


ORIGINAL ARTICLE



Seasonal variation and host sex affect bat–bat fly interaction networks in the Amazonian savannahs

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Abstract

Bats are the second-most diverse group of mammals in the world, and bat flies are their main parasites. However, significant knowledge gaps remain regarding these antagonistic interactions, especially since diverse factors such as seasonality and host sex can affect their network structures. Here, we explore the influence of such factors by comparing species richness and composition of bat flies on host bats, as well as specialization and modularity of bat–bat fly interaction networks between seasons and adult host sexes. We captured bats and collected their ectoparasitic flies at 10 sampling sites in the savannahs of Amapá State, northeastern region of the Brazilian Amazon. Despite female bats being more parasitized and recording greater bat fly species richness in the wet season, neither relationship was statistically significant. The pooled network could be divided into 15 compartments with 54 links, and all subnetworks comprised >12 compartments. The total number of links ranged from 27 to 48 (for the dry and wet seasons, respectively), and female and male subnetworks had 44 and 41 links, respectively. Connectance values were very low for the pooled network and for all subnetworks. Our results revealed higher bat fly species richness and abundance in the wet season, whereas specialization and modularity were higher in the dry season. Moreover, the subnetwork for female bats displayed higher specialization and modularity than the male subnetwork. Therefore, both seasonality and host sex contribute in different ways to bat–bat fly network structure. Future studies should consider these factors when evaluating bat–bat fly interaction networks.

Key words: Amapá, Amazon biome, bat flies, bats, interaction networks

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INTRODUCTION

Rates of bat fly parasitism in Neotropical bats are sensitive to many different factors, including season and host sex (Pilosof *et al.* 2012; Bezerra & Bocchiglieri 2018; Salinas-Ramos *et al.* 2018; Barbier *et al.* 2019). This scenario arises because bat flies completely rely on their hosts for space and food (Overal 1980; Dick *et al.* 2009), and host roost and environmental conditions affect their pupal development, reproductive success, and, consequently, their abundance (ter Hofstede & Fenton 2005; Patterson *et al.* 2007; Dittmar *et al.* 2009). Accordingly, season and host sex are very important factors influencing bat fly population dynamics, especially since the reproductive behavior of their bat hosts is dependent on seasonal resources (Kunz & Hood 2000; Carvalho *et al.* 2019; Ocampo-González *et al.* 2021), and given that host sex defines their roosting, seasonal, and reproductive behaviors (McCracken & Wilkinson 2000).

In the Neotropics, bat fly parasitism has been shown previously to be incompletely correlated with seasonal and spatial patterns of prevalence and mean intensity, independently of bat fly species and host species (Komeno & Linhares 1999; Rui & Graciolli 2005; Patterson *et al.* 2007; Presley & Willig 2008; Pilosof *et al.* 2012; Salinas-Ramos *et al.* 2018; Barbier *et al.* 2019), most likely because bats exhibit a lot of heterogeneity in terms of morphology, ecology, and behavior. For example, sociality in bats ranges from solitary to groups that form only in the mating season, and extends to bats that roost in colonies year-round (McCracken & Wilkinson 2000). Consequently, bats that form bigger colonies have a higher probability of parasite transfer, and so present higher rates of parasitism (Rifkin *et al.* 2012). Bat group size is limited by roost type, roost size, and availability (Racey & Entwistle 2000; Patterson *et al.* 2007; Dittmar *et al.* 2009), highlighting the significant influence of environment on rates of parasitism by bat flies on bats (ter Hofstede & Fenton 2005; Patterson *et al.* 2007; Dittmar *et al.* 2009).

Network analysis has been adopted as a novel approach for exploring the antagonistic relationships between bats and their ectoparasites (Zarazúa-Carbajal *et al.* 2016; Saldaña-Vázquez *et al.* 2019; Urbieta *et al.* 2021). By calculating network parameters, network analysis provides information on interactions at the community level (Dormann *et al.* 2008; Blüthgen *et al.* 2011; Beckett 2015, 2016). Those network parameter values are influenced by factors such as network size, latitude, altitude, type of habitat, and disturbance (Saldaña-Vázquez *et al.* 2019; Júnior *et al.* 2020; Urbieta *et al.* 2021). However, to date,

only two studies have tested for the influence of seasonality (Zarazúa-Carbajal *et al.* 2016; Rivera-García *et al.* 2017), and to our knowledge, no study has addressed the influence of host sex using this approach. Although most previous studies have reported a similar general pattern for bat–bat fly interaction networks in the Neotropics, displaying low connectance, high specialization, and high modularity (Hernández-Martínez *et al.* 2019; Saldaña-Vázquez *et al.* 2019; Júnior *et al.* 2020), these metrics still vary across broad scales given the considerable latitudinal variation of the Neotropics (Júnior *et al.* 2020). Thus, it is necessary to study the influence of season and sexual behavior to establish structural patterns (Webber *et al.* 2016). We anticipated that bat–bat fly network structures would exhibit the same variability as parasitism rates (Webber *et al.* 2016).

