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Are cocoa plantations suitable habitats? Network between parasites (Diptera: Hippoboscidea) and hosts (Mammalia: Chiroptera) in cocoa-dominated landscapes of the Brazilian Amazon

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Introduction: The relationship between ectoparasitic flies and bats is influenced by anthropogenic changes in natural environments. In the Amazon, various forms of disturbance contribute to ecosystem imbalance, potentially leading to the local extinction and disruption of ecological functions. Cacao cultivation has been expanding in the Amazon, but studies on its impacts on bat diversity are still limited, hindering the development of effective conservation strategies. This study aims to assess bat and batfly species to understand how land-use changes affect antagonistic interaction networks between ectoparasitic flies and Phyllostomidae bats.

Methods: We sampled urban areas, natural vegetation, and cacao plantations using 10 mist nets over 69 nights at 36 sites across 10 municipalities in Pará.

Results: The overall interaction network showed 42 host species and 52 ectoparasite species, showing high specialization, low connectivity, and insignificant nesting and parasite vulnerability. The highest ectoparasites richness was observed in natural vegetation (47), followed by cacao (30) and urban areas (29). The cacao-dominated network exhibited high modularity, natural areas had the highest occurrence of infracommunities, followed by urban areas and cocoa. Five bat species were present in all three environments, each infested with infracommunities. Notably, infracommunal associations were common among ectoparasite genera *Speiseria, Strebla*, and *Trichobius*.

Discussion: The species richness observed highlights Pará as a region of exceptional diversity for dipteran ectoparasites of bats (with 60 species). Our study suggests that cacao plantations can serve as suitable habitats for both

bats and flies. Notably, we conducted this research on a small, family-run farm. While these types of farms are not substitutes for natural vegetation, they may help mitigate the impacts of rapid land-use and land-cover change. In fact, these small, family-operated farms demonstrated habitat suitability close to that of natural vegetation areas, supporting greater biodiversity within agricultural landscapes.

KEYWORDS

Streblidae, Nycteribiidae, infracommunity, Phyllostomidae, Trichobius tuttlei, Speiseria peytoni, Mastoptera guimaraesi, Basilia manu

1 Introduction

Parasites represent a large proportion of species diversity in ecosystems (Dobson et al., 2008), with associations so specific that they often drive co-speciation and mirror the phylogenetic relationships of their hosts (Hafner et al., 1994). In particular, bats and their ectoparasitic flies frequently form co-evolutionary or co-adaptive relationships (Poulin et al., 2011), shaped by ecological interactions (Janzen, 1980). Mammals are commonly parasitized by arthropods (Whitaker, 1988; Graciolli and Bianconi, 2007; Torres et al., 2019), especially ectoparasitic Diptera from the families Streblidae and Nycteribiidae, which are exclusive to Chiroptera (Graciolli, 2004; Rui and Graciolli, 2005; Santos et al., 2012). Bats, the only mammals capable of true flight, 1,487 species globally (Simmons and Cirranello, 2025), with 288 species in the Neotropics and 181 in Brazil (Garbino et al., 2024). Their morphological and dietary diversity allows them to occupy varied habitats and provide essential ecological services, such as pollination, seed dispersal, and insect control (Kunz et al., 2011; Aguiar et al., 2021), making them key species in tropical forests, like the (Silva et al., 2020).

Streblidae includes 299 species exclusive to the New World (Dick et al., 2016; Graciolli and Linardi, 2002). In Brazil, 24 genera, 101 species – 9 of which are endemic – and 2 subspecies are currently known (Graciolli, 2024). The Nycteribiidae family is distributed worldwide, with 28 species recorded in Brazil, 12 of which are endemic and belong to 2 genera (Graciolli and Hrycyna, 2024). These ectoparasitic flies reproduce through adrenotropic viviparity (Dittmar et al., 2015), where each female deposits a pre-pupa that develops in approximately three weeks (Dick and Patterson, 2007). The pre-pupa is deposited on the surface of the host's shelter, and once it hatches, the young fly must quickly find a host to survive (Dittmar et al., 2009).

The development of these flies in limited by the shelter microclimatic (Dittmar et al., 2009; Morse et al., 2012) and behavior (Reckardt and Kerth, 2007), and host traits such as sex, age, size, and reproductive stage, which can influence the abundance of ectoparasitic flies (Patterson et al., 2008; Esbérard et al., 2012). These interactions are also influenced by human activity (Salkeld et al., 2013), which leads to habitat degradation and loss, reduced habitat host and parasite diversity (Bojsen and Jacobsen, 2003; Kleine and Trivinho-Strixino, 2005) and potentially causing local species extinctions (Ramírez-Mejía et al., 2020). Alterations in parasitic relationships are also evident due to changes in land use and land cover, habitat loss and fragmentation, urbanization, and climate change (Davidson et al., 2012; Urbieta et al., 2014; Bolívar-Cimé et al., 2018; Palheta et al., 2020; Mendes, 2021). In fact, the subfamily Phyllostominae, which is primarily composed of insectivorous, carnivorous, and omnivorous gleaning bats, is described as a potential indicator of disturbed areas (Silva, 2012) and are highly adaptable, occupying both natural and anthropogenic environments (Morales et al., 2012; Heer et al., 2015).

In Pará, the natural landscape has been directly affected by climate change and rapid agricultural development (Galford et al., 2010). Changes in land use and cover are, in fact, the main drivers of biodiversity loss in the Neotropics (Meyer et al., 2016). In this context, numerous sources of anthropogenic disturbance are observed, such as deforestation, the opening of pastures, fires (Fearnside, 1995; Fearnside et al., 2013; Defries and Rosenzweig, 2010), short-cycle crops like soybeans (Nepstad et al., 2008; Barona et al., 2010), and long-cycle crops like cocoa, both in the cabruca system and in traditional monoculture (Brainer, 2021; Franca et al., 2023). The advance of cocoa farming in the Amazon is evident, despite the state of Pará having a smaller planted area than Bahia (152,881 ha vs. 440,050 ha, respectively) (IBGE/SIDRA/LSPA, 2023). Nevertheless, with a production of over 129,000 tons of cocoa in 2019, Pará became the largest cocoa producer in Brazil, surpassing Bahia, which produced 105,000 tons (Agencia Para, 2021).

Cocoa plantations are typically located near forest fragments, with cocoa trees ranging from three to twenty meters in height (SENAR, 2018). These areas, which exhibit low anthropogenic modification, represent productive environments with high bat activity (Faria, 2006). In Pará, cocoa is cultivated through conventional monoculture, extractivist systems, and cabruca-type Agroforestry Systems (AFS), where cocoa is grown alongside tall canopy trees. Cabruca AFS involve mixed and polyculture systems, often pairing cocoa with species like rubber, açaí, African mahogany, or Australian cedar, which can include native or exotic species of economic interest (SENAR, 2018; