

RESEARCH ARTICLE

Spatiotemporal trends in floral visitation and interaction networks reveal shifting niches for bats in a Neotropical savanna

Ugo Mendes Diniz^{1,2}  | Ludmilla Moura de Souza Aguiar² 

¹Technische Universität München, Freising, Germany

²University of Brasília, Brasília, Brazil

Correspondence

Ugo Mendes Diniz

Email: ugomdiniz@gmail.com**Funding information**

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 304989/2019-3; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 88882.347259/2019-01; Rufford Foundation, Grant/Award Number: 24878-1

Handling Editor: Clare Stawski**Abstract**

1. Flower-visiting bats are important components of tropical pollinator communities, yet little is known about the structure of their pollination networks and how resource availability through time (seasons) and space (habitat heterogeneity) affects the extent to which bats interact with plants within a community-wide context. This information is key for the conservation of threatened nectarivore species, such as the Cerrado-endemic *Lonchophylla dekeyseri*, for which data on its specialization on floral-resources is scarce.
2. Within a seasonal and heterogeneous savanna in the central Brazilian Cerrado, we performed a year-round assessment of an inclusive assemblage of flower-visiting bats (both nectarivores and other guilds that can also feed on nectar) within a savanna-edge-forest gradient, the phenological trends and spatial distribution of bat and their resource plants, and the resultant temporal and spatial interaction networks between bats and plants in order to associate network structure to resource availability.
3. Clear spatiotemporal trends emerged in the community. Nectarivores dominated the flower-visiting niche outside forests and were prolific floral visitors, resulting in networks with lower specialization and modularity. These bats diverged into savanna foragers active during the wet season and the wet-dry transition, and edge foragers active mostly during the dry season. The latter group encompassed *L. dekeyseri*, which visited mostly *Bauhinia* species. Frugivores took over as main floral visitors within forests, as well as during peak dry season, when fewer fruits were available, resulting in more specialized and modular networks.
4. Our work shows that the turnover of floral resources across seasons and vegetation types has a defining role in bat-plant interactions and relates to network structure, as bat trophic guilds interact with plants in distinct habitats and times of the year. Frugivores dominate the flower-visiting niche in certain temporal and spatial subsets of the network, which calls for the inclusion of this guild in future studies. Moreover, the high visitation to *Bauhinia* species by *L. dekeyseri* during

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

the dry season might reduce competition with other nectarivores and is relevant to the management of the species, although more data is needed on its resource consumption on a larger time frame and across its geographic range.

KEYWORDS

bat pollination, Cerrado, chiropterophily, habitat heterogeneity, interaction networks, *Lonchophylla dekeyseri*, modularity, phenology

1 | INTRODUCTION

Plant–pollinator interactions are one of the foundations of ecosystem functioning worldwide. While pollen dispersal by animals ensures pollen flow and determines the reproductive success and demographics of plant species (Handel, 1983), flowering plants offer a valuable resource to a large variety of animals that is key to their survival, mainly pollen and nectar (Willmer, 2011). Resource availability, however, is not constant and entails a temporal (phenology) and a spatial (plant ranges and habitat heterogeneity) component, which leads to variable pollinator communities and interactions across seasons and along the landscape (Ogilvie & Forrest, 2017; Viana et al., 2012; Wray & Elle, 2015). As a result, pollination networks are often driven by the spatiotemporal overlap between plant and animal species (Olesen et al., 2007; Vázquez et al., 2009), especially in seasonal and structurally complex tropical environments (Chávez-González et al., 2020; Diniz & Aguiar, 2023a; Maruyama et al., 2014).

However, some pollinator groups present remarkable plasticity in their feeding niche, which may buffer them against the oscillations in the abundance of specific resource plants. This has been observed in pollinators that often feed on plants outside of their designed pollination syndromes, such as polylectic bees (Cane & Dunne, 2014), hummingbirds (Maruyama et al., 2013), and bats (Cordero-Schmidt et al., 2021; Heithaus et al., 1975). Bats, in turn, are a key part of tropical pollinator communities (Fujita & Tuttle, 1991; Machado & Lopes, 2004) and are recognized as relatively flexible floral visitors, feeding on a wide variety of flowering plants within (but incidentally also outside) the chiropterophilous syndrome and thus presenting temporal stability in their interactions (Cordero-Schmidt et al., 2021) and ensuring a steady energetic intake. However, even though bats are relatively opportunistic, diet-flexible pollinators, early evidence suggests that spatiotemporal overlap seems to play a defining role in their pollination networks (Diniz & Aguiar, 2023a).

This early evidence suggests the usage of foraging optimization by bats, which select foraging areas based on nectar density (Rothenwöhrer et al., 2011), and shows that, even though bats are morphologically able to visit a wide variety of flowers, they may refrain from doing so when their preferred resource is in flowering period and locally present. However, the study of bat–pollination networks is a nascent field, and little is known about the variables that lead to partner selection and network structure in this system. Recent studies on bat–flower networks have started to explore network topology and patterns of specialization in the Paleotropics

(Sritongchuay & Bumrungsri, 2016; Stewart & Dudash, 2017), and later in the neotropics Neotropics (Cordero-Schmidt et al., 2021; Queiroz et al., 2020), as well as drivers of network structure (Diniz & Aguiar, 2023a; Liévano-Latorre et al., 2023) and the effects of landscape structure on bat–flower interactions (Sritongchuay et al., 2019). However, still little is known about how the community-wide distribution of flowering resources in time and space affects the intensity with which bats from different trophic guilds engage in floral visitation and pollination networks and the structure of the resultant networks. Additionally, although there has been some work on the role of frugivores in pollination networks in the Paleotropics (Sritongchuay & Bumrungsri, 2016; Sritongchuay et al., 2019; Stewart & Dudash, 2017), these gaps are particularly strong also for Neotropical frugivores, which, although engaging in floral visitation when fruit availability is low (Heithaus et al., 1975), have so far received little attention in pollination and network studies (see Cordero-Schmidt et al., 2021; Queiroz et al., 2020).

Understanding how flower-visiting bats respond to shifts in the flowering plant community is not only key for understanding the ecology of bat pollination but also crucial for conserving Neotropical bat species. The biodiversity hotspot of the Brazilian Cerrado, the most diverse savanna in the world (Myers et al., 2000), is home to one of the few threatened nectar bat species in Brazil. *Lonchophylla dekeyseri* (Phyllostomidae) is a nectar bat endemic to the Cerrado classified as Endangered by the IUCN Red List and the Brazilian Environmental Ministry (Aguiar et al., 2006; Aguiar & Bernard, 2016). While its main threats are the loss of suitable habitats and roosting sites, more information about its basic ecology is needed to improve conservation strategies (Aguiar et al., 2006, 2010). Unfortunately, data on the dietary specialization and foraging pattern of *L. dekeyseri* are scarce and dated (see Aguiar et al., 2006; Coelho & Marinho-Filho, 2002). The species would thus profit from an expansion of its primary ecological data, as well as having its dietary specialization inserted in a community-wide context where the interaction (and potential competition) with other species can be assessed.

Thus, we aimed to explore how the spatiotemporal distribution of plant species affects bat activity, their role as floral visitors, and the structure of their interaction networks in a highly seasonal and heterogeneous Neotropical savanna. Specifically, we sampled an entire assemblage of plant visiting bats and inferred floral visitation via pollen analysis in order to understand how the occurrence of flower-visiting bats from different trophic guilds (e.g. nectarivores and frugivores) and the structure of their interaction networks with plants vary (i) throughout the year (in response to phenological turnover)

and (ii) across space (in response to the contrast between neighbouring habitat types in a vegetation mosaic), and how these variations are associated with shifts in the plant community.

2 | MATERIALS AND METHODS

2.1 | Study site and assessment of plant community

Data collection was carried out at the Parque Nacional de Brasília (PNB), Distrito Federal, Brazil, a Protected Area within the national capital Brasília (15°47'10.4"S, 47°54'26.3"W). The park has an area of 42,000 ha and is a representative site in terms of the variety of habitats found in the Brazilian Cerrado, specifically of the Central Brazilian Plateau, characterized chiefly by grasslands, savannas, flooded palm groves, and enclaves of humid and shaded gallery forests (Silva et al., 2006). The region is classified as a tropical wet savanna (Aw, Köppen scale) with a well-defined dry season between April and September (mean precipitation of 30 mm) and a wet season between October and March (210 mm) (precipitation data from the National Institute for Meteorology, <https://portal.inmet.gov.br/>). Therefore, plant phenology in the region is highly seasonal, with flowering periods generally confined to a few weeks or months (Batalha & Martins, 2004).

Within the PNB, we set eight fixed sampling sites where all subsequent data was collected. The sites were selected in a way to cover the entirety of the park's area, being separated by ca. 2 km from each other. Moreover, the sites encompassed the different vegetation seen in the savannas of the Central Brazilian Plateau that form the typical mosaic conformation of bushy savannas surrounding habitats of dense and shaded (ombrophilous) gallery forests along rivers (Silva et al., 2006). Therefore, we aimed to cover the environments within this savanna-forest gradient, thus resulting in the following sites: four typical savannas (SA) sites (P1–15°40'49.1"S, 48°04'07.9"W; P3–15°44'18.2"S, 47°59'10.0"W; P5–15°39'05.3"S, 48°00'06.7"W; P6–15°41'59.5"S, 47°59'52.2"W), dominated by dense, bushy vegetation and an assortment of small (<5 m) trees, dotted by few and isolated large trees (ca. 10 m). Two forest edge (FE) sites (P7–15°42'50.0"S, 48°03'38.9"W; P8–15°38'12.3"S, 47°56'11.7"W), spanning from the border of a gallery forest until 10 m towards the savanna. FEs usually harbour significantly distinct species assemblages, resembling a transitional community, and comprise a diversity of bushes, large herbs, small-to-medium trees (<10 m), palms, and vines. Finally, two forest interior (FI) sites (P2–15°37'36.8"S, 48°01'04.9"W; P4–15°41'38.5"S, 47°58'12.0"W), marked by humid and ombrophilous forests characterized by large trees (10–20 m) and some patches of a dense understory in areas with secondary growth.

