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Modularity and specialization in bat–fly interaction networks are remarkably consistent across patches within urbanized landscapes and spatial scales

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Abstract

Patterns of specialization and the structure of interactions between bats and ectoparasitic flies have been studied mostly on non-urban environments and at local scales. Thus, how anthropogenic disturbances influence species interactions and network structure in this system remain poorly understood. Here, we investigated patterns of interaction between Phyllostomidae bats and ectoparasitic Streblidae flies, and variations in network specialization and structure across Cerrado patches within urbanized landscapes in Brazil and between local and regional scales. We found high similarity in the richness and composition of bat and fly species across communities, associated with low turnover of interactions between networks. The high specialization of bat–streblid interactions resulted in little connected and modular networks, with the emergence of modules containing subsets of species that interact exclusively or primarily with each other. Such similarities in species and interaction composition and network structure across communities and scales suggest that bat–fly interactions within Cerrado patches are little affected by the degree of human modification in the surrounding matrix. This remarkable consistency is likely promoted by specific behaviors, the tolerance of Phyllostomidae bats to surrounding urbanized landscapes as well as by the specificity of the streblid–bat interactions shaped over evolutionary time.

Key words: Chiroptera, ectoparasites, host–parasite network, neotropics, Streblidae, urbanization

Urbanization may deeply influence bat communities which, in turn, can affect species associated with them (Russo and Anciollotto 2015). Notably, the urban environment often have increased availability of fruits, nectar, preys, and shelters which may facilitate bat reproduction and the stability of their colonies (Pacheco et al. 2010; Almeida et al. 2011; Nunes et al. 2017). However, some bat species are less tolerant to anthropogenic disturbances (e.g., artificial lighting) which can generate drastic changes in their behavior and

reproduction (Russo et al. 2017). Consequently, urbanization as well as other anthropogenic disturbances often present near urbanized landscapes (e.g., crops and pastures), can influence other organisms that are closely associated with bats, such as ectoparasitic flies of the Streblidae family. Streblidae encompasses approximately 100 species in the Americas that are often widely distributed in the Neotropical region (Dick and Miller 2010; Alcantara et al. 2019; Guerrero 2019). Owing to profound morphological adaptations related to the use of bats as hosts, such as lateral and ventral compression of the body, reduced eyes, curved claws, elongated legs (Peterson and Wenzel 1987; Meier et al. 1999; Dick and Patterson 2006), and dependency on bat shelters to find new hosts (Marshall 1982; Dittmar et al. 2015), ectoparasitic flies may be highly susceptible to environmental changes that affect their host bats.

How urbanization and habitat fragmentation influence the relationship between bats and streblid flies remains poorly understood. The abundance of these flies is known to be affected by increased human density in urbanized landscapes and habitat fragmentation as well as to respond to environmental variation in precipitation, temperature, and elevation (Pilosof et al. 2012; Frank et al. 2016; Bolivar-Cimé et al. 2018), which can affect host–parasite interaction patterns. In fact, evidence indicates that parasitic specificity of flies on their hosts tends to be lower in more urbanized environments which may be associated with habitat modification and shelter sharing among bat species (Urbieta et al. 2018).