Here, we assessed how seasonality and host sex affect the structure of antagonistic networks between bats and their ectoparasitic flies in the savannahs of Amapá State, northeastern Brazil. Considering that variation in parasitism rates likely correlate with those variables, we also aimed to test if seasonality and host sex influence specialization and modularity in bat–bat fly networks. To our knowledge, only one other study examined seasonal differences in the specialization of bat–bat fly interaction networks (Rivera-García *et al.* 2017; but also see Luna *et al.* 2017). Since bats in the Neotropics typically start breeding around the beginning of the wet season (Racey & Entwistle 2000; Carvalho *et al.* 2019), we expected bat fly abundance to be higher during this period because of host births and immigration (due to the mating season for certain species) (see Rifkin *et al.* 2012). In turn, competition among bat flies for space and food would be enhanced, prompting them to switch host species during the wet season. Therefore, we predicted higher specialization and modularity in bat–bat fly interaction networks in the dry season. Moreover, we hypothesized greater bat fly abundance and a higher degree of exclusivity for bat–bat fly interactions for female hosts due to their more gregarious habits (ter Hofstede & Fenton 2005; Patterson *et al.* 2007; Rifkin *et al.* 2012), which would be reflected in greater specialization and modularity for that interaction subnetwork.

MATERIALS AND METHODS

Study area

We captured bats from 10 sites within forest patches of the savannah of Amapá State in the northeastern

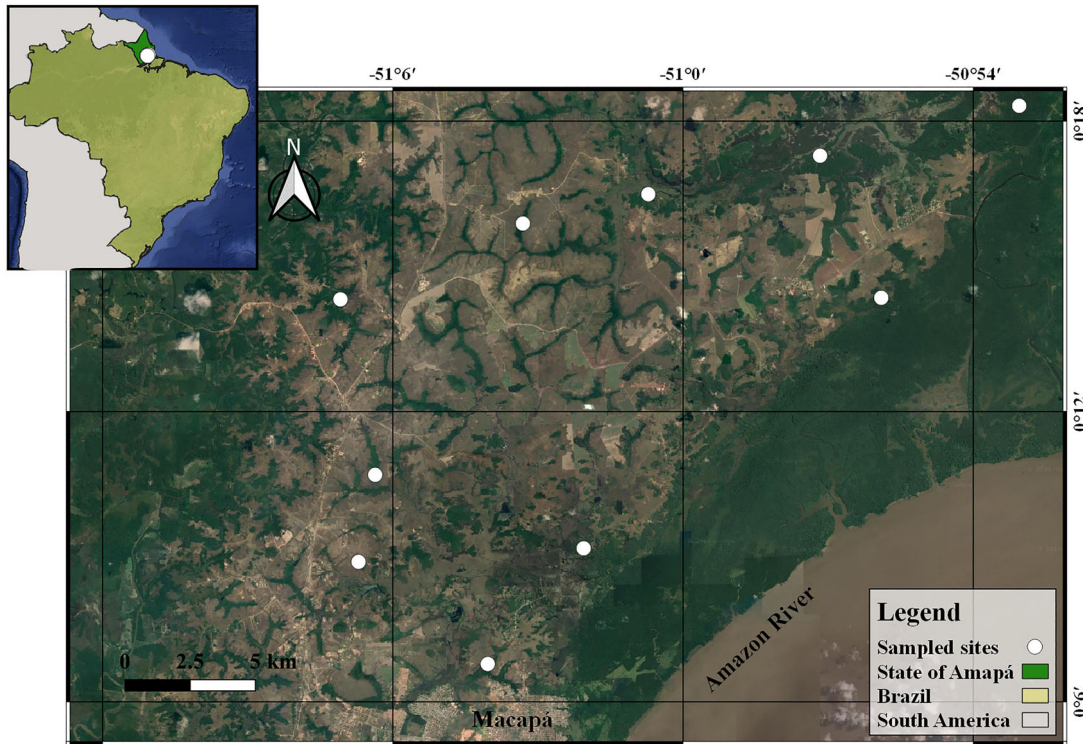


Figure 1 Map showing Amapá State in Brazil and the 10 sites where bats were captured and their bat flies collected. Sampling was conducted between 2016 and 2018.

portion of the Brazilian Amazon (Fig. 1). The Amapá savannahs represent the fourth largest block of Amazonian savannahs, characterized by grasslands hosting forest patches, flooded fields, and gallery forests dominated by *Mauritia flexuosa* (Carvalho & Mustin 2017; Mustin *et al.* 2017). We selected particular forest patches based on their accessibility by roads and trails, all of which are embedded in a type of savannah featuring open canopy cover and trees of <2 m (Costa-Neto 2017), locally called “parkland cerrado” (Mustin *et al.* 2017). All 10 sampling sites were equidistant from each other (by 2.5 km), as individuals of some bat species tend to travel up to 2.5 km per night in Amazonian savannahs (Bernard & Fenton 2003). The average vegetation height for the sampled forest patches was 7 m, with some trees exceeding 25 m in height (Carvalho *et al.* 2023). The region is characterized by a tropical monsoon climate (according to Köppen’s classification), featuring a wet season from December to July and a dry season from August to November, with local temperatures not varying greatly throughout the year (annual average = 27°C) (Tavares 2014).

Bat capture, bat fly collection, and species identification

We captured bats between August 2016 and August 2018 in transects of ~110 m, which were set at least 30 m from the edge of the forest patch at each site to minimize edge effects on bat capture (Meyer *et al.* 2015). We used nine mist nets (12 × 3 m, mesh size = 14 mm; Luz *et al.* 2019) over four nights—two nights in the wet season and two nights in the dry season at each site, for a total of 40 sampling nights. We ensured a minimum interval of 30 days for sampling nights at a given site to reduce the effects of sampling over consecutive nights (Esbérard 2006; Marques *et al.* 2013). Our sampling effort was 12 960 square meters of mistnet per hour for each station (*sensu* Straube & Bianconi 2002). Further details about our bat capture methodology have been reported previously (Carvalho *et al.* 2021, 2023).

