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Centro de Ciências Biológicas e da Saúde
Universidade Federal de Mato Grosso Do Sul

Forest loss and isolation impacts on mutualistic bat-plant interaction networks in a Brazilian Cerrado

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Campo Grande
Abril 2025

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Dedico aos meus pais, Jussara e Geraldo,
que por mim fizeram tantos sacrifícios e me
guiam até hoje com muito amor, carinho e
dedicação.
Sem vocês, eu nada seria.

Agradecimentos

Primeiramente agradeço imensamente aos meus pais, Jussara C. P. Carlos e Geraldo D. Carlos, pelo amor incondicional e toda luta e sacrifícios que enfrentaram para que hoje eu esteja aqui e possa continuar seguindo meus sonhos. Tudo que eu fiz e fizer por vocês não poderá recompensar todo esse amor e dedicação, mais uma vez obrigada por serem os melhores pais do mundo.

Em conjunto agradeço a todos da minha família que me apoiaram e incentivaram a continuar tentando, se alegram com minhas conquistas alcançadas e entenderem a ausência física durante muitos períodos. Porém, meu muito obrigada especial ao meu tio Jair P. Filho, Bruna Pacheco e Matheus Pacheco que tanto me incentivam a caminhar sempre mais e vencer inúmeras barreiras.

Ao meu orientador Erich Fischer por mais um ciclo de apoio, conselhos e conhecimento doado que foram essenciais para a realização e qualidade deste trabalho. Aos meus coorientadores Fernando Gonçalves, que além de me auxiliar com muita atenção e dedicação é um grande amigo, e ao Maurício Silveira, pelas revisões. Ao meu supervisor Bo Dalsgaard, por toda atenção, tempo desprendido, conselhos e bom humor. Muito obrigada, este trabalho não teria sido realizado sem a ajuda de vocês.

Aos meus eternos amigos de outros carnavais Camila, Carol, Celso, Erika, Hanna, Luanna e Maria Julia, não há palavras para agradecer. Obrigada por serem meus confidentes, conselheiros e companheiros de cerveja. Obrigada por me ajudarem tanto e entenderem minhas ausências, carregarei essas amizades para a vida, independentemente da localidade geográfica.

Aos novos amigos que os tempos de doutorado, em Campo Grande e Copenhague, me deram; em especial para a Aline, Jeane e Max. Obrigada por serem tão especiais, ouvirem minhas lamentações e alegrarem meus dias. Carregarei sempre vocês comigo. E a todos os amigos do Programa de Pós-Graduação em Ecologia e Conservação, obrigada pelos conselhos e boas risadas.

Obrigada a todos os pesquisadores do Programa de Pós-Graduação em Ecologia e Conservação da UFMS pelos conselhos e conhecimentos compartilhados, e à Alêny e Liliana por toda atenção e carinho oferecido.

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General abstract

In recent decades, human land use has led tropical forests to fragmentation and isolation, disrupting biological communities and changing species interactions, like the plant-animal interactions with implication for pollination and seed-dispersal. Altered landscapes affect environmental conditions and resource quality and availability, impacting the roles of nectarivorous and frugivorous animals in sustaining ecosystem functions. Against this backdrop, my research investigates two interconnected questions: (1) how forest loss and isolation of fragments from large continuous forests influence the abundance and richness of interacting bat and plant species, as well as the structure of the local bat-plant interaction networks; and (2) how the modularity of the regional metanetwork correlates with bat body mass, forest cover, and isolation from large continuous forest. I used a seven-year dataset of interacting bats and plants (pollen and seeds surveyed from the bats' faeces) across 20 sites at variable distances to the Serra da Bodoquena National Park, a continuous deciduous-semideciduous forest in southwestern Brazil. Forest cover was measured at two spatial scales (1 and 2.5 km radius buffers around each site), and isolation was calculated as the linear distance between each site and the nearest border of the national park. The results revealed that forest loss and increased isolation significantly affect bat and plant species richness and abundance, as well as bat-plant network connectance, modularity, and nestedness. Along continuous gradients of forest cover loss and isolation in the landscapes, bat and plant species richness and abundance followed a hump-shaped pattern, peaking at intermediate values (around 50% forest cover). Local network modularity was highest and connectance lowest in landscapes with approximately 30% forest cover. In addition, the modularity of the Serra da Bodoquena metanetwork varied along environmental gradients, suggesting that bat body mass was the strongest predictor of modular structure, followed by forest cover and isolation. In conclusion, local bat-plant networks tended to be smaller, more connected, and less modular in sites embedded in highly deforested and isolated, while the emergence of modules of the metanetwork is greatly associated with bat size and forest loss and isolation. Overall results emphasize that conservation of interacting bats and plants should prioritize the maintenance of at least 30 to 50% forest cover in areas designed for land use, along with the preservation of large continuous forests in the region.

Keywords: ecological resilience, habitat connectivity, community dynamics, environmental changes, ecological transformations

Resumo geral

Nas últimas décadas, o uso humano do solo levou à fragmentação e ao isolamento das florestas tropicais, causando a desestruturação das comunidades biológicas e alterando as interações entre espécies, como as interações planta-animal, com implicações para a polinização e a dispersão de sementes. Paisagens alteradas afetam as condições ambientais e a qualidade e disponibilidade de recursos, impactando o papel de animais nectarívoros e frugívoros na manutenção das funções ecossistêmicas. Diante desse cenário, minha pesquisa investiga duas questões interconectadas: (1) como a perda de floresta e o isolamento de fragmentos em relação a grandes áreas contínuas influenciam a abundância e a riqueza de espécies de morcegos e plantas interagentes, bem como a estrutura das redes locais de interação morcego-planta; e (2) como a modularidade da metarrede regional se correlaciona com a massa corporal dos morcegos, a cobertura florestal e o isolamento em relação à floresta contínua. Utilizei um conjunto de dados de sete anos sobre interações entre morcegos e plantas (com pólen e sementes obtidos das fezes dos morcegos) em 20 sítios localizados a distâncias variáveis do Parque Nacional da Serra da Bodoquena, uma floresta contínua decídua-semi-decídua no sudoeste do Brasil. A cobertura florestal foi medida em duas escalas espaciais (buffers de 1 e 2,5 km de raio ao redor de cada sítio), e o isolamento foi calculado como a distância linear entre cada sítio e o limite mais próximo do parque nacional. Os resultados revelaram que a perda de floresta e o aumento do isolamento afetam significativamente a riqueza e a abundância de espécies de morcegos e plantas, bem como a conectância, a modularidade e a aninhamento das redes morcego-planta. Ao longo de gradientes contínuos de perda de cobertura florestal e isolamento nas paisagens, a riqueza e a abundância de espécies de morcegos e plantas seguiram um padrão em forma de curva, com pico em valores intermediários (cerca de 50% de cobertura florestal). A modularidade das redes locais foi maior e a conectância menor em paisagens com aproximadamente 30% de cobertura florestal. Além disso, a modularidade da metarrede da Serra da Bodoquena variou ao longo de gradientes ambientais, sugerindo que a massa corporal dos morcegos foi o preditor mais forte da estrutura modular, seguido pela cobertura florestal e pelo isolamento. Em conclusão, as redes locais de interação morcego-planta tenderam a ser menores, mais conectadas e menos modulares em sítios inseridos em paisagens altamente desmatadas e isoladas, enquanto a emergência de módulos na metarrede esteve fortemente associada ao tamanho corporal dos morcegos, à perda de floresta e ao isolamento. Os resultados como um todo enfatizam que a conservação de morcegos e plantas interagentes deve priorizar a manutenção de pelo menos 30 a 50% de cobertura florestal em áreas destinadas ao uso do solo, juntamente com a preservação de grandes áreas contínuas de floresta na região.

Palavras-chave: resiliência ecológica, conectividade de habitat, dinâmica de comunidades, mudanças ambientais, transformações ecológicas.

General introduction

Tropical ecosystems have undergone unprecedented transformation in recent decades, and the Brazilian Cerrado is one of the most severely affected biodiversity hotspots globally, having already lost more than 50 percent of its native vegetation due to mechanised agriculture, cattle ranching and infrastructure expansion (Haddad et al., 2015; Newbold et al., 2016). These landscape changes create patchy resource distributions and increase the spatial isolation of habitats, disproportionately affecting specialist species that have narrow ecological niches and limited dispersal abilities, while favouring more generalist species adapted to disturbed environments (Haddad et al., 2015; Winfree et al., 2011). These widespread changes lead to declines in ecosystem functions and services, as well as in genetic diversity across both plants and animals (Caughlin et al., 2015; Fahrig, 2003). Mutualistic interactions, such as pollination and seed dispersal, are particularly vulnerable, as they rely on spatial and temporal synchrony between species, which is disrupted by habitat fragmentation through reduced resource availability and increased isolation (González-Varo et al., 2017; Tylianakis et al., 2008).

Studies approaching landscape ecology have explored how habitat loss affects mutualisms by reducing resource availability and increasing spatial isolation (González-Varo et al., 2017; Hadley & Betts, 2012; Kormann et al., 2016; Tylianakis et al., 2008). In recent decades, network analysis has emerged as a powerful framework for capturing the complexity of ecological interactions by assessing patterns such as specialization, modularity, and connectivity, which can, in turn, buffer or amplify the impacts of disturbances (Bascompte & Jordano, 2007). While there is a considerable body of work examining mutualistic networks involving plants, birds, and insects (e.g., Bonfim et al., 2023; Chama et al., 2013; Emer et al., 2018, 2020; Vidal et al., 2019; Winfree et al., 2011), bat-plant interaction networks also been increasingly studied (e.g., Diniz & Aguiar, 2023b; Laurindo et al., 2019; Muylaert et al., 2016; Zamora-Gutierrez et al., 2018). However, few studies address fragmented landscapes or simultaneously consider both frugivory and nectarivory, this limits our understanding of how multifunctional bat mutualisms respond to real-world gradients of forest loss and isolation.

Neotropical bat-fruit networks often exhibit high generalization and modularity, reflecting dietary flexibility and niche partitioning (Mello et al., 2011a, 2011c). Additionally, preliminary evidence suggests that bat-flower networks might display distinct structural patterns, but assessments within specific domains such as the Cerrado, are still very limited (Diniz & Aguiar, 2023a). Such discrepancies call for an integrated approach that considers both the direct impacts of landscape changes and the underlying network structure of ecological interactions.

This thesis addresses critical gaps in understanding how habitat loss and spatial isolation reshape bat-plant mutualistic networks in Brazil's Cerrado. It is divided into two chapters. The first chapter aims to elucidate how forest cover and isolation influence bat and plant abundance, richness, and local network structure, including metrics such as connectance, modularity and nestedness. The second chapter investigates the relative importance of environmental factors, such as forest cover and isolation, and intrinsic bat traits, such as body size, in shaping network modularity at a regional scale. Overall, my findings underscore the need for conservation strategies that prioritize both biodiversity and the integrity of ecological interactions in human-modified landscapes, particularly in the threatened Cerrado domain.

Chapter 1 – Forest loss and isolation effects on mutualistic plant-bat interactions in a Neotropical savanna

(Published in Forest Ecology and Management)

Forest loss and isolation effects on mutualistic plant-bat interactions in a Neotropical savanna

Abstract

Human-induced habitat loss and isolation have severe impacts on biodiversity, with indirect effects on plant-animal interactions. We investigate how forest loss and isolation (distance) from a large continuous forest affect mutualistic plant-bat interaction networks based on a seven-years survey across 20 sites surrounding the Serra da Bodoquena National Park, Brazil. Our results showed that landscapes with 30 to 70% forest cover at 1 km-radius buffer had more species (9 bat species: $r^2 = 0.50$, $p = 0.01$; 24 plant species: $r^2 = 0.54$, $p = 0.001$) and interactions than those at the extremes, either heavily deforested or fully forested landscapes. Plant-bat networks were also larger and more modular (0.60), with lower connectivity (0.18), in landscapes with intermediate than in extremes forest cover values ($r^2 = 0.51$, $p = 0.03$; $r^2 = 0.73$, $p = 0.002$; respectively). Richness of interacting bats (9 species) and network modularity (0.60) were higher at 10 km from the park's continuous forest than in sites closer or further away ($r^2 = 0.39$, $p = 0.05$; $r^2 = 0.54$, $p = 0.002$; respectively). Overall results indicate that forest loss and isolation from the park nonlinearly affect the size and structure of plant-bat networks, with intermediate levels of forest cover and isolation supporting larger and more modular networks. These outcomes highlight the importance of keeping a considerable area of forest remnants in human-modified landscapes, and the crucial role of large protected forests to maintain pollination and seed-dispersal plant-bat interactions.

Keywords: biodiversity; interaction network; karst; moderate disturbance; Pantanal, Cerrado

Resumo

A perda e o isolamento de habitat induzidos por ações humanas têm impactos severos sobre a biodiversidade, com efeitos indiretos sobre as interações planta-animal. Investigamos como a perda de floresta e o isolamento (distância) em relação a floresta contínua afetam redes de interações mutualísticas planta-morcego, com base em um levantamento de sete anos em 20 áreas ao redor do Parque Nacional da Serra da Bodoquena, Brasil. Nossos resultados mostraram que paisagens com 30 a 70% de cobertura florestal em um buffer de 1 km de raio apresentaram mais espécies (9 espécies de morcegos: $r^2 = 0.50$, $p = 0.01$; 24 espécies de plantas: $r^2 = 0.54$, $p = 0.001$) e mais interações do que aquelas nos extremos, seja em paisagens fortemente desmatadas ou totalmente florestadas. As redes planta-morcego também foram maiores e mais modulares (0.60), com menor conectividade (0.18), em áreas com cobertura florestal intermediária do que em valores extremos de cobertura florestal ($r^2 = 0.51$, $p = 0.03$; $r^2 = 0.73$, $p = 0.002$; respectivamente). A riqueza de interações de morcegos (9 espécies) e a modularidade da rede (0.60) foram maiores a 10 km da floresta contínua que em locais mais próximos ou mais distantes ($r^2 = 0.39$, $p = 0.05$; $r^2 = 0.54$, $p = 0.002$; respectivamente). Os resultados gerais indicam que a perda de floresta e o isolamento em relação ao parque afetam de forma não linear o tamanho e a estrutura das redes planta-morcego, sendo que níveis intermediários de cobertura florestal e de isolamento sustentam redes maiores e mais modulares. Esses resultados destacam a importância de manter uma área considerável de remanescentes florestais em paisagens modificadas pelo homem, e o papel crucial de grandes florestas protegidas para manter interações planta-morcego de polinização e dispersão de sementes.

Palavras-chave: biodiversidade; rede de interações; carste; distúrbio moderado; Pantanal, Cerrado

1. Introduction

Tropical forests face significant deforestation rates due to human activities, leading to the loss of natural habitats, fragmentation and isolation of forest patches (Fischer & Lindenmayer, 2007). Although the fragmentation per se – i.e., without changes in total forest coverage – may have positive effects on biodiversity (Fahrig, 2017), forest reduction and isolation often negatively affect different dimensions of biodiversity, as taxonomic and functional diversity of communities and populational genetic structure (Gonçalves et al., 2017; Ibouroi et al., 2024; Lino et al., 2019; Melo et al., 2018; Rosa et al., 2021). Consequently, forest loss can lead to changes on the structure of interaction networks, with potential cascading effects on pollination and seed dispersal services involving mutualistic animal species (Cazetta & Fahrig, 2022; Chama et al., 2013; De Assis Bomfim et al., 2018; Menke et al., 2012; Spiesman & Inouye, 2013). The maintenance of interaction networks structures may be influenced by the intensity of landscape changes, and identifying critical thresholds of forest loss could inform effective conservation policies (Vidal et al., 2019). In addition, examining ecological networks provides insights into how interactions unfold and evolve within biological communities, and the structural attributes of these networks allow inferences about interaction resilience (Bastolla et al., 2009; Fortuna & Bascompte, 2006; Ligo et al., 2024).

Since species diversity may peak in moderately disturbed environments, the interactions they perform may also vary nonlinearly along the gradient of forest loss (Muylaert et al., 2016; Vidal et al., 2019). Nonlinear dynamics can also reveal critical disturbance thresholds that may trigger profound shifts in the structure of mutualistic interaction (Muylaert et al., 2016; Vidal et al., 2019). Interaction networks metrics provide an effective way to assess community-level changes in mutualistic interactions (Okuyama

& Holland, 2008), with networks presenting high connectivity and low specialization often thought to have great resilience after disturbances (Memmott et al., 2004; Palacio et al., 2016). In addition, the combination of high connectivity and nestedness, with low modularity, contribute to more structurally resistant networks (Bascompte et al., 2003; Bastolla et al., 2009).

Flower- and fruit-visiting bats contribute significantly to pollination and seed dispersal of tropical angiosperms (Fleming et al., 2009). Their role as pollen and seed vectors may depend on the spatial arrangement of food sources, roosting sites, and the connectivity of habitat patches in altered landscapes (Galindo-González et al., 2000; García-Morales et al., 2012). Moreover, the maintenance of their populations relies heavily on the availability of flowers and fruits throughout the year (García-Morales et al., 2012; Ripperger et al., 2015). However, despite the importance of bats as pollinators and seed dispersers, little has been investigated on the impact of landscape changes on plant-bat networks (Sritongchuay et al., 2019, 2022; Sritongchuay & Bumrungsri, 2016). Here, we asked how forest loss and isolation affect plant-bat networks, as well as the richness of interacting plants and bats, in 20 landscapes from Bodoquena Plateau, Brazil. We hypothesized that interaction networks will be larger and more compartmentalized in moderately forested landscapes and sites less isolated from large continuous forests, represented by the Serra da Bodoquena National Park. We predict that the richness of interacting species, as well as network size and modularity, will peak at intermediate levels of forest cover and in areas closer to the national park. To assess whether the effects of forest cover and isolation on plant-bat interactions are linear, hump-shaped, or exhibit thresholds of change, we compared the fit of linear, quadratic, and piecewise models.

2. Methods

2.1. Study region and sample sites

The study was conducted in the karstic plateau of Serra da Bodoquena (150–800 m elevation, 18,000 km²), southwestern Brazilian Cerrado (Fig. 1). The climate is Aw of Koppen, with marked wet and dry seasons. Annual temperature averages 22–26 ◦C and annual rainfall, 1200-1300 mm. The original vegetation is predominantly composed of deciduous or semi-deciduous forests. The Serra da Bodoquena National Park constitutes the far largest (>76,000 ha) and continuous forests in the region (Fig. 1b), surrounded by landscapes transformed into pastures and croplands with remaining forest fragments (Eriksson et al., 2023; Lino et al., 2021).

To obtain 20 sampling sites at varying distances from the park, distributed across landscapes with a forest cover gradient, we first divided the entire plateau into 360 hexagonal grids of 5000 ha each and measured their forest cover using satellite images. Subsequently, we selected 20 hexagons representing a gradient from 3 % to 100 % forest cover (Fig. 1b); additional criteria were accessibility, presence of watercourses, and avoidance of nearby hexagons with similar forest cover.

2.2 Data collection

Seven surveys were conducted between 2015 and 2021 in four dry and three rainy seasons (Table S1). At each survey, we mistnetted bats for one night per site using ten 12x2.6 m-nets opened for six hours following the sunset. Captured bats were kept 30-45 min in cloth bags to defecate, then identified, marked with numbered collars, and released. We did not reuse bags on the same night and washed them between uses to avoid contamination. Faecal samples were stored in glycerine and subsequently examined in laboratory for seeds and pollen under stereomicroscope and light microscope, respectively. Seeds and pollen were identified to species level, whenever possible, based on a reference collection of seeds and pollen from plants in the study region. When the morphology matched the group but differed from the species in the collection, identification was made at the genus or family level. Of the pollen and seed species, 33% and 42%, respectively, were morphotyped. We assumed that the presence of pollen or seeds in faeces indicates plant-bat pollination or seed-dispersal interactions. With the exception of *Bauhinia blakeana* (Lau et al., 2005), all identified pollen and seeds were from species known to be pollinated or dispersed by bats (Ferreira et al., 2024; Fischer et al., 2018).

We measured forest cover around the 20 sites at two spatial scales, in concentric buffers of 1 and 2.5 km radius (Fig. 1c), which encompass expected ranges for responses of phytophagous bats (Mendes & Srbek-Araujo, 2021; Pinto & Keitt, 2008). Measures were based on MapBiomas 2021-collection 6 images (https://brasil.mapbiomas.org/) using QGIS 3.10 (QGIS Development Team, 2019); no detectable differences of forest cover occurred for each site between 2015 and 2021, period of field samplings. For isolation from large continuous forest, we used ESRI Satellite plugin to measure the distances between each site and the nearest boundary of the national park.