The detection of the effects of disturbance on interaction patterns may be complex. In this sense, network analyses provide a valuable conceptual and analytical framework to describe how host–parasite interaction patterns vary across communities with disparate environmental characteristics and disturbance levels (Poulin 2010; Galiana et al. 2019). Although this approach has been used to describe different types of interactions (e.g. predation, herbivory, and mutualisms; Dehling 2018), parasitism has been comparatively less explored and, in particular, the relationship between bats and ectoparasitic flies (Zarazúa-Carbajal et al. 2016; Durán et al. 2018). The high degree of specificity of flies to their hosts constitutes a relationship of high "intimacy" (*sensu* Pires and Guimarães 2012) which can generate high niche partitioning among species and define network structure such as the emergence of interaction modules, that is, subsets of species that interact more with each other than with other species in the community (Cordeiro et al. 2020). In fact, previous studies recorded high specificity and modularity in bat–fly interaction networks in the Neotropical region (Zarazúa-Carbajal et al. 2016; Rivera-García et al. 2017; Durán et al. 2018; Hernández-Martínez et al. 2018; Saldaña-Vázquez et al. 2019). Although network structure is known to be influenced by variation in species richness (Saldaña-Vázquez et al. 2019), behavioral ecology, type of shelter used by the hosts (Fagundes et al. 2017; Hernández-Martínez et al. 2018; Saldaña-Vázquez et al. 2019), vegetation (Zarazúa-Carbajal et al. 2016; Durán et al. 2018), and seasonality (Rivera-García et al. 2017), few studies have investigated how the structure of bat–streblid networks varies across communities inserted within natural areas surrounded by urbanized landscapes (Hernández-Martínez et al. 2018).

Additionally, interaction patterns may dependent on the spatial scale investigated. In fact, defining the appropriate scales for describing ecological phenomena is one of the major challenges in ecology (Levin 1992; Dáttilo et al. 2019; Cordeiro et al. 2020). Recent studies demonstrated that both consistent and inconsistent interaction patterns between spatial scales can reveal different ecological and evolutionary processes shaping species interactions (Vizentin-Bugoni et al. 2019; Cordeiro et al. 2020). However, few studies have evaluated the effect of scales on host–parasite networks (e.g., Galiana et al. 2019) and, to the best of our knowledge, no study has addressed spatial scales explicitly for bat–fly interaction networks.

Herein, we investigated the specialization and structure of phyllostomid–fly interaction networks at local (3 communities) and regional (meta-network) scales in 3 Cerrado patches within urbanized areas with distinct degrees of anthropogenic modification. Specifically, we described species richness, connectance, complementary specialization, modularity, and nestedness for networks in each community and scale. Considering that streblid flies depend on bats for food, have part of their life cycle on bat shelters and that bat diversity and abundance may decrease with urbanization, we expect the level of modification in the urbanized landscapes surrounding the patches to negatively affect species richness and bat–fly interactions across communities and spatial scales. Specifically, we predict bat and fly richness, specialization, and modularity will be lower in more modified landscapes and, owing to the lower richness in local communities, we expect local networks to present less modules and lower complementary specialization (i.e., niche partitioning) than the regional network.

Materials and Methods

Study area

We sampled 3 patches of Cerrado vegetation surrounded by human modified areas with variable levels of urbanization and other secondary disturbances (especially habitat fragmentation and isolation by crops and pastures) in the Campo Grande, Mato Grosso do Sul, Brazil. Instituto de Pesquisa São Vicente (IPS) (20°23′08.5″ S, 054°36′28.8″ W) covers 190 hectares, Área de Preservação do Córrego Bandeira (APABAND) (20°29′ 31″ S, 54°34′45″ W) covers 17 hectares, and Centro de Educação Ambiental do Imbirussu (CEAIMB) (20°26′53″ S, 54°41′38″ W) covers 14 hectares (Figure 1). Despite being the larger area, approximately 95% of the IPS has been converted to pasture, agriculture, and urban areas. All these areas encompass Cerrado patches (Figure 1) which are remnants of native vegetation including grasslands and shrublands ("Cerrado *stricto sensu*" and "Cerradão") and gallery forests (Planurb-Instituto Municipal de Planejamento Urbano 2016). The mean distance between study sites was 12.29 ± 0.71 km (mean $\pm$ SD). The climate is tropical with dry winter and wet summer with average annual precipitation of 1,745 mm and average annual temperature of 24°C (climate type Aw, according to the classification of Köppen; Peel et al. 2007).