Captured bats were placed in individual cotton bags to prevent sample contamination (i.e. accidental parasitism *sensu* Dick 2007). We recorded sex and age, classifying the bats as either adults or juveniles based on differences

in the degree of epiphyseal ossification (Anthony 1988). We identified bats according to Lim and Engstrom (2001), Gardner (2008), Reis *et al.* (2017), and López-Baucells *et al.* (2018). We adopted the bat species nomenclature of Garbino *et al.* (2020), and handled the bats according to the protocol of the American Society of Mammalogists (Sikes & Animal Care & Use Committee of the American Society of Mammalogists 2016). All bat flies on the captured bats were removed on-site using fine-tipped forceps and stored individually in microtubes containing 70% ethanol. The fly samples were taken to the Laboratory of Morpho-physiological and Parasitological Studies at the Federal University of Amapá (LEMP-UNIFAP) and identified according to Graciolli *et al.* (2010), Guerrero (1993, 1994a,b, 1995a,b, 1996), and Theodor and Peterson (1964). For statistical analyses, we considered *Trichobius dugesioides dugesioides* (parasitizing *Trachops cirrhosus*) and *T. dugesioides phyllostomus* (parasitizing *Phyllostomus elongatus*) as *Trichobius dugesioides* and *Trichobius phyllostomus*, respectively, due to morphological differences found by G. Graciolli (Unpublished data).

Data analysis

We used the complete adult host database to create a pooled network, which we split to create subnetworks for each season (wet vs. dry) and host sex (male vs. female), in order to check if these subnetworks display structural differences. We used Hill numbers to evaluate sample coverage by comparing the values among subnetworks, allowing us to determine if any differences among the subnetworks are attributable to sampling success rather than to biological processes. Hill numbers are an appropriate measure for comparing datasets, as well as for evaluating species richness and sampling success according to coverage (Chao *et al.* 2014; Roswell & Dushoff 2021). Here, sampling coverage means the proportion of fly species found on more than a single bat. Since bats can host more than a single bat fly (in some cases >20 on a single individual—e.g. Wenzel 1976; also see table 2), we used the number of infected hosts per bat fly species as a measure of sample size. We calculated coverage using the R package “iNEXT” (Hsieh *et al.* 2014), estimating species richness ($q = 0$) based on the number of bats (knots = 100; an 84% confidence interval [se = TRUE, conf = 0.84]; and 1000 iterations [nboot = 1000]).

Hill numbers can also be used to estimate species richness. We constructed species richness curves considering a sample size of up to twice the size of the smallest sample

of bat fly species, as recommended by Chao *et al.* (2014). Thus, to compare between male and female host and seasons, we used total sample of infected bats. To compare the expected species richness curves for the subnetworks, we determined overlap of their confidence intervals (CI) (Chao & Chiu 2016), so that whenever the 84% CI did not overlap, we considered the difference significant at $\alpha = 0.05$ (Cumming & Finch 2005; MacGregor-Fors & Payton 2013). However, when the 84% CI overlapped, we used diversity estimates and standard errors to establish statistical significance, as proposed by Schenker and Gentleman (2001).

We also compared fly abundance between seasons (wet vs. dry) and host sex (males vs. females) by means of a Mann–Whitney *U* Test using the R package “stats” (R Core Team 2021). We evaluated the species composition of bat flies among subnetworks by conducting a similarity analysis (ANOSIM) and using the Bray–Curtis index (Clarke 1993), which allowed us to construct a dissimilarity matrix for seasonality and host sex. To estimate the statistical significance of our ANOSIM, we ran a permutation test with 9999 iterations and conducted nonmetrical multidimensional scaling (NMDS) to visualize differences. ANOSIM and NMDS were processed in the R package “vegan” (Oksanen *et al.* 2022).

To assess the network metrics between bats and bat flies, we assessed the pooled network (representing the complete dataset, but excluding juvenile bats) and the four subnetworks considering season and host sex. The pooled network encompasses all species and interactions found in the Amapá savannahs, whereas the subnetworks illuminate different perspectives of the structure of the pooled network. We constructed each network using a weighted data matrix in which rows correspond to bat species, columns correspond to bat fly species, and each cell shows the number of infected bats. We calculated bat species richness, bat fly species richness, number of links, number of compartments, specialization (H2' index), and modularity for the pooled network and all subnetworks. Links represent the interactions between bat and bat fly species, represented by lines in the network figures. Compartments are independent groups of species with no connection to other groups in the network/subnetwork (Dormann & Strauss 2014). Specialization (H2') reflects the degree of exclusivity for connections in the network/subnetwork and can be considered a measure of niche differentiation (Blüthgen & Klein 2011). The values of the H2' index range from 0 to 1, with 1 indicating “perfect specialization.” Modularity can be used to identify subgroups of species that are more connected to each other than to the rest of the network/subnetwork (modules).

Modularity values also range from 0 to 1, with a value of 1 evidencing a highly modular network (Dormann & Strauss 2014). We used the DIRTLPawb + algorithm to calculate modularity (Beckett 2016). All these metrics adequately describe patterns of specificity in interaction networks and, in our case, can be used to quantify how bat fly species share hosts as resources (Blüthgen *et al.* 2007; Almeida-Neto & Ulrich 2011; Beckett 2016). Furthermore, we used a null model to test the significance of specialization (H_2') and modularity based on 1000 matrices generated using the “shuffle.web” algorithm (Dormann *et al.* 2009). Bat flies are highly specific ectoparasites (Esbérard *et al.* 2005; Dick & Patterson 2007; Lourenço *et al.* 2016), so low connectance is a typical property of bat–bat fly interaction networks (Júnior *et al.* 2020). Accordingly, we chose an algorithm that maintains this characteristic to build our null model. Marginal totals can encompass geographic variability due to divergent environmental characteristics (Dick & Dick 2006; Patterson *et al.* 2007; Dittmar *et al.* 2009), so we maintained them as variable factors in our model. We compared estimated index values with the 95% CI of the null model to establish if they differed significantly from values expected by chance (Dormann *et al.* 2009). We performed this analysis in the R package “bipartite” (Dormann *et al.* 2019), and drew the network using the R package “igraph” (R Core Team 2021).