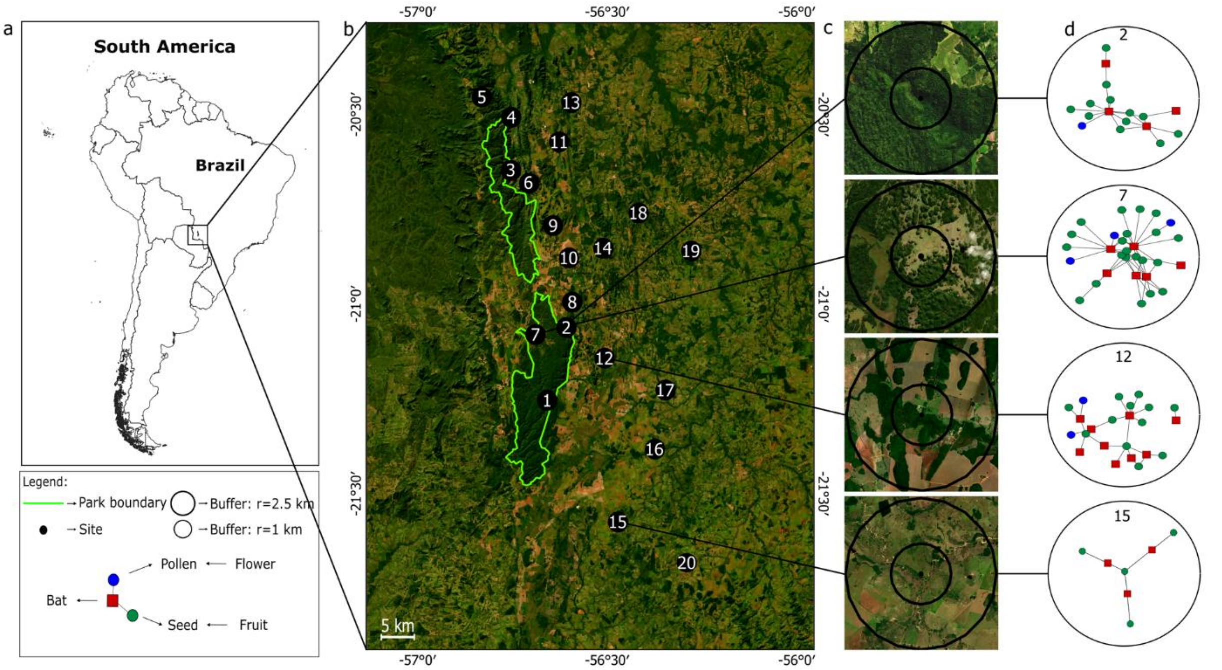

Fig. 1 Location of Serra da Bodoquena plateau in South America (a), distribution of the 20 sample sites surrounding the two continuous forest areas (green-line polygons) of the Serra da Bodoquena National Park (b), and four examples of landscapes measured in two circular buffers (c) with their respective plant-bat interaction networks (d).

2.3. Data analyses

We assigned species interactions based on the presence of pollen or seed species in the bats' faeces. The number of interactions for each bat species was counted per site as the number of individuals whose faeces contained a given pollen or seed species, and the number of interactions of each plant species was the number of faecal samples in which their seeds or pollen were present. These counts are hereafter referred to as abundance of interacting bats and plants, respectively. For plant-bat networks in each site we calculated connectance (proportion of actual connections out of all possible connections), specialization (degree to which species interact with specific partners), nestedness (a pattern where less connected species tend to interact with subsets of the species that highly connected species interact with), robustness (network resilience to species removal), and modularity (the extent to which species form subgroups of more frequent interactions). Significance of metrics was assessed through z-scores and Method 3 null model, which randomizes matrices while preserving row and column totals (Table S2), in the "bipartite" R package (Dormann et al., 2008).

To evaluate how interacting species and network metrics relate to forest cover and isolation from the park, we compared linear, quadratic, and piecewise regression models. Our response variables included the richness and abundance of interacting plants and bats, as well as interaction network metrics. We performed all analyses in R version 4.3.2 (R Core Team, 2023) and the "segmented" package for piecewise regressions (Muggeo, 2008), considering each site as a sampling unit. The response variables and the residuals of the significant relationships did not show spatial autocorrelation (Moran's I; Table S3). In addition, to explore how the abundance of interactions of each species may vary with forest cover and isolation, we also ran the same three models for each species occurring in 10 or more sites; and included as supplementary material.

3. Results

3.1. Abundance and richness of interacting species

We captured 966 bat individuals comprising 12 Phyllostomidae species (Table S4). Among them, 779 individuals (80%) defecated seeds and/or pollen, with 743 (95%) samples containing seeds and 63 (8%) containing pollen. We recorded 38 seed and nine pollen species belonging to the families: Moraceae (11 spp.), Piperaceae (7 spp.), Fabaceae (6 spp.), Solanaceae (2 spp.), Myrtaceae (1 spp.), Salicaceae (1 spp.), and Urticaceae (1 spp.) (Table S5). The abundance of bats per site was 31.4 ± 40.0 (mean ± SD) individuals, ranging from 12 to 152 (Table S6), and mean bat species richness per site was 5 ± 1.6, ranging from three to nine species. Mean plant abundance was 38.5 ± 32.2 occurrences, ranging from 25 to 172 (44.3 ± 32.3, from 10 to 163 for seeds; and 3.3 ± 3.3, from 0 to 9 for pollen); and mean plant richness was 13 ± 4.1, ranging from six to 24 (12 ± 3.9, from 5 to 21 for seeds; 2 ± 1.6, from 0 to 6 for pollen) (Table S6).

The abundance of interacting bat individuals was not significantly related with park-isolation (Fig. 2a), but it showed a hump-shaped relationship with forest cover (Table 1), peaking in sites with 50-60% forest cover at 2.5 km-radius buffer (Fig. 2b). Bat species richness presented hump-shaped relationships with forest cover and distance to the park, peaking in 50-60% forest cover at 10 km from the park (Fig. 2c-d). The abundance of plants linearly decreased as distance to the park increased and showed a hump-shaped relationship with forest cover (Fig. 2e), being higher in 75% forest cover at 1 km-radius buffer; however, with a broad 95% confidence interval (Fig. 2f). Plant species richness was not related with distance to the park (Fig. 2g), but non-linearly related with forest cover, peaking around 55% forest cover at 1 km-radius buffer (Fig. 2h).

Abundance of three bat and six seed species responded to the predictor variables (Table S7). *Artibeus planirostris* peaked at 20 km from the park (Fig. S1a), whereas the abundance of *Carollia perspicillata* decreased up to 20 km and kept low as distance increased (Fig. S1b). *Platyrrhinus lineatus* tended to decrease in abundance as park-isolation increases, but it was not significant (Fig. S1e). Abundances of these three bats showed hump-shaped relationships, peaking at 50% forest cover for *A. planirostris* (Fig. S1b) and 75% forest cover for *C. perspicillata* and *P. lineatus* (Fig. S1d-f). Among plants, abundance of *Piper aduncum* and *Piper angustifolium* seeds decreased as park-isolation increased (Fig. S2c-g), and those of *Ficus pertusa*, *Piper aduncum,* and *Piper tuberculatum* showed hump-shaped relationships, peaking between 65 and 80% forest cover (Fig. S2b-d-j). Abundance of *Piper amalago* and *Piper angustifolium* linearly increased with forest cover increasing (Fig. S2f-h).

3.2. Plant-bat mutualistic network

From 779 faecal samples, we recorded 134 different interactions between 47 plant species (seeds or pollen) and 12 phyllostomid species (Table S8). Connectance and modularity of plant-bat networks showed hump-shaped relationships with both forest cover and park-isolation, though in opposite directions (Fig. 3). Connectance decreased while modularity increased up to 10 km from the park, with reversed tendencies beyond this distance. These metrics also showed hump-shaped relationships with forest cover, with lower connectance and higher modularity near 30% forest cover at 1 km-radius buffer (Fig. 3b-d). In turn, nestedness decreased as forest cover increased until 60% at 2.5 km-radius buffer (Fig. 3f), but it was not significantly related with distance to the park. Network specialization and robustness did not significantly vary with forest cover or park-isolation (Table 2).

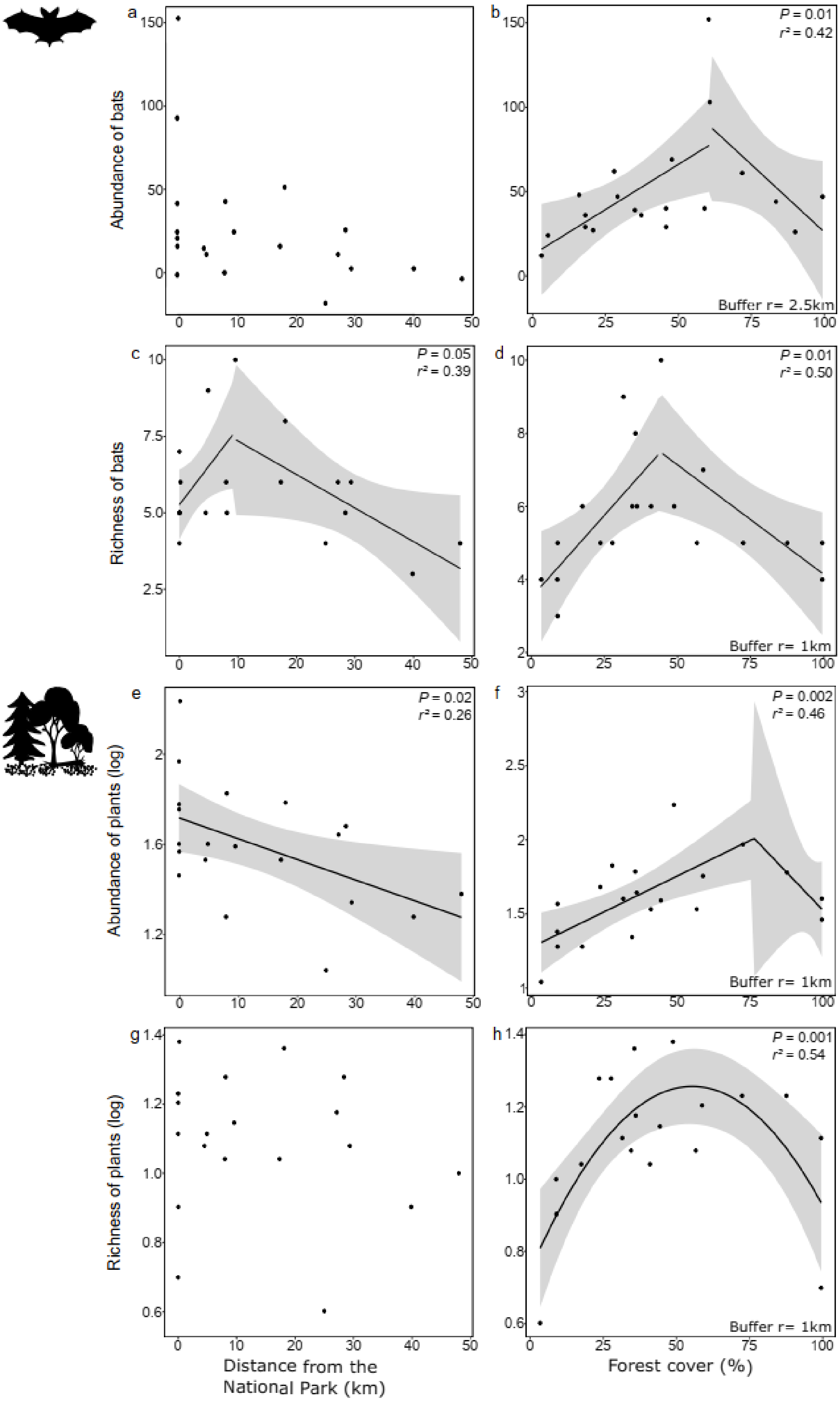

Fig. 2. Relationships (lines and shadows for 95% Confidence Interval) that returned the highest r² (see Table 1) for abundance and richness of interacting plants and bats with forest cover and distance to the national park; and values for non-significant relationships (a, g).

Table 1. Results for linear, piecewise, and quadratic regressions of bat and plant (seeds or pollen) abundance and species richness on distance to the national park and percentage of forest cover in two buffer sizes across 20 landscapes at Serra da Bodoquena plateau. Bold indicates significant *p* values.

Models	Distance to the national park	Forest cover	
		1 km-radius buffer	2.5 km-radius buffer
	r^2 (*p*)	r^2 (*p*)	r^2 (*p*)
Linear			
Bat abundance	0.18 (0.06)	0.07 (0.27)	0.10 (0.17)
Bat richness	0.08 (0.23)	0.00 (0.90)	0.00 (0.91)
Plant abundance	**0.26 (0.02)**	0.17 (0.07)	**0.19 (0.05)**
Plant richness	0.04 (0.39)	0.03 (0.45)	0.01 (0.65)
Piecewise			
Bat abundance	0.23 (0.98)	**0.36 (0.01)**	**0.42 (0.01)**
Bat richness	**0.39 (0.05)**	**0.50 (0.01)**	**0.37 (0.03)**
Plant abundance	0.30 (0.98)	**0.46 (0.002)**	**0.43 (0.002)**
Plant richness	0.04 (0.39)	0.55 (0.39)	**0.39 (0.05)**
Quadratic			
Bat abundance	0.19 (0.16)	0.30 (0.28)	0.28 (0.06)
Bat richness	0.25 (0.09)	**0.42 (0.01)**	0.26 (0.08)
Plant abundance	0.25 (0.07)	**0.46 (0.004)**	**0.39 (0.02)**
Plant richness	0.05 (0.63)	**0.54 (0.001)**	**0.37 (0.02)**

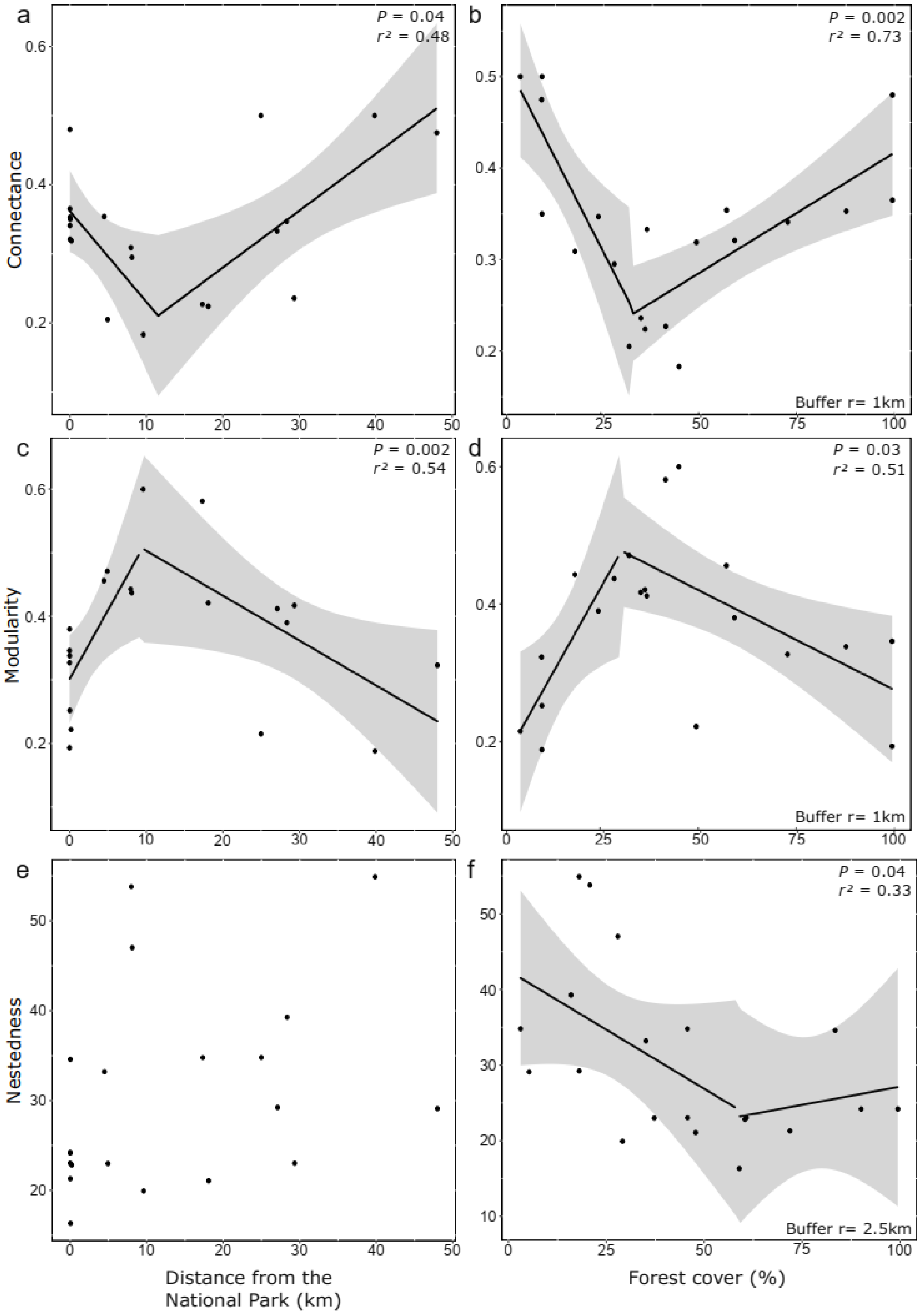

Fig. 3. Relationships (lines and shadows for 95% Confidence Interval) that returned the highest r^2 (see Table 2) for plant-bat network metrics (connectance, modularity, and nestedness) with forest cover and distance to the national park; and values for one non-

significant relationship (e).

Table 2. Results for linear, piecewise, and quadratic regressions of plant-bat network metrics on distance to the national park and percentage of forest cover in two buffer sizes across 20 landscapes at the Serra da Bodoquena plateau. Bold indicates significant *p* values.

Models	Distance to the national park	Forest cover	
		1 km-radius buffer	2.5 km-radius buffer
	r^2 (*p*)	r^2 (*p*)	r^2 (*p*)
Linear			
Connectance	0.09 (0.20)	0.00 (0.85)	0.00 (0.77)
Modularity	0.00 (0.83)	0.00 (0.94)	0.04 (0.39)
Nestedness	0.12 (0.13)	0.13 (0.13)	**0.23 (0.03)**
Robustness	0.01 (0.73)	0.00 (0.97)	0.03 (0.43)
Specialization	0.07 (0.26)	0.00 (0.82)	0.02 (0.54)
Piecewise			
Connectance	**0.48 (0.04)**	**0.73 (0.00)**	**0.68 (0.00)**
Modularity	**0.54 (0.00)**	**0.51 (0.03)**	**0.48 (0.02)**
Nestedness	0.23 (0.43)	0.19 (0.18)	**0.33 (0.04)**
Robustness	0.09 (0.50)	0.15 (0.30)	0.10 (0.42)
Specialization	0.15 (0.16)	0.05 (0.54)	0.15 (0.28)
Quadratic			
Connectance	**0.37 (0.02)**	**0.59 (0.00)**	**0.61 (0.00)**
Modularity	0.26 (0.07)	**0.44 (0.01)**	**0.30 (0.05)**
Nestedness	0.14 (0.27)	0.16 (0.22)	0.27 (0.07)
Robustness	0.08 (0.47)	0.02 (0.83)	0.04 (0.68)
Specialization	0.09 (0.45)	0.04 (0.74)	0.07 (0.54)

4. Discussion

Overall results highlight the importance of large protected forests and the maintenance of forest remnants in modified areas for conserving plant-bat interactions. The decline in richness and abundance of interacting species towards more isolated sites indicates that the park plays a role as source area for species undergoing metapopulation dynamics, whose presence in isolated fragments depends on dispersal from large forested areas (Leibold & Miller, 2004). Although there is a lack of studies on population dynamics in our study region, the role of the park as a source area is reinforced with the observed loss of genetic diversity with increasing distance to the park for the bat *Carollia perspicillata* (Lino et al., 2021). Another general finding was that landscapes with intermediate forest cover (nearly 50%) boost the richness and abundance of interacting species, likely related with an enhanced habitat heterogeneity at intermediate than at high or low forest cover levels (Muylaert et al., 2016; Viljur et al., 2022). In contrast, several studies apply linear models for assessing effects of forest cover and isolation (Ferreira et al., 2020; Gómez-Martínez et al., 2020; Ren et al., 2023; Sritongchuay et al., 2022; Zhang et al., 2023), and few indicate nonlinear patterns (Bonfim et al., 2023; Vidal et al., 2019). Likewise, few studies included landscapes comprising a nearly entire range (0-100%) of forest cover (Ferreira et al., 2020; Laurindo et al., 2019; Ren et al., 2023), though it proved critical to understanding the relationships. As most relationships adjusted better to quadratic or piecewise models, discrepant results would arise if including only part of this gradient. The nonlinear effects of forest cover highlight that interpretations should account for the measured forest cover range.

Although the spatial scale often matters for understanding landscape effects (Pinto

& Keitt, 2008; Stewart et al., 2024), we did not find a marked difference between the two scales measured, 1 km- and 2.5 km-radius buffers (628 and 3,927 ha, respectively), with a slightly better fit to the small scale for most relationships, but overall bat abundance and network nestedness adjusted better to forest cover at the large scale. As we selected sites based on a forest cover continuum measured in a still higher scale (5,000 ha hexagons, see Methods), this may have contributed to correlation ($r = 0.73$, $p < 0.001$) of forest cover proportion between our buffer sizes. If the selection of landscapes based on pre-analysis of an entire region can reduce differences between spatial scales (Pinto & Keitt, 2008; Stewart et al., 2024), then the results could be simpler and more easily applicable to conservation.

To some extent, increasing modularity and declining connectance of the network occurred along with the increase in species richness and abundance. However, the highest partition of interacting plant and bat subgroups occurred in landscapes with nearly 30% forest cover, while the maximum richness was at 50% forest cover. This difference indicates that modularity does not co-vary linearly with network size, being lower in both, the most species-poor and species-rich networks. Nestedness was low from high to medium forest cover, but increased towards extensively deforested landscapes, reflecting an increasing of generalist species that interact with most partners (Bascompte et al., 2003). In addition, modularity was maximal and connectance minimal at 10 km from the park, indicating that more compartmentalized networks occur at intermediate park-isolation. The scenario in the Serra da Bodoquena thus supports that forest cover and park-isolation affect plant-bat network size and structure through changes in species richness and abundance, generating larger and more modular networks in areas with 50 and 30% forest cover, respectively, and smaller and more connected networks in highly deforested or park-isolated landscapes, a similar pattern reported for plant-bee and plant-frugivore networks in other tropical forests

(Ferreira et al., 2020; Menke et al., 2012). On the other hand, landscapes near to 100% forest cover and close to the park also contained low richness and abundance of interacting species, forming less modular and more connected networks. This reinforces that interacting plants and bats take advantage of a certain level of forest disturbance (Medina et al., 2007; Muylaert et al., 2016), representing a system associated with early- to mid-stage of forest regeneration. Density of these species inside large preserved forests would be low because the low intensity and frequency of natural disturbances, such as treefall gaps, compared to land use changes.