Capture and identification of bats and flies

In each area, we captured bats during 3 expeditions (November 2016, February 2017, and April 2017), each one encompassing 15 consecutive nights. We used 6 mist nests (6.0 m $\times$ 3.0 m) installed between 0.5 and 3.5 m from the ground. Mist nests were installed along trails and on forest gaps, edges, and interior. Mist nests were opened for 6 h starting at the sunset and being reviewed every 15 min, summing up a total sampling effort of 29.160 h/m^2 (*sensu* Straube and Bianconi 2002). Each bat caught was put in a separate cloth bags that was used only once per expedition in order to avoid contamination, that is, flies from an individual moving to another individual (*sensu* Dick 2007). In addition, to mitigate escape of parasites or cross-host contamination, we inspected mist nets at short
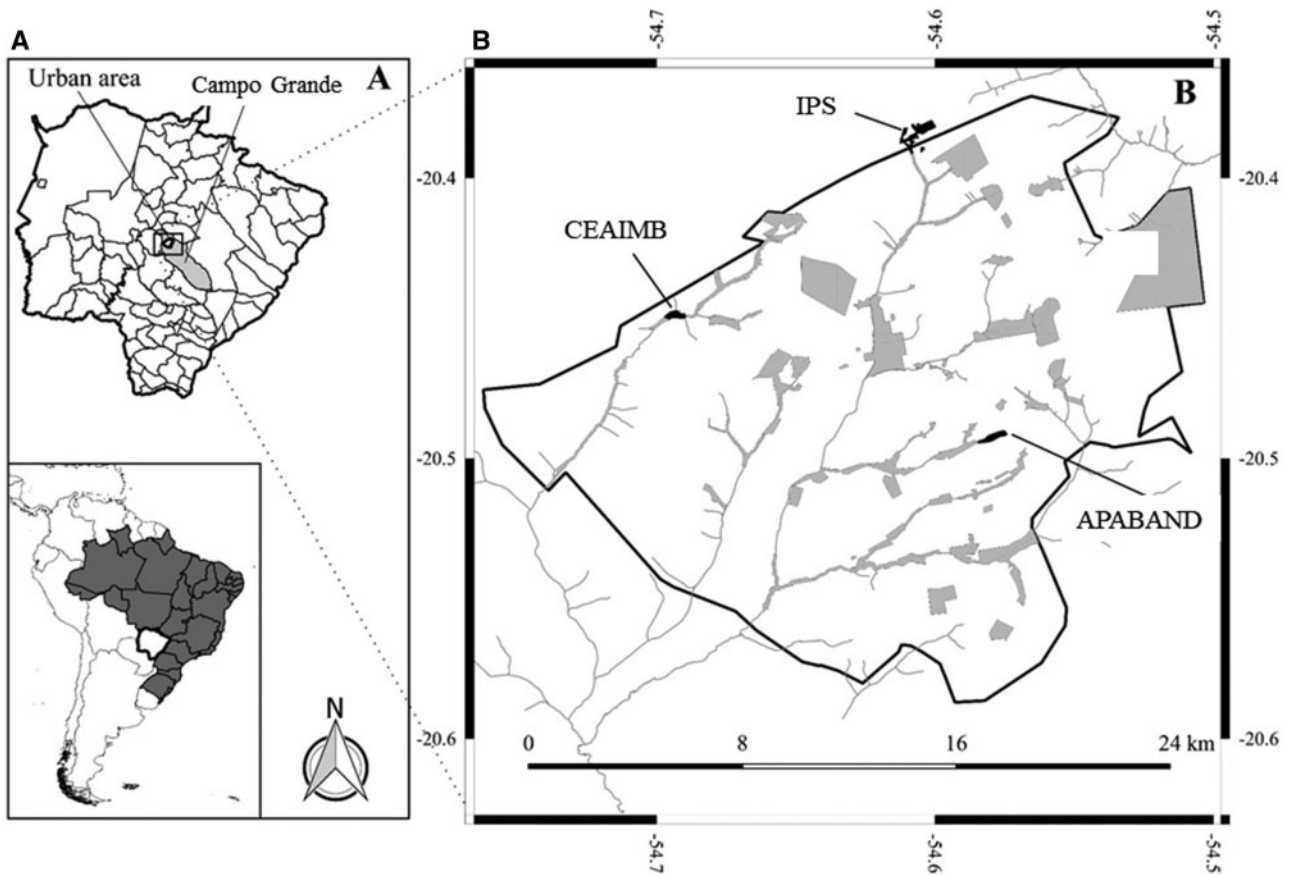
Figure 1. (**A**) Campo Grande city, Mato Grosso do Sul state, Brazil, and (**B**) the 3 study sites—Instituto de Pesquisa São Vicente (IPS), Área de Preservação do Córrego Bandeira (APABAND), and Centro de Educação Ambiental do Imbirussu (CEAIMB)—with Cerrado patches (gray) within the Campo Grande human modified (mostly urban) matrix (white).