Ethics statement

Animal ethics approval for the present project was obtained from the Comitê de Ética no Uso de Animais of Universidade Federal do Amapá.

RESULTS

Bat and ectoparasitic fly assemblage structure, composition, and richness

We captured 1073 bats belonging to 54 species, out of which 397 individuals from 26 species were parasitized by bat flies (Table 2). Bats parasitized by bat flies belonged to the Phyllostomidae and Vespertilionidae families. The most abundant bat species were *Artibeus planirostris* ($n = 239$), *Carollia perspicillata* ($n = 188$), and *Artibeus lituratus* ($n = 129$). Overall, 37.00% SE 1.47 of the host bats harbored ectoparasitic flies, with bats being more parasitized in the wet season (41.27% SE 1.91 of bats; average bat fly abundance = 105.2 SD 48.59) than in the dry season (30.07% SE 2.27 of bats; average bat

fly abundance = 33.6 SD 42.63) ($U = 18.5$; $P = 0.018$). Female bats were more parasitized (41.76% SE 2.11 of hosts; average bat fly abundance = 82.6 SD 49.84) than males (32.07% SE 2.03 of hosts; average bat fly abundance = 56.2 SD 27.95), but this difference was not statistically significant ($U = 35$; $P = 0.279$).

We collected 1388 ectoparasitic flies belonging to 40 species of the families Streblidae (38 species) and Nycteribiidae (2 species). The most abundant fly species were *Trichobius joblingi* ($n = 521$), *Trichobius parasiticus* ($n = 126$), *Speiseria ambigua* ($n = 76$), *Strebla wiedemanni* ($n = 86$), and *Mastoptera minuta* ($n = 71$). We recorded higher bat fly species richness in the wet season (Table 1), although overlap in the 84% CI of respective Hill number values indicated that this difference was not statistically significant (Fig. 2a). Despite greater bat fly species richness on female hosts (Table 1), again the 84% CI overlapped between the female and male datasets, supporting that this difference was not statistically significant (Fig. 2b). Bat fly species composition did differ significantly between seasons (Global $R = 0.263$; $P = 0.002$; Fig. 3a). However, we found no differences in bat fly species composition between female and male hosts (Global $R = -0.023$; $P = 0.609$; Fig. 3b).

Interaction network topology, specialization, and modularity

We found the pooled network (Fig. 4) to be highly specialized (0.88) and modular (0.73), with specific bat–bat fly interactions in the network forming 15 compartments (Table 1). Overall, we identified subnetworks with wide variation in the number of bat species (15–23), bat fly species (25–36), links (27–48), as well as in bat fly abundance (336–1052) and number of compartments (12–14) (Table 1). Among all subnetworks, dry season proved to be more specialized (0.99) and modular (0.82) because fewer bat species were parasitized by fewer species of bat flies relative to the wet season when abundances of both species' groups were greater. Intriguingly, the female subnetwork was slightly more specialized (0.88) and modular (0.73) due to their having greater numbers of bat and bat fly species relative to males. Furthermore, the pooled network and the subnetworks presented low connectance with sample coverage >94% (Table 1).

DISCUSSION

As anticipated, parasitized bats and their ectoparasitic flies were more abundant during the wet season, and

Table 1 Network structure and bat–bat fly interaction networks for the Amapá savannah, northeastern Brazil

METRICS	Wet	Dry	Female	Male	Pooled
Coverage	0.977	0.969	0.962	0.947	0.982
Bat richness	23	15	22	20	26
Bat fly richness	36	25	34	32	40
Bat individuals parasitized	274	123	228	169	397
Bat fly abundance	1052	336	826	562	1388
Links	48	27	44	41	54
Compartments	14	13	14	12	15
Connectance	0.058	0.072	0.059	0.064	0.052
Specialization ($H2'$)	0.842	0.990	0.882	0.873	0.875
Null Model ($H2'$)	0.937–0.944	0.975–0.981	0.938–0.947	0.930–0.938	0.939–0.946
Modularity	0.654	0.829	0.732	0.676	0.730
QuanBiMo	0.802–0.814	0.842–0.856	0.822–0.834	0.809–0.821	0.811–0.819

Values in bold represent statistically significant results, that is, the observed value differs from the null model 95% confidence interval.

