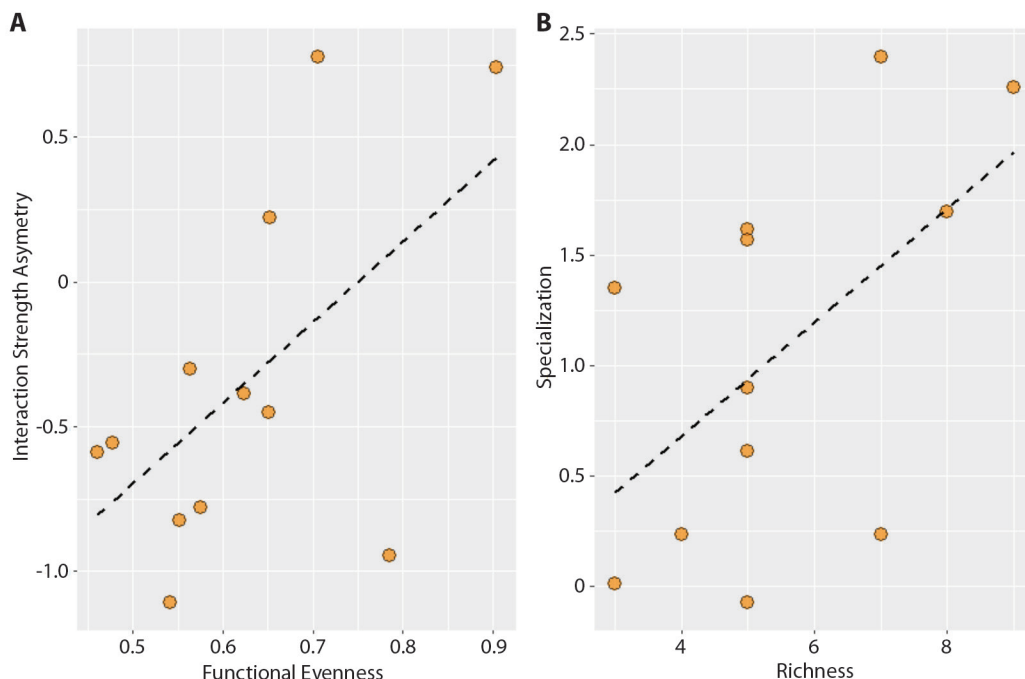


Fig. 2. Relationships between diversity metrics and structural network characteristics. **A.** Positive correlation between functional evenness and interaction strength asymmetry, indicating that networks with higher functional balance exhibit greater interaction asymmetry. **B.** Positive relationship between species richness and specialization, suggesting that networks with higher richness tend to show greater specialization in interaction patterns. Dashed lines represent linear fits illustrating observed trends in the data.

DISCUSSION

Our study investigated how multiple dimensions of biodiversity influence mutualistic networks in highly fragmented Neotropical landscapes. Based on our initial hypothesis that functional diversity would be the primary driver of network structure, we expected to find strong correlations between the range of bat functional traits and key network metrics. However, our results did not corroborate this hypothesis. Instead, we found that network structure reflected the effects of habitat alteration that filtered species composition by favoring resilient generalists over specialized frugivores. Two overarching patterns emerged from our findings: first, we observed a fundamental reorganization of bat-plant interactions under anthropogenic pressure, and second, despite the inherent sampling limitations of

fragmented landscapes, we detected consistent ecological signatures characteristic of human-modified ecosystems. These insights underscore that fragmentation not only reduces biodiversity but also fundamentally reshapes interaction networks, an insight that is critical for conservation efforts in the context of accelerating land-use change. The persistence of certain plant-bat associations, alongside the disappearance of others, underscores both the vulnerability and adaptability capacity of seed dispersal networks in anthropogenic environments.

Network structure and diversity patterns: We found that our networks were more modular than nested and exhibited lower ISA values than expected by chance. In contrast, they showed higher values of SA and H_2 than expected by the null models. These patterns are likely driven by non-random associations

between specific bat and plant genera. Previous studies have shown that certain bat species prefer fruit from particular plant genera (e.g., *Carollia* prefers *Piper*, *Sturnira* prefers *Solanum*, and *Artibeus* prefers *Ficus* and *Cecropia*) (Laurindo et al., 2020). Such specialized interactions contribute to the modular organization and higher specialization observed in the networks.

Our results for functional indices revealed contrasting response patterns. Although functional dispersion and evenness were low, overall functional diversity was notably high. In contrast, taxonomic indices exhibited low Shannon diversity and richness, but high evenness. Low functional evenness indicates an uneven distribution of traits, with most species clustering around similar trait values, while a few outliers expand the total functional space. This pattern is consistent with ecological theory, which predicts that environmental filtering in human-modified landscapes promotes trait convergence in core species while allowing niche differentiation among a few remaining specialists (Hillebrand & Matthiessen, 2009). Phylogenetic indices indicated that the bat species exhibited low phylogenetic uniformity and a tendency toward greater phylogenetic distance among co-occurring bat species. This pattern is ecologically relevant as greater genetic divergence within communities reflects higher evolutionary diversity in the species in the pool (Cianciaruso et al., 2009).

Sampling completeness was low for some networks, which may have affected the sensitivity of certain metrics (Fründ et al., 2016), highlighting the need for increased sampling efforts to detect additional species and interactions (Costa et al., 2016). This underestimation may be partially related to the degree of habitat fragmentation and disturbance in the study region, as habitat loss reduces plant richness and consequently the diversity of zoochoric species (Pessoa et al., 2017). In addition, this methodological factor can may have contributed to low completeness. Then use of mist-nets to capture bats is influenced by several variables, including habitat structure, climate, or behavior and body size of bats (Larsen et

al., 2007), potentially biasing which species are sampled. Moreover, the method used to detect interactions, seed recovery from fecal samples, may also influence network structure. Networks constructed from fecal samples tend to be less symmetrical compared to those built from visitation censuses (Escribano-Avila et al., 2018). It is also important to note that seed dispersal networks are generally smaller and include fewer disperser species than pollination networks. Therefore, it is expected that studies on seed dispersal may require relatively less sampling effort to achieve comparable completeness (Costa et al., 2016).