Network specialization and robustness were not significantly related with the studied gradients, suggesting a complex response of these metrics to joint factors not evaluated here, like forest patch connectivity and edge length (Menke et al., 2012; Ren et al., 2023). As the number of fragments and edge length can vary while keeping a given amount of forest cover, our analyses did not account for these factors on network structure. However, our plant-bat networks with significant specialization values > 0.4 occurred between 25 and 60% forest cover and at 5 to 20 km from the park, coherent with the lower connectance and higher modularity of networks at moderate forest cover and park-isolation.

Our 20 landscapes spanning the spatial forest cover continuum in the same original formation may resemble changes over time. For instance, as deforestation begins, the richness and abundance of interacting plants and bats would increase, as well as network size and modularity, because the introduction of forest edges and human-modified areas. As deforestation advances beyond a critical level, specialized species would be gradually eliminated, filtering out the most generalist and resistant interactions that conduct to smaller and more connected networks at extreme deforested landscapes. Thus, these robust networks in terms of species extinction (Bascompte et al., 2003; Bastolla et al., 2009) represent an outcome of intense landscape degradation.

Seed-dispersal interactions were markedly predominant over pollination ones in our study region, with four times more interacting seeds than pollen species and 97% of the recorded interactions corresponding to four frugivorous and only one nectarivorous bat species. This low frequency of interactions with flowers could be due to a relatively low detectability of pollen in bat faeces, but the predominance of frugivores over nectarivores would be sufficient to provide a preponderance of seed dispersal interactions. Among bats, *Artibeus planirostris*, the largest and most dietary generalist species (Fischer et al., 2018), peaked in abundance at 50% forest cover, whereas abundance of the smaller bats *Platyrrhinus lineatus* and *Carollia perspicillata* peaked at 75% forest cover. As costs for moving across forest patches are expected to be lower for larger bats, *A. planirostris* could more frequently use fragmented landscapes by outcompeting small bats (Medina et al., 2007; Pinto & Keitt, 2008; Silveira et al., 2018; Stewart et al., 2024). The abundances of *Cecropia pachystachya* and most *Ficus* species, whose fruits were largely consumed by *A. planirostris*, were unrelated with forest cover or park-isolation. This may reflect the use of *A. planirostris* as seed disperser combined with the fact that *Ficus* trees are commonly kept in pastures to provide shade for livestock and *C. pachystachya* are pioneer trees that may take advantage of logging and forest edges (Esquivel-Mimenza et al., 2011). *Platyrrhinus lineatus* also extensively consume fruits of *C. pachystachya* and *Ficus* species (Munin et al., 2011), but its small size could restrain its occurrence into more isolated or deforested landscapes. In turn, *C. perspicillata* feeds mainly on fruits of *Piper* shrubs, which are removed from managed areas due to potential invasion and shading of pastures (Mello et al., 2011b; Pinto & Keitt, 2008), likely contributing to most *Piper* species peak at high forest cover (60–85%) or continuously increase in abundance as forest cover increases. Likewise, higher abundance of *A. planirostris* occurred at 20 km isolation from the park while abundances of *P. lineatus* and *C. perspicillata*, and of *Piper* species as well, tended to continuously decrease as park-isolation increases.

5. Conclusions

We show comprehensive results indicating that, considering the full amplitude (near zero to 100%) of forest cover gradient, plant-bat interaction networks are larger and more modular at 30 to 50% forest cover. On the one hand, these results reflect that interacting Neotropical plant and bat species are particularly associated with forest regeneration, which benefit of a certain level of disturbance. On the other hand, complex and species-rich networks depend on landscapes with at least one-third of the area covered by forest remnants. The non-linear responses and thresholds found along this gradient seem to be fundamental aspects to consider in predictive models applied to tropical forest management, reconciling land use and the sustainability of species-rich natural ecosystems. However, repetitions are necessary to establish a more precise range of values for forest cover before applying it to conservation policies, considering other determining factors and regional characteristics. Additionally, the presence of large preserved forests in the region, such as the Serra da Bodoquena National Park, could be critical to sustain subpopulations throughout forest fragments in altered landscapes. A strong reduction in forest cover and an increase in isolation from large continuous forests probably filter generalist species with greater dispersal capacity, as the frugivore *A. planirostris* and the trees of *Ficus* and *Cecropia* at our study region, making networks structurally more resilient, though species-poor. In contrast, combining large forest reserves and mosaics of used areas with at least one third covered by forest remnants may ensure the sustainability of plant-bat interactions in Neotropical regions.

6. Supplementary material

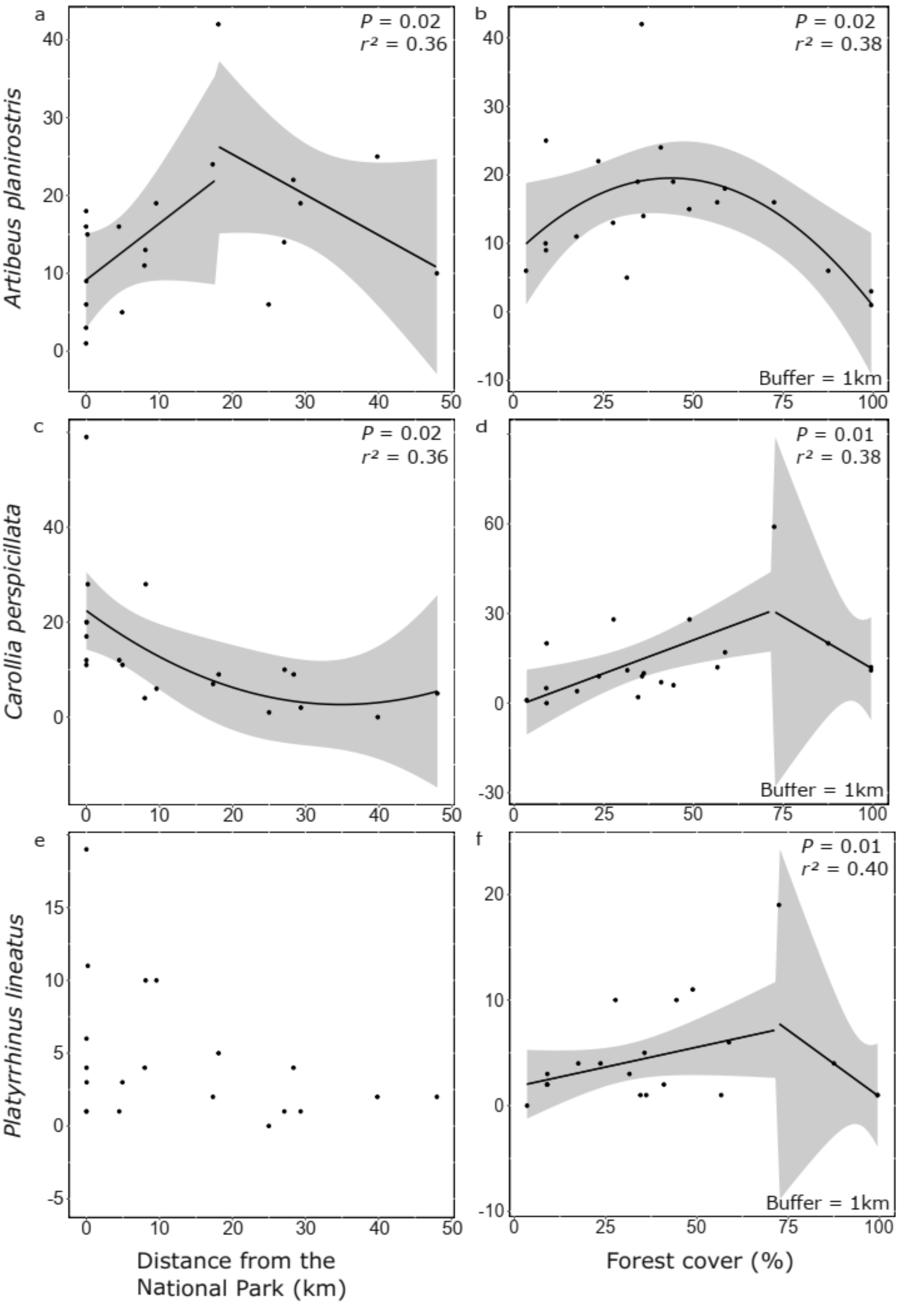

Fig. S1. Relationships (lines and 95% Confidence Interval shadows) that returned the highest r² (see Table S7) for number of individuals of three bat species which interact with plants as a function of forest cover and distance to the Serra da Bodoquena National Park; and values for one non-significant relationship (e).

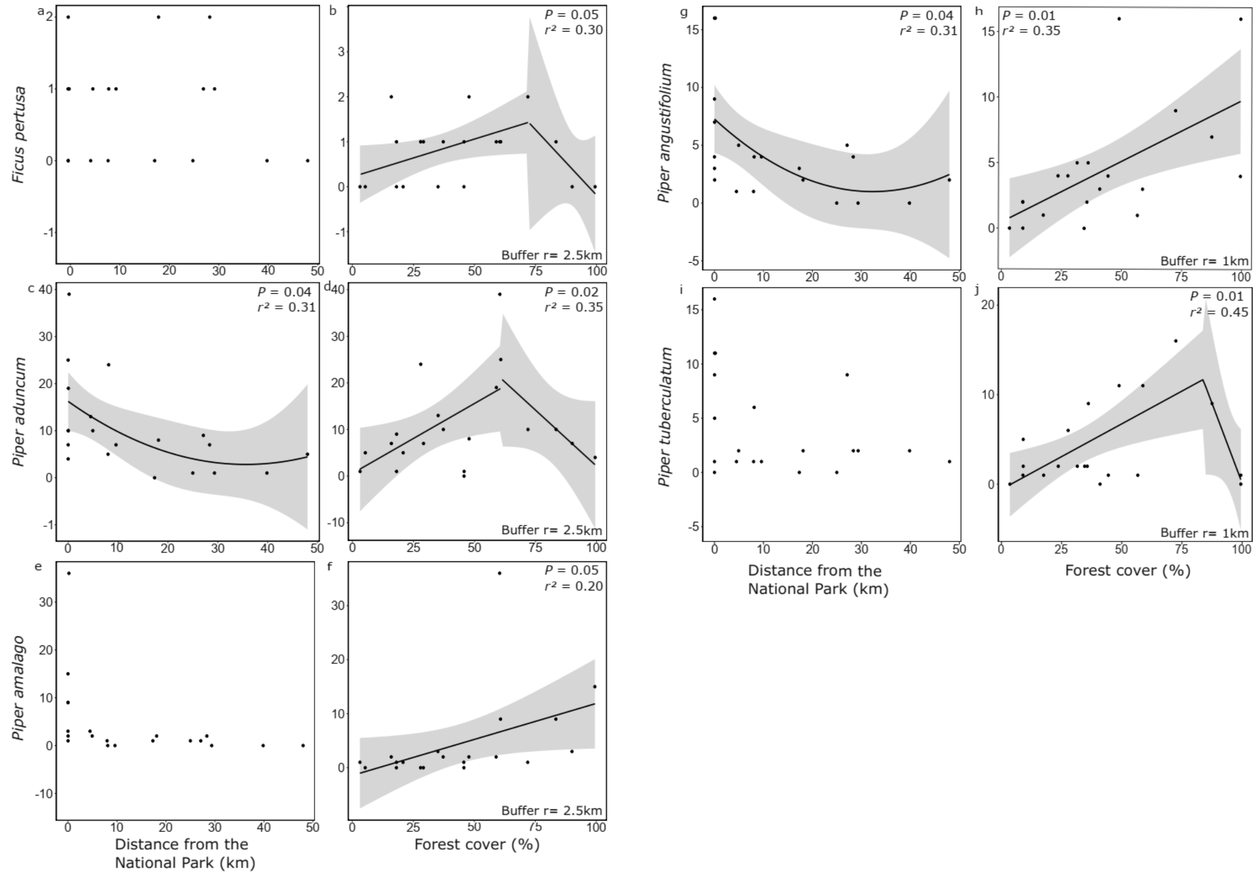

Fig. S2. Relationships (lines and 95% Confidence Interval shadows) that returned the highest r² (see Table S7) for number of interactions with bats of five seed species as a function of forest cover and distance to the Serra da Bodoquena National Park; and values for non-significant relationships.

Table S1. Years and months of field expeditions for sampling plant-bat interactions in 20 sites in the Serra da Bodoquena, southwestern Brazil.

Year	Rainy season			Dry season			
	January	February	March	June	July	August	September
2015				X	X		
2016	X	X	X	X	X	X	X
2017	X	X	X	X	X	X	X
2019		X	X				
2021						X	X

Table S2. Values (V) of connectance, modularity, nestedness, robustness, and specialization for 20 plant-bat interaction networks across the Serra da Bodoquena region, southwestern Brazil. Nonsignificant Z values (Z > │1.65│) are in bold.

Site	Connectance		Modularity		Nestedness		Robustness (HL)		Specialization (H2)	
	V	Z	V	Z	V	Z	V	Z	V	Z
1	0.480	-5.69	0.193	-5.71	24.198	-3.77	0.674	-5.68	0.323	-5.70
2	0.365	-7.04	0.346	-7.05	24.188	-3.24	0.737	-6.98	0.355	-7.05
3	0.341	-8.77	0.327	-8.77	23.022	-4.82	0.815	-8.68	0.395	-8.76
4	0.321	-7.33	0.380	-7.32	21.298	-4.11	0.791	-7.26	0.361	-7.32
5	0.353	-8.45	0.338	-8.45	34.584	-2.54	0.842	-8.36	0.371	-8.45
6	0.350	-4.77	0.252	-4.78	16.334	-3.16	0.658	-4.74	0.177	-4.79
7	0.319	-11.27	0.222	-11.30	22.826	-6.39	0.841	-11.16	0.279	-11.28
8	0.354	-8.51	0.456	-8.48	**33.210**	**-0.42**	0.773	-8.41	0.550	-8.46
9	0.205	-5.92	0.471	-5.86	**22.983**	**-1.38**	0.698	-5.82	0.426	-5.87
10	0.309	-5.50	0.443	-5.48	53.812	5.10	0.788	-5.41	0.204	-5.52
11	0.295	-7.09	0.437	-7.06	47.013	2.78	0.860	-6.97	0.486	-7.05
12	0.183	-5.58	0.600	-5.47	**19.931**	**-0.63**	0.677	-5.45	0.495	-5.50
13	0.227	-4.31	0.581	-4.23	34.779	3.10	0.682	-4.21	0.772	-4.19
14	0.224	-7.65	0.421	-7.61	21.067	-3.45	0.738	-7.54	0.468	-7.60
15	0.500	-3.25	0.215	-3.27	**34.794**	**-1.03**	0.719	-3.23	0.256	-3.26
16	0.333	-7.62	0.412	-7.61	29.230	-2.28	0.789	-7.54	0.347	-7.62
17	0.347	-8.05	0.390	-8.04	**39.272**	**-0.24**	0.864	-7.94	0.367	-8.05
18	0.236	-4.93	0.417	-4.90	**23.020**	**-1.14**	0.668	-4.86	0.306	-4.92
19	**0.500**	**-1.18**	**0.188**	**-1.20**	54.900	2.91	**0.731**	**-1.16**	**1.000**	**-1.14**
20	0.475	-4.83	0.323	-4.85	**29.102**	**-1.74**	0.854	-4.80	0.264	-4.86

Table S3. Results of Moran's I tests of spatial autocorrelation for the response variables and the residuals of significant relationships with forest cover and distance from the Serra da Bodoquena National Park.

Response variables	Tests for variables	Tests for relationships' residuals[1]		
		Distance to the park	Forest cover 1km buffer	Forest cover 2.5km buffer
	Moran I (*p*)	Moran I (*p*)	Moran I (*p*)	Moran I (*p*)
Bat abundance	-0.055 (0.51)		-0.172 (0.80)	-0.205 (0.85)
Bat richness	-0.114 (0.64)	-0.209 (0.82)	-0.129 (0.67)	-0.149 (0.72)
Plant abundance	-0.036 (0.45)	-0.282 (0.95)	-0.169 (0.82)	-0.186 (0.84)
Plant richness	-0.081 (0.57)		-0.130 (0.67)	-0.121 (0.65)
Connectance	0.088 (0.21)	-0.033 (0.45)	0.075 (0.23)	0.048 (0.28)
Modularity	-0.027 (0.44)	-0.047 (0.49)	-0.026 (0.44)	0.017 (0.34)
Nestedness	-0.222 (0.84)		-0.256 (0.88)	-0.215 (0.83)
Robustness	-0.143 (0.69)			
Specialization	-0.070 (0.55)			

Table S4. Number of Phyllostomidae bats that interacted with plants in 20 sample sites in the Serra da Bodoquena, southwestern Brazil.

Subfamily Species	Sites																				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Carolliinae																					
Carollia perspicillata	12	11	59	17	20	20	28	12	11	4	28	6	7	9	1	10	9	2	0	5	271
Glossophaginae																					
Glossophaga soricina	1	0	3	6	4	5	11	0	2	3	5	0	4	1	3	3	7	1	0	0	59
Anoura caudifer	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	4
Lonchophylla dekeyseri	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2
Phyllostominae																					
Phyllostomus hastatus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Micronycteris microtis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Stenodermatinae																					
Artibeus planirostris	1	3	16	18	6	9	15	16	5	11	13	19	24	42	6	14	22	19	25	10	294
Sturnira lilium	32	11	6	12	10	3	86	9	10	4	6	2	2	8	2	7	6	5	2	7	230
Platyrrhinus lineatus	1	1	19	6	4	3	11	1	3	4	10	10	2	5	0	1	4	1	2	2	90
Platyrrhinus helleri	0	0	0	0	0	0	0	0	2	0	0	5	0	0	0	0	0	0	0	0	7
Artibeus lituratus	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	1	0	0	5
Vampyressa pusilla	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1

Table S5. Number of bat faecal samples containing seeds or pollen species in 20 sample sites in the Serra da Bodoquena, southwestern Brazil. Morphs are unidentified species.

Plant family and species			Sites																				Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Seeds	Moraceae	*Ficus citrifolia*	0	0	7	3	4	0	2	2	2	2	0	3	6	4	1	2	5	2	5	3	53
		Ficus maxima	0	0	5	3	0	0	4	3	1	2	7	0	2	9	0	5	0	2	5	0	48
		Ficus obtusifolia	0	2	1	0	0	0	1	3	0	1	0	0	0	5	0	2	5	0	1	4	25
		Ficus insipida	0	1	2	1	0	0	0	0	1	2	0	12	0	1	0	0	2	0	0	2	24
		Ficus crocata	0	0	3	1	1	0	1	0	0	0	1	1	7	3	0	0	1	1	0	0	20
		Ficus pertusa	0	0	1	2	1	1	1	0	1	0	1	1	0	2	0	1	2	1	0	0	15
		Ficus carautana	0	0	2	0	0	0	0	0	0	0	0	3	1	1	0	1	1	0	0	0	9
		Ficus lagoensis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	4
		Ficus adhatodifolia	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
		Ficus sp. 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
		Maclura tinctoria	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	0	0	6
	Piperaceae	*Piper aduncum*	4	7	25	10	10	19	39	13	10	5	24	7	0	8	1	9	7	1	1	5	205
		Piper amalago	15	3	9	1	9	2	36	3	2	1	0	0	1	2	1	1	2	0	0	0	88
		Piper angustifolium	16	4	9	3	7	2	16	1	5	1	4	4	3	2	0	5	4	0	0	2	88
		Piper tuberculatum	0	1	16	11	9	5	11	1	2	1	6	1	0	2	0	9	2	2	2	1	82
		Piper hispidum	0	1	1	0	0	0	0	0	0	0	0	1	0	4	0	0	1	0	0	0	8
		Piper macedoi	0	2	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	7
		Piper sp. 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	5
	Salicaceae	*Banara arguta*	0	0	0	0	3	0	11	2	0	0	0	0	0	0	0	2	0	0	0	3	21
	Solanaceae	*Solanum* sp. 1	1	0	0	0	0	0	4	0	0	1	2	0	2	3	0	1	0	0	1	0	15
		Solanum paniculatum	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	0	5
	Urticaceae	*Cecropia pachystachya*	3	8	3	7	2	2	14	2	4	2	6	6	2	5	5	7	7	9	6	3	103
	Unknown	Morph seed 1	0	0	0	0	0	0	6	2	0	0	1	1	0	1	2	0	1	3	4	0	21
		Morph seed 10	0	0	0	1	0	0	7	1	0	0	0	0	0	0	0	0	0	1	2	0	12
		Morph seed 14	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	3
		Morph seed 2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
		Morph seed 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
		Morph seed 4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
		Morph seed 7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
		Morph seed 12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
		Morph seed 13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
		Morph seed 15	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 16	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Pollen	Fabaceae	*Bauhinia ungulata*	0	0	1	4	1	1	7	1	6	1	1	1	5	1	0	0	2	1	0	0	33
		Hymenaea courbaril	0	0	0	2	0	0	1	0	0	0	1	0	2	0	0	2	2	0	0	0	10
		Bauhinia sp. 1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	2	0	0	0	0	8
		Bauhinia sp. 2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	3
		Bauhinia blakeana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
		Inga sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	Myrtaceae	sp. 1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
	Unknown	Morph pollen 2	0	0	0	0	0	0	1	0	0	0	3	0	0	1	0	1	0	0	0	0	6
		Morph pollen 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

Table S6. Distance to Serra da Bodoquena National Park, forest cover in 1 km- and 2.5 km-radius buffers, and bat and plant abundance (individuals and presence in faecal samples, respectively) and richness across plant-bat networks in 20 sites at Serra da Bodoquena region, southwestern Brazil.