time intervals and bats were readily screened for easily excitable fly species (Barbier and Bernard 2017). In order to not sample the same individual more than once, we marked bats forearms with non-toxic permanent ink. We identified bats in the field following Gregorin and Taddei (2002), Gardner (2008), and Aguirre et al. (2009). We collected ectoparasitic flies using brushes moistened with ethanol and individualized them in microtubes containing ethanol 70%. These flies were identified at the Laboratório de Sistemática, Ecologia e Evolução (LSEE) of the Universidade Federal de Mato Grosso do Sul (UFMS), following Guerrero (1993, 1994a, 1994b, 1995, 1996) and then deposited in the Zoological Reference Collection of the UFMS (ZUFMS), in Campo Grande. The data used here are part of the study previously conducted by Urbieta et al. (2018). For our analyses, we only considered Phyllostomidae species which comprised 82.9% of all individuals caught (445 out of 537 individuals; Supplementary Table S1) and were the only bats parasitized by Strelidae (see Urbieta et al. 2018). All capture and collection procedures were authorized under the license issued by the Biodiversity Information and Authorization System (SISBIO) (process number: 10.566).

Measuring urbanization

Urbanization was quantified within a buffer with 5 km from the center of each study area, which is conservatively expected to encompass the foraging area of most bat species occurring in the region, as well as the scale in which bats respond to local biotic and abiotic

factors (Gorresen et al. 2005; Pilosof et al. 2012; but see Muylaert et al. 2016). We used Google Earth polygon tools and images from *landsat8* to quantify the proportion of the area covered by impermeable surface (i.e., paved roads) and constructions (i.e., buildings and houses) within the 5-km radius buffers (Moll et al. 2019).

Data analysis

We built a network for each of the 3 areas (*local* scale) and pooled together all interactions of the 3 areas to build a meta-network (*regional* scale) (Supplementary Material S1). Thus, the *regional* scale comprises the entire pool of species and interactions found on the 3 local communities. Each network is represented by a matrix where each row corresponds to a bat species i, each column corresponds to a fly species j, and the intersections correspond to the frequency of interactions a_{ij}, which is the number of samples of a bat i in which a fly j was present. For each network, we calculated: bat richness, fly richness, number of links, number of interactions (N flies), connectance (C), specialization (H_2' index), nestedness (wNODF) and modularity (Q). Connectance is defined as the proportion of links observed in relation to the total possible. The H_2' index can be interpreted as a measure of complementary specialization, that is, how species partition their interactions (Blüthgen et al. 2006). H_2' varies from 0 to 1 which indicates extreme generalization or specialization, respectively. For nestedness, we used the wNODF metric (Almeida-Neto and Ulrich 2011) which calculates the non-overlap and decreasing fill of interactions for quantitative matrices. It ranges

Table 1. Urban coverage and network structure in 3 local (IPS, APABAND, and CEAIMB) and 1 regional bat–fly interaction networks in Cerrado patches within urbanized landscapes in the Campo Grande city, Brazil