Savannas had double the number of sites compared to other vegetation types to balance capture rates, as its sparse density of plants and lack of natural flying corridors lead to lower chances of intercepting bats. Grasslands, the emblematic habitats in the biome, were excluded from the sampling as terrestrial herbs are rarely pollinated

by bats (Diniz et al., 2019; Fleming et al., 2009). To characterize the composition and phenology of the plant community in the sites, we set a 1 km transect in each along the vegetation type of interest. We walked along the eight transects monthly for a phenological year (Jan–Feb 2020, Aug–Dec 2020, Mar–Jul 2021), recording the number of flowering individuals from plant species of interest by free observation in a radius of ca. 10 m in each sampling date. Species of interest were any flowering species that (i) are known to be bat-pollinated according to literature or (ii) had chiropterophilous traits (criteria of Faegri & Van Der Pijl, 2013). Additionally, as bats may visit plants from other syndromes, any plant that (iii) produced nectar and/or pollen as a main floral reward and that simultaneously had a corolla diameter (or inflorescence diameter, in the case of species with pseudanthia sensu Classen-Bockhoff, 1990) of at least 1 cm to allow bat visitation were included as species of interest. In individual flowers, this measure refers either to the opening of the corolla tube (in tubular flowers) or the diameter of the corolla base where nectar is produced and accumulated (in non-tubular flowers). Besides recording their abundance, we collected pollen from open anthers from these species to build a palynological inventory for reference. Plants were identified to the lowest-possible taxonomical level, and vouchers were deposited at the Herbarium at Universidade de Brasília, DF, Brazil (Herbário UB).

2.2 | Bat community and interactions with plants

Bats and their interactions with flowering plants were also sampled monthly via direct captures in all eight sites. In each sampling night, 10 mist nets (2.6 × 12 m, polyester, denier 75/2, 36 mm mesh, Avinet, Japan) were set randomly at the understory (in FE and FI sites, nets were placed strategically along natural flight corridors) and left open from 18:00 until 00:00, at least 5 days before or after full moons to avoid interference. Sampling months were Oct 2019–Feb 2020, Aug–Sep 2020, and Mar–Jul 2021, and resulted in 172,224 m²h of sampling effort (sensu Straube & Bianconi, 2002). All captured bats from the family Phyllostomidae were processed for pollen. First, pollen was collected directly after removal from the net via safranin-stained gelatin cubes (Voigt et al., 2009) rubbed throughout the entire external body of bats, including all patagia. Tools were sterilized and rubber gloves were used and exchanged between bat individuals to avoid contamination. Cubes were then stored individual for further analysis. To potentially complement interaction data, bats were placed inside cotton bags for at least 30 min and faecal samples were collected occasionally, whenever bats defecated. Faecal samples were stored in individual paper bags for further analysis. Afterwards, bats were identified according to a specialized key (Díaz et al., 2016) and released. Vouchers of bat species, when the collection was possible, were deposited in the Mammal Collection of the Universidade de Brasília (permissions to handle and collect bats were issued by relevant institutions, CEUA 23106.119660/2019-07, SISBIO 70268).

Pollen samples were analysed individually via optical microscopy, and pollen grains were identified using our personal palynological

collection (see section above). Identification was made to the lowest-possible taxonomical level, and morphotypes were, when possible, associated with plants occurring at the site. The presence of pollen on the bodies of bats was thus assumed to correspond to floral visitation, and only pollen grains of a morphotype numbering five or more in a sample (or 10 or more, for small grains with less than $40\mu\text{m}$ of polar diameter) were considered an interaction between the associated plant and the individual of the bat species. Faecal samples were analysed via optical microscopy by a specialist (see Acknowledgements).

2.3 | Data analysis

2.3.1 | Temporal patterns

We searched for phenological trends in the flowering plants visited by bats and the year-round bat species' activity (measured as number of captures) using circular statistics. This is a widespread and effective method to identify aggregate (non-random) distributions of a biological phenomenon within a given timeframe (Morellato et al., 2010). We used the absolute number of captures of each bat species (pooled across all sampling points) per month as a proxy for the activity intensity. For plants, we used the number of flowering individuals of each species (summed across all transects) as a value of monthly flowering intensity. Months were transformed into degree values (0° – 360° , 30° intervals), and, for all species, we measured the mean degree of the Rho vector (r) and its length for each variable to test for aggregation. The r vector varies from zero to one. Higher values indicate aggregated data, suggesting seasonality. A Rayleigh test was performed for each variable to test the significance of data aggregation (Fisher, 1995).

Additionally, bat species were pooled into either nectarivores (subfamilies Glossophaginae and Lonchophyllinae) or other dietary guilds (frugivores or insectivores). Plants were pooled in either chiropterophilous or plants of other syndromes (see Section 2.3 above). The same procedure to test for aggregate data was repeated for each of the four groups to test for seasonality at the trophic guild level. Analyses were performed in R 4.1.0 (R Core Team, 2021) using the CIRCULAR package (Lund et al., 2017).

2.3.2 | Spatial patterns

We employed principal component analysis (PCA) to ordinate sampling sites according to species occurrences and obtain a graphical summary of community composition according to vegetation type (SA, FE and FI). Species were used as ordination variables and their absolute frequencies were used to assemble a matrix of species occurrences per sampling site, pooling all months. As defined above, bat species' frequencies in a site correspond to the sum of captured bats in that site, whereas plant species' frequencies correspond to the abundance of flowering individuals found in the transection belonging to the site.

2.3.3 | Spatiotemporal trends of nectarivory and bat-plant interactions

In order to quantify the activity of different groups of flower-visiting bats (nectarivores and non-nectarivores) and their engagement in floral visitation, we measured the two following variables: (i) the ratio of nectarivores (RON), or the ratio of Glossophaginae and Lonchophyllinae bats captured concerning total captures in a given time or location, and (ii) participation of other guilds (POG), or the proportion of interactions with plants that were made by non-nectarivores concerning all interactions in a given time or location. RON and POG values were assigned for each sampling month (using sites as replicates) and each sampling site (using months as replicates). To detect potential seasonality in RON and POG, we employed circular statistics as described in the section *Temporal patterns* above. To assess spatial trends, RON and POG were compared across the three vegetation types through one-way ANOVAs.

In order to explore how interactions are distributed across different seasons and vegetation types, we assembled weighted bipartite networks between bats and plants. Network analysis is a powerful tool to assess how interactions scale up among several sets of species and yields insights into community assembly (Proulx et al., 2005). Thus, we created a set of networks corresponding to different seasons or habitats. Four temporal networks were built, each corresponding to the bats captured and their interactions with plants in distinct seasonal windows in the study site characterized by their own assemblages of flowering plants: peak dry season (May–July), dry-wet transition (August–October), peak rainy season (November–January) and rainy-dry transition (February–April). Likewise, we assembled three spatial networks corresponding to the bats and their interactions captured in each vegetation type included in the study (SA, FE, and FI). In all networks, interactions (i.e. matrix cells a_{ij}) corresponded to the number of bat individuals of species i interacting with plant species j .

For each of the networks, we calculated two structural indices that translate different aspects of interaction distribution. First, complementary specialization ($H2'$), which measures to which extent interactions between species overlap (Blüthgen, 2010). Lower values ($H2' \rightarrow 0$) suggests a generalized network where interactions are not complementary, while high values ($H2' \rightarrow 1$) indicate high specialization. Second, weighted modularity (Q_w). Modularity in pollination networks is often associated with niche specialization, as species of consumers (floral visitors) tend to interact more frequently with a certain group of plants due to morphological specialization or environmental variables, thus creating interaction modules (Olesen et al., 2007). Low Q_w values ($Q_w \rightarrow 0$) suggest a non-modular network without subgroups, while high values ($Q_w \rightarrow 1$) indicate a modular network will well-defined modules. Q_w was quantified using the DIRTLPAwb+ algorithm (Beckett, 2016), and both metrics were estimated in the BIPARTITE package (Dormann et al., 2008).

3 | RESULTS

3.1 | Community and spatiotemporal patterns

We captured a total of 386 bats, from which 369 from 12 species belonged to the family Phyllostomidae and subfamilies Carollinae, Glossophaginae, Lonchophyllinae, Micronycterinae and Stenodermatinae. From these individuals, 162 were transporting pollen. A total of 302 interactions with 35 pollen types were registered, associated with both chiropterophilous and non-chiropterophilous species. Out of this species pool, 17 plant species (251 interactions with 138 bats of 12 species) were found in the site and could have spatiotemporal data tracked, thus being included in the study. An overview of bats and flowering plants included in the study is illustrated in Figure 1, and a list of species composing the interactions network and their occurrence by vegetation types can be found in Table S1. Additionally, a thorough list with all bat species captured and all the plants species of interest registered in the site are found in Tables S2 and S3, respectively.