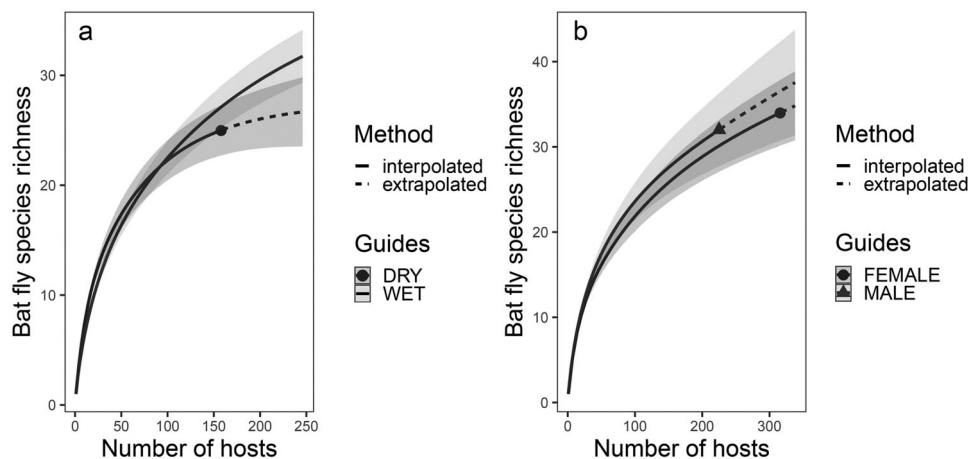


Figure 2 Species richness, as estimated by Hill numbers ($q = 0$), of bat flies parasitizing bats according to season (a) and host sex (b). The shaded area represents the 84% confidence interval.

specialization and modularity were higher in the dry season (Table 1). The higher values of specialization and modularity for the dry season subnetwork reflect fewer resources, that is, fruits, flowers, insects, and roosts, being available at this time, so contact between host species and bat fly species in roosts is reduced. Thus, usual or accidental contacts, that is, when a fly parasitizes a non-primary host, directly affect the structure of interactions. Moreover, as hypothesized, female hosts harbored more bat flies than males, as reflected in network specialization, modularity, and topology metrics. Our findings complement knowledge from other ecosystems in northern

Brazil and Amazonian savannahs (Gracioli & Bernard 2002; Gracioli & Linardi 2002; Dias *et al.* 2009; Santos *et al.* 2009, 2013; Hrycyna *et al.* 2019; Palheta *et al.* 2020), revealing seasonal differences, together with an influence of host sex, in bat–bat fly relationships in the Amazonian savannah.

Impact of seasonality on bat–bat fly interactions

We found that a greater number of interactions occurred between bats and their ectoparasitic flies during

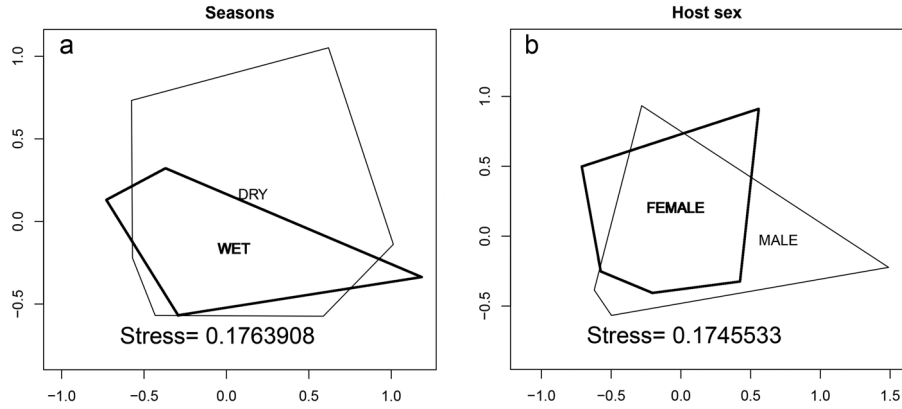


Figure 3 Nonmetric multidimensional scaling (NMDS) ordination chart, showing differences in bat fly species composition according to season (a) and host sex (b). Bold lines match to the names in bold.