Site ID	Distance to the national park (km)	Forest cover 1 km buffer (%)	Forest cover 2.5 km buffer (%)	Abundance		Richness	
				Bat	Plant	Bat	Plant
1	0.000	99.5	99.4	47	40	5	5
2	0.000	99.5	90.0	26	29	4	13
3	0.000	72.5	60.8	103	93	5	17
4	0.012	58.8	71.9	61	57	7	16
5	0.018	87.5	83.4	44	60	5	17
6	0.036	9.0	58.9	40	37	5	8
7	0.189	48.9	60.4	152	172	6	24
8	4.498	56.6	35.1	38	34	4	12
9	4.937	31.5	37.2	36	40	9	13
10	7.989	17.5	20.8	26	19	5	11
11	8.115	27.7	28.0	62	67	5	19
12	9.591	44.4	29.1	46	39	9	14
13	17.328	41.0	45.7	40	34	6	11
14	18.101	35.7	47.8	68	61	7	23
15	24.984	4.0	3.1	12	11	4	4
16	27.104	36.1	18.9	35	44	5	15
17	28.359	23.6	16.0	48	48	5	19
18	29.337	34.5	45.8	29	22	6	12
19	39.848	9.0	18.0	29	19	3	8
20	47.997	8.9	5.3	24	24	4	10
Mean	13.4	42.3	43.8	48.3	47.5	5.5	13.6
Standard Deviation	14.88	29.26	27.83	31.40	35.21	1.57	5.37

Table S7. Results for linear, piecewise, and quadratic regression models examining the influence of percentage of forest cover and distance to Serra da Bodoquena National Park on the abundance of interacting plant and bat species that occurred in 10 or more sampling sites in the Serra da Bodoquena region, Brazil. Significant values are in bold. Fc 1 = forest cover in 1 km-radius buffer; Fc 2 = forest cover in 2.5 km-radius buffer; Dist = distance to Serra da Bodoquena National Park.

	Linear						Piecewise						Quadratic					
Species	Fc 1		Fc 2		Dist		Fc 1		Fc 2		Dist		Fc 1		Fc 2		Dist	
	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P
Bats																		
Artibeus planirostris	0.08	0.21	0.07	0.27	0.11	0.15	0.39	0.12	0.42	0.10	**0.36**	**0.02**	**0.38**	**0.02**	**0.36**	**0.02**	0.27	0.07
Carollia perspicillata	0.15	0.10	0.15	0.09	**0.30**	**0.01**	**0.38**	**0.01**	**0.36**	**0.01**	0.38	0.35	0.20	0.14	0.25	0.09	**0.36**	**0.02**
Glossophaga soricina	0.01	0.75	0.01	0.67	0.09	0.20	0.11	0.53	0.20	0.11	0.12	0.98	0.09	0.45	0.08	0.51	0.09	0.43
Platyrrhinus lineatus	0.03	0.48	0.02	0.59	0.14	0.10	**0.40**	**0.01**	**0.29**	**0.04**	0.16	0.29	0.21	0.13	0.20	0.15	0.15	0.24
Sturnira lilium	0.08	0.22	0.13	0.12	0.11	0.16	0.15	0.18	0.13	0.30	0.21	0.43	0.10	0.40	0.13	0.31	0.17	0.21
Plants																		
Seeds																		
Cecropia pachystachya	0.00	0.92	0.00	0.89	0.00	0.78	0.12	0.29	0.03	0.56	0.06	0.46	0.07	0.56	0.01	0.88	0.01	0.91
Ficus citrifolia	0.00	0.88	0.02	0.51	0.07	0.26	0.33	0.12	0.18	0.62	0.09	0.83	0.14	0.27	0.12	0.33	0.07	0.53
Ficus crocata	0.01	0.68	0.01	0.62	0.00	0.88	0.26	0.07	0.31	0.12	0.29	0.29	0.20	0.14	0.22	0.13	0.12	0.34
Ficus maxima	0.01	0.64	0.01	0.63	0.00	0.83	0.25	0.18	0.24	0.15	0.10	0.39	0.24	0.10	0.24	0.10	0.07	0.53
Ficus obtusifolia	0.02	0.55	0.09	0.20	0.18	0.06	0.07	0.45	0.17	0.41	0.20	0.34	0.02	0.82	0.10	0.42	0.18	0.19
Ficus pertusa	0.00	0.95	0.01	0.68	0.02	0.55	0.32	0.31	**0.30**	**0.05**	0.14	0.58	0.28	0.06	0.22	0.13	0.08	0.49
Piper aduncum	0.02	0.56	0.05	0.34	**0.26**	**0.02**	0.20	0.08	**0.35**	**0.02**	0.32	0.34	0.13	0.30	0.22	0.13	**0.31**	**0.04**
Piper amalago	0.15	0.09	**0.20**	**0.05**	0.17	0.07	0.16	0.23	0.23	0.11	0.32	0.23	0.16	0.24	0.20	0.16	0.24	0.10
Piper angustifolium	**0.35**	**0.01**	**0.33**	**0.01**	**0.24**	**0.03**	0.35	0.78	0.45	0.14	0.38	0.96	**0.35**	**0.02**	**0.35**	**0.02**	**0.31**	**0.04**
Piper tuberculatum	0.07	0.25	0.09	0.21	0.14	0.10	**0.45**	**0.01**	**0.40**	**0.01**	0.31	0.96	0.21	0.14	0.19	0.16	0.20	0.16
Pollen																		
Bauhinia ungulata	0.07	0.26	0.06	0.30	0.06	0.29	0.22	0.43	0.11	0.95	0.16	0.70	0.15	0.25	0.08	0.50	0.09	0.43

Table S8. Number of bats' faecal samples containing seed or pollen species in the Serra da Bodoquena region, southwestern Brazil.

Plants		Bats												Total
		Carollia perspicillata	*Sturnira lilium*	*Artibeus planirostris*	*Platyrrhinus lineatus*	*Glossophaga soricina*	*Platyrrhinus helleri*	*Artibeus lituratus*	*Lonchophylla dekeyseri*	*Anoura caudifer*	*Phyllostomus hastatus*	*Micronycteris microtis*	*Vampyressa pusilla*	
Seeds	*Piper aduncum*	102	61	19	7	14	0	0	1	0	0	1	0	**205**
	Cecropia pachystachya	7	15	38	24	12	1	3	0	1	2	0	0	**103**
	Piper amalago	40	38	2	3	5	0	0	0	0	0	0	0	**88**
	Piper angustifolium	43	37	3	1	2	0	0	2	0	0	0	0	**88**
	Piper tuberculatum	43	23	12	1	2	0	0	1	0	0	0	0	**82**
	Ficus citrifolia	2	2	39	10	0	0	0	0	0	0	0	0	**53**
	Ficus maxima	1	0	41	6	0	0	0	0	0	0	0	0	**48**
	Ficus obtusifolia	2	4	15	4	0	0	0	0	0	0	0	0	**25**
	Ficus insipida	0	4	6	9	0	3	1	0	0	0	0	1	**24**
	Banara arguta	10	10	0	1	0	0	0	0	0	0	0	0	**21**
	Morph seed 1	12	6	0	1	2	0	0	0	0	0	0	0	**21**
	Ficus crocata	1	0	13	5	0	1	0	0	0	0	0	0	**20**
	Ficus pertusa	2	1	10	1	0	1	0	0	0	0	0	0	**15**
	Solanum sp. 1	0	2	10	3	0	0	0	0	0	0	0	0	**15**
	Morph seed 10	5	7	0	0	0	0	0	0	0	0	0	0	**12**
	Ficus carautana	2	2	3	1	0	0	1	0	0	0	0	0	**9**
	Piper hispidum	4	0	4	0	0	0	0	0	0	0	0	0	**8**
	Piper macedoi	6	0	0	1	0	0	0	0	0	0	0	0	**7**
	Maclura tinctoria	1	4	1	0	0	0	0	0	0	0	0	0	**6**
	Piper sp. 1	3	1	1	0	0	0	0	0	0	0	0	0	**5**
	Solanum paniculatum	1	2	1	1	0	0	0	0	0	0	0	0	**5**
	Ficus lagoensis	0	2	1	1	0	0	0	0	0	0	0	0	**4**
	Ficus adhatodifolia	0	0	2	1	0	0	0	0	0	0	0	0	**3**
	Morph seed 14	1	2	0	0	0	0	0	0	0	0	0	0	**3**
	Ficus sp. 1	0	0	0	1	0	0	0	0	0	0	0	0	**1**
	Morph seed 2	0	0	1	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 3	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 4	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 5	0	0	0	0	1	0	0	0	0	0	0	0	**1**
	Morph seed 6	1	0	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 7	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 8	0	0	0	1	0	0	0	0	0	0	0	0	**1**
	Morph seed 9	1	0	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 11	1	0	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 12	0	0	0	0	0	1	0	0	0	0	0	0	**1**
	Morph seed 13	0	0	1	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 15	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Morph seed 16	1	0	0	0	0	0	0	0	0	0	0	0	**1**

Pollen	*Bauhinia ungulata*	11	3	0	0	19	0	0	0	1	0	0	0	**34**
	Hymenaea courbaril	1	1	1	0	7	0	0	0	0	0	0	0	**10**
	Bauhinia sp. 1	2	1	3	0	1	1	0	0	0	0	0	0	**8**
	Morph pollen 2	4	0	1	1	0	0	0	0	0	0	0	0	**6**
	Bauhinia sp. 2	1	0	0	0	1	0	0	0	1	0	0	0	**3**
	Myrtaceae sp. 1	2	0	0	0	0	0	0	0	0	0	0	0	**2**
	Bauhinia blakeana	0	0	1	0	0	0	0	0	0	0	0	0	**1**
	Inga sp. 1	0	0	0	0	1	0	0	0	0	0	0	0	**1**
	Morph pollen 1	1	0	0	0	0	0	0	0	0	0	0	0	**1**
	Total	**314**	**232**	**229**	**84**	**67**	**8**	**5**	**4**	**3**	**2**	**1**	**1**	**950**

Chapter 2 - Bat body mass, forest loss and isolation determine modularity in a mutualistic bat-plant metanetwork in a Neotropical savanna

Bat body mass, forest loss and isolation determine modularity in a mutualistic bat-plant metanetwork in a Neotropical savanna

Abstract

Mutualistic networks exhibit modularity in the form of semi-independent subgroups of species interactions. Yet, how anthropogenic habitat loss alters this modular structure remains poorly understood, particularly in tropical ecosystems. Here, we investigate the modularity of bat-plant interaction networks in Brazil's Serra da Bodoquena, a karstic region experiencing extensive forest loss. Using data from 20 sites, we constructed a meta-network and evaluated its modularity. To identify drivers of module formation, we analysed three ecological variables - bat body mass, forest cover, and isolation from large continuous forest - using MANOVA, ANOVA, post-hoc Tukey tests, and PCA. Our results revealed moderate modularity (0.35), indicating the presence of distinct modules with some level of connectivity between them, with bat body mass emerging as the strongest predictor of module composition, followed by forest cover and spatial isolation. This highlights how size-dependent traits and environmental factors such as forest cover and spatial isolation jointly structure mutualistic networks in forest fragments. These findings underscore that modularity arises from an interplay of species traits and habitat attributes. Our findings demonstrate how modularity in bat-plant networks responds to bat body mass, forest cover loss, and spatial isolation, offering practical insights for biodiversity conservation in landscapes modified for land use.

Keywords: functional trait diversity; pollinator; seed dispersal; anthropogenic impacts; species assemblages; trophic specialization; Cerrado

Resumo

Redes mutualísticas exibem modularidade na forma de subgrupos semi-independentes de interações entre espécies. No entanto, ainda é pouco compreendido como a perda de habitat causada por atividades humanas altera essa estrutura modular, especialmente em ecossistemas tropicais. Neste estudo, investigamos a modularidade de redes de interação entre morcegos e plantas na Serra da Bodoquena, uma região cárstica do Brasil que enfrenta intensa perda florestal. Utilizando dados de 20 sítios, construímos uma metarrede e avaliamos sua modularidade. Para identificar os fatores que determinam a formação dos módulos, analisamos três variáveis ecológicas - massa corporal dos morcegos, cobertura florestal e isolamento em relação a grandes áreas contínuas de floresta - por meio de MANOVA, ANOVA, testes de Tukey pós-hoc e PCA. Nossos resultados revelaram modularidade moderada (0,35), indicando a presença de módulos distintos com algum nível de conectividade entre eles, sendo que a massa corporal dos morcegos se destacou como o principal preditor da composição dos módulos, seguida pela cobertura florestal e pelo isolamento espacial. Isso destaca como características relacionadas ao tamanho e fatores ambientais, como cobertura florestal e isolamento espacial, estruturam conjuntamente redes mutualísticas em fragmentos florestais. Esses resultados reforçam que a modularidade surge da interação entre traços das espécies e atributos do habitat. Nossos achados demonstram como a modularidade em redes morcego-planta responde à massa corporal dos morcegos, à perda de cobertura florestal e ao isolamento espacial, oferecendo subsídios práticos para a conservação da biodiversidade em paisagens modificadas pelo uso do solo.

Palavras-chave: diversidade de características funcionais; polinizador; dispersão de sementes; impactos antrópicos; agrupamentos de espécies; especialização trófica; Cerrado

1. Introduction

The structure and dynamics of ecological networks are fundamental to understanding biodiversity maintenance and ecosystem functioning because mutualistic interactions, such as bat–plant pollination and seed dispersal, underpin key tropical processes (Bascompte & Jordano, 2007; Thébault & Fontaine, 2010). Mutualistic network play a pivotal role in sustaining critical ecosystem processes like pollination and seed dispersal, particularly in tropical ecosystems (Bascompte & Jordano, 2007; Emer et al., 2020). These networks often exhibit modularity, in which subgroups of species interacting more frequently within their module than across others (Dáttilo et al., 2016; Olesen et al., 2007). Modular structures are thought to enhance stability and resilience by localizing the effects of disturbances (e.g., species loss or habitat loss) within specific modules, thereby buffering the entire network from collapse (Dunne et al., 2002; Schleuning et al., 2016). Such compartmentalization may also reflect niche specialization or coevolutionary dynamics, which are critical for maintaining biodiversity in heterogeneous landscapes (Dáttilo et al., 2016; Mello et al., 2019).

Tropical landscapes are increasingly fragmented due to human activities, leading to forest loss and spatial isolation that reshape ecological communities (Haddad et al., 2015; Newbold et al., 2016). These processes can reduce species richness and alter the structure of interaction networks (Emer et al., 2020; Farneda et al., 2015). In the Cerrado, recent work has shown that forest cover and distance from large remnants affect both the size and modularity of bat–plant networks, with more pronounced effects in highly degraded areas (Carlos et al., 2025). In fragmented landscapes, species with certain traits, particularly larger body mass, tend to be more vulnerable to local extinction (Colombo et al., 2023; Farneda et al., 2015). By playing a central role as nocturnal pollinators and seed dispersers, bats support key tropical ecosystem processes, such as forest regeneration and genetic connectivity (Kunz et al., 2011; Pinto & Keitt, 2008). However, forest cover loss and habitat isolation can disrupt these processes by reducing resource availability and increasing spatial constraints, which may limit species' movements, filter interaction partners, and ultimately alter the modular structure of mutualistic networks (Emer et al., 2020; Farneda et al., 2015; Tylianakis et al., 2010). Understanding this structure is vital to predict community reorganization under environmental change and to design conservation strategies that preserve interaction resilience (Emer et al., 2020; Tylianakis et al., 2010).

Modularity analyses in fragmented landscapes have shown that species interactions may either cluster into distinct modules or become homogenised, reflecting how networks reorganise under anthropogenic disturbance (Emer et al., 2018). Trait-based studies, including information on body mass, diet, and movement behaviour, are essential to elucidate how bats' responses to habitat characteristics shape interaction patterns (Farneda et al., 2015; Pinto & Keitt, 2008). Among these traits, body mass plays a particularly important role, as it influences both behaviour strategies and home range size (Colombo et al., 2023; Wood et al., 2024). Heavier bat species tend to forage across large distances, while lighter species are more restricted to nearby areas, which may facilitate resource partitioning and reduce interspecific competition (Colombo et al., 2023; Wood et al., 2024). Despite its importance, the extent to which body mass structures interaction modules in bat–plant networks remains unclear, especially in the Cerrado, where studies integrating functional traits and network modularity are still scarce (Mello et al., 2011c, 2011b). Additionally, the potential role of trophic guilds (nectarivores vs. frugivores) and resource type (flowers vs. fruits) in module formation remains underexplored (Laurindo et al., 2019; Muylaert et al., 2016).

The Serra da Bodoquena, a karstic region in southwestern Brazil, hosts rich biodiversity but faces severe habitat loss due to agricultural expansion (Lino et al., 2021). The region provides an ideal system to investigate how bat–plant interaction networks are structured and what ecological factors drive module formation, as recently demonstrated in the Serra da Bodoquena (Carlos et al., 2025). In this study, we combined network theory and multivariate analyses to (1) assess the modular structure of bat-plant interactions across 20 sites in Serra da Bodoquena, (2) identify the relative importance of bat body mass, forest cover, and isolation from a large continuous forest (represented by the Serra da Bodoquena National Park) in shaping these modules, and (3) test the hypothesis that differences in module composition are associated with spatial (habitat isolation), environmental (forest cover), and morphological (variation in bat body mass) gradients, while also exploring whether trophic guilds and resource types contribute to module differentiation. Our findings aim show how modularity in bat-plant networks emerges influenced by bat body mass, forest cover loss, and spatial isolation, providing a framework for understanding mutualistic network reorganization in fragmented landscapes and offering insights into how species traits and environmental gradients jointly shape interaction structures.

2. Methods

2.1 Data collection

To investigate bat–plant interactions in Serra da Bodoquena National Park, Brazil, we built a quantitative metanetwork by integrating data from 20 sites, as described in Chapter 1, sections 2.1 and 2.2. The analytical procedures used to identify these interactions are detailed in Chapter 1, section 2.3. Captured bats, which were held in cloth bags, also had their body mass measured using spring scales.

2.2. Data analyses

We performed modularity analysis on the metanetwork using the “bipartite” R package (Dormann et al., 2008) allowing us to analyse, visualise, and calculate network metrics. Modularity is a metric that quantifies the degree to which the network is subdivided into distinct modules or compartments, with values ranging from 0 to 1; values closer to 1 indicate a highly modular network, where species interact more frequently within modules than between them. We used the computeModules function with the DIRTLPAwb+ algorithm and high number of steps (1E9) to ensure results. This integrative approach allowed us to quantify the relationship between module structure and both environmental and functional heterogeneity across sampled sites (i.e. bat body mass, forest cover, and isolation).

To test the significance of the observed modularity, we generated 100 randomised matrices using the “nullmodel” function with the "r2dtable" method, recalculated modularity for each, and compared the observed value with the 2.5% and 97.5% quantiles of the null distribution. Values outside this range were considered significant.

We further explored the relationship between module composition and three ecological variables: bat body mass (g), forest cover (%), and isolation by the distance from the Serra da Bodoquena National Park (km) (Table S3). Modules were identified using the modularity analysis, and each bat individual was assigned to a specific module based on its interaction patterns. This information was then used to test whether species grouped within each module shared similar ecological characteristics.

To assess the influence of these variables on module formation, we performed a multivariate analysis of variance (MANOVA), using the “MASS” R package (Ripley, 2020). In the MANOVA, module identity was used as the categorical response variable, and the three ecological variables as predictors. The significance of each individual variable was further examined through individual ANOVAs for bat body mas, forest cover, and isolation. Post-hoc Tukey's Honest Significant Difference (HSD) tests were applied to assess pairwise differences between modules, offering detailed insights into how each variable varied across modules.

To assess the underlying multivariate relationships among the variables, we performed a Principal Component Analysis (PCA) using the continuous variables bat body mass, forest cover, and isolation. Modularity results were visualised with a biplot created using the "factoextra" R package (Kassambara & Mundt, 2016), while relationships among modules were illustrated with the "ggplot2" R package (Wickham, 2009). This analytical approach allowed us to identify ecological variables influencing module formation by relating module composition to bat body mass, forest cover, and isolation, and to assess the robustness of the observed modular structure by comparing it to a distribution of modularity values from 100 randomised matrices. All analyses were performed in R version 4.3.2 (R Core Team, 2023).

3. Results

A total of 966 individuals from 12 species of Phyllostomidae bats were captured during the study (Table S4). Of these, 779 bats (80%) provided samples containing seeds and/or pollen. Among the positive samples, 743 (95%) contained seeds, while 63 (8%) had pollen. We identified 38 plant species from seed samples and nine from pollen, representing families such as Moraceae (11 species), Piperaceae (7), Fabaceae (6), Solanaceae (2), and one species each from Myrtaceae, Salicaceae, and Urticaceae (Table S6).

The Serra da Bodoquena bat-plant metanetwork revealed three distinct modules, with a moderate modularity of 0.3512 (95% CI: 0.0856 - 0.1141) (Figure 2, 3). The distribution of null likelihoods ranged between the 2.5% and 97.5%, with values from 0.0834 to 0.1119, respectively. The observed likelihood of 0.3512 falls well outside this range, confirming that the observed modularity is significantly higher than expected by chance.