Metrics	IPS	CEAIMB	APABAND	REGIONAL
Urban cover (km^2)	2.47	12.69	17.75	–
Bat species	7	7	6	7
Fly species	10	10	8	12
Links	13	12	12	20
Number of interactions (N individual flies)	154	157	69	379
Number of modules	6	6	6	6
Connectance	0.20	0.17	0.25	0.23
Specialization (H_2')	**0.82** (0.22–0.82)*	**0.96** (0.29–0.89)*	**0.93** (0.27–0.80)*	**0.86** (0.12–0.51)*
Nestedness (wNODF)	1.51 (10.60–34.98)^{ns}	4.54 (6.06–33.33)^{ns}	0 (9.30–37.20)^{ns}	2.10 (21.54–42.24)^{ns}
Modularity (Q)	**0.54** (0.14–0.51)*	**0.64** (0.19–0.57)*	**0.64** (0.19–0.56)*	**0.61** (0.10–0.39)*

Bold indicates statistically significant results, that is, when the observed value is higher than the 95% confidence interval (presented between parenthesis).

from 0 to 100, with high values representing high nestedness. For modularity, we use the Q metric and the DIRTLPAwb+ algorithm, which searches for the optimal division of the matrix into subsets of highly connected species (Beckett 2016). A network is modular when subsets of species interact more among themselves than with other members of the community. As DIRTLPAwb+ is an optimization algorithm, there may be variation in results between rounds, so we select the highest value detected in 10 repetitions. We considered the observed H_2', wNODF, and Q statistically significant when they were higher than the 95% confidence intervals generated by the *vaznull* null model (Vázquez et al. 2007). This model reshuffles interactions while preserving marginal total (i.e., sum of rows and columns) and connectance as the observed network. All analyzes were performed using the *bipartite* package (Dormann et al. 2009) in the software R (R Core Team 2018).

Results

We captured 445 phyllostomid bats distributed among 10 species (Table 1 and Supplementary Table S1). At least 1 individual of each bat species was parasitized, summing up 104 individuals parasitized by 379 streblids distributed among 12 species (Figure 2 and Supplementary Material S1). Local networks had similar number of bat species (6 or 7), fly species (8–10), and links (12 or 13) (Figure 2) and the similarity in species composition among communities was high (Figure 3). The number of flies collected per communities was 157 (CEAIMB), 154 (IPS), and 69 individuals (APABAND). All networks presented low connectance (<0.25), and were significantly specialized (>0.82) and modular (0.54–0.64), but nestedness did not differ from the random expectation produced by the null model (<4.54) (Table 1). All local networks had 6 modules with similar species composition (Figure 2). Each local network included most of the species present in the regional network, which had 7 bats and 12 flies. Similarly to the local networks, the regional meta-network was not more nested than the null expectation, but it was highly specialized and modular, presenting 6 modules (Table 1). Urban coverage—which is the main source of habitat modification in the matrix surrounding the sites—varied between areas (IPS = 2.47 km^2, CEAIMB = 12.69 km^2, and APABAND = 17.75 km^2) (Figure 2). Network structure was consistent across areas, presenting slightly lower levels of specialization and modularity in the site surrounded by less urbanized area (i.e., IPS; Figure 2).

Discussion

Contrary to our predictions, bat and streblid richness were similar between communities, having low turnover of species and interactions, regardless of the degree of human modification in the surrounding urbanized landscape (Figures 2 and 3). Consequently, all 3 networks presented similar structure being specialized and modular, with modules having species composition remarkably similar across communities. Because of these similarities across communities, the same patterns of interaction were consistent between local and regional scales, underlining the high degree of specialization of bat–fly interactions.