Bats and their resource plants showed conspicuous trends in their distribution across time and space. Concerning plant phenology, flowering periods and the abundance of flowering plants were seasonal and strongly skewed towards the transition between the dry and wet seasons for chiropterophilous plants, peaking in September (Figure 2a,b), due mainly to the flowering of the abundant and seasonal species *Caryocar brasiliense* and *Bauhinia goyazensis* (Figure 2a; Table S1). During the dry season, resource availability was maintained by less abundant plants, such as *Bauhinia rufa* and *Pseudobombax* spp. (Figure 2a; Table S1). The flowering of non-chiropterophilous plants was also seasonal and complementary to chiropterophilous plants, with higher intensity during the wet season and showing an apparent bimodal distribution with flowering peaks in March due to the flowering of the ornithophilous and abundant *Psittacanthus robustus*, and in October due to *Lamanonia ternata* (Figure 2b; Table S1).

Bat capture rates were also seasonal, though not as conspicuous as plant flowering. The detectability of nectarivores peaked during the wet season (November), synchronized with the peak flowering of chiropterophilous plants and continuing shortly after (Figure 2c,d). Only the nectarivores *L. dekeyseri* and *Anoura caudifer* were registered (Figure 2c) during dry season peak (June–July). A surge in the abundance of nectarivores, specifically the common *Glossophaga soricina*, also occurred at peak wet season and was aligned with the flowering of the ornithophilous *P. robustus*. Capture rates of frugivores were variable and showed little seasonality (Figure 2c,d), with a slight peak in the wet season (January) but also occurring in large numbers throughout the dry season.

In terms of the spatial distribution of species, vegetation types diverged considerably in species compositions. The principal components for bat and plant species compositions, explained, respectively, 64.55% and 53.39% of all variation in the data (Figure 3). FI sites were strongly characterized by the occurrence of all species of

primarily frugivorous Stenodermatinae bats and negatively related to the occurrence of nectarivores, the other frugivore *Carollia perspicillata* (Carollinae) and the insectivore *Micronycteris schmidtorum* (Figure 3a). In terms of plant composition, FI sites had few plants of interest recorded but were marked mainly by *Combretum fruticosum* (Combretaceae), which was visited exclusively by frugivores, and *Hymenaea courbaril* (Fabaceae), visited by nectarivores (Figure 3b).

Forest edge sites were strongly correlated with the occurrence of the nectarivores *Lonchophylla dekeyseri* and *A. caudifer* (Figure 3a), as well as the resources mostly consumed by these species, that is *Bauhinia goyazensis*, *B. rufa* and *Lafoensia pacari* (Figure 3b). *Lonchophylla dekeyseri* was particularly associated to FE sites, with 20 individuals (90.1% of total captures) being registered in this type of environment and 12 (55.0%) within the P8 site, which was strongly correlated with *Bauhinia* spp. (Figure 3b). FEs were also somewhat associated with the generalized frugivore *C. perspicillata*, which fed strongly on *L. pacari*. *Lamanonia ternata* (Cunoniaceae), which was exclusively visited by Stenodermatinae frugivores, was also mostly found in this environment. SA sites were in turn characterized by an increased abundance of *G. soricina* and the larger *Anoura geoffroyi*, as well as *C. perspicillata* and of *M. schmidtorum* (Figure 3a).

3.2 | Spatiotemporal trends in floral visitation and interaction networks

The relevance of different bat groups as floral visitors and the structure of their interaction network varied across seasons and vegetation types (Figures 4 and 5). Nectarivore ratios were aggregate ($r=0.31$, $p<0.001$), peaking in the dry-rainy transition (October, mean degree = $276.11^\circ \pm 86.7^\circ$) (Figure 4a). *Caryocar brasiliense* was the most-consumed floral resource in this period, mainly by the common *G. soricina*, and the network during this period was the most generalized and least modular (Figure 4b). Although its interactions were concentrated between October and November (17 interactions, or 50.0%), *L. dekeyseri* rarely visited abundant species with copious nectar that were flowering at the time (e.g. *C. brasiliense* and *P. robustus*), sticking to *Bauhinia* spp, mainly *B. goyazensis*. The peak-dry network was the only one that did not include *G. soricina* and had the lowest nectarivore diversity, while *L. dekeyseri* and *A. caudifer* remained and visited mainly the tube-flowered *Bauhinia* spp. The peak-dry period also frugivores overtaking as main floral visitors (June, $r=0.33$, $p<0.001$, $d=157.58^\circ \pm 85.19^\circ$) (Figure 5a), especially the large *Artibeus planirostris* and *Platyrrhinus lineatus* visiting the wide-flowered *C. pentandra*, *Pseudobombax* spp. and *L. pacari*. The peak dry network was the most specialized and most modular (Figure 4b).

In FI sites, nectarivorous bats were rarely recorded in comparison to other environments, resulting in a significantly lower RON ($F_{2,33}=6.42$, $p<0.005$) (Figure 5a). Within these environments, other guilds (mainly frugivores, considering a single interaction from an insectivore) showed the highest participation as floral visitors in forest-interior sites ($F_{2,33}=4.36$, $p<0.05$) (Figure 5a), interacting mostly with

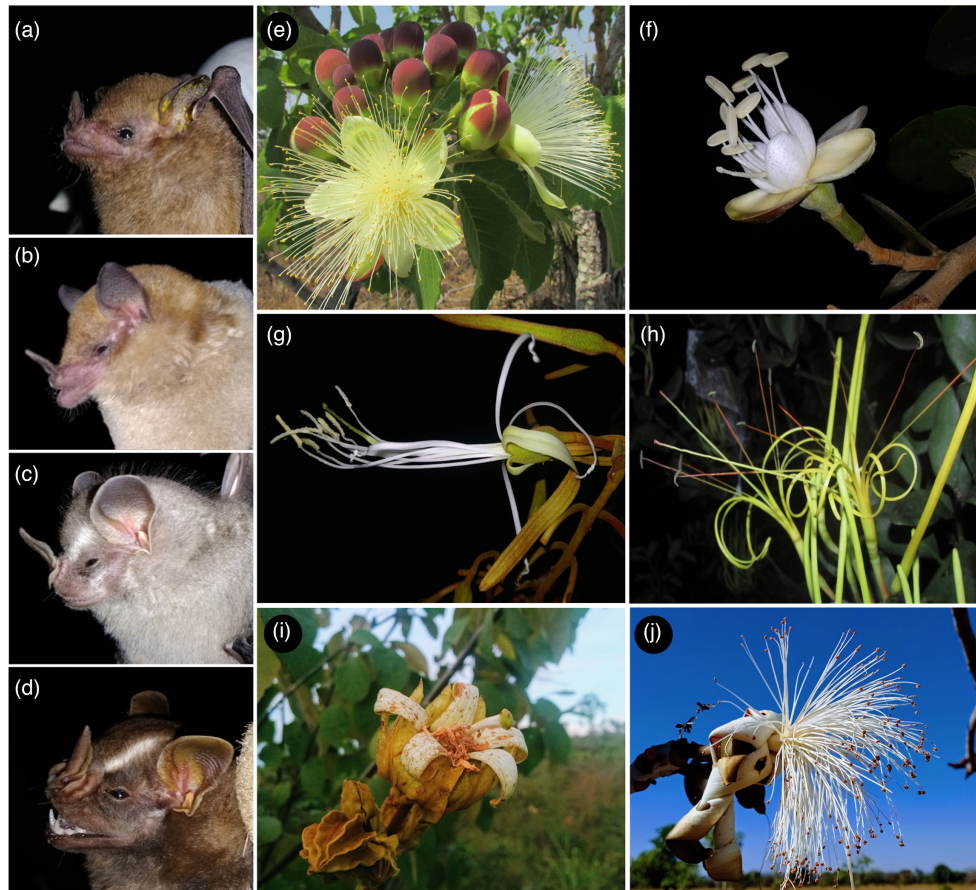


FIGURE 1 The study site has a selection of flower-visiting bat species (a–d) and bat-visited plants (e–j). Nectarivores: (a) *Glossophaga soricina* (Glossophaginae) and (b) *Lonchophylla dekeyseri* (Lonchophyllinae). Frugivores (Stenodermatinae): (c) *Dermanura cinerea* and (d) *Artibeus lituratus*. Open-flowered plants: (e) *Caryocar brasiliense* (Caryocaraceae) and (f) *Hymenaea stigonocarpa* (Fabaceae). Tube-flowered plants: (g) *Bauhinia goyazensis* (Fabaceae) and (h) *Psittacanthus robustus* (Loranthaceae). (i) *Luehea grandiflora* (Malvaceae) and (j) *Pseudobombax longiflorum* (Malvaceae).

FI (*C. pentandra*, *C. fruticosum*) or FE plants (*L. ternata*) and forming the most specialized and modular network (Figure 5b). The nectarivores *A. caudifer* and *L. dekeyseri* were more frequent visitors in FE, especially to *Bauhinia* spp. The SA network was dominated by the *G. soricina*, which visited a diverse range of typical savanna plants (*C. brasiliense*, *P. robustus* and *H. stigonocarpa*). It was also the most generalized and least modular (Figure 5b). Although nectarivores were sporadically captured inside forests, they only interacted with plants in SA or FE.