A multivariate analysis of variance (MANOVA) demonstrated that the formation of these modules was significantly influenced by the variables bat body mass (g), forest cover (%), and isolation (km) (Pillai's trace = 0.1674, approximate $F = 51.137$, $df = 3$, $p < 0.001$). Further analysis using ANOVAs for each response variable confirmed significant differences among modules for bat body mass ($F_{1,765} = 130.42$, $p < 0.001$), forest cover ($F_{1,765} = 41.017$, $p < 0.001$), and isolation ($F_{1,765} = 45.957$, $p < 0.001$).

Additionally, Post-hoc Tukey tests revealed significant differences between modules for all three variables (Table 1). For bat body mass, all comparisons were significant: module 2 vs. 1 (*diff* = 22.50, $p < 0.0001$), module 3 vs. 1 (*diff* = -8.33, $p < 0.0001$), and module 3 vs. 2 (*diff* = -33.83, $p < 0.0001$). Regarding forest cover, significant differences were found between module 2 vs. 1 (*diff* = -13.14, $p < 0.0001$) and module 3 vs. 1 (*diff* = -8.58, $p = 0.03$), but not between modules 3 vs. 2 (*diff* = 4.55, $p = 0.39$). For isolation, significant differences were found between module 2 vs. 1 (*diff* = 8.04, $p < 0.0001$) and 3 vs. 2 (*diff* = -4.65, $p = 0.03$), with no significant difference between module 3 vs. 1 (*diff* = 3.38, $p = 0.14$) (Figure 4).

Module 2 was primarily composed of heavier bat species found in more isolated sites with lower forest cover. Module 3, in contrast, was characterised by lighter species predominantly composed of nectarivorous bats and associated with more forested and less isolated areas. Module 1 showed intermediate values for all three variables, suggesting a mixed composition. The results suggest that bat body mass was the most influential variable in differentiating modules, followed by forest cover and isolation, highlighting the ecological importance of these factors in shaping the network's modular structure.

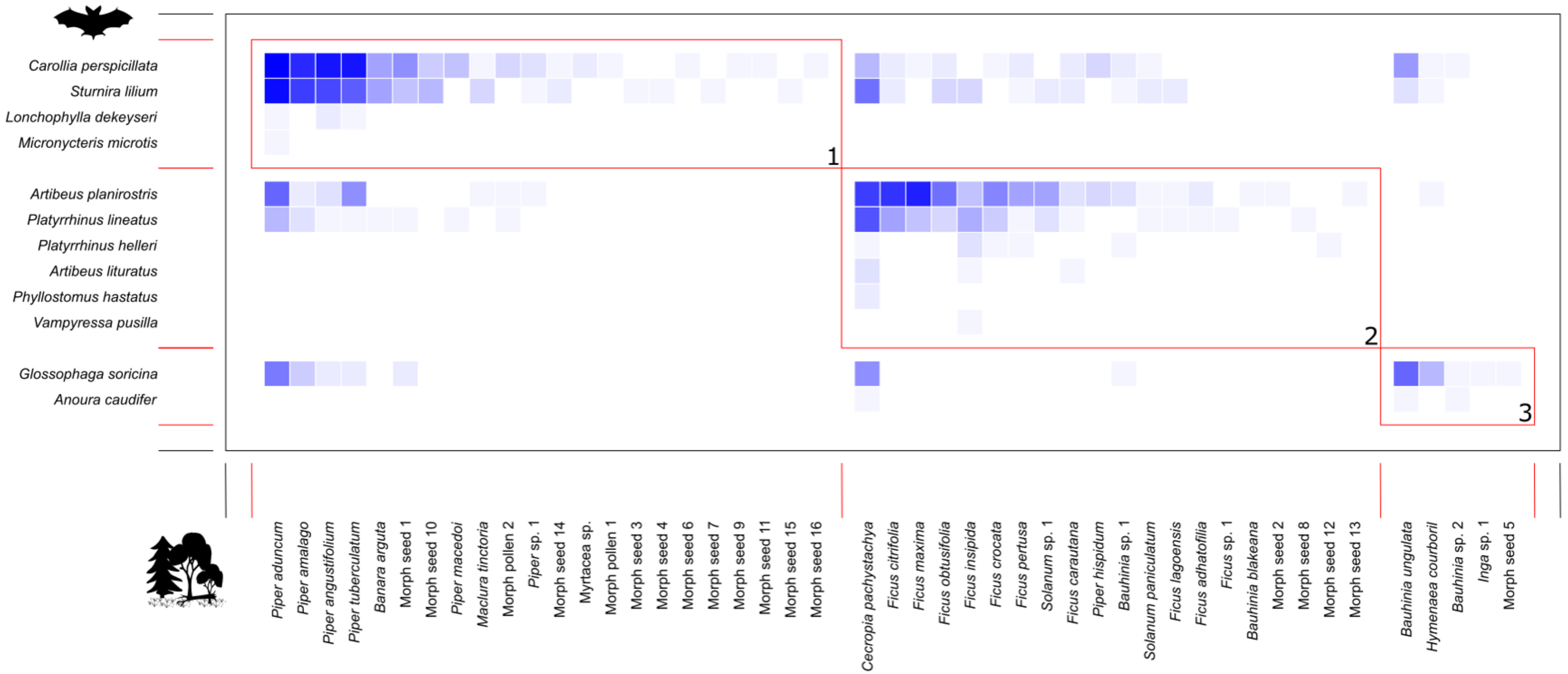

Figure 2. Bat-plant interaction metanetwork in the Serra da Bodoquena, organised in modules, with higher interaction frequencies indicated by darker blue shades and three modules (labelled 1, 2, and 3) indicated by red rectangles.

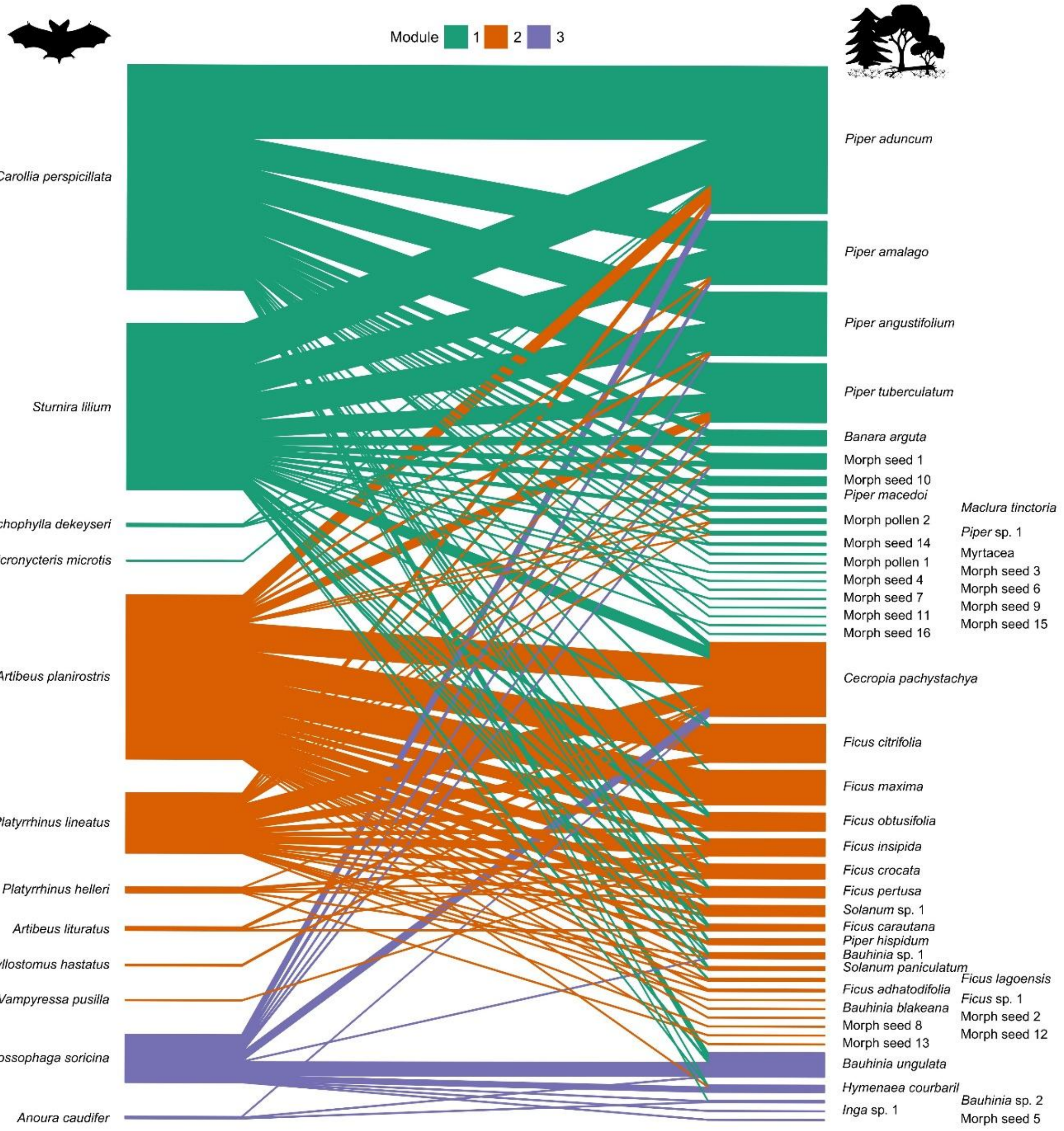

Figure 3. Bat-plant interaction metanetwork in the Serra da Bodoquena region, organised into three distinct modules (green, orange, and purple), based on interaction patterns. Lines between bats and plants observed interactions, with line thickness proportional to relative strength of the interaction frequency.

Table 1. Results of the Multivariate Analysis of Variance (MANOVA) testing differences in ecological variables (bat body mass, forest cover, isolation) across three modules of the bat-plant interaction metanetwork. Significant multivariate effects (Pillai's Trace) and univariate ANOVA results (F-values, p-values) are shown, with significant differences highlighted.

	Module	*diff*	*lwr*	*upr*	*p adj*
Bat body mass (g)	**2 - 1**	22.50	20.97	24.04	**0.00**
	3 - 1	-8.33	-11.35	-5.31	**0.00**
	3 - 2	-30.83	-33.92	-27.74	**0.00**
Forest cover (%)	**2 - 1**	-13.14	-17.20	-9.08	**0.00**
	3 - 1	-8.58	-16.58	-0.59	**0.03**
	3 - 2	4.55	-3.63	12.73	0.39
Isolation (km)	**2 - 1**	8.04	5.92	10.15	**0.00**
	3 - 1	3.38	-0.78	7.54	0.14
	3 - 2	-4.65	-8.91	-0.40	**0.03**

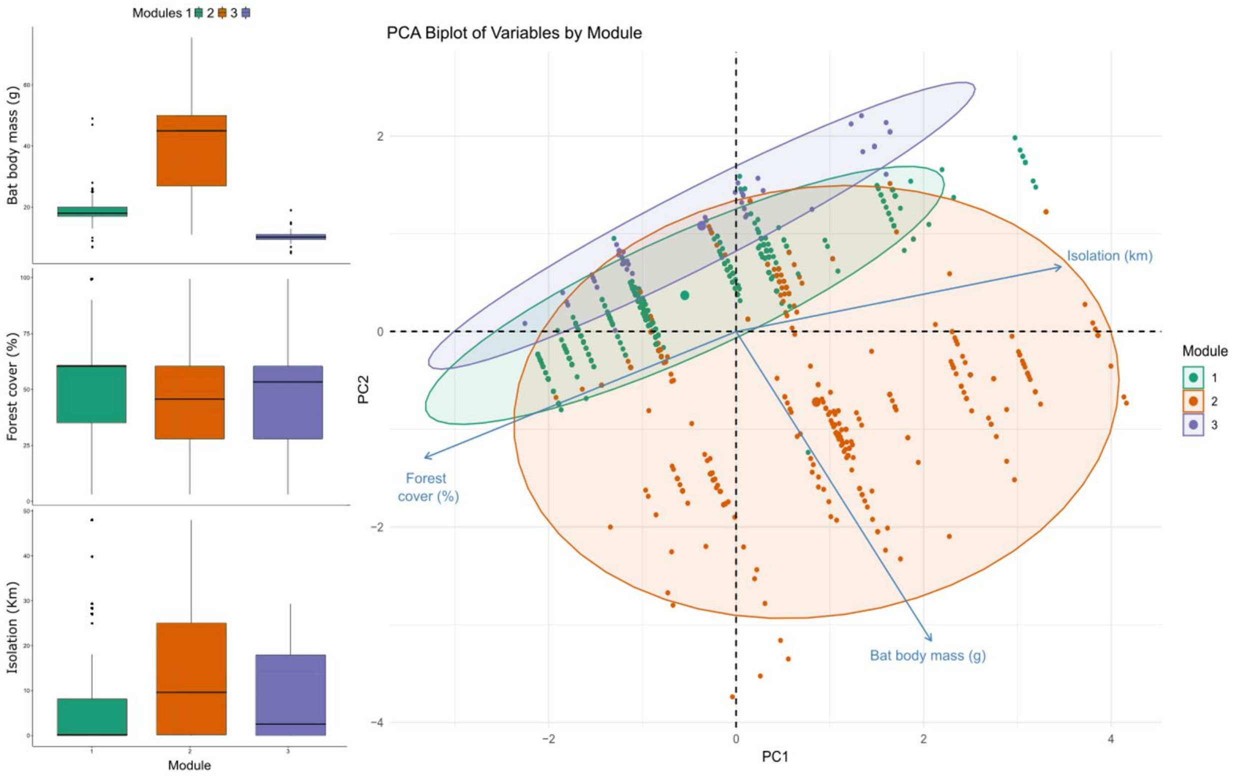

Figure 4. Principal Component Analysis (PCA) biplot of bat-plant interaction across ecological modules. Left: boxplots of bat body mass (g), forest cover (%), and isolation (km) by module. Right: PCA with bat-plant interactions (points) coloured by module. Ellipses represent 95% confidence intervals around module centroids; arrows indicate variable contributions (bat body mass and forest cover dominate PC1, isolation drives PC2).

4. Discussion

Our analysis of a large dataset from the Serra da Bodoquena National Park in Brazil reveals a moderate modular bat-plant interaction network, structured into three distinct modules. This modularity is driven primarily by bat body mass, followed by forest cover and isolation. The results may reflect resource selection patterns or niche differentiation, with size-related traits playing a fundamental role in module formation (Emer et al., 2020; Pinto & Keitt, 2008). Spatial and environmental factors, such as forest cover and isolation, further reinforce this modular structure by influencing species interactions within and between modules (Dáttilo et al., 2016; González-Varo et al., 2017). These findings underscore the complexity and structured nature of ecological networks, where modularity arises from a combination of species traits, spatial dynamics, and environmental gradients. This modular structure, however, also reveals vulnerabilities important to consider for conservation.

The observed modularity underscores the complexity and structured nature of these ecological interactions, consistent with patterns observed in other mutualistic networks (Bascompte & Jordano, 2007; Mello et al., 2011b, 2011c; Olesen et al., 2007). These modules represent functional sub-networks within the ecosystem, shaped by niche differentiation and spatial proximity (Dáttilo et al., 2016; Poisot et al., 2015). High modularity, by grouping species into these semi-independent units, may enhance the resilience and adaptability of the network, since disturbances affecting one module are less likely to spread and destabilise the entire system (Thébault & Fontaine, 2010; Tylianakis et al., 2010). Such flexibility in ecological responses is especially important given the increasing anthropogenic pressures and climate change, which pose significant risks to the stability of ecological dynamics (Emer et al., 2020). Beyond species traits, spatial variables such as isolation add another layer influencing modular structure, as revealed in our study.

The bat size-dependent structuring of modules also highlights a critical vulnerability: despite their greater dispersal ability, larger bats require larger and more continuous habitats to sustain viable populations, making them more vulnerable to local extinction in fragmented landscapes due to their specialized ecological needs (Farneda et al., 2015; Jones et al., 2009). In contrast, Module 3, composed of small-sized nectarivores (*Glossophaga soricina* and *Anoura caudifer*), illustrates how smaller body size may buffer against some extinction risks; however they are dependent on specific floral resources. As habitat loss disproportionately impacts larger frugivorous bats, their decline weakens pollination and seed dispersal networks, further compromising forest regeneration (Henry & Jouard, 2007; Laurindo et al., 2019; Ripperger et al., 2015). This pattern aligns with broader trends observed in mammals, where larger-bodied species are more susceptible to ecological disturbances and population declines (Cardillo et al., 2005; Sanders et al., 2024). The loss of larger species could lead to the collapse of entire sub-groups, disrupting the network's modular structure and overall functionality.

Spatial and environmental factors, such as forest cover and isolation, also play crucial roles in shaping the modular structure of bat-plant networks. Gradients of forest cover reveal that densely wooded sites harbour modules dominated by small-bodied frugivores associated with more preserved forest remnants, whereas sparsely forested areas are associated with modules formed by disturbance-tolerant species. Differences in module composition along isolation gradients suggest that spatial proximity promotes interactions among co-occurring species, reinforcing the spatial structuring of the network (Emer et al., 2020; González-Varo et al., 2017). Because our isolation metric captures the distance from each site to the continuous forest of Serra da Bodoquena National Park, it reflects landscape permeability rather than classical patch-scale fragmentation. This inference is supported by the observation that larger-bodied bats, capable of traversing fragmented landscapes, tend to dominate in more isolated habitats, whereas smaller species are often restricted to continuous forest areas (Emer et al., 2018; Silveira et al., 2018; Stewart et al., 2024). These large-bodied bats also act as connectors: in Fig. 3 their interaction links (e.g., the orange lines) bridge plants belonging to different modules, thus maintaining pollen and seed flows across the broader network. These patterns indicate that spatial isolation filters species according to their mobility, which in turn shapes the configuration of interaction modules. When such connector species are lost, interactions become trapped within modules, eroding cohesion and functional redundancy across the entire network. As a result, habitat fragmentation may reduce the likelihood of interactions across modules and increase the risk of losing key species. This underscores the importance of maintaining habitat connectivity to preserve the structure and stability of ecological networks. Together, these findings highlight how species traits, spatial dynamics, and environmental factors interact to shape modularity, offering valuable insights for conservation strategies under ongoing habitat loss.

These findings align with previous studies that emphasize the role of ecological and environmental traits in shaping community structure and interaction patterns (Araujo et al., 2018; Dáttilo & Rico-Gray, 2018). The clear differentiation of modules based on these variables underscores the complexity of ecological networks and the multifaceted drivers of their modularity, which include species traits, spatial dynamics, and environmental gradients (González-Varo et al., 2017; Thébault & Fontaine, 2010). Understanding these drivers is critical for predicting how changes in ecological factors - such as habitat loss, fragmentation, or shifts in traits species - may impact the stability and function of interaction networks (Carlos et al., 2025; Emer et al., 2020; Farneda et al., 2015). This insight highlights the need for conservation strategies that consider the structural organisation of ecological networks. For example, maintaining forest cover can support the internal integrity of modules, while ensuring habitat connectivity helps preserve the role of mobile species that facilitate interactions across modules. Protecting both local habitat conditions and broader landscape connectivity can enhance the resilience of mutualistic networks in the face of environmental change, ultimately contributing to the long-term preservation of biodiversity and ecosystem function.

5. Supplementary material

Table S1. Years and months of field expeditions for sampling plant-bat interactions in 20 sites in the Serra da Bodoquena, southwestern Brazil.

Year	Rainy season			Dry season			
	January	February	March	June	July	August	September
2015				X	X		
2016	X	X	X	X	X	X	X
2017	X	X	X	X	X	X	X
2019		X	X				
2021						X	X

Table S2. Significant correlations between isolation to Serra da Bodoquena National Park and forest cover in 2.5 km-radius buffers for 20 sites in the Serra da Bodoquena region, southwestern Brazil.

	Forest cover (%)		Isolation (km)	
	r	P	r	P
Forest cover (%)	–	–	0.53	**0.0003**
Isolation (Km)	0.53	**0.0003**	–	–

Table S3: Bat body mass, isolation to Serra da Bodoquena National Park, forest cover in 2.5 km-radius buffers across plant-bat networks in 20 sites at Serra da Bodoquena region, southwestern Brazil.