Owing to the high specialization, the richness and composition of ectoparasitic flies assemblages are expected to be highly dependent on the composition of the local host assemblage (Dick and Gettinger 2005; Eriksson et al. 2019). However, the composition and similarity of flies in communities may also depend on whether different bat species share shelters, as this may increase chances of ectoparasitic flies exchanging hosts, which may influence network structure (Fagundes et al. 2017). In fact, shelter sharing may explain flies parasitizing unusual hosts, resulting in accidental infestations (Barbier and Bernard 2017). For instance, the fly *Trichobius joblingi* is typically found on *Carollia perspicillata* (Wenzel 1976; Dick and Gettinger 2005; Tello et al. 2008) but here we detected on *Glossophaga soricina*, which likely occurred because *C. perspicillata* and *G. soricina* shared shelters. Interestingly, we recorded more "accidental interactions" in the site whose surrounding matrix was more modified (Figure 2), suggesting that landscape modification may increase opportunities for such associations. In fact, habitat loss and fragmentation are known to induce host aggregations and may promote reduced specialization in streblid–bat interaction networks (Hernández-Martínez et al. 2018) via "accidental interactions." For example, although less urbanized than APABAND and CEAIMB, the matrix surrounding IPS has historically gone through fragmentation and deforestation, which may have promoted bat aggregation and the presence of "accidental interactions," making networks in this site structurally similar to the sites surrounded by more modified matrices. This suggests that historical fragmentation and deforestation may also contribute at some extent to the present patterns of interactions between streblids and bats. In long-term, accidental interactions may change the patterns of interaction between flies and bats with possible implications on the evolutionary trajectories of such relationships. However, specific studies are needed to properly test whether bat species share shelters more frequently in more fragmented and isolated patches within
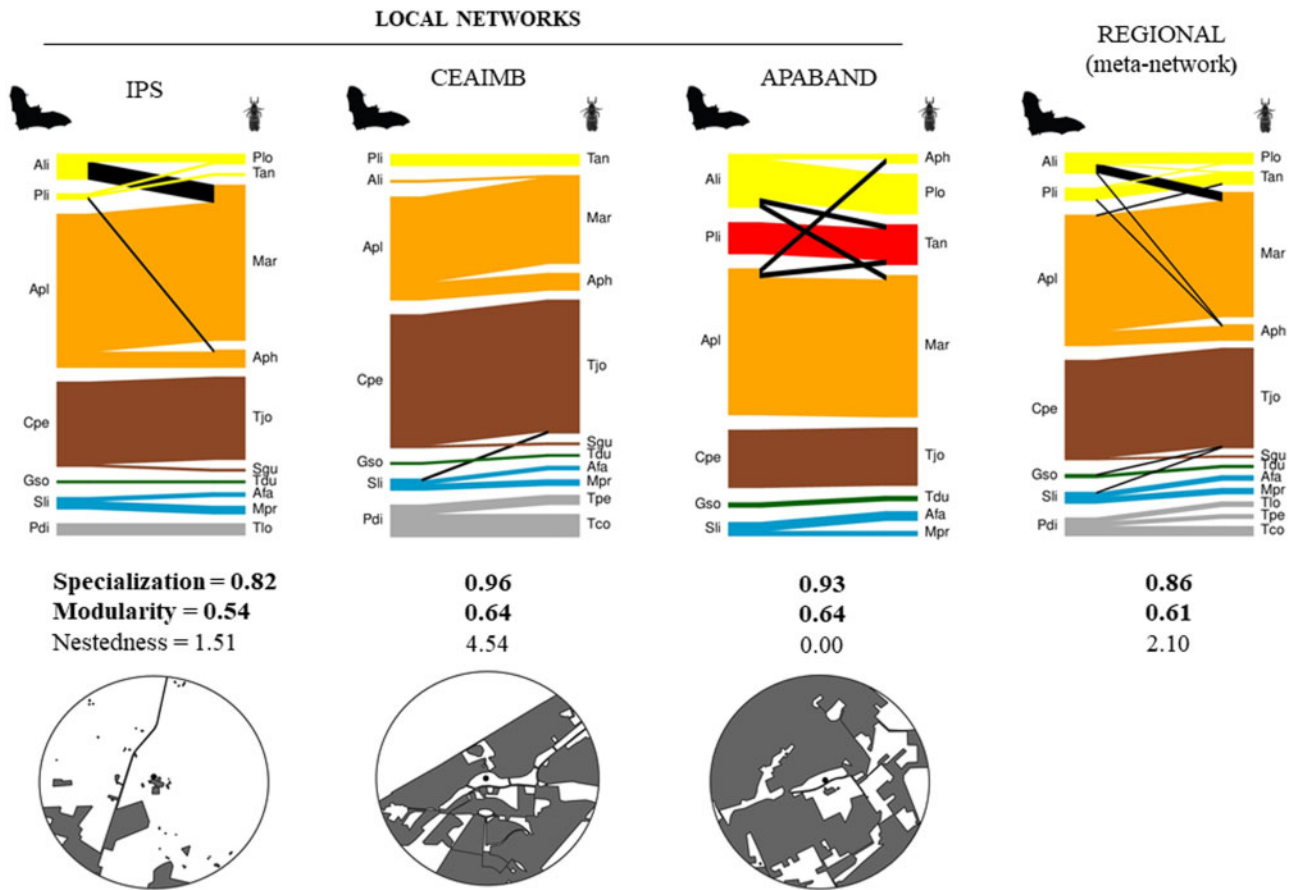
Figure 2. Modularity of bat–fly interaction networks in 3 Cerrado patches within urbanized landscapes (IPS, APABAND, and CEAIMB) in Brazil and a regional meta-network consisting of all 3 sites pooled together. Distinct colors represent distinct modules, with black links representing interactions between species from distinct modules; these associations are unusual and may be considered "accidental interactions" (see text). Line thickness indicates interaction frequencies. Circles show urban coverage (gray) and other types of coverage, that is, Cerrado patches, urban voids, pastures and crops (white) within a 5-km radius around each study site. Bat acronyms: Pli, *Platyrrhinus lineatus*; Ali, *Artibeus lituratus*; Apl, *Artibeus planirostris*; Sli, *Stunira lilium*; Gso, *Glossophaga soricina*; Cpe, *Carollia perspicillata*; and Pdi, *Phyllostomus discolor*. Fly (Streblidae) acronyms: Tan, *Trichobius angulatus*; Plo, *Paratrichobius longicrus*; Mar, *Megistopoda aranea*; Aph, *Aspidoptera phyllostomatis*; Afa, *Aspidoptera falcata*; Mpr, *Megistopoda proxima*; Tdu, *Trichobius dugesii*; Tjo, *Trichobius joblingi*; Sgu, *Strebla guajiro*; Tlo, *Trichobius longipes*; Tco, *Trichobius costalimai*; and Tpe, *Trichobioides perspicillatus*.
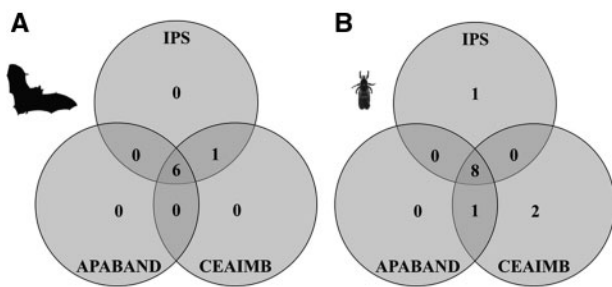