4 | DISCUSSION

Our work provides the first assessment of the temporal and spatial patterns of an entire assemblage of flower-visiting bats, their resource plants and interaction networks. Our results largely reaffirm the generalized nature of bat-plant networks (Cordero-Schmidt et al., 2021; González-Gutiérrez et al., 2022; Mello et al., 2011; Queiroz et al., 2020), corroborating the relatively high trophic plasticity of phytophagous bats. However, we show evidence of a strong shift in bat species engaging in floral visitation, and in the structures of interaction networks across seasons

and habitat types in a Neotropical savanna. We thus extend the evidence of network stability across years brought by Cordero-Schmidt et al. (2021) to show that such stability might be achieved by an intra-annual variability of bat niches. We also show that network structure is not only affected by anthropogenic variations in the landscape (Sritongchuy et al., 2019) but also by naturally occurring habitat heterogeneity.

Moreover, we highlight that other trophic guilds, such as large frugivores, not only are relevant components of pollen-transport networks (González-Gutiérrez et al., 2022; Mello et al., 2019; Sritongchuy & Bumrungsri, 2016) but can in fact dominate the floral visitation niche under particular spatiotemporal circumstances. In the following sections, we will address the temporal and spatial axes that seem to drive community-wide bat-flower interactions.

4.1 | Seasonality in the Cerrado: Niche turnover for flower-visiting bats

Temporal interaction networks revealed a species turnover not only in the key flowering species in the community, which is expected within

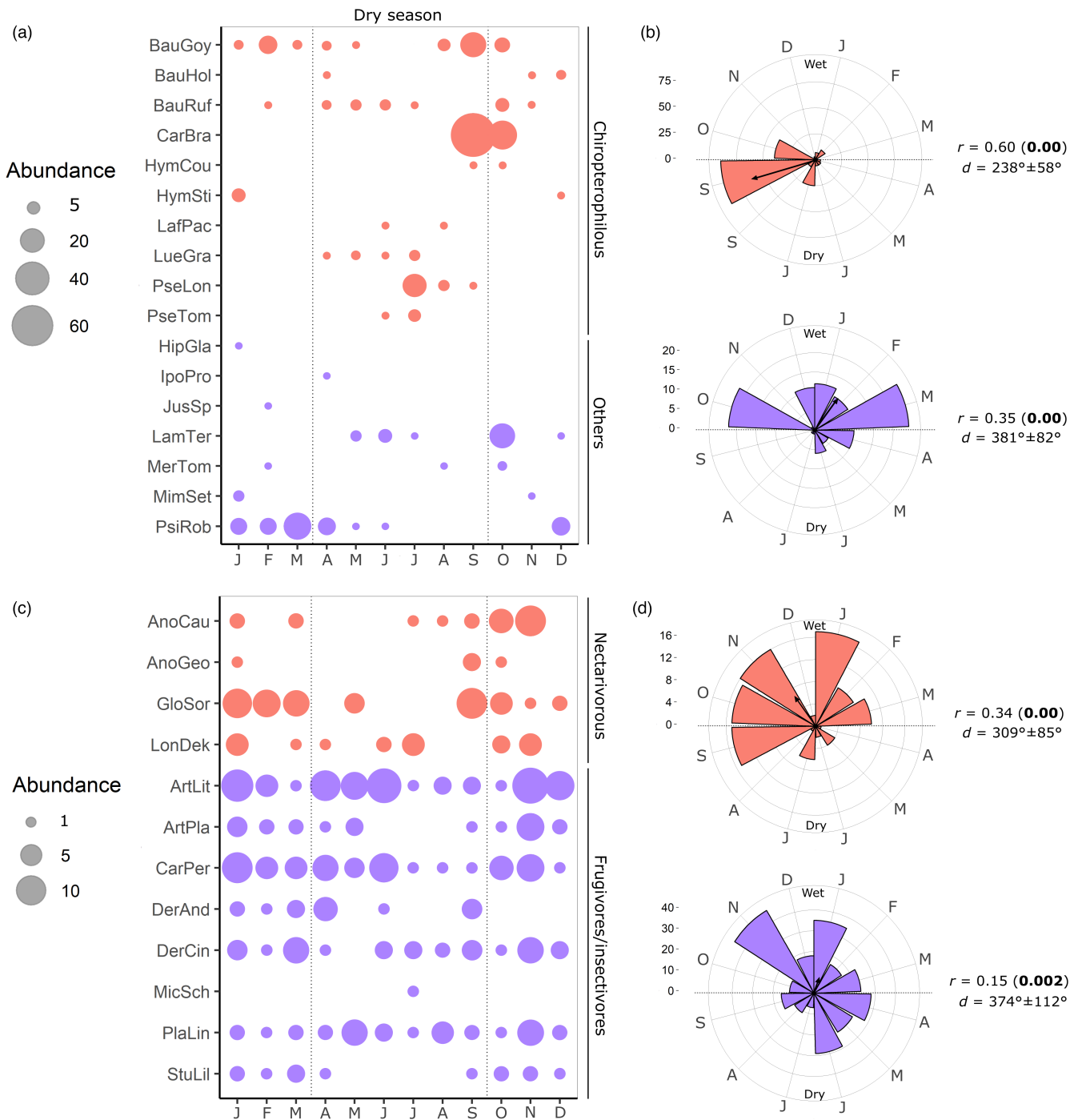


FIGURE 2 Flowering phenology of plants consumed by bats (a, b) and the distribution of the abundance of flower-visiting bat species across time (c, d) in a Cerrado site. Species in both panels are divided by colour as associated with specialized bat-pollination systems (nectarivores and chiropterophilous plants in salmon) or with not (frugivorous or insectivorous bats and non-chiropterophilous plants in purple). (a) and (c) picture species-specific abundances, whereas (b) and (d) picture the circular distribution of pooled species in each group, followed by the length of the Rho vector (r) with the significance between parenthesis, and the mean degree (d). The dry and wet seasons are separated by dashed lines. Species codes are found in Table S1.

the highly seasonal Cerrado environment (Batalha & Martins, 2004) but also in the bat species engaging in nectarivory and interacting with plants. Nectarivores diverged into two groups: those active during the wet-dry transition (*G. soricina*, *A. caudifer*), and those that sustained themselves through the dry season (*L. dekeyseri*), the former

associated with the flowering of abundant plants with copious nectar such as *Caryocar brasiliense* (Caryocaraceae) (Gribel & Hay, 1993) and *Psittacanthus robustus* (Loranthaceae) (Diniz et al., 2022). This turnover agrees with previous evidence of an energetic niche divergence among bats. Tschapka (2004) showed that after peak nectar