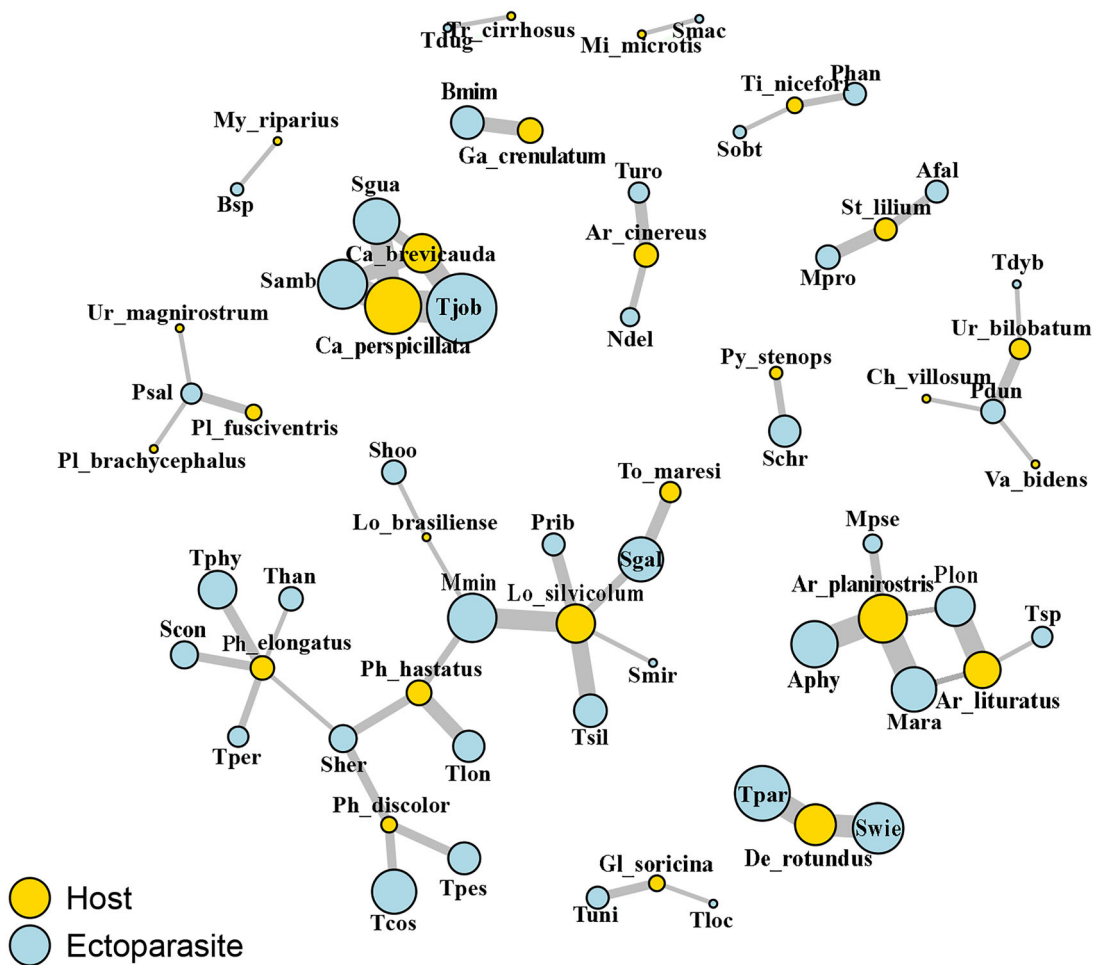


Figure 4 Local interaction network for bats and their bat flies in forest patches of Amapá savannah, northeastern Brazil. Node and link weights have been log-transformed. Abbreviations are explained in Table 2.

Table 2 List of bat species and their ectoparasitic fly species, as recorded in the Amapá savannah between 2016 and 2018, with species name abbreviations, number of parasitized bats, and bat fly abundance data

No.	SPECIES	Abbreviation	No. examined bats	No. parasitized bats	Bat fly abundance	Occurrence	
						Season	Sex
Phyllostomidae							
1	<i>Ametrida centurio</i>		2			wd	m
2	<i>Artibeus (Dermanura) sp.</i>		2			d	fm
3	<i>Artibeus cinereus</i>	Ar_cinereus	48	7		wd	fm
	<i>Neotrichobius delicatus</i>	Ndel			4	wd	fm
	<i>Trichobius urodermae</i>	Turo			5	wd	fm
4	<i>Artibeus concolor</i>		3			w	f
5	<i>Artibeus gnomus</i>		9			wd	fm
6	<i>Artibeus lituratus</i>	Ar_lituratus	129	24		wd	fm
	<i>Megistopoda aranea</i>	Mara			2	w	f
	<i>Paratrichobius longicrus</i>	Plon			30	wd	fm
	<i>Trichobius sp.</i>	Tsp			5	w	f
7	<i>Artibeus obscurus</i>		44			wd	fm
8	<i>Artibeus planirostris</i>	Ar_planirostris	239	69		wd	fm
	<i>Aspidoptera phyllostomatis</i>	Aphy			59	wd	fm
	<i>Megistopoda aranea</i>	Mara			48	wd	fm
	<i>Metelasmus pseudopterus</i>	Mpse			4	wd	fm
	<i>Paratrichobius longicrus</i>	Plon			1	w	m
9	<i>Carollia brevicauda</i>	Ca_brevicauda	36	29		w	fm
	<i>Speiseria ambigua</i>	Samb			12	w	fm
	<i>Strebla guajiro</i>	Sgua			9	w	f
	<i>Trichobius joblingi</i>	Tjob			67	w	fm
10	<i>Carollia perspicillata</i>	Ca_perspicillata	188	142		wd	fm
	<i>Speiseria ambigua</i>	Samb			64	wd	fm
	<i>Strebla guajiro</i>	Sgua			46	wd	fm
	<i>Trichobius joblingi</i>	Tjob			454	wd	fm
11	<i>Chiroderma trinitatum</i>		1			w	m
12	<i>Chiroderma villosum</i>	Ch_villosum	1	1		w	m
	<i>Paratrichobius dunnii</i>	Pdun			1	w	m
13	<i>Desmodus rotundus</i>	De_rotundus	41	36		wd	fm
	<i>Strebla wiedemanni</i>	Swie			86	wd	fm
	<i>Trichobius parasiticus</i>	Tpar			126	wd	fm
14	<i>Glossophaga soricina</i>	Gl_soricina	7	3		w	m
	<i>Trichobius lonchophyllae</i>	Tloc			1	w	m
	<i>Trichobius uniformis</i>	Tuni			6	w	m

(Continued)

Table 2 (Continued)