Figure 3. Venn diagram with (**A**) the number of bat and (**B**) Streblidae fly species shared in 3 Cerrado patches (IPS, APABAND, and CEAIMB) within urbanized landscapes in the Campo Grande city, in Brazil.

urban landscapes and whether this is the cause for the increase of accidental interactions.

Although other antagonistic networks (e.g., Tachinid–arthropod interactions; Corcos et al. 2019) and interactions between ectoparasitic flies and bats (Pilosof et al. 2012) are known to be affected by anthropogenic disturbances, we found only slight association between human modification in the surrounding matrix and the

structure of bat–fly interaction networks. Specifically, we found slightly lower richness of bats and flies, and lower number of interactions in the more modified site, while slightly lower levels of specialization and modularity were found in less modified areas. These results may be related to high tolerance of the bat species studied here to matrix modification and urbanization and the dominance of frugivorous bat species (71% of all species) which usually have low shelter fidelity (Lewis 1995; Patterson et al. 2007), reducing changes of parasites to switch hosts and, ultimately, leading to similar patterns of interactions regardless of the degree of human modification in the surrounding urbanized landscape. Thus, the minor effect of degree of human modification in the surrounding matrix on network structure may also be related to the behavior of the bats in the assemblages as well as their tolerance to anthropogenic disturbances which make species richness and composition vary little among communities.