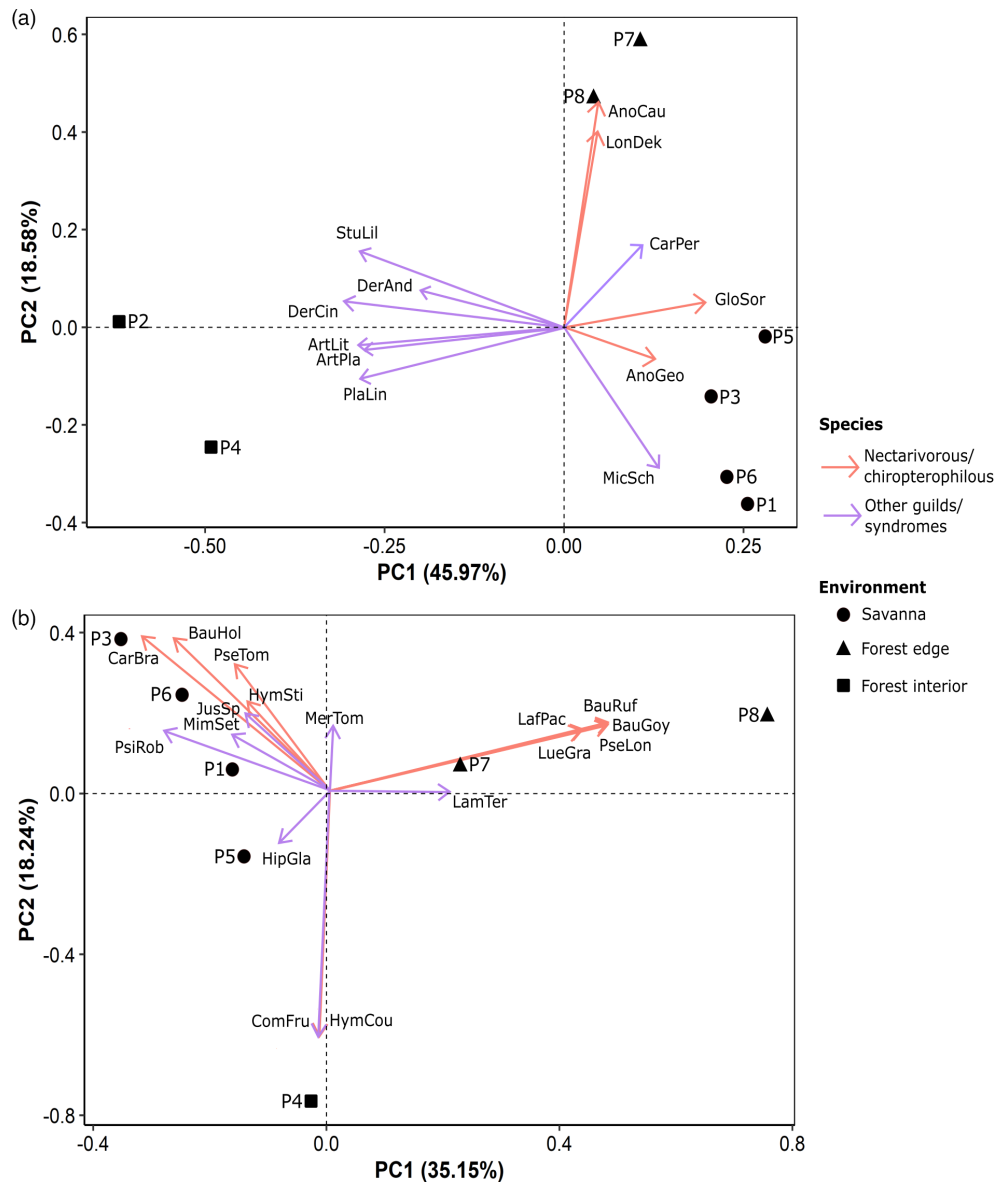


FIGURE 3 Distribution of sampling sites across the two main principal components (PC, followed by % of explained variation) according to bat (a) and plant (b) species compositions. Species loadings (arrows) are coloured according to their association with the bat-pollination system (nectarivores and chiropterophilous plants in salmon) or with not (frugivorous or insectivorous bats and non-chiropterophilous plants in blue). One of the forest interior sites (P2) had no interest plants recorded, and thus does not appear in panel (b). Species labels can be found in [Table S1](#).

availability in a plant community in Costa Rica, *Glossophaga comissaris* shifted to frugivory while rarer and more specialized bats remained and fed on remaining flowers. Indeed, some nectarivores shift to an insect- or fruit-based diet if nectar reaches an availability threshold (Clare et al., 2014), depending on their ability to consume harder food items (e.g. bats with shorter and more robust rostra) (Santana et al., 2012).

This would explain the permanence of *L. dekeyseri*, the most morphologically specialized bat in the assemblage (Diniz & Aguiar, 2023a), which would sustain itself with the various tubular *Bauhinia* flowering year-round in the area. Gonzalez-Terrazas et al. (2012) showed that longer-tongued bats are more efficient in removing lower quantities of nectar from smaller and tubular flowers, such as in *Bauhinia*

(Hokche & Ramirez, 1990), which could have led other bat species to resort to alternative resource types or emigrate locally when nectar was running low, while *L. dekeyseri* remained. The overall result is a smaller, more specialized network with more defined modules during peak dry season, highlighting the role of energy density as a key niche axis for nectar bats. Coelho and Marinho-Filho (2002) and Aguiar et al. (2006) also found high frequencies of *Bauhinia* pollen on *L. dekeyseri* at roosts in a nearby area, alongside a high consumption of insects and fruits during the rainy season, which would aid the species in keeping a steady energy intake throughout the year. However, the low to no visitation to abundant chiropterophilous plants during the wet season and the wet-dry transition in both the literature and in the current work is truly remarkable and points to a

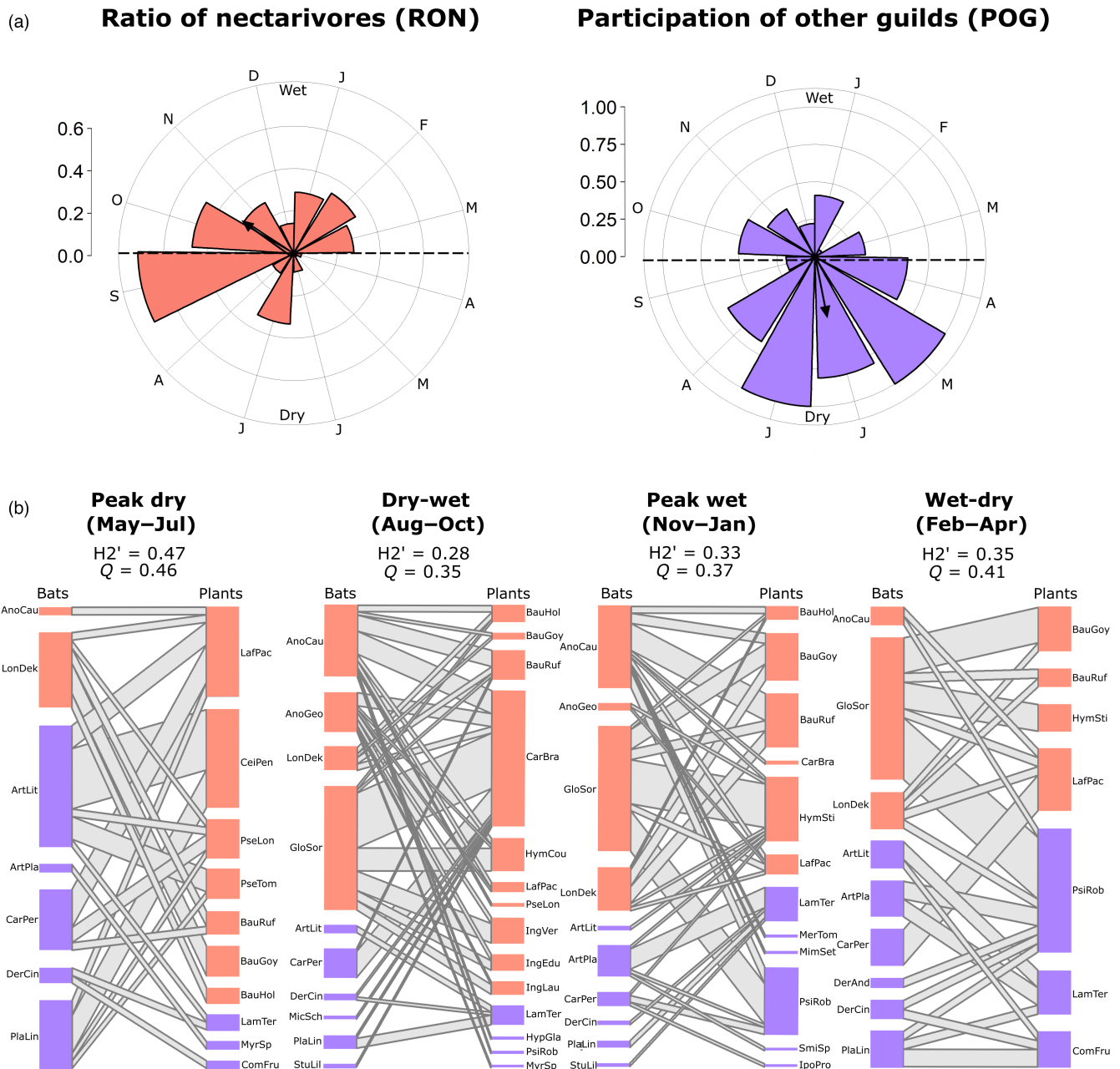


FIGURE 4 Temporal trends in the interaction networks between flower-visiting bats and plants in the Brasília National Park. (a) Temporal variation in the ratio between nectarivores and frugivores (left) and the proportion of frugivores that visited plants (right). Arrows indicate the angle and length of the vector. (b) Partial networks from the different periods during one seasonal year and their respective specialization and modularity indices. Species are separated by colour as within chiropterophily (nectarivores and chiropterophilous plants) and outside chiropterophily (frugivores and non-chiropterophilous plants). Species labels are found in [Tables S1](#), except for the following pollen types that were not identified to the species level and could not be associated to a species, or that were not found on transections: CeiPen—*Ceiba pentandra* (Malvaceae); MyrSp—Myrtaceae; IngVer—*Inga vera* (Fabaceae); IngEdu—*I. edulis*; IngLau—*I. laurina*; SmiSp—*Smilax* sp. (Smilacaceae).

preference to this specific plant genus, likely a result of niche partitioning with sympatric nectarivores.

Frugivores greatly contributed to the seasonal specialization of the network. The dry season in the Cerrado is marked by low availability of fruiting chiropterocoric trees (Amaral et al., 2016), and Stenodermatinae and Carollinae bats may resort to nectar during such periods (Heithaus et al., 1975). Their dominance as

floral visitors during the dry season would thus correspond to an attempt to keep up with energetic needs. Although able to feed on a variety of complementary dietary items, including insects (Pellón et al., 2022), pollen and nectar (Fleming et al., 2009) and even leaves (Rocha et al., 2017), frugivorous bats in our study appear to be much more constrained (“specialized”) in the plants that they consume for nectar or pollen, differing from the prolific nectarivore counterparts