Bat specie	Site ID	Bat body mass (g)	Forest cover (%)	Isolation (km)
Anoura caudifer	9	12.5	37.2	4.937
Anoura caudifer	12	11	29.1	9.591
Anoura caudifer	14	11	47.8	18.101
Artibeus lituratus	9	59	37.2	4.937
Artibeus lituratus	12	64	29.1	9.591
Artibeus lituratus	14	62	47.8	18.101
Artibeus lituratus	14	62	47.8	18.101
Artibeus lituratus	18	66	45.7	29.337
Artibeus planirostris	1	44	99.4	0.000
Artibeus planirostris	2	57	90.0	0.000
Artibeus planirostris	2	59	90.0	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	45	60.8	0.000
Artibeus planirostris	3	46	60.8	0.000
Artibeus planirostris	3	47.25	60.8	0.000
Artibeus planirostris	3	50	60.8	0.000
Artibeus planirostris	3	50	60.8	0.000
Artibeus planirostris	3	62	60.8	0.000
Artibeus planirostris	3	66	60.8	0.000
Artibeus planirostris	3	72	60.8	0.000
Artibeus planirostris	3	75	60.8	0.000
Artibeus planirostris	4	32	71.9	0.012
Artibeus planirostris	4	41	71.9	0.012
Artibeus planirostris	4	41.5	71.9	0.012
Artibeus planirostris	4	43	71.9	0.012
Artibeus planirostris	4	43	71.9	0.012
Artibeus planirostris	4	43	71.9	0.012
Artibeus planirostris	4	44	71.9	0.012
Artibeus planirostris	4	45	71.9	0.012
Artibeus planirostris	4	45	71.9	0.012
Artibeus planirostris	4	45	71.9	0.012
Artibeus planirostris	4	45	71.9	0.012
Artibeus planirostris	4	47	71.9	0.012
Artibeus planirostris	4	54	71.9	0.012
Artibeus planirostris	5	42	83.4	0.018
Artibeus planirostris	5	43	83.4	0.018
Artibeus planirostris	5	46	83.4	0.018
Artibeus planirostris	5	52	83.4	0.018
Artibeus planirostris	5	75.5	83.4	0.018
Artibeus planirostris	6	20	58.9	0.036
Artibeus planirostris	6	43	58.9	0.036
Artibeus planirostris	6	50	58.9	0.036
Artibeus planirostris	6	52.5	58.9	0.036
Artibeus planirostris	6	61	58.9	0.036
Artibeus planirostris	7	29	60.4	0.189
Artibeus planirostris	7	37	60.4	0.189

Artibeus planirostris	7	42	60.4	0.189
Artibeus planirostris	7	43	60.4	0.189
Artibeus planirostris	7	45	60.4	0.189
Artibeus planirostris	7	46	60.4	0.189
Artibeus planirostris	7	47	60.4	0.189
Artibeus planirostris	7	48	60.4	0.189
Artibeus planirostris	7	48	60.4	0.189
Artibeus planirostris	7	48	60.4	0.189
Artibeus planirostris	7	50	60.4	0.189
Artibeus planirostris	7	50	60.4	0.189
Artibeus planirostris	7	57	60.4	0.189
Artibeus planirostris	8	37	35.1	4.498
Artibeus planirostris	8	40	35.1	4.498
Artibeus planirostris	8	40	35.1	4.498
Artibeus planirostris	8	41	35.1	4.498
Artibeus planirostris	8	42	35.1	4.498
Artibeus planirostris	8	42.5	35.1	4.498
Artibeus planirostris	8	46	35.1	4.498
Artibeus planirostris	8	50	35.1	4.498
Artibeus planirostris	8	51	35.1	4.498
Artibeus planirostris	8	53	35.1	4.498
Artibeus planirostris	8	55	35.1	4.498
Artibeus planirostris	8	57	35.1	4.498
Artibeus planirostris	8	60	35.1	4.498
Artibeus planirostris	9	46	37.2	4.937
Artibeus planirostris	9	51.8	37.2	4.937
Artibeus planirostris	9	54.2	37.2	4.937
Artibeus planirostris	10	47	20.8	7.989
Artibeus planirostris	10	48	20.8	7.989
Artibeus planirostris	10	49	20.8	7.989
Artibeus planirostris	11	45	28.0	8.115
Artibeus planirostris	11	45.5	28.0	8.115
Artibeus planirostris	11	47	28.0	8.115
Artibeus planirostris	11	48	28.0	8.115
Artibeus planirostris	11	50	28.0	8.115
Artibeus planirostris	11	51	28.0	8.115
Artibeus planirostris	11	51	28.0	8.115
Artibeus planirostris	11	52.5	28.0	8.115
Artibeus planirostris	12	11	29.1	9.591
Artibeus planirostris	12	42	29.1	9.591
Artibeus planirostris	12	45	29.1	9.591
Artibeus planirostris	12	45	29.1	9.591
Artibeus planirostris	12	48	29.1	9.591
Artibeus planirostris	12	48	29.1	9.591
Artibeus planirostris	12	50	29.1	9.591
Artibeus planirostris	12	50.5	29.1	9.591
Artibeus planirostris	12	58	29.1	9.591
Artibeus planirostris	12	69	29.1	9.591
Artibeus planirostris	13	35.5	45.7	17.328
Artibeus planirostris	13	38.5	45.7	17.328
Artibeus planirostris	13	38.5	45.7	17.328
Artibeus planirostris	13	43	45.7	17.328
Artibeus planirostris	13	45	45.7	17.328
Artibeus planirostris	13	46.5	45.7	17.328
Artibeus planirostris	13	47	45.7	17.328
Artibeus planirostris	13	47	45.7	17.328
Artibeus planirostris	13	47.5	45.7	17.328
Artibeus planirostris	13	48	45.7	17.328

Artibeus planirostris	13	48	45.7	17.328
Artibeus planirostris	13	49	45.7	17.328
Artibeus planirostris	13	50	45.7	17.328
Artibeus planirostris	13	50	45.7	17.328
Artibeus planirostris	13	50	45.7	17.328
Artibeus planirostris	13	50	45.7	17.328
Artibeus planirostris	14	27	47.8	18.101
Artibeus planirostris	14	40.5	47.8	18.101
Artibeus planirostris	14	41	47.8	18.101
Artibeus planirostris	14	42	47.8	18.101
Artibeus planirostris	14	42	47.8	18.101
Artibeus planirostris	14	43	47.8	18.101
Artibeus planirostris	14	44	47.8	18.101
Artibeus planirostris	14	44.5	47.8	18.101
Artibeus planirostris	14	45	47.8	18.101
Artibeus planirostris	14	46	47.8	18.101
Artibeus planirostris	14	46	47.8	18.101
Artibeus planirostris	14	46	47.8	18.101
Artibeus planirostris	14	46	47.8	18.101
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Artibeus planirostris	14	46	47.8	18.101
Artibeus planirostris	14	46	47.8	18.101
Artibeus planirostris	14	46.5	47.8	18.101
Artibeus planirostris	14	47	47.8	18.101
Artibeus planirostris	14	48	47.8	18.101
Artibeus planirostris	14	49	47.8	18.101
Artibeus planirostris	14	50	47.8	18.101
Artibeus planirostris	14	52	47.8	18.101
Artibeus planirostris	14	55	47.8	18.101
Artibeus planirostris	14	55	47.8	18.101
Artibeus planirostris	14	56	47.8	18.101
Artibeus planirostris	14	56	47.8	18.101
Artibeus planirostris	14	57	47.8	18.101
Artibeus planirostris	14	58	47.8	18.101
Artibeus planirostris	14	60	47.8	18.101
Artibeus planirostris	14	65	47.8	18.101
Artibeus planirostris	15	33	3.1	24.984
Artibeus planirostris	15	50	3.1	24.984
Artibeus planirostris	15	50	3.1	24.984
Artibeus planirostris	15	55	3.1	24.984
Artibeus planirostris	16	38	18.1	27.104
Artibeus planirostris	16	44	18.1	27.104
Artibeus planirostris	16	44.5	18.1	27.104
Artibeus planirostris	16	45	18.1	27.104
Artibeus planirostris	16	45	18.1	27.104
Artibeus planirostris	16	46	18.1	27.104
Artibeus planirostris	16	48	18.1	27.104
Artibeus planirostris	16	48	18.1	27.104
Artibeus planirostris	16	49	18.1	27.104
Artibeus planirostris	16	50	18.1	27.104
Artibeus planirostris	16	50	18.1	27.104
Artibeus planirostris	16	52	18.1	27.104
Artibeus planirostris	17	40	16.0	28.359
Artibeus planirostris	17	40	16.0	28.359
Artibeus planirostris	17	41	16.0	28.359
Artibeus planirostris	17	41.5	16.0	28.359
Artibeus planirostris	17	42	16.0	28.359
Artibeus planirostris	17	44	16.0	28.359

Artibeus planirostris	17	45	16.0	28.359
Artibeus planirostris	17	47	16.0	28.359
Artibeus planirostris	17	47	16.0	28.359
Artibeus planirostris	17	54	16.0	28.359
Artibeus planirostris	17	55	16.0	28.359
Artibeus planirostris	17	55	16.0	28.359
Artibeus planirostris	17	57	16.0	28.359
Artibeus planirostris	17	61	16.0	28.359
Artibeus planirostris	17	64	16.0	28.359
Artibeus planirostris	18	36	45.7	29.337
Artibeus planirostris	18	43	45.7	29.337
Artibeus planirostris	18	43	45.7	29.337
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Artibeus planirostris	18	45.5	45.7	29.337
Artibeus planirostris	18	50	45.7	29.337
Artibeus planirostris	18	50	45.7	29.337
Artibeus planirostris	18	54	45.7	29.337
Artibeus planirostris	19	43	18.1	39.848
Artibeus planirostris	19	45.5	18.1	39.848
Artibeus planirostris	19	46	18.1	39.848
Artibeus planirostris	19	46	18.1	39.848
Artibeus planirostris	19	47	18.1	39.848
Artibeus planirostris	19	47.5	18.1	39.848
Artibeus planirostris	19	47.5	18.1	39.848
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Artibeus planirostris	19	49	18.1	39.848
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Artibeus planirostris	19	50	18.1	39.848
Artibeus planirostris	19	52	18.1	39.848
Artibeus planirostris	19	52	18.1	39.848
Artibeus planirostris	19	54	18.1	39.848
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Artibeus planirostris	20	46	5.3	47.997
Artibeus planirostris	20	47	5.3	47.997
Artibeus planirostris	20	48	5.3	47.997
Artibeus planirostris	20	48	5.3	47.997
Artibeus planirostris	20	48	5.3	47.997
Artibeus planirostris	20	53	5.3	47.997
Artibeus planirostris	20	58	5.3	47.997
Artibeus planirostris	20	59	5.3	47.997
Carollia perspicillata	1	16	99.4	0.000
Carollia perspicillata	1	16	99.4	0.000
Carollia perspicillata	1	17	99.4	0.000
Carollia perspicillata	1	17	99.4	0.000
Carollia perspicillata	1	17	99.4	0.000
Carollia perspicillata	1	19	99.4	0.000
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Carollia perspicillata	2	17	90.0	0.000

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Carollia perspicillata	2	19	90.0	0.000
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Carollia perspicillata	3	20	60.8	0.000
Carollia perspicillata	3	21	60.8	0.000
Carollia perspicillata	3	21	60.8	0.000
Carollia perspicillata	3	22	60.8	0.000
Carollia perspicillata	3	24	60.8	0.000
Carollia perspicillata	3	24	60.8	0.000
Carollia perspicillata	3	24	60.8	0.000
Carollia perspicillata	3	24	60.8	0.000
Carollia perspicillata	3	26	60.8	0.000
Carollia perspicillata	4	14	71.9	0.012
Carollia perspicillata	4	14	71.9	0.012
Carollia perspicillata	4	15	71.9	0.012
Carollia perspicillata	4	15	71.9	0.012
Carollia perspicillata	4	16	71.9	0.012
Carollia perspicillata	4	16.5	71.9	0.012
Carollia perspicillata	4	16.5	71.9	0.012
Carollia perspicillata	4	17	71.9	0.012
Carollia perspicillata	4	17	71.9	0.012
Carollia perspicillata	4	17	71.9	0.012

Carollia perspicillata	4	17.5	71.9	0.012
Carollia perspicillata	4	18	71.9	0.012
Carollia perspicillata	4	18	71.9	0.012
Carollia perspicillata	4	18	71.9	0.012
Carollia perspicillata	4	20	71.9	0.012
Carollia perspicillata	4	23	71.9	0.012
Carollia perspicillata	5	14	83.4	0.018
Carollia perspicillata	5	15	83.4	0.018
Carollia perspicillata	5	15	83.4	0.018
Carollia perspicillata	5	15	83.4	0.018
Carollia perspicillata	5	15	83.4	0.018
Carollia perspicillata	5	15.5	83.4	0.018
Carollia perspicillata	5	16	83.4	0.018
Carollia perspicillata	5	16	83.4	0.018
Carollia perspicillata	5	17	83.4	0.018
Carollia perspicillata	5	17	83.4	0.018
Carollia perspicillata	5	17	83.4	0.018
Carollia perspicillata	5	18	83.4	0.018
Carollia perspicillata	5	18	83.4	0.018
Carollia perspicillata	5	19	83.4	0.018
Carollia perspicillata	5	19	83.4	0.018
Carollia perspicillata	5	20	83.4	0.018
Carollia perspicillata	5	21	83.4	0.018
Carollia perspicillata	5	21	83.4	0.018
Carollia perspicillata	6	15.5	58.9	0.036
Carollia perspicillata	6	15.5	58.9	0.036
Carollia perspicillata	6	16	58.9	0.036
Carollia perspicillata	6	16	58.9	0.036
Carollia perspicillata	6	16	58.9	0.036
Carollia perspicillata	6	17	58.9	0.036
Carollia perspicillata	6	18	58.9	0.036
Carollia perspicillata	6	18	58.9	0.036
Carollia perspicillata	6	19	58.9	0.036
Carollia perspicillata	6	20	58.9	0.036
Carollia perspicillata	6	20	58.9	0.036
Carollia perspicillata	6	21	58.9	0.036
Carollia perspicillata	6	22	58.9	0.036
Carollia perspicillata	6	22	58.9	0.036
Carollia perspicillata	6	22	58.9	0.036
Carollia perspicillata	6	23	58.9	0.036
Carollia perspicillata	6	23	58.9	0.036
Carollia perspicillata	6	23	58.9	0.036
Carollia perspicillata	7	14	60.4	0.189
Carollia perspicillata	7	15	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	16	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189
Carollia perspicillata	7	17	60.4	0.189

Carollia perspicillata	7	18	60.4	0.189
Carollia perspicillata	7	18	60.4	0.189
Carollia perspicillata	7	18	60.4	0.189
Carollia perspicillata	7	19	60.4	0.189
Carollia perspicillata	7	19	60.4	0.189
Carollia perspicillata	7	19	60.4	0.189
Carollia perspicillata	7	19	60.4	0.189
Carollia perspicillata	7	19	60.4	0.189
Carollia perspicillata	7	20	60.4	0.189
Carollia perspicillata	7	21	60.4	0.189
Carollia perspicillata	7	22	60.4	0.189
Carollia perspicillata	7	22	60.4	0.189
Carollia perspicillata	8	14	35.1	4.498
Carollia perspicillata	8	14	35.1	4.498
Carollia perspicillata	8	15	35.1	4.498
Carollia perspicillata	8	15	35.1	4.498
Carollia perspicillata	8	18	35.1	4.498
Carollia perspicillata	8	19	35.1	4.498
Carollia perspicillata	8	19	35.1	4.498
Carollia perspicillata	8	20	35.1	4.498
Carollia perspicillata	8	20	35.1	4.498
Carollia perspicillata	8	22	35.1	4.498
Carollia perspicillata	9	13	37.2	4.937
Carollia perspicillata	9	14	37.2	4.937
Carollia perspicillata	9	16	37.2	4.937
Carollia perspicillata	9	17	37.2	4.937
Carollia perspicillata	9	18	37.2	4.937
Carollia perspicillata	9	18	37.2	4.937
Carollia perspicillata	9	19	37.2	4.937
Carollia perspicillata	9	19	37.2	4.937
Carollia perspicillata	9	19	37.2	4.937
Carollia perspicillata	9	23	37.2	4.937
Carollia perspicillata	9	24	37.2	4.937
Carollia perspicillata	10	19	20.8	7.989
Carollia perspicillata	10	19	20.8	7.989
Carollia perspicillata	10	24.5	20.8	7.989
Carollia perspicillata	11	9	28.0	8.115
Carollia perspicillata	11	13	28.0	8.115
Carollia perspicillata	11	14.5	28.0	8.115
Carollia perspicillata	11	15.5	28.0	8.115
Carollia perspicillata	11	16	28.0	8.115
Carollia perspicillata	11	16	28.0	8.115
Carollia perspicillata	11	17	28.0	8.115
Carollia perspicillata	11	17	28.0	8.115
Carollia perspicillata	11	17	28.0	8.115
Carollia perspicillata	11	17	28.0	8.115
Carollia perspicillata	11	17	28.0	8.115
Carollia perspicillata	11	18	28.0	8.115
Carollia perspicillata	11	18	28.0	8.115
Carollia perspicillata	11	18	28.0	8.115
Carollia perspicillata	11	18	28.0	8.115
Carollia perspicillata	11	18	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	19	28.0	8.115

Carollia perspicillata	11	19	28.0	8.115
Carollia perspicillata	11	20	28.0	8.115
Carollia perspicillata	11	20	28.0	8.115
Carollia perspicillata	11	20	28.0	8.115
Carollia perspicillata	12	14	29.1	9.591
Carollia perspicillata	12	17	29.1	9.591
Carollia perspicillata	12	18	29.1	9.591
Carollia perspicillata	12	19	29.1	9.591
Carollia perspicillata	12	20	29.1	9.591
Carollia perspicillata	12	22	29.1	9.591
Carollia perspicillata	13	16	45.7	17.328
Carollia perspicillata	13	18	45.7	17.328
Carollia perspicillata	13	18	45.7	17.328
Carollia perspicillata	13	19	45.7	17.328
Carollia perspicillata	13	21	45.7	17.328
Carollia perspicillata	14	16	47.8	18.101
Carollia perspicillata	14	17	47.8	18.101
Carollia perspicillata	14	17	47.8	18.101
Carollia perspicillata	14	20	47.8	18.101
Carollia perspicillata	14	20	47.8	18.101
Carollia perspicillata	14	21	47.8	18.101
Carollia perspicillata	14	21	47.8	18.101
Carollia perspicillata	14	23	47.8	18.101
Carollia perspicillata	16	15.5	18.1	27.104
Carollia perspicillata	16	15.5	18.1	27.104
Carollia perspicillata	16	16	18.1	27.104
Carollia perspicillata	16	17	18.1	27.104
Carollia perspicillata	16	17	18.1	27.104
Carollia perspicillata	16	18	18.1	27.104
Carollia perspicillata	16	19	18.1	27.104
Carollia perspicillata	16	20	18.1	27.104
Carollia perspicillata	16	22	18.1	27.104
Carollia perspicillata	17	17	16.0	28.359
Carollia perspicillata	17	17	16.0	28.359
Carollia perspicillata	17	17	16.0	28.359
Carollia perspicillata	17	18	16.0	28.359
Carollia perspicillata	17	18	16.0	28.359
Carollia perspicillata	17	18	16.0	28.359
Carollia perspicillata	17	47	16.0	28.359
Carollia perspicillata	18	18	45.7	29.337
Carollia perspicillata	18	19	45.7	29.337
Carollia perspicillata	20	16	5.3	47.997
Carollia perspicillata	20	18	5.3	47.997
Carollia perspicillata	20	19	5.3	47.997
Glossophaga soricina	1	11	99.4	0.000
Glossophaga soricina	3	9.5	60.8	0.000
Glossophaga soricina	3	11	60.8	0.000
Glossophaga soricina	4	10	71.9	0.012
Glossophaga soricina	4	10.5	71.9	0.012
Glossophaga soricina	4	11	71.9	0.012
Glossophaga soricina	4	12	71.9	0.012
Glossophaga soricina	4	19	71.9	0.012
Glossophaga soricina	5	10	83.4	0.018
Glossophaga soricina	5	11.5	83.4	0.018
Glossophaga soricina	5	12	83.4	0.018
Glossophaga soricina	6	9.5	58.9	0.036
Glossophaga soricina	6	11	58.9	0.036
Glossophaga soricina	6	11.5	58.9	0.036

Glossophaga soricina	6	13	58.9	0.036
Glossophaga soricina	7	8	60.4	0.189
Glossophaga soricina	7	9	60.4	0.189
Glossophaga soricina	7	9	60.4	0.189
Glossophaga soricina	7	9	60.4	0.189
Glossophaga soricina	7	10	60.4	0.189
Glossophaga soricina	7	10.5	60.4	0.189
Glossophaga soricina	7	11	60.4	0.189
Glossophaga soricina	7	11	60.4	0.189
Glossophaga soricina	7	12	60.4	0.189
Glossophaga soricina	7	15	60.4	0.189
Glossophaga soricina	9	10.5	37.2	4.937
Glossophaga soricina	9	11	37.2	4.937
Glossophaga soricina	10	9	20.8	7.989
Glossophaga soricina	10	11	20.8	7.989
Glossophaga soricina	11	8	28.0	8.115
Glossophaga soricina	11	9.5	28.0	8.115
Glossophaga soricina	11	10	28.0	8.115
Glossophaga soricina	13	9	45.7	17.328
Glossophaga soricina	13	10	45.7	17.328
Glossophaga soricina	13	11	45.7	17.328
Glossophaga soricina	14	7	47.8	18.101
Glossophaga soricina	15	8.5	3.1	24.984
Glossophaga soricina	15	10	3.1	24.984
Glossophaga soricina	15	10	3.1	24.984
Glossophaga soricina	16	5.5	18.1	27.104
Glossophaga soricina	16	10	18.1	27.104
Glossophaga soricina	17	5	16.0	28.359
Glossophaga soricina	17	10	16.0	28.359
Glossophaga soricina	17	10	16.0	28.359
Glossophaga soricina	17	10	16.0	28.359
Glossophaga soricina	17	14.5	16.0	28.359
Glossophaga soricina	18	13	45.7	29.337
Lonchophylla dekeyseri	7	7	60.4	0.189
Lonchophylla dekeyseri	12	9	29.1	9.591
Phyllostomus hastatus	4	75	71.9	0.012
Phyllostomus hastatus	13	19	45.7	17.328
Platyrrhinus helleri	9	13	37.2	4.937
Platyrrhinus helleri	9	15	37.2	4.937
Platyrrhinus helleri	12	22	29.1	9.591
Platyrrhinus helleri	12	24	29.1	9.591
Platyrrhinus helleri	12	24	29.1	9.591
Platyrrhinus helleri	12	25	29.1	9.591
Platyrrhinus helleri	12	25	29.1	9.591
Platyrrhinus lineatus	1	23	99.4	0.000
Platyrrhinus lineatus	2	24	90.0	0.000
Platyrrhinus lineatus	3	22	60.8	0.000
Platyrrhinus lineatus	3	22	60.8	0.000
Platyrrhinus lineatus	3	24	60.8	0.000
Platyrrhinus lineatus	3	24	60.8	0.000
Platyrrhinus lineatus	3	25	60.8	0.000
Platyrrhinus lineatus	3	25	60.8	0.000
Platyrrhinus lineatus	3	25	60.8	0.000
Platyrrhinus lineatus	3	25	60.8	0.000
Platyrrhinus lineatus	3	25	60.8	0.000
Platyrrhinus lineatus	3	26	60.8	0.000
Platyrrhinus lineatus	3	26	60.8	0.000
Platyrrhinus lineatus	3	26	60.8	0.000