Patterns of host phenotypic similarity and their phylogenetic relationships may also influence the observed interaction patterns. For example, despite the high host–parasite specialization in this system, we detected both *Artibeus lituratus* and *Artibeus planirostris* being parasitized by *Megistopoda aranea*, *Aspidoptera phyllostomatis*, and *Trichobius angulatus* (Figure 2). It is possible that the

phenotypic similarities between these phylogenetically related bats act filtering parasite species with similar ecological traits (Lima-Junior et al. 2012; Wiens et al. 2013). Furthermore, attributes such as host behavior, phylogeny, and immunology can also play a fundamental role on interactions because host–parasite interactions often depend on the evolutionary history of the hosts and their antiparasitic defenses as well as on the parasites' abilities to disperse and colonize hosts (Galbe and Oliver-Junior 1992; Krasnov et al. 2012). Thus, phylogenetically closely related bats may have similar attributes that facilitate parasitism by specific flies able to overcome antiparasitic defenses, forming highly specialized interactions that lead to the emergence of interaction modules within the networks (Fagundes et al. 2017) as we documented here. This is the case for other parasitic interactions such as those between mammals and fleas, where hosts phylogenetic relationship is associated with network specialization and modularity, which may indicate cospeciation (Krasnov et al. 2012; Lima-Junior et al. 2012). Thus, the consistent interaction patterns observed across communities and scales reinforce the specificity of the streblid–bat (Urbieta et al. 2018) which is likely derived from processes that shaped species phenotypes and ecologies over evolutionary time.

The networks studied here were not nested (i.e., the assumptions of the null model were not sufficient to reproduce the observed low level of nestedness) but were modular at both local and regional scales, which are patterns present in other systems with high specialization (Cordeiro et al. 2020). In parasite–host networks involving fish and their ectoparasites and endoparasites, for example, nestedness may occur (Lima-Junior et al. 2012). However, our findings support previous studies with bats and flies in non-urban environments that detected non-nested but modular network structure (Zarazúa-Carbajal et al. 2016; Fagundes et al. 2017; Rivera-García et al. 2017; Durán et al. 2018, but see Patterson et al. 2009). In antagonistic networks, nestedness is related to generalism and opportunism (Bellay et al. 2013), while its absence (as well as the presence of modularity) may be related to high niche partitioning (Cordeiro et al. 2020), which in host–parasite interactions often results from profound adaptation of parasites' traits to their specific hosts (Krasnov et al. 2012) as observed in bat–fly interaction networks. Therefore, the consistent lack of nestedness and presence of high modularity in bat–fly interaction networks structure across communities and scales (local and regional) as we detected here is likely a product of high specialization of these interactions which, associated to bats behavior and their tolerance to human modification of the surrounding urban landscape, lead to similar interaction patterns across communities.

In summary, our study shows that the richness and composition of species of bats and ectoparasitic flies and the degree of specialization of bat–fly interaction networks vary little across Cerrado patches surrounded by modified (mostly urban) landscapes in the Neotropical communities studied. The low turnover of species associated with the host–parasite specificity generates structurally similar interaction networks that are highly modular, and whose modules present remarkably similar composition between communities and spatial scales. We recommend further studies directly assessing the effects of urbanization and habitat isolation and fragmentation on shelter sharing, the occurrence of accidental interactions and their implications for host–parasite interactions. Furthermore, our study is restricted to one city and more studies including other cities with distinct human population densities and green cover are necessary before generalizations. Despite the 3 study sites evaluated here varied in the extent of urbanization in the surrounding matrix, we encourage future studies including more sites in order to encompass a full gradient (i.e., from not urbanized to highly urbanized areas) to confirm the trends we reported here.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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