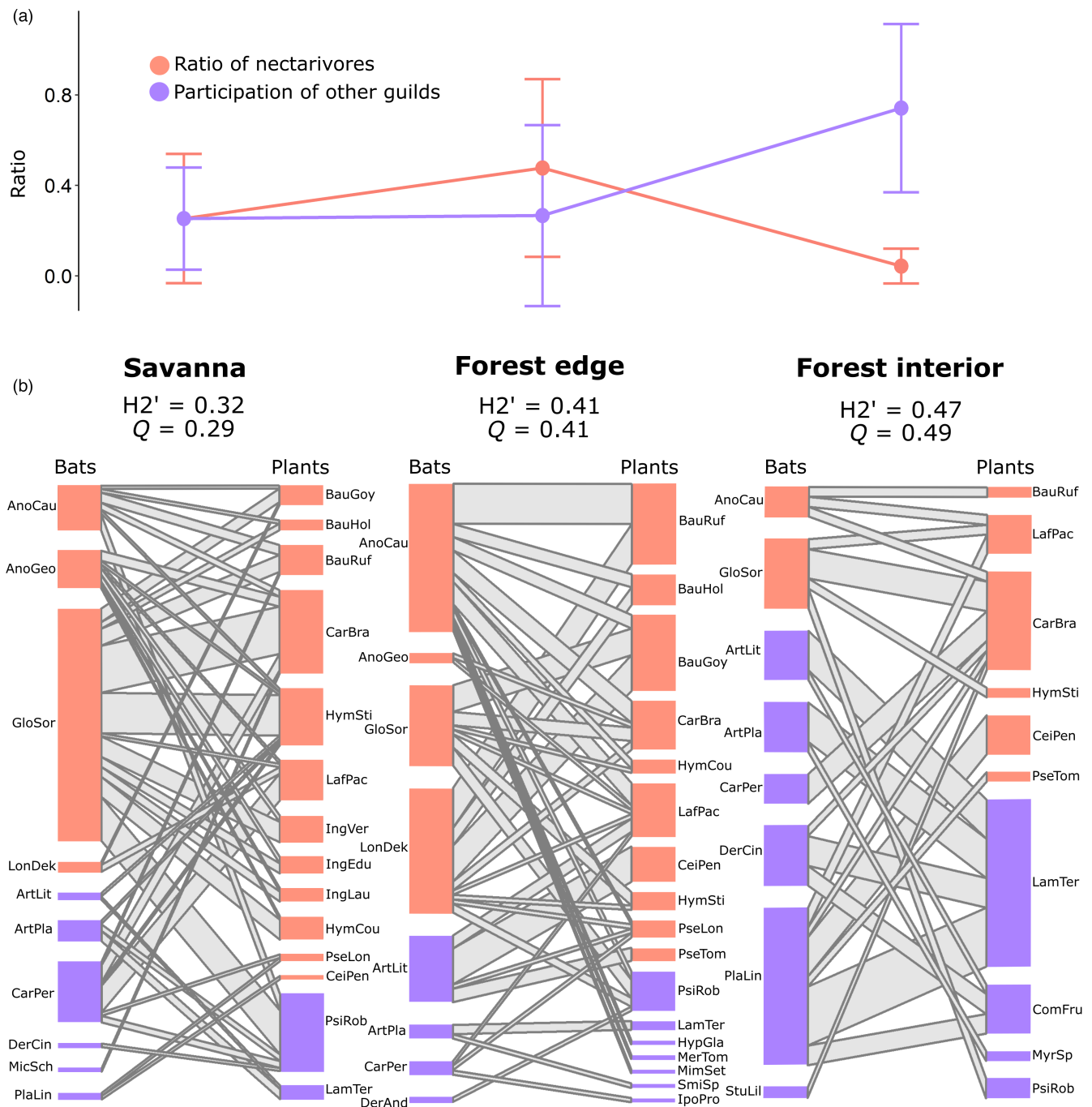


FIGURE 5 Spatial trends of the interaction network between flower-visiting bats and plants. (a) Variation in the ratio between nectarivores and frugivores and the importance of frugivores as floral visitors across the different vegetation types. (b) Partial networks from the different vegetation types in which bats were captured. Species are separated as within chiropterophily (nectarivores and chiropterophilous plants) and outside chiropterophily (frugivores and non-chiropterophilous plants). Species labels are found in Tables S1, except for the following pollen types that were not identified to the species level, or that were not found on transections: CeiPen—*Ceiba pentandra* (Malvaceae); MyrSp—Myrtaceae; IngVer—*Inga vera* (Fabaceae); IngEdu—*I. edulis*; IngLau—*I. laurina*; SmiSp—*Smilax* sp. (Smilacaceae).

likely due to morphological constraints, as they do not possess the fine morphophysiological traits to hover and visit small tubular flowers, and thus require large open flowers or inflorescences (Fleming et al., 2009). Moreover, pollen, and not nectar, may be actively searched for by frugivorous bats. *Pseudobombax* flowers, for instance, are large and rich in pollen (sometimes only offering

pollen as a reward, such as in *P. munguba*; Gribel & Gibbs, 2002), and often have large frugivore or insectivore bats, as well as non-volant mammals, as their main visitors (Gribel, 1988; Gribel & Gibbs, 2002; Heithaus et al., 1975). The visitation of certain species by frugivores for pollen (e.g. *P. longiflorum*, *P. tomentosum*) could also result in a smaller pool of realized interactions in the study system, further

increasing network specialization. The relatively modular and specialized network observed during the dry season, therefore, reflects the predominance of bats with a narrower range of interacting partners, be it the long-tongued nectarivorous *Lonchophylla* bats or Stenodermatinae frugivores.

4.2 | Spatial heterogeneity as a source of resource specialization

The central highlands of the Cerrado offers distinct spatial niches that encompass contrasting microclimatic traits and plant species composition that affect animal species distributions (Silva et al., 2006). The stark contrast of thin strips of dense and shaded forests surrounded by a matrix of savannas and grasslands greatly determines bat distributions and foraging areas of bats. Frugivorous bats, for instance, particularly from the subfamily Stenodermatinae, roost within gallery forests and feed on the abundant chiropterocoric plants found therein (Oliveira et al., 2019). In the present work, this pattern translated into a clear preference of frugivorous Stenodermatinae bats for forest interiors, while showing that floral visitation in these types of environments is also dominated by these opportunistic floral visitors, which apparently choose not to deviate much from their preferred foraging areas to seek floral resources when fruits are scarce in the dry season. Forest edges, although an intermediate vegetation type with an equal presence of nectarivores and frugivores, likely aided frugivores in their permanence within forests by buffering their exit due to the high abundances of the tree *Lamanonia ternata*, a species with large inflorescences and exposed flowers frequently visited by frugivores.

Nectarivores, in turn, were rarely captured in forest interiors, and those captured there (*G. soricina*, *A. caudifer*) had pollen from matrix plants. This may suggest that these bat species use the forest for other needs besides feeding, such as roosting (both species are known to roost in hollow trees and logs, Gardner, 2008), whereas *L. dekeyseri* is a strict cave-dweller (Aguiar et al., 2010), and thus does not need to interact with forests. Interestingly, forest-roosting nectarivores normally engage with chiropterophilous plants within other, more homogeneous forested biomes, such as the Atlantic Forest (Sazima et al., 1999). The stark spatial heterogeneity of the Cerrado, coupled with a higher diversity of unique species in the matrix than within forests (Lenza et al., 2015) may have aided in keeping nectarivores out of this vegetation type and into the bushy savanna, particularly as terrestrial bat-pollinated plants seem to be more frequent in open or edge environments with sparse vegetation (Diniz et al., 2019; Machado et al., 1998; Machado & Lopes, 2004).

Additionally, nectarivores have a higher field metabolic rate than frugivores and require many more visits to flowers to meet their daily energetic needs in comparison to the foraging intensity required by fruit-consuming bats (Voigt et al., 2006). Therefore, nectarivores engage in a precise and effective trap-lining behaviour, often between sparsely distributed plants, to meet energetic needs

via nectar consumption, optimizing their foraging range and duration according to nectar availability (Fleming, 1982; Rothenwöhler et al., 2011). Therefore, a preference for the matrix and forest edges where chiropterophilous plants are more abundant is warranted for nectarivores but is unattractive for larger frugivores, which may consume a series of other food items more efficiently. Although able to have large home ranges sizes, frugivores appear to stick mostly to core forested areas where roosts and fruits are found (Loayza & Loiselle, 2008; Ripperger et al., 2015), while, apparently, consuming nectar only as a secondary and complementary resource in times of lower fruit availability.

Even within nectarivores outside forests, different foraging strategies seem to be employed, also resulting in a partitioning of the spatial niche. Nectarivores tend to have foraging areas based on nectar density (Rothenwöhler et al., 2011), which likely led to the preferences of certain bat species for energy-dense flowers found in savannas only (e.g. *C. brasiliense*) and the high adherence of the more specialized *L. dekeyseri* to species with lower nectar density found in edges. This niche partitioning may be facilitated by the enhanced spatial working memory and reinforced learning used by nectarivorous bats (Goldshtein et al., 2020; Henry & Stoner, 2011), which explains the fidelity of *L. dekeyseri* to a specific edge site where *Bauhinia* was found in highest densities in the park.

Therefore, although *L. dekeyseri* may reach up to 3.8km in distance from its core area while foraging, thus being resistant to fragmentation (Aguiar et al., 2014), the species appears to stick to reliable and predictable resource patches where its interaction partners are found. When considering conservation measures for the species, which has its distribution centered in the Cerrado highlands where the work was conducted (Aguiar et al., 2014), it is thus key to consider the maintenance of these very short savanna-forest transitional habitats close to known roosts, as they seemingly account for a large proportion of the floral resources consumed by the species.

AUTHOR CONTRIBUTIONS

Ugo Mendes Diniz and Ludmilla Moura de Souza Aguiar conceived the study and the methodology. Ugo Mendes Diniz performed data collection, curation and analyses, and prepared the original draft of the manuscript. Ugo Mendes Diniz and Ludmilla Moura de Souza Aguiar contributed to the final version of the manuscript.