Platyrrhinus lineatus	3	27	60.8	0.000
Platyrrhinus lineatus	3	30	60.8	0.000
Platyrrhinus lineatus	3	46	60.8	0.000
Platyrrhinus lineatus	4	23	71.9	0.012
Platyrrhinus lineatus	4	24	71.9	0.012
Platyrrhinus lineatus	4	25	71.9	0.012
Platyrrhinus lineatus	4	25	71.9	0.012
Platyrrhinus lineatus	5	18	83.4	0.018
Platyrrhinus lineatus	5	21	83.4	0.018
Platyrrhinus lineatus	5	25	83.4	0.018
Platyrrhinus lineatus	6	16	58.9	0.036
Platyrrhinus lineatus	6	20.5	58.9	0.036
Platyrrhinus lineatus	6	26.5	58.9	0.036
Platyrrhinus lineatus	7	15	60.4	0.189
Platyrrhinus lineatus	7	17	60.4	0.189
Platyrrhinus lineatus	7	19	60.4	0.189
Platyrrhinus lineatus	7	20	60.4	0.189
Platyrrhinus lineatus	7	24	60.4	0.189
Platyrrhinus lineatus	7	25	60.4	0.189
Platyrrhinus lineatus	7	25	60.4	0.189
Platyrrhinus lineatus	7	27	60.4	0.189
Platyrrhinus lineatus	7	30	60.4	0.189
Platyrrhinus lineatus	8	17	35.1	4.498
Platyrrhinus lineatus	9	23	37.2	4.937
Platyrrhinus lineatus	9	27	37.2	4.937
Platyrrhinus lineatus	9	27	37.2	4.937
Platyrrhinus lineatus	10	21	20.8	7.989
Platyrrhinus lineatus	10	23	20.8	7.989
Platyrrhinus lineatus	10	25	20.8	7.989
Platyrrhinus lineatus	10	26	20.8	7.989
Platyrrhinus lineatus	11	22	28.0	8.115
Platyrrhinus lineatus	11	23	28.0	8.115
Platyrrhinus lineatus	11	23	28.0	8.115
Platyrrhinus lineatus	11	23	28.0	8.115
Platyrrhinus lineatus	11	24	28.0	8.115
Platyrrhinus lineatus	11	24	28.0	8.115
Platyrrhinus lineatus	11	25	28.0	8.115
Platyrrhinus lineatus	11	26	28.0	8.115
Platyrrhinus lineatus	12	11	29.1	9.591
Platyrrhinus lineatus	12	22	29.1	9.591
Platyrrhinus lineatus	12	23	29.1	9.591
Platyrrhinus lineatus	12	25	29.1	9.591
Platyrrhinus lineatus	12	26	29.1	9.591
Platyrrhinus lineatus	12	26	29.1	9.591
Platyrrhinus lineatus	12	28	29.1	9.591
Platyrrhinus lineatus	12	29	29.1	9.591
Platyrrhinus lineatus	13	24	45.7	17.328
Platyrrhinus lineatus	13	25	45.7	17.328
Platyrrhinus lineatus	14	20	47.8	18.101
Platyrrhinus lineatus	14	23	47.8	18.101
Platyrrhinus lineatus	14	26.5	47.8	18.101
Platyrrhinus lineatus	14	29	47.8	18.101
Platyrrhinus lineatus	14	30	47.8	18.101
Platyrrhinus lineatus	16	23	18.1	27.104
Platyrrhinus lineatus	17	16	16.0	28.359
Platyrrhinus lineatus	17	25	16.0	28.359
Platyrrhinus lineatus	18	21	45.7	29.337
Platyrrhinus lineatus	20	28	5.3	47.997

Platyrrhinus lineatus	20	28	5.3	47.997
Sturnira lilium	1	16	99.4	0.000
Sturnira lilium	1	16.5	99.4	0.000
Sturnira lilium	1	17	99.4	0.000
Sturnira lilium	1	17	99.4	0.000
Sturnira lilium	1	17.5	99.4	0.000
Sturnira lilium	1	18	99.4	0.000
Sturnira lilium	1	18	99.4	0.000
Sturnira lilium	1	19	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	20	99.4	0.000
Sturnira lilium	1	22	99.4	0.000
Sturnira lilium	1	22	99.4	0.000
Sturnira lilium	1	24	99.4	0.000
Sturnira lilium	1	24	99.4	0.000
Sturnira lilium	1	24	99.4	0.000
Sturnira lilium	1	25	99.4	0.000
Sturnira lilium	2	17.5	90.0	0.000
Sturnira lilium	2	18	90.0	0.000
Sturnira lilium	2	19	90.0	0.000
Sturnira lilium	2	19	90.0	0.000
Sturnira lilium	2	19	90.0	0.000
Sturnira lilium	2	20	90.0	0.000
Sturnira lilium	2	20	90.0	0.000
Sturnira lilium	2	20	90.0	0.000
Sturnira lilium	2	25.5	90.0	0.000
Sturnira lilium	3	15.5	60.8	0.000
Sturnira lilium	3	19	60.8	0.000
Sturnira lilium	3	25	60.8	0.000
Sturnira lilium	3	26	60.8	0.000
Sturnira lilium	4	17	71.9	0.012
Sturnira lilium	4	18	71.9	0.012
Sturnira lilium	4	18	71.9	0.012
Sturnira lilium	4	20	71.9	0.012
Sturnira lilium	4	21	71.9	0.012
Sturnira lilium	4	22	71.9	0.012
Sturnira lilium	4	25	71.9	0.012
Sturnira lilium	5	17	83.4	0.018
Sturnira lilium	5	17	83.4	0.018
Sturnira lilium	5	18	83.4	0.018
Sturnira lilium	5	18	83.4	0.018
Sturnira lilium	5	18	83.4	0.018
Sturnira lilium	5	20	83.4	0.018
Sturnira lilium	5	22	83.4	0.018
Sturnira lilium	5	22	83.4	0.018
Sturnira lilium	5	25	83.4	0.018
Sturnira lilium	6	17.5	58.9	0.036
Sturnira lilium	6	19	58.9	0.036
Sturnira lilium	6	25	58.9	0.036
Sturnira lilium	7	14	60.4	0.189
Sturnira lilium	7	15	60.4	0.189

Sturnira lilium	7	15	60.4	0.189
Sturnira lilium	7	15	60.4	0.189
Sturnira lilium	7	15	60.4	0.189
Sturnira lilium	7	15	60.4	0.189
Sturnira lilium	7	15	60.4	0.189
Sturnira lilium	7	16	60.4	0.189
Sturnira lilium	7	16	60.4	0.189
Sturnira lilium	7	16	60.4	0.189
Sturnira lilium	7	16	60.4	0.189
Sturnira lilium	7	16.5	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17	60.4	0.189
Sturnira lilium	7	17.5	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
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Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18	60.4	0.189
Sturnira lilium	7	18.5	60.4	0.189
Sturnira lilium	7	18.5	60.4	0.189
Sturnira lilium	7	19	60.4	0.189
Sturnira lilium	7	19	60.4	0.189
Sturnira lilium	7	19	60.4	0.189
Sturnira lilium	7	19	60.4	0.189
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Sturnira lilium	7	19	60.4	0.189
Sturnira lilium	7	19.5	60.4	0.189
Sturnira lilium	7	20	60.4	0.189
Sturnira lilium	7	20	60.4	0.189
Sturnira lilium	7	20	60.4	0.189
Sturnira lilium	7	20	60.4	0.189
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Sturnira lilium	7	20	60.4	0.189

Sturnira lilium	7	20	60.4	0.189
Sturnira lilium	7	20	60.4	0.189
Sturnira lilium	7	21	60.4	0.189
Sturnira lilium	7	21	60.4	0.189
Sturnira lilium	7	21	60.4	0.189
Sturnira lilium	7	21	60.4	0.189
Sturnira lilium	7	21	60.4	0.189
Sturnira lilium	7	22	60.4	0.189
Sturnira lilium	7	22	60.4	0.189
Sturnira lilium	7	22	60.4	0.189
Sturnira lilium	7	22	60.4	0.189
Sturnira lilium	7	22	60.4	0.189
Sturnira lilium	7	23	60.4	0.189
Sturnira lilium	7	23	60.4	0.189
Sturnira lilium	7	23	60.4	0.189
Sturnira lilium	7	24	60.4	0.189
Sturnira lilium	8	16	35.1	4.498
Sturnira lilium	8	19	35.1	4.498
Sturnira lilium	8	20	35.1	4.498
Sturnira lilium	8	20	35.1	4.498
Sturnira lilium	8	21	35.1	4.498
Sturnira lilium	8	22	35.1	4.498
Sturnira lilium	8	22.5	35.1	4.498
Sturnira lilium	8	49	35.1	4.498
Sturnira lilium	9	16.5	37.2	4.937
Sturnira lilium	9	18	37.2	4.937
Sturnira lilium	9	18	37.2	4.937
Sturnira lilium	9	20	37.2	4.937
Sturnira lilium	9	20	37.2	4.937
Sturnira lilium	9	21	37.2	4.937
Sturnira lilium	9	21	37.2	4.937
Sturnira lilium	9	22	37.2	4.937
Sturnira lilium	9	23	37.2	4.937
Sturnira lilium	9	23	37.2	4.937
Sturnira lilium	10	17	20.8	7.989
Sturnira lilium	10	20	20.8	7.989
Sturnira lilium	10	20	20.8	7.989
Sturnira lilium	10	21	20.8	7.989
Sturnira lilium	11	10	28.0	8.115
Sturnira lilium	11	16	28.0	8.115
Sturnira lilium	11	17	28.0	8.115
Sturnira lilium	11	17	28.0	8.115
Sturnira lilium	11	20	28.0	8.115
Sturnira lilium	11	28	28.0	8.115
Sturnira lilium	12	19	29.1	9.591
Sturnira lilium	12	21	29.1	9.591
Sturnira lilium	13	18	45.7	17.328
Sturnira lilium	14	16	47.8	18.101
Sturnira lilium	14	17.5	47.8	18.101
Sturnira lilium	14	20	47.8	18.101
Sturnira lilium	14	23	47.8	18.101
Sturnira lilium	14	23	47.8	18.101
Sturnira lilium	14	25	47.8	18.101
Sturnira lilium	15	18	3.1	24.984
Sturnira lilium	15	25	3.1	24.984
Sturnira lilium	16	18	18.1	27.104
Sturnira lilium	16	20	18.1	27.104
Sturnira lilium	16	21	18.1	27.104

Sturnira lilium	16	22	18.1	27.104
Sturnira lilium	16	22	18.1	27.104
Sturnira lilium	16	22	18.1	27.104
Sturnira lilium	16	26	18.1	27.104
Sturnira lilium	17	17	16.0	28.359
Sturnira lilium	17	18	16.0	28.359
Sturnira lilium	17	18	16.0	28.359
Sturnira lilium	17	20	16.0	28.359
Sturnira lilium	17	25	16.0	28.359
Sturnira lilium	18	21	45.7	29.337
Sturnira lilium	18	23	45.7	29.337
Sturnira lilium	19	16	18.1	39.848
Sturnira lilium	19	20.5	18.1	39.848
Sturnira lilium	20	19	5.3	47.997
Sturnira lilium	20	20	5.3	47.997
Sturnira lilium	20	20	5.3	47.997
Sturnira lilium	20	20	5.3	47.997
Sturnira lilium	20	23	5.3	47.997
Sturnira lilium	20	24	5.3	47.997
Vampyressa pusilla	9	12	37.2	4.937

Table S4. Abundance of Phyllostomidae bat species (separated into subfamilies) in 20 sample sites in the Serra da Bodoquena region, southwestern Brazil.

Subfamily Species	Sites																				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Carolliinae																					
Carollia perspicillata	12	11	59	17	20	20	28	12	11	4	28	6	7	9	1	10	9	2	0	5	271
Glossophaginae																					
Glossophaga soricina	1	0	3	6	4	5	11	0	2	3	5	0	4	1	3	3	7	1	0	0	59
Anoura caudifer	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	4
Lonchophylla dekeyseri	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2
Phyllostominae																					
Phyllostomus hastatus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Micronycteris microtis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Stenodermatinae																					
Artibeus planirostris	1	3	16	18	6	9	15	16	5	11	13	19	24	42	6	14	22	19	25	10	294
Sturnira lilium	32	11	6	12	10	3	86	9	10	4	6	2	2	8	2	7	6	5	2	7	230
Platyrrhinus lineatus	1	1	19	6	4	3	11	1	3	4	10	10	2	5	0	1	4	1	2	2	90
Platyrrhinus helleri	0	0	0	0	0	0	0	0	2	0	0	5	0	0	0	0	0	0	0	0	7
Artibeus lituratus	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	1	0	0	5
Vampyressa pusilla	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1

Table S5. Number of bat faecal samples containing seed and/or pollen species (separated into families and subfamilies) across 20 sample sites in the Serra da Bodoquena region, southwestern Brazil. Morphs are unidentified species.

Plant family and species		Site																				Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Seed																						
Moraceae	*Ficus citrifolia*	0	0	7	3	4	0	2	2	2	2	0	3	6	4	1	2	5	2	5	3	53
	Ficus maxima	0	0	5	3	0	0	4	3	1	2	7	0	2	9	0	5	0	2	5	0	48
	Ficus obtusifolia	0	2	1	0	0	0	1	3	0	1	0	0	0	5	0	2	5	0	1	4	25
	Ficus insipida	0	1	2	1	0	0	0	0	1	2	0	12	0	1	0	0	2	0	0	2	24
	Ficus crocata	0	0	3	1	1	0	1	0	0	0	1	1	7	3	0	0	1	1	0	0	20
	Ficus pertusa	0	0	1	2	1	1	1	0	1	0	1	1	0	2	0	1	2	1	0	0	15
	Ficus carautana	0	0	2	0	0	0	0	0	0	0	0	3	1	1	0	1	1	0	0	0	9
	Ficus lagoensis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	4
	Ficus adhatodifolia	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	Ficus sp. 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
	Maclura tinctoria	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	0	0	6
Piperaceae	*Piper aduncum*	4	7	25	10	10	19	39	13	10	5	24	7	0	8	1	9	7	1	1	5	205
	Piper amalago	15	3	9	1	9	2	36	3	2	1	0	0	1	2	1	1	2	0	0	0	88
	Piper angustifolium	16	4	9	3	7	2	16	1	5	1	4	4	3	2	0	5	4	0	0	2	88
	Piper tuberculatum	0	1	16	11	9	5	11	1	2	1	6	1	0	2	0	9	2	2	2	1	82
	Piper hispidum	0	1	1	0	0	0	0	0	0	0	0	1	0	4	0	0	1	0	0	0	8
	Piper macedoi	0	2	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	7
	Piper sp. 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	5
Salicaceae	*Banara arguta*	0	0	0	0	3	0	11	2	0	0	0	0	0	0	0	2	0	0	0	3	21
Solanaceae	*Solanum* sp. 1	1	0	0	0	0	0	4	0	0	1	2	0	2	3	0	1	0	0	1	0	15
	Solanum paniculatum	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	0	5
Urticaceae	*Cecropia pachystachya*	3	8	3	7	2	2	14	2	4	2	6	6	2	5	5	7	7	9	6	3	103
Morphotype	Morph seed 1	0	0	0	0	0	0	6	2	0	0	1	1	0	1	2	0	1	3	4	0	21
	Morph seed 10	0	0	0	1	0	0	7	1	0	0	0	0	0	0	0	0	0	1	2	0	12
	Morph seed 14	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	3
	Morph seed 2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	Morph seed 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Morph seed 4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Morph seed 5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Morph seed 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

		Morph seed 7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
		Morph seed 12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
		Morph seed 13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
		Morph seed 15	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Morph seed 16	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pollen																							
	Fabaceae	*Hymenaea courbaril*	0	0	0	2	0	0	1	0	0	0	1	0	2	0	0	2	2	0	0	0	10
		Bauhinia sp. 1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	2	0	0	0	0	8
		Bauhinia ungulata	0	0	1	4	1	1	7	1	6	1	1	1	5	1	0	0	2	1	0	0	4
		Bauhinia sp. 2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	3
		Bauhinia blakeana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
		Inga sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	Myrtaceae	sp. 1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
	Morphotype	Morph pollen 2	0	0	0	0	0	0	1	0	0	0	3	0	0	1	0	1	0	0	0	0	6
		Morph pollen 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

Table S6. Number of faecal samples containing seed and/or pollen species from 12 bat species in the Serra da Bodoquena region, southwestern Brazil.

Plants	Bats												Total
	Carollia perspicillata	*Sturnira lilium*	*Artibeus planirostris*	*Platyrrhinus lineatus*	*Glossophaga soricina*	*Platyrrhinus helleri*	*Artibeus lituratus*	*Lonchophylla dekeyseri*	*Anoura caudifer*	*Phyllostomus hastatus*	*Micronycteris microtis*	*Vampyressa pusilla*	
Seed													
Piper aduncum	102	61	19	7	14	0	0	1	0	0	1	0	**205**
Cecropia pachystachya	7	15	38	24	12	1	3	0	1	2	0	0	**103**
Piper amalago	40	38	2	3	5	0	0	0	0	0	0	0	**88**
Piper angustifolium	43	37	3	1	2	0	0	2	0	0	0	0	**88**
Piper tuberculatum	43	23	12	1	2	0	0	1	0	0	0	0	**82**
Ficus citrifolia	2	2	39	10	0	0	0	0	0	0	0	0	**53**
Ficus maxima	1	0	41	6	0	0	0	0	0	0	0	0	**48**
Ficus obtusifolia	2	4	15	4	0	0	0	0	0	0	0	0	**25**
Ficus insipida	0	4	6	9	0	3	1	0	0	0	0	1	**24**
Banara arguta	10	10	0	1	0	0	0	0	0	0	0	0	**21**
Morph seed 1	12	6	0	1	2	0	0	0	0	0	0	0	**21**
Ficus crocata	1	0	13	5	0	1	0	0	0	0	0	0	**20**
Ficus pertusa	2	1	10	1	0	1	0	0	0	0	0	0	**15**
Solanum sp. 1	0	2	10	3	0	0	0	0	0	0	0	0	**15**
Morph seed 10	5	7	0	0	0	0	0	0	0	0	0	0	**12**
Ficus carautana	2	2	3	1	0	0	1	0	0	0	0	0	**9**
Piper hispidum	4	0	4	0	0	0	0	0	0	0	0	0	**8**
Piper macedoi	6	0	0	1	0	0	0	0	0	0	0	0	**7**
Maclura tinctoria	1	4	1	0	0	0	0	0	0	0	0	0	**6**
Piper sp. 1	3	1	1	0	0	0	0	0	0	0	0	0	**5**
Solanum paniculatum	1	2	1	1	0	0	0	0	0	0	0	0	**5**
Ficus lagoensis	0	2	1	1	0	0	0	0	0	0	0	0	**4**
Ficus adhatodifolia	0	0	2	1	0	0	0	0	0	0	0	0	**3**
Morph seed 14	1	2	0	0	0	0	0	0	0	0	0	0	**3**
Ficus sp. 1	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Morph seed 2	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Morph seed 3	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 4	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 5	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Morph seed 6	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 7	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 8	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Morph seed 9	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 11	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 12	0	0	0	0	0	1	0	0	0	0	0	0	**1**
Morph seed 13	0	0	1	0	0	0	0	0	0	0	0	0	**1**

Morph seed 15	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Morph seed 16	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Pollen													
Bauhinia ungulata	11	3	0	0	19	0	0	0	1	0	0	0	**34**
Hymenaea courbaril	1	1	1	0	7	0	0	0	0	0	0	0	**10**
Bauhinia sp. 1	2	1	3	0	1	1	0	0	0	0	0	0	**8**
Morph pollen 2	4	0	1	1	0	0	0	0	0	0	0	0	**6**
Bauhinia sp. 2	1	0	0	0	1	0	0	0	1	0	0	0	**3**
Myrtaceae sp. 1	2	0	0	0	0	0	0	0	0	0	0	0	**2**
Bauhinia blakeana	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Inga sp. 1	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Morph pollen 1	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Total	**314**	**232**	**229**	**84**	**67**	**8**	**5**	**4**	**3**	**2**	**1**	**1**	**950**

General conclusion

This dissertation integrates ecological network theory, species interaction dynamics, and landscape ecology to explore the mutual dependencies between bats and plants in Neotropical environments, with a particular focus on the Brazilian Cerrado. Across the two chapters, the findings collectively highlight the importance of ecological traits, habitat structure, and species-specific responses in shaping network modularity and complexity.

The First Chapter expands this understanding by demonstrating the threshold-drive dynamics between forest cover, isolation and network complexity. Plant-bat networks exhibit peak species richness at 50% forest cover but become more modular and less connected at 30% forest cover. This non-linear relationship indicates that increases in network size do not necessarily lead to higher modularity. Moderate forest disturbance thus fosters a balance between ecological diversity and compartmentalised interaction structures. Such thresholds highlight the fragility of mutualistic networks in homogenised (e.g., intact forest) or over-disturbed habitats (e.g., deforested areas). However, landscapes with at least 50% forest cover are critical to sustaining complex networks. The presence of large preserved forests (e.g., Serra da Bodoquena National Park) appears to play a key role in maintaining subpopulations and preventing biodiversity loss. These insights have direct applications in tropical forest management, highlighting the importance of mosaic landscapes that combine forest reserves with moderately disturbed areas to sustain rich and functionally robust networks.