No.	SPECIES	Abbreviation	No. examined bats	No. parasitized bats	Bat fly abundance	Occurrence	
						Season	Sex
15	<i>Lophostoma brasiliense</i>	Lo_brasiliense	2	1		w	m
	<i>Mastoptera minuta</i>	Mmin			23	w	m
	<i>Strebla hoogstragaali</i>	Shoo			7	w	m
16	<i>Lophostoma silvicola</i>	Lo_silvicola	50	29		wd	fm
	<i>Mastoptera minuta</i>	Mmin			46	wd	fm
	<i>Pseudostrebla riberoi</i>	Prib			6	wd	fm
	<i>Strebla galindoi</i>	Sgal			18	w	fm
	<i>Strebla mirabilis</i>	Smir			1	w	m
	<i>Trichobius silvicolae</i>	Tsil			17	wd	fm
	<i>Mesophylla macconnelli</i>				6	wd	fm
18	<i>Micronycteris megalotis</i>		4		wd	fm	
19	<i>Gardnerycteris crenulatum</i>	Ga_crenulatum	38	8		wd	fm
	<i>Basilina mimoni</i>	Bmim			17	wd	fm
20	<i>Micronycteris microtis</i>	Mi_microtis	4	1		d	f
	<i>Strebla machadoi</i>	Smac			1	d	f
21	<i>Micronycteris schmidtorum</i>		1		w	f	
22	<i>Micronycteris</i> sp.		1		w	f	
23	<i>Phyllostomus discolor</i>	Ph_discolor	3	3		w	fm
	<i>Strebla hertigi</i>	Sher			4	w	fm
	<i>Trichobioides perspicillatus</i>	Tpes			16	w	fm
	<i>Trichobius costalimai</i>	Tcos			49	w	fm
24	<i>Phyllostomus elongatus</i>	Ph_elongatus	10	7		wd	fm
	<i>Strebla consocia</i>	Scon			10	wd	f
	<i>Strebla hertigi</i>	Sher			3	w	f
	<i>Trichobius phyllostomus</i>	Tphy			27	w	f
	<i>Trichobius handleyi</i>	Than			7	w	m
	<i>Trichobius persimilis</i>	Tper			5	d	fm
25	<i>Phyllostomus hastatus</i>	Ph_hastatus	8	8		wd	fm
	<i>Mastoptera minuta</i>	Mmin			2	wd	fm
	<i>Strebla hertigi</i>	Sher			3	d	fm
	<i>Trichobius longipes</i>	Tlon			15	wd	fm
26	<i>Phylloiderma stenops</i>	Py_stenops	2	2		d	fm
	<i>Strebla christinae</i>	Schr			15	d	fm
27	<i>Platyrrhinus brachycephalus</i>	Pl_brachycephalus	6	1		d	f
	<i>Paratrichobius salvini</i>	Psal			1	d	f
28	<i>Platyrrhinus fusciventris</i>	Pl_fusciventris	22	3		wd	f
	<i>Paratrichobius salvini</i>	Psal			3	wd	f

(Continued)

Table 2 (Continued)

No.	SPECIES	Abbreviation	No. examined bats	No. parasitized bats	Bat fly abundance	Occurrence	
						Season	Sex
29	<i>Platyrrhinus incarum</i>		7			wd	fm
30	<i>Platyrrhinus</i> sp.		5			wd	fm
31	<i>Rhinophylla pumilio</i>		26			wd	fm
32	<i>Sturnira lilium</i>	St_lilium	7	6		w	fm
	<i>Aspidoptera falcata</i>	Afal			6	w	fm
	<i>Megistopoda proxima</i>	Mpro			7	w	fm
33	<i>Tonatia maresi</i>	To_maresi	12	5		wd	fm
	<i>Strebla galindoi</i>	Sgal			31	wd	fm
34	<i>Trachops cirrhosus</i>	Tr_cirrhosus	1	1		w	f
	<i>Trichobius dugesioides</i>	Tdug			1	w	f
35	<i>Trinycteris nicefori</i>	Ti_nicefori	4	3		w	fm
	<i>Parastrebla handleyi</i>	Phan			6	w	fm
	<i>Strebla obtusa</i>	Sobt			2	w	f
36	<i>Uroderma bilobatum</i>	Ur_bilobatum	46	5		wd	fm
	<i>Paratrichobius dunni</i>	Pdun			4	wd	fm
	<i>Trichobius dybasi</i>	Tdyb			1	d	m
37	<i>Uroderma magnirostrum</i>	Ur_magnirostrum	8	1		w	f
	<i>Paratrichobius salvini</i>	Psal			1	w	f
38	<i>Vampyriscus bidens</i>	Va_bidens	5	1		w	m
	<i>Paratrichobius dunni</i>	Pdun			1	w	m
39	<i>Vampyriscus brocki</i>		1			w	f
40	<i>Vampyrodes caraccioli</i>		1			w	f
	Vespertilionidae						
41	<i>Myotis riparius</i>	My_riparius	1	1		w	f
	<i>Basilina</i> sp.	Bsp			2	w	f
	Molossidae						
42	<i>Eumops delticus</i>		1			w	m
43	<i>Molossus coibensis</i>		4			w	fm
44	<i>Molossus molossus</i>		4			wd	f
45	<i>Molossus rufus</i>		1			d	f
	Emballonuridae						
46	<i>Cormura brevirostris</i>		3			wd	fm
47	<i>Peropteryx leucoptera</i>		3			wd	fm
48	<i>Peropteryx pallidoptera</i>		2			w	f
49	<i>Rhynchonycteris naso</i>		4			wd	fm
50	<i>Saccopteryx bilineata</i>		1			w	f
51	<i>Saccopteryx canescens</i>		4			wd	fm

(Continued)

Table 2 (Continued)

No.	SPECIES	Abbreviation	No. examined bats	No. parasitized bats	Bat fly abundance	Occurrence	
						Season	Sex
52	<i>Saccopteryx leptura</i>		14			wd	fm
	Thyropteridae						
53	<i>Thyroptera tricolor</i>		1			d	m
		Total	1073	397	1388		

Bat families are shown in bold and bat species numbered. For bat species, under “Occurrence,” we show the season in which the species was captured, and the sexes recorded. For bat fly species, under “Occurrence,” we show the season and host sex in which an interaction was recorded (w = only wet season; d = only dry season; wd = both seasons; f = only female hosts; m = only male hosts; fm = both sexes). Genus abbreviations are as follows: Ar, *Artibeus*; Ca, *Carollia*; Ch, *Chiroderma*; De, *Desmodus*; Gl, *Glossophaga*; Lo, *Lophostoma*; Ga, *Gardnerycteris*; Mi, *Micronycteris*; My, *Myotis*; Ph, *Phyllostomus*; Py, *Phylloderma*; Pl, *Platyrrhinus*; St, *Sturnira*; To, *Tonatia*; Tr, *Trachops*; Ti, *Trinycteris*. Note that we only add the parasitized bat species to the interaction network plot.