ACKNOWLEDGEMENTS

This work was funded by the Rufford Foundation (24878-1), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (88882.347259/2019-01), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (304989/2019-3) and supported logistically by FINATEC (Brasília). We thank the staff of the Brasília National Park for supporting fieldwork; and Igor Daniel Bueno-Rocha, Priscilla Petrazzini and Guilherme Dantas for their help in the field; and Lucas de Toledo Lauretto University of Brasília/Mamiraua Institute for processing faecal contents and aiding fieldwork. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the GitHub Digital Repository <https://doi.org/10.5281/zenodo.7814619> (Diniz & Aguiar, 2023b).

ORCID

Ugo Mendes Diniz  <https://orcid.org/0000-0003-3360-8314>

Ludmilla Moura de Souza Aguiar  <https://orcid.org/0000-0002-9180-5052>

REFERENCES

- Aguiar, L., & Bernard, E. (2016). *Lonchophylla dekeyseri*. The IUCN red list of threatened species 2016, e.T12264A22038149. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T12264A22038149.en>
- Aguiar, L., Bernard, E., & Machado, R. B. (2014). Habitat use and movements of *Glossophaga soricina* and *Lonchophylla dekeyseri* (Chiroptera: Phyllostomidae) in a Neotropical savannah. *Zoologia (Curitiba)*, 31, 223–229. <https://doi.org/10.1590/S1984-46702014000300003>
- Aguiar, L., Brito, D., & Machado, R. B. (2010). Do current vampire bat (*Desmodus rotundus*) population control practices pose a threat to Dekeyser's nectar bat's (*Lonchophylla dekeyseri*) long-term persistence in the Cerrado? *Acta Chiropterologica*, 12(2), 275–282. <https://doi.org/10.3161/150811010X537855>
- Aguiar, L. M. S., Machado, R. B., Ditchfield, A. D., Zortéa, M., Marinho-Filho, J., & Coelho, D. (2006). *Plano de Ação Para a conservação do morceguinho do cerrado Lonchophylla dekeyseri/action plan for Lonchophylla dekeyseri, the Cerrado bat*. Ministry of Environment–PROBIO/and ICMBio.
- Amaral, T. S., Macário, L. M., & Aguiar, L. M. S. (2016). Testing the co-existence of *Artibeus lituratus* and *A. planirostris* in a Neotropical savanna. *Acta Chiropterologica*, 18(2), 441–449. <https://doi.org/10.3161/15081109ACC2016.18.2.011>
- Batalha, M. A., & Martins, F. R. (2004). Reproductive phenology of the cerrado plant community in Emas National Park (Central Brazil). *Australian Journal of Botany*, 52(2), 149–161. <https://doi.org/10.1071/BT03098>
- Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, 3(1), 140536. <https://doi.org/10.1098/rsos.140536>
- Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology*, 11(3), 185–195. <https://doi.org/10.1016/j.baae.2010.01.001>
- Cane, J. H., & Dunne, R. (2014). Generalist bees pollinate red-flowered *Penstemon eatonii*: Duality in the hummingbird pollination syndrome. *The American Midland Naturalist*, 171(2), 365–370. <https://doi.org/10.1674/0003-0031-171.2.365>
- Chávez-González, E., Vizin-Bugoni, J., Vázquez, D. P., MacGregor-Fors, I., Dáttilo, W., & Ortiz-Pulido, R. (2020). Drivers of the structure of plant–hummingbird interaction networks at multiple temporal scales. *Oecologia*, 193(4), 913–924. <https://doi.org/10.1007/s00442-020-04727-4>
- Clare, E. L., Goerlitz, H. R., Drapeau, V. A., Holderied, M. W., Adams, A. M., Nagel, L., Dumont, E. R., Hebert, P. D., & Fenton, B. M. (2014). Trophic niche flexibility in *Glossophaga soricina*: How a nectar seeker sneaks an insect snack. *Functional Ecology*, 28(3), 632–641. <https://doi.org/10.1111/1365-2435.12192>
- Classen-Bockhoff, R. (1990). Pattern analysis in pseudanthia. *Plant Systematics and Evolution*, 171(1), 57–88. <https://doi.org/10.1007/BF00940596>
- Coelho, D. C., & Marinho-Filho, J. (2002). Diet and activity of *Lonchophylla dekeyseri* (Chiroptera, Phyllostomidae) in the Federal District, Brazil. *Mammalia*, 66(3), 319–330. <https://doi.org/10.1515/mamm.2002.66.3.319>
- Cordero-Schmidt, E., Maruyama, P. K., Vargas-Mena, J. C., Pereira Oliveira, P., de Assis, R., Santos, F., Medellín, R. A., Rodríguez-Herrera, B., & Venticinque, E. M. (2021). Bat–flower interaction networks in Caatinga reveal generalized associations and temporal stability. *Biotropica*, 53(6), 1546–1557. <https://doi.org/10.1111/btp.13007>
- Díaz, M. M., Solari, S., Aguirre, L. F., Aguiar, L., & Barquez, R. M. (2016). *Clave de identificación de los murciélagos de Sudamérica/Chave de identificação dos morcegos da América do Sul*. Publicación Especial No. 2.
- Diniz, U. M., & Aguiar, L. M. S. (2023a). The interplay between spatiotemporal overlap and morphology as determinants of microstructure suggests no 'perfect fit' in a bat–flower network. *Scientific Reports*, 13, 2737. <https://doi.org/10.1038/s41598-023-29965-3>
- Diniz, U. M., & Aguiar, L. M. S. (2023b). Data from: Spatiotemporal trends in floral visitation and interaction networks reveal shifting niches for bats in a Neotropical savanna. *GitHub Digital Repository*, <https://doi.org/10.5281/zenodo.7814619>
- Diniz, U. M., Domingos-Melo, A., & Machado, I. C. (2019). Flowers up! The effect of floral height along the shoot axis on the fitness of bat-pollinated species. *Annals of Botany*, 124(5), 809–818. <https://doi.org/10.1093/aob/mcz116>
- Diniz, U. M., Fischer, N. L. S., & Aguiar, L. M. S. (2022). Changing the main course: strong bat visitation to the ornithophilous mistletoe *Psittacanthus robustus* (Loranthaceae) in a Neotropical savanna. *Biotropica*, 54(2), 478–489. <https://doi.org/10.1111/btp.13070>
- Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analyzing ecological networks. *R News*, 8(2), 8–11.
- Faegri, K., & Van Der Pijl, L. (2013). *Principles of pollination ecology*. Pergamon Press.
- Fisher, N. I. (1995). *Statistical analysis of circular data*. Cambridge University Press.
- Fleming, T. H. (1982). Foraging strategies of plant-visiting bats. In T. H. Kunz (Ed.), *Ecology of bats* (pp. 287–325). Plenum Press.
- Fleming, T. H., Geiselman, C., & Kress, W. J. (2009). The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, 104, 1017–1043. <https://doi.org/10.1093/aob/mcp197>
- Fujita, M. S., & Tuttle, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): Threatened animals of key ecological and economic importance. *Conservation Biology*, 5(4), 455–463. <https://doi.org/10.1111/j.1523-1739.1991.tb00352.x>
- Gardner, A. L. (2008). *Mammals of South America, volume 1: Marsupials, xenarthrans, shrews, and bats*. University of Chicago Press.
- Goldshtein, A., Handel, M., Eitan, O., Bonstein, A., Shaler, T., Collet, S., Greif, S., Medellín, R. A., Emek, Y., Korman, A., & Yovel, Y. (2020). Reinforcement learning enables resource partitioning in foraging bats. *Current Biology*, 30(20), 4096–4102. <https://doi.org/10.1016/j.cub.2020.07.079>
- González-Gutiérrez, K., Castaño, J. H., Pérez-Torres, J., & Mosquera-Mosquera, H. R. (2022). Structure and roles in pollination networks between phyllostomid bats and flowers: a systematic review for the Americas. *Mammalian Biology*, 102(1), 21–49. <https://doi.org/10.1007/s42991-021-00202-6>
- Gonzalez-Terrazas, T. P., Medellín, R. A., Knörnschild, M., & Tschapka, M. (2012). Morphological specialization influences nectar extraction efficiency of sympatric nectar-feeding bats. *Journal of Experimental Biology*, 215(22), 3989–3996. <https://doi.org/10.1242/jeb.068494>
- Gribel, R. (1988). Visits of *Caluromys lanatus* (Didelphidae) to flowers of *Pseudobombax tomentosum* (Bombacaceae): A probable case of pollination by marsupials in Central Brazil. *Biotropica*, 20(4), 344–347.
- Gribel, R., & Gibbs, P. E. (2002). High outbreeding as a consequence of selfed ovule mortality and single vector bat pollination in