Although sampling completeness was relatively low in some networks, we emphasize that this is a common challenge in ecological network studies, particularly in tropical fragmented landscapes (Fründ et al., 2016). While limited completeness may lead to underestimation of network metrics or reduced statistical power, recent studies have demonstrated that structural patterns in network and diversity effects often remain consistent even in partially sampled networks, especially when analyzed across multiple replicates, as in our case (Blütgen, 2010; Trøjelsgaard & Olesen, 2013). Furthermore, the moderate p -values observed (e.g., $0.05 < p < 0.1$) suggest trends that, although not statistically significant under conventional thresholds, are biologically meaningful and likely to gain significance with increased sampling. These patterns are consistent with theoretical expectations and contribute valuable insights into the ecological processes shaping mutualistic networks. Importantly, the integration of multiple dimensions of diversity and the use of replicated networks enhance the robustness of our inferences, mitigating the potential effects of site-specific sampling bias. Nonetheless, we acknowledge the need for further studies with greater sampling completeness to validate and extend these findings.

Indices of diversity and interaction networks: Pearson correlation analysis indicated associations between network structure and diversity indices, aiding in the understanding



of mutualistic network dynamics. A key finding was the negative trend between nestedness and species richness. Nestedness in ecological networks is often associated with hierarchical structures, where some species occupy central positions and interact with a broad range of partners, while others are more peripheral, interacting with fewer species (Vázquez et al., 2007; Laurindo et al., 2020). This hierarchical structure can limit the number of species that co-occur in the network, as abundant species dominate the interactions, and less abundant species are restricted to specific modules. The observed relationship between nestedness and species richness suggests that network structure may influence species diversity by reflecting both the complementarity of species traits (Rezende et al., 2007) and the unequal abundance of species (Vázquez et al., 2007), where more abundant species tend to interact with more plant species and occupy more central positions in the network (Laurindo et al., 2020).

However, the lack of significance for nestedness relative to the null model suggests that the trend, while present, might not be a robust and stable pattern after accounting for random network assembly. The correlation analysis indicated a potential relationship between nestedness and species richness; however, the results of the null model suggested that this relationship may not be consistent when considering the inherent randomness in network formation. Additionally, while nested structures have been shown to favor diversity in mutualistic networks by reducing competition (Bastolla et al., 2009), caution is required when interpreting our results. The observed trends may be influenced by low sampling completeness (Fründ et al., 2016). However, it is worth noting that the WNODF metric used in this study has been shown to be less biased by sampling completeness than other indices (Fründ et al., 2016). Therefore, future studies with more comprehensive sampling efforts are needed to accurately assess the role of nestedness in shaping species richness and network structure.

The moderate correlation between modularity and species richness, along with Shannon

diversity, suggests that modularity may contribute to maintaining network diversity. While many frugivorous bats in our study are generalists, studies have documented genera-level preferences, such as *Carollia* for *Piper*, *Sturnira* for *Solanum*, and *Artibeus* for *Ficus* and *Cecropia*, which can lead to the formation of distinct modules (Laurindo et al., 2020; Lobova et al., 2009). Therefore, rather than reflecting niche partitioning alone, the observed modularity may also result from morphological compatibility, spatial or temporal segregation, or habitat filtering (Schleuning et al., 2014; Silva et al., 2016). Nevertheless, we recognize that modularity may be partially inflated by low sampling completeness, which can underestimate interactions and reduce the apparent connectivity between species (Fründ et al., 2016). Taken together, these patterns suggest that modularity, even if influenced by sampling limitations, reflects the underlying ecological processes that help organize interactions into more structured and potentially stable subgroups.

The significant positive correlation between interaction strength asymmetry and functional evenness is particularly interesting, as it suggests that networks with a more regular distribution of functional traits tend to exhibit greater asymmetry in their interaction strengths. This result provides valuable insights into the role of functional diversity in the network architecture. Functional evenness, which measures the evenness of functional trait distribution across species in a community (Villéger et al., 2008), can influence interaction patterns by promoting a more equitable distribution of interaction strengths. This, in turn, could enhance network robustness by reducing the likelihood of cascading effects in mutualistic networks (Gaiarsa & Guimarães, 2019).

Asymmetric interaction networks, in which some species are more heavily involved in interactions than others, may offer greater resilience to disturbances, as they can buffer the effects of disruptions in key interactions. This idea is supported by previous studies that have shown how asymmetric architectures can minimize interspecific competition, facilitating

the coexistence of species with complementary functional roles (Xi et al., 2020).

Overall, our results highlight the importance of considering taxonomic, functional, and phylogenetic diversity indices when analyzing mutualistic networks. Although our primary hypothesis regarding the predominant role of functional diversity was not confirmed, the observed trends suggest a crucial association between functional traits and specific network properties, such as interaction asymmetry. The inclusion of functional and phylogenetic indices provides a more nuanced understanding of the mechanisms driving network structure and species coexistence (Cisneros et al., 2014). Our study demonstrates that both taxonomic and functional diversity indices may influence the bat-plant interaction networks in different ways, with functional diversity indices playing a particularly crucial role in explaining potential relationships with asymmetry metrics and the distribution of interaction strengths. This highlights the need for a more integrated approach to studying mutualistic networks, where both the evolutionary history of species and their functional roles are considered to better understand the dynamics of ecological communities.

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See supplementary material
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