the wet season. Upon emerging from the pupal stage, bat flies need to find a host immediately to feed on (Overall 1980; Dick & Patterson 2007; Dittmar *et al.* 2009). Consequently, greater bat species richness in the wet season has been postulated to enhance the probability of bat flies switching hosts, mainly to phylogenetically related bat species (Fagundes *et al.* 2017; Saldaña-Vázquez *et al.* 2019), since new bat species are added to the host pool during this time. Moreover, both *Carollia* spp. and *Artibeus* spp. display reproductive peaks in the wet season (Carvalho *et al.* 2019), increasing their abundance and forcing them to share scarce roost sites (Kunz 1982; Aguirre *et al.* 2003). Consequently, ectoparasitic exchange is promoted between bat species with similar roosting habits (see Urbieta *et al.* 2022). Bat social dynamics also change during the mating season. As described by McCracken and Wilkinson (2000) and Wilkinson (1986), individuals are constantly exchanged between groups of group-living bats, with males seeking to establish harems and competing for their control, and females searching for higher-ranked males. Therefore, in multispecies roost sites, bats of different species but with similar mating systems and roosting behaviors can exchange ectoparasites (Garbino & Tavares 2018). Hence, similarities in bat roosting behavior and individual mobility (McKee *et al.* 2019) likely explain seasonal interactions, such as we observed for *Megistopoda aranea* with *Artibeus lituratus*, as well as for *Paratrachobius longicrus* with *Artibeus planirostris* (Table 2), and as also reported by Urbieta *et al.* (2021). Notably, rates of bat capture (see Carvalho *et al.* 2018) and bat fly collection (Table 1) tend to be higher in the wet season, and the greater

combined host species richness at this time enhances the probability of bat flies switching hosts within bat roosts (Dick 2007; Hiller *et al.* 2021). Although Zarazúa-Carbajal *et al.* (2016) found that season alone could influence bat fly species composition in their interaction network, we postulate that it affects network structure in combination with other variables (such as those mentioned above) in patchy sites like our study area. Therefore, together, all these factors increase the number of links in the bat–bat fly interaction network and modify their extent, thereby reducing specialization in the wet season subnetwork.

Interestingly, network specialization and modularity were also impacted during the dry season, likely because at this time bat reproductive rates are lower (Mello *et al.* 2004; Klingbeil & Willig 2010; Carvalho *et al.* 2019), juveniles disperse (Dobson 1982; Morrison & Handley 1991), and males become solitary (McCracken & Wilkinson 2000). Accordingly, group sizes are reduced and contact between bat individuals and species is diminished, reducing the rate of ectoparasite transfer (Rifkin *et al.* 2012). In addition, food is scarcer during the dry season, so some host species must disperse to search for resources (Janzen & Schoener 1967; Racey 1982; Lewis 1995; McCracken & Wilkinson 2000; Pinheiro *et al.* 2002; Mello *et al.* 2004; Klingbeil & Willig 2010; Ramos *et al.* 2010). Together, these influences contribute to a dry-season interaction network that involves fewer bat species than that for the wet season, highlighting how a more depauperate host community means fewer ectoparasites (Barbier & Bernard 2017). Bat flies display diminished survival on atypical host species (Overall 1980; Marshall

1982; Dick & Patterson 2006), so network specialization and modularity are higher in the dry season when there are fewer host species for bat flies.

Impact of host sex on bat–bat fly interactions

We uncovered greater specialization and modularity for the female host subnetwork. Although the number of parasitized females was statistically similar to males, the nature of the aggregate parasitism of the bat flies and the behavior of the females seem to have affected the subnetworks. Notably, the social behavior of female bats is more stable throughout the year, with most species being colony-forming and establishing harems only during the mating season (Lewis 1995; McCracken & Wilkinson 2000; Christie *et al.* 2007). Although individuals can switch between harems, such exchange is generally restricted to groups within a common colony (McCracken & Wilkinson 2000; Kerth 2008), especially for species that form large colonies. In comparison, males tend to move further, switch roosts more frequently, and change location while competing for harems (Morrison 1979; Morrison & Handley 1991; Kunz & McCracken 1996), all of which tend to reduce the exclusivity of their relationships with bat flies. Our interaction networks reflect these sex-biased relationships, despite no apparent significant differences in bat fly species richness or bat fly species composition between sexes being detected (Figs 2b and 3). Therefore, although male and female hosts display the same ectoparasitism rates (i.e. abundances of bat flies), bat fly species richness, and bat fly species composition, the female subnetwork had higher values of specialization and modularity, which may indicate a stronger association with bat fly species than that presented by males.

CONCLUSIONS

Here, we present novel data on bat–bat fly interactions in the fourth largest block of Amazonian savannah (Carvalho & Mustin 2017), revealing that the wet season drives lower specialization and modularity in the interaction network, and that the female subnetwork shows higher specialization and modularity than the male subnetwork. Our findings add to the growing body of knowledge on interaction networks between bats and their ectoparasitic flies, yet ours is one of few studies that have considered seasonality and host sex as factors. Moreover, our data prompt the question as to how these variables may affect interaction networks in other Neotropical

regions of contrasting precipitation regimes, where bat and bat fly responses might differ.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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