- the Amazonian tree *Pseudobombax munguba* (Bombacaceae). *International Journal of Plant Sciences*, 163(6), 1035–1043.
- Gribel, R., & Hay, J. D. (1993). Pollination ecology of *Caryocar brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. *Journal of Tropical Ecology*, 9(2), 199–211. <https://doi.org/10.1017/S0266467400007173>
- Handel, S. N. (1983). Pollination ecology, plant population structure, and gene flow. In L. Real (Ed.), *Pollination biology* (pp. 163–211). Elsevier.
- Heithaus, E. R., Fleming, T. H., & Opler, P. A. (1975). Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, 56(4), 841–854. <https://doi.org/10.2307/1936295>
- Henry, M., & Stoner, K. E. (2011). Relationship between spatial working memory performance and diet specialization in two sympatric nectar bats. *PLoS ONE*, 6(9), e23773. <https://doi.org/10.1371/journal.pone.0023773>
- Hokche, O., & Ramirez, N. (1990). Pollination ecology of seven species of *Bauhinia* L. (Leguminosae: Caesalpinioideae). *Annals of the Missouri Botanical Garden*, 77(3), 559–572. <https://doi.org/10.2307/2399520>
- Lenza, E., Santos, J. O., & Maracahipes-Santos, L. (2015). Species composition, diversity, and vegetation structure in a gallery forest-cerrado sensu stricto transition zone in eastern Mato Grosso, Brazil. *Acta Botânica Brasileira*, 29, 327–338.
- Liévano-Latorre, L. F., Varassin, I. G., & Zanata, T. B. (2023). Evolutionary history and precipitation seasonality shape niche overlap in neotropical bat-plant pollination networks. *Biotropica*, 55(1), 246–255. <https://doi.org/10.1111/btp.13181>
- Loayza, A. P., & Loiselle, B. A. (2008). Preliminary information on the home range and movement patterns of *Sturnira lilium* (Phyllostomidae) in a naturally fragmented landscape in Bolivia. *Biotropica*, 40(5), 630–635.
- Lund, U., Agostinelli, C., & Agostinelli, M. C. (2017). Package 'circular'. Repository CRAN. <https://cran.r-project.org/web/packages/circular/circular.pdf>
- Machado, I. C., & Lopes, A. V. (2004). Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry forest. *Annals of Botany*, 94(3), 365–376. <https://doi.org/10.1093/aob/mch152>
- Machado, I. C. S., Sazima, I., & Sazima, M. (1998). Bat pollination of the terrestrial herb *Irlbachia alata* (Gentianaceae) in northeastern Brazil. *Plant Systematics and Evolution*, 209, 231–237.
- Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B., & Oliveira, P. E. (2013). Pollination syndromes ignored: Importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, 100(11), 1061–1068. <https://doi.org/10.1007/s00114-013-1111-9>
- Maruyama, P. K., Vizenin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B. (2014). Morphological and spatio-temporal mismatches shape a Neotropical savanna plant-hummingbird network. *Biotropica*, 46(6), 740–747. <https://doi.org/10.1111/btp.12170>
- Mello, M. A., Felix, G. M., Pinheiro, R. B., 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.
- Mello, M. A. R., Marquitti, F. M. D., Guimaraes, P. R., Jr., Kalko, E. K. V., Jordano, P., & de Aguiar, M. A. M. (2011). The missing part of seed dispersal networks: Structure and robustness of bat-fruit interactions. *PLoS ONE*, 6(2), e17395.
- Morellato, L. P. C., Alberti, L. F., & Hudson, I. L. (2010). Applications of circular statistics in plant phenology: A case studies approach. In I. L. Hudson & M. R. Keatley (Eds.), *Phenological research* (pp. 339–359). Springer.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, 21, 75–82. <https://doi.org/10.1016/j.cois.2017.05.015>
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104(50), 19891–19896. <https://doi.org/10.1073/pnas.0706375104>
- Oliveira, H. F. M., Camargo, N. F., Gager, Y., Muylaert, R. L., Ramon, E., & Martins, R. C. C. (2019). Protecting the Cerrado: Where should we direct efforts for the conservation of bat-plant interactions? *Biodiversity and Conservation*, 28(11), 2765–2779. <https://doi.org/10.1007/s10531-019-01793-w>
- Pellón, J. J., Medina-Espinoza, E. F., Lim, B. K., Cornejo, F., & Medellín, R. A. (2022). Eat what you can, when you can: Relatively high arthropod consumption by frugivorous bats in Amazonian Peru. *Mammalian Biology*, 1-8, 137–144. <https://doi.org/10.1007/s42991-022-00327-2>
- Proulx, S. R., Promislow, D. E., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- Queiroz, J. A., Diniz, U. M., Vázquez, D. P., Quirino, Z. M., Santos, F. A. R., Mello, M. A. R., & Machado, I. C. (2020). Bats and hawkmoths form mixed modules with flowering plants in a nocturnal interaction network. *Biotropica*, 53(2), 596–607. <https://doi.org/10.1111/btp.12902>
- R Development Core Team. (2021). *R: A language and environment for statistical computing*. The R Foundation for Statistical Computing. <https://www.r-project.org/>
- Ripperger, S. P., Kalko, E. K., 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.
- Rocha, P. A., Pereira, A. S., Silvestre, S. M., Santana, J. P., Beltão-Mendes, R., Zortéa, M., & Ferrari, S. F. (2017). Consumption of leaves by *Platyrrhinus lineatus* (Chiroptera, Stenodermatinae): Are these bats primarily frugivorous or broadly phytophagous? *Zoology*, 121, 44–48. <https://doi.org/10.1016/j.zool.2016.12.004>
- Rothenwöhler, C., Becker, N. I., & Tschapka, M. (2011). Resource landscape and spatio-temporal activity patterns of a plant-visiting bat in a Costa Rican lowland rainforest. *Journal of Zoology*, 283(2), 108–116. <https://doi.org/10.1111/j.1469-7998.2010.00748.x>
- Santana, S. E., Grosse, I. R., & Dumont, E. R. (2012). Dietary hardness, loading behavior, and the evolution of skull form in bats. *Evolution: International Journal of Organic Evolution*, 66(8), 2587–2598. <https://doi.org/10.1111/j.1558-5646.2012.01615.x>
- Sazima, M., Buzato, S., & Sazima, I. (1999). Bat-pollinated flower assemblages and bat visitors at two Atlantic Forest sites in Brazil. *Annals of Botany*, 83(6), 705–712. <https://doi.org/10.1006/anbo.1999.0876>
- Silva, J. F., Fariñas, M. R., Felfili, J. M., & Klink, C. A. (2006). Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. *Journal of Biogeography*, 33(3), 536–548. <https://doi.org/10.1111/j.1365-2699.2005.01422.x>
- 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/10.1016/j.gecco.2019.e00702>
- 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/10.26786/1920-7603\(2016\)7](https://doi.org/10.26786/1920-7603(2016)7)
- Stewart, A. B., & Dudash, M. R. (2017). Flower-visiting bat species contribute unequally toward agricultural pollination ecosystem services in southern Thailand. *Biotropica*, 49(2), 239–248. <https://doi.org/10.1111/btp.12401>
- Straube, F. C., & Bianconi, G. V. (2002). Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de rede-de-neblina. *Chiroptera Neotropical*, 8(2), 150–152.
- Tschapka, M. (2004). Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats.

Journal of Zoology, 263(1), 7–21. <https://doi.org/10.1017/S0952836903004734>

- Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology*, 90(8), 2039–2046. <https://doi.org/10.1890/08-1837.1>
- Viana, B. F., Boscolo, D., Lopes, L., Lopes, A., Ferreira, P., Pigozzo, C. M., & Primo, L. (2012). How well do we understand landscape effects on pollinators and pollination services? *Journal of Pollination Ecology*, 7(5), 31–34. [https://doi.org/10.26786/1920-7603\(2012\)2](https://doi.org/10.26786/1920-7603(2012)2)
- Voigt, C. C., Kelm, D. H., Bradley, B. J., & Ortman, S. (2009). Dietary analysis of plant-visiting bats. In T. H. Kunz & S. Parsons (Eds.), *Ecological and behavioral methods for the study of bats* (pp. 593–609). Johns Hopkins University Press.
- Voigt, C. C., Kelm, D. H., & Visser, G. H. (2006). Field metabolic rates of phytophagous bats: Do pollination strategies of plants make life of nectar-feeders spin faster? *Journal of Comparative Physiology B*, 176(3), 213–222.
- Willmer, P. (2011). *Pollination and floral ecology*. Princeton University Press.
- Wray, J. C., & Elle, E. (2015). Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. *Landscape Ecology*, 30(2), 261–272. <https://doi.org/10.1007/s10980-014-0121-0>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: List of captured flower-visiting bats and plants whose pollen was found on bats in the research area (Brasília National Park, Brazil). Species are followed by their codes used in Figures 3–6 in the main manuscript, their ecological guild (bats) or flowering syndromes (plants), their total abundance in the site (N) (number of captures for bats, the abundance of flowering individuals in transects for plants) and their abundance per habitat type (SA: savanna or Cerrado sensu stricto, FE: forest edge, FI: forest interior). Dashed cells indicate that

the plant corresponding to the pollen type was not found in the transects.

Table S2: A list of all bat individuals captured in the Brasília National Park, followed by their trophic guild, their absolute abundance (in parenthesis: the proportion in relation to the total, or relative abundance), the habitat types in which they were registered (SA: savanna, FE: forest edge, FI: forest interior, All: found in all types) and the number of pollen carriers (in parenthesis: the proportion of pollen carriers in relation to the total of individuals captured of that species).

Table S3: A list of all the plant species of interest registered in the transections of the Brasília National Park that were classified as potential resources for bats. Species are followed by the habitat types (SA: savanna, FE: forest edge, FI: forest interior) in which they are found, their syndromes according to Faegri and Van Der Pijl (2013), criteria for inclusion (i—chiropterophilous and with bat-pollination described in the literature; ii—chiropterophilous; iii—not chiropterophilous, but had nectar and/or pollen as nectar reward and at least 1 cm of corolla diameter; see main manuscript for a thorough description of the criteria), the reference for criteria i (literature) or ii (traits used to classify as chiropterophilous), and whether the species had pollen found on bats throughout the research.

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