The Second Chapter underscores how ecological trait and environmental gradients collectively drive the formation of modular structures in interaction metanetwork. Species traits, spatial dynamics, and environmental gradients are key determinants of network modularity, with implications for predicting the impact of habitat alterations on network stability and resilience. Results indicated that body size was a key predictor of module composition, while isolation and forest cover also played significant roles. This chapter emphasizes the necessity of conservation strategies aimed at preserving habitat connectivity to maintain resilient ecological networks.

Taken together, these findings underscore the critical role of habitat loss in shaping ecological dynamics within bat-plant interaction networks. The interplay between forest cover, isolation and network modularity responses to landscape structure suggests that conservation efforts should prioritize maintaining large forest reserves while ensuring moderately disturbed habitats that support biodiversity and ecological connectivity. This research contributes to a broader understanding of how biodiversity self-organizes in human-modified landscapes and provides insights for designing effective conservation strategies that reconcile land use demands with the persistence of species-rich ecosystems in the Neotropics.

References

Araujo, A. C., Martín González, A. M., Sandel, B., Maruyama, P. K., Fischer, E., Vizentin-Bugoni, J., De Araújo, F. P., Coelho, A. G., Faria, R. R., Kohler, G., Las-Casas, F. M. G., Lopes, A. V., Machado, A. O., Machado, C. G., Machado, I. C., McGuire, J. A., Moura, A. C., Oliveira, G. M., Oliveira, P. E., … Svenning, J. (2018). Spatial distance and climate determine modularity in a cross-biomes plant–hummingbird interaction network in Brazil. *Journal of Biogeography*, *45*(8), 1846–1858. https://doi.org/10.1111/jbi.13367

Bascompte, J., & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383–9387. https://doi.org/10.1073/pnas.1633576100

Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, *458*(7241), 1018–1020. https://doi.org/10.1038/nature07950

Bonfim, F. C. G., Dodonov, P., Guimarães, P. R., & Cazetta, E. (2023). Habitat loss shapes the structure and species roles in tropical plant–frugivore networks. *Oikos*, *2023*(4), e09399. https://doi.org/10.1111/oik.09399

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Carlos, P. P., Dalsgaard, B., Gonzales, F., Silveira, M., Acero-Murcia, A. C., Eriksson, A., Santos, C. S., & Fischer, E. (2025). *Forest loss and isolation effects on mutualistic plant-bat interactions in a Neotropical savanna*. https://doi.org/doi.org/10.1016/j.foreco.2025.122710

Caughlin, T. T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S., & Levey, D. J. (2015). Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1798), 20142095. https://doi.org/10.1098/rspb.2014.2095

Cazetta, E., & Fahrig, L. (2022). The effects of human-altered habitat spatial pattern on frugivory and seed dispersal: A global meta-analysis. *Oikos*, *2022*(2), oik.08288. https://doi.org/10.1111/oik.08288

Chama, L., Berens, D. G., Downs, C. T., & Farwig, N. (2013). Habitat Characteristics of Forest Fragments Determine Specialisation of Plant-Frugivore Networks in a Mosaic Forest Landscape. *PLoS ONE*, *8*(1), e54956. https://doi.org/10.1371/journal.pone.0054956

Colombo, G. T., Di Ponzio, R., Benchimol, M., Peres, C. A., & Bobrowiec, P. E. D. (2023). Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. *Functional Ecology*, *37*(1), 99–111. https://doi.org/10.1111/1365-2435.14118

Dáttilo, W., Lara-Rodríguez, N., Jordano, P., Guimarães, P. R., Thompson, J. N., Marquis, R. J., Medeiros, L. P., Ortiz-Pulido, R., Marcos-García, M. A., & Rico-Gray, V. (2016). Unravelling Darwin's entangled bank: Architecture and robustness of mutualistic networks with multiple interaction types. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161564. https://doi.org/10.1098/rspb.2016.1564

Dáttilo, W., & Rico-Gray, V. (Orgs.). (2018). *Ecological Networks in the Tropics: An Integrative Overview of Species Interactions from Some of the Most Species-Rich*

Habitats on Earth. Springer International Publishing. https://doi.org/10.1007/978-3-319-68228-0

De Assis Bomfim, J., Guimarães, P. R., Peres, C. A., Carvalho, G., & Cazetta, E. (2018). Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. *Ecography*, *41*(11), 1899–1909. https://doi.org/10.1111/ecog.03592

Diniz, U. M., & Aguiar, L. M. D. S. (2023a). Spatiotemporal trends in floral visitation and interaction networks reveal shifting niches for bats in a Neotropical savanna. *Journal of Animal Ecology*, *92*(7), 1442–1455. https://doi.org/10.1111/1365-2656.13941

Diniz, U. M., & Aguiar, L. M. D. S. (2023b). The interplay between spatiotemporal overlap and morphology as determinants of microstructure suggests no 'perfect fit' in a bat-flower network. *Scientific Reports*, *13*(1), 2737. https://doi.org/10.1038/s41598-023-29965-3

Dormann, C. F., Gruber, B., & Fründ, J. (2008). *Introducing the bipartite Package: Analysing Ecological Networks*. *8*.

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Emer, C., Galetti, M., Pizo, M. A., Guimarães, P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. *Ecology Letters*, *21*(4), 484–493. https://doi.org/10.1111/ele.12909

Emer, C., Jordano, P., Pizo, M. A., Ribeiro, M. C., Da Silva, F. R., & Galetti, M. (2020). Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. *Biotropica*, *52*(1), 81–89. https://doi.org/10.1111/btp.12738

Eriksson, A., Filion, A., Labruna, M. B., Muñoz-Leal, S., Poulin, R., Fischer, E., & Graciolli, G. (2023). Effects of forest loss and fragmentation on bat-ectoparasite interactions. *Parasitology Research*, *122*(6), 1391–1402. https://doi.org/10.1007/s00436-023-07839-x

Esquivel-Mimenza, H., Ibrahim, M., Harvey, C. A., Benjamin, T., & Sinclair, F. L. (2011). DISPERSED TREES IN PASTURELANDS OF CATTLE FARMS IN A TROPICAL DRY ECOSYSTEM. *Tropical and Subtropical Agroecosystems*, *14*(3). https://doi.org/10.56369/tsaes.1075

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D., & Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, *52*(5), 1381–1391. https://doi.org/10.1111/1365-2664.12490

Ferreira, F. F., Silva, S. G., Vitorino, B. D., Frota, A. V. B., & Guilherme, F. A. G. (2024). Seed Dispersal Networks in Neotropical Forest Areas of the Amazon, Cerrado, and Associated Ecotone: Abundance as the Driver of Bat Roles. *Acta Chiropterologica*, *26*(1). https://doi.org/10.3161/15081109ACC2024.26.1.002

Ferreira, P. A., Boscolo, D., Lopes, L. E., Carvalheiro, L. G., Biesmeijer, J. C., Da Rocha, P. L. B., & Viana, B. F. (2020). Forest and connectivity loss simplify tropical pollination networks. *Oecologia*, *192*(2), 577–590. https://doi.org/10.1007/s00442-019-04579-7

Fischer, E., Silveira, M., Munin, R. L., Camargo, G., Santos, C. F., Pereira, M. J. R., Fischer, W., & Eriksson, A. (2018). *Bats in the dry and wet Pantanal*.

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, *16*(3), 265–280.

https://doi.org/10.1111/j.1466-8238.2007.00287.x

Fleming, T. H., Geiselman, C., & Kress, W. J. (2009). The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, *104*(6), 1017–1043. https://doi.org/10.1093/aob/mcp197

Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters*, *9*(3), 281–286. https://doi.org/10.1111/j.1461-0248.2005.00868.x

Galindo-González, J., Guevara, S., & Sosa, V. J. (2000). Bat- and Bird-Generated Seed Rains at Isolated Trees in Pastures in a Tropical Rainforest. *Conservation Biology*, *14*(6), 1693–1703. https://doi.org/10.1111/j.1523-1739.2000.99072.x

García-Morales, R., Chapa-Vargas, L., Galindo-González, J., & Badano, E. I. (2012). Seed Dispersal Among Three Different Vegetation Communities in the Huasteca Region, Mexico, Analyzed from Bat Feces. *Acta Chiropterologica*, *14*(2), 357. https://doi.org/10.3161/150811012X661675

Gómez-Martínez, C., Aase, A. L. T. O., Totland, Ø., Rodríguez-Pérez, J., Birkemoe, T., Sverdrup-Thygeson, A., & Lázaro, A. (2020). Forest fragmentation modifies the composition of bumblebee communities and modulates their trophic and competitive interactions for pollination. *Scientific Reports*, *10*(1), 10872. https://doi.org/10.1038/s41598-020-67447-y

Gonçalves, F., Fischer, E., & Dirzo, R. (2017). Forest conversion to cattle ranching differentially affects taxonomic and functional groups of Neotropical bats. *Biological Conservation*, *210*, 343–348. https://doi.org/10.1016/j.biocon.2017.04.021

González-Varo, J. P., Carvalho, C. S., Arroyo, J. M., & Jordano, P. (2017). Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. *Molecular Ecology*, *26*(16), 4309–4321. https://doi.org/10.1111/mec.14181

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Hadley, A. S., & Betts, M. G. (2012). The effects of landscape fragmentation on pollination dynamics: Absence of evidence not evidence of absence. *Biological Reviews*, *87*(3), 526–544. https://doi.org/10.1111/j.1469-185X.2011.00205.x

Henry, M., & Jouard, S. (2007). Effect of Bat Exclusion on Patterns of Seed Rain in Tropical Rain Forest in French Guiana. *Biotropica*, *39*(4), 510–518. https://doi.org/10.1111/j.1744-7429.2007.00286.x

Ibouroi, M. T., Arnal, V., Montgelard, C., & Besnard, A. (2024). Habitat fragmentation increases genetic distance between fruit bat subpopulations. *African Journal of Ecology*, *62*(2), e13261. https://doi.org/10.1111/aje.13261

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., … Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, *90*(9), 2648–2648. https://doi.org/10.1890/08-1494.1

Kassambara, A., & Mundt, F. (2016). *Package 'factoextra'—Extract and Visualize the Results of Multivariate Data Analyses*. http://www.sthda.com/english/rpkgs/factoextra

Kormann, U., Scherber, C., Tscharntke, T., Klein, N., Larbig, M., Valente, J. J., Hadley, A. S., & Betts, M. G. (2016). Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1823), 20152347. https://doi.org/10.1098/rspb.2015.2347

Kunz, T. H., Braun De Torrez, E., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*(1), 1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Lau, C. P. Y., Ramsden, L., & Saunders, R. M. K. (2005). Hybrid origin of “ *Bauhinia blakeana* ” (Leguminosae: Caesalpinioideae), inferred using morphological, reproductive, and molecular data. *American Journal of Botany*, *92*(3), 525–533. https://doi.org/10.3732/ajb.92.3.525

Laurindo, R. S., Novaes, R. L. M., Vizentin-Bugoni, J., & Gregorin, R. (2019). The effects of habitat loss on bat-fruit networks. *Biodiversity and Conservation*, *28*(3), 589–601. https://doi.org/10.1007/s10531-018-1676-x

Leibold, M. A., & Miller, T. E. (2004). From Metapopulations to Metacommunities. Em *Ecology, Genetics and Evolution of Metapopulations* (p. 133–150). Elsevier. https://doi.org/10.1016/B978-012323448-3/50008-8

Ligo, A. B., Laurindo, R. D. S., Faria, L. D. B., & Gregorin, R. (2024). Climatic, geographic and anthropogenic factors shape the structure of bat–fruit networks in the Neotropical region. *Austral Ecology*, *49*(1), e13328. https://doi.org/10.1111/aec.13328

Lino, A., Ferreira, E., Fonseca, C., Fischer, E., & Ramos Pereira, M. J. (2021). Species–genetic diversity correlation in phyllostomid bats of the Bodoquena plateau, Brazil. *Biodiversity and Conservation*, *30*(2), 403–429. https://doi.org/10.1007/s10531-020-02097-0

Lino, A., Fonseca, C., Rojas, D., Fischer, E., & Ramos Pereira, M. J. (2019). A meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals. *Mammalian Biology*, *94*, 69–76. https://doi.org/10.1016/j.mambio.2018.09.006

Medina, A., Harvey, C. A., Merlo, D. S., Vílchez, S., & Hernández, B. (2007). Bat Diversity and Movement in an Agricultural Landscape in Matiguás, Nicaragua. *Biotropica*, *39*(1), 120–

128. https://doi.org/10.1111/j.1744-7429.2006.00240.x

Mello, M. A. R., Felix, G. M., Pinheiro, R. B. P., Muylaert, R. L., Geiselman, C., Santana, S. E., Tschapka, M., Lotfi, N., Rodrigues, F. A., & Stevens, R. D. (2019). Insights into the assembly rules of a continent-wide multilayer network. *Nature Ecology & Evolution*, *3*(11), 1525–1532. https://doi.org/10.1038/s41559-019-1002-3

Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & De Aguiar, M. A. M. (2011a). The Missing Part of Seed Dispersal Networks: Structure and Robustness of Bat-Fruit Interactions. *PLoS ONE*, *6*(2), e17395. https://doi.org/10.1371/journal.pone.0017395

Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & De Aguiar, M. A. M. (2011b). The Missing Part of Seed Dispersal Networks: Structure and Robustness of Bat-Fruit Interactions. *PLoS ONE*, *6*(2), e17395. https://doi.org/10.1371/journal.pone.0017395

Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & De Aguiar, M. A. M. (2011c). The modularity of seed dispersal: Differences in structure and robustness between bat– and bird–fruit networks. *Oecologia*, *167*(1), 131. https://doi.org/10.1007/s00442-011-1984-2

Melo, I., Ochoa-Quintero, J. M., Oliveira Roque, F., & Dalsgaard, B. (2018). A review of threshold responses of birds to landscape changes across the world. *Journal of Field Ornithology*, *89*(4), 303–314. https://doi.org/10.1111/jofo.12272

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1557), 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Mendes, P., & Srbek-Araujo, A. C. (2021). Effects of land-use changes on Brazilian bats: A review of current knowledge. *Mammal Review*, *51*(1), 127–142.

https://doi.org/10.1111/mam.12227

Menke, S., Böhning-Gaese, K., & Schleuning, M. (2012). Plant–frugivore networks are less specialized and more robust at forest–farmland edges than in the interior of a tropical forest. *Oikos*, *121*(10), 1553–1566. https://doi.org/10.1111/j.1600-0706.2011.20210.x

Muggeo, V. M. R. (2008). *segmented: An R Package to Fit Regression Models with Broken-Line Relationships*. *8*.

Munin, R. L., Da Costa, P. C., & Fischer, E. (2011). Differential ingestion of fig seeds by a Neotropical bat, Platyrrhinus lineatus. *Mammalian Biology*, *76*(6), 772–774. https://doi.org/10.1016/j.mambio.2010.12.006

Muylaert, R. L., Stevens, R. D., & Ribeiro, M. C. (2016). Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. *Ecological Applications*, *26*(6), 1854–1867. https://doi.org/10.1890/15-1757.1

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B. I., … Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, *353*(6296), 288–291. https://doi.org/10.1126/science.aaf2201

Okuyama, T., & Holland, J. N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, *11*(3), 208–216. https://doi.org/10.1111/j.1461-0248.2007.01137.x

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, *104*(50), 19891–19896. https://doi.org/10.1073/pnas.0706375104

Palacio, R. D., Valderrama-Ardila, C., & Kattan, G. H. (2016). Generalist Species Have a

Central Role In a Highly Diverse Plant–Frugivore Network. *Biotropica*, *48*(3), 349–355. https://doi.org/10.1111/btp.12290

Pinto, N., & Keitt, T. H. (2008). *Scale-dependent responses to forest cover displayed by frugivore bats*.

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*(3), 243–251. https://doi.org/10.1111/oik.01719

QGIS Development Team. (2019). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. http://www.qgis.org/

R Core Team. (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ren, P., Didham, R. K., Murphy, M. V., Zeng, D., Si, X., & Ding, P. (2023). Forest edges increase pollinator network robustness to extinction with declining area. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01973-y

Ripley, B. (2020). *Package MASS - Support Functions and Datasets for Venables and Ripley's MASS* (K. Hornik & A. Gebhardt, Trads.). University of Oxford, Department of Statistics. http://www.stats.ox.ac.uk/pub/MASS4/

Ripperger, S. P., Kalko, E. K. V., Rodríguez-Herrera, B., Mayer, F., & Tschapka, M. (2015). Frugivorous Bats Maintain Functional Habitat Connectivity in Agricultural Landscapes but Rely Strongly on Natural Forest Fragments. *PLOS ONE*, *10*(4), e0120535. https://doi.org/10.1371/journal.pone.0120535

Rosa, M. R., Brancalion, P. H. S., Crouzeilles, R., Tambosi, L. R., Piffer, P. R., Lenti, F. E. B., Hirota, M., Santiami, E., & Metzger, J. P. (2021). Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. *Science Advances*, *7*(4), eabc4547. https://doi.org/10.1126/sciadv.abc4547

Sanders, E., Wassens, S., Michael, D. R., Nimmo, D. G., & Turner, J. M. (2024). Extinction risk of the world's freshwater mammals. *Conservation Biology*, *38*(1), e14168. https://doi.org/10.1111/cobi.14168

Schleuning, M., Fründ, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., Beil, M., Benadi, G., Blüthgen, N., Bruelheide, H., Böhning-Gaese, K., Dehling, D. M., Dormann, C. F., Exeler, N., Farwig, N., Harpke, A., Hickler, T., Kratochwil, A., Kuhlmann, M., … Hof, C. (2016). Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications*, *7*(1), 13965. https://doi.org/10.1038/ncomms13965

Silveira, M., Tomas, W. M., Fischer, E., & Bordignon, M. O. (2018). Habitat occupancy by Artibeus planirostris bats in the Pantanal wetland, Brazil. *Mammalian Biology*, *91*, 1–6. https://doi.org/10.1016/j.mambio.2018.03.003

Spiesman, B. J., & Inouye, B. D. (2013). Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology*, *94*(12), 2688–2696. https://doi.org/10.1890/13-0977.1

Sritongchuay, T., & Bumrungsri, S. (2016). Specialized and facultative nectar-feeding bats have different effects on pollination networks in mixed fruit orchards, in Southern Thailand. *Journal of Pollination Ecology*, *19*, 98–103. https://doi.org/10.26786/1920-7603(2016)7

Sritongchuay, T., Dalsgaard, B., Wayo, K., Zou, Y., Simla, P., Tanalgo, K. C., Orr, M. C., & Hughes, A. C. (2022). Landscape-level effects on pollination networks and fruit-set of crops in tropical small-holder agroecosystems. *Agriculture, Ecosystems & Environment*, *339*, 108112. https://doi.org/10.1016/j.agee.2022.108112

Sritongchuay, T., Hughes, A. C., & Bumrungsri, S. (2019). The role of bats in pollination networks is influenced by landscape structure. *Global Ecology and Conservation*, *20*, e00702. https://doi.org/10.1016/j.gecco.2019.e00702

Stewart, A. B., Srilopan, S., Wayo, K., Hassa, P., Dudash, M. R., & Bumrungsri, S. (2024). Bat pollinators: A decade of monitoring reveals declining visitation rates for some species in Thailand. *Zoological Letters*, *10*(1), 5. https://doi.org/10.1186/s40851-024-00228-x

Thébault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*, *329*(5993), 853–856. https://doi.org/10.1126/science.1188321

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*(10), 2270–2279. https://doi.org/10.1016/j.biocon.2009.12.004

Vidal, M. M., Banks-Leite, C., Tambosi, L. R., Hasui, É., Develey, P. F., Silva, W. R., Guimarães, P. R., & Metzger, J. P. (2019). Predicting the non-linear collapse of plant–frugivore networks due to habitat loss. *Ecography*, *42*(10), 1765–1776. https://doi.org/10.1111/ecog.04403

Viljur, M., Abella, S. R., Adámek, M., Alencar, J. B. R., Barber, N. A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B. R., Chao, A., Chergui, B., Choi, C., Cleary, D. F. R., Davis, T. S., Dechnik-Vázquez, Y. A., Downing, W. M., Fuentes-Ramirez, A., Gandhi, K. J. K., Gehring, C., … Thorn, S. (2022). The effect of natural disturbances on forest biodiversity: An ecological synthesis. *Biological Reviews*, *97*(5), 1930–1947. https://doi.org/10.1111/brv.12876

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer New York. https://doi.org/10.1007/978-0-387-98141-3

Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011). Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 1–22.

https://doi.org/10.1146/annurev-ecolsys-102710-145042

Wood, M. R., De Vries, J. L., Monadjem, A., & Markotter, W. (2024). Review and meta-analysis of correlates of home range size in bats. *Journal of Mammalogy*, *105*(5), 1044–1056. https://doi.org/10.1093/jmammal/gyae036

Zamora-Gutierrez, V., Pearson, R. G., Green, R. E., & Jones, K. E. (2018). Forecasting the combined effects of climate and land use change on Mexican bats. *Diversity and Distributions*, *24*(3), 363–374. https://doi.org/10.1111/ddi.12686

Zhang, X., Dalsgaard, B., Staab, M., Zhu, C., Zhao, Y., Gonçalves, F., Ren, P., Cai, C., Qiao, G., Ding, P., & Si, X. (2023). Habitat fragmentation increases specialization of multi-trophic interactions by high species turnover. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2009), 20231372. https://doi.org/10.1098/rspb.2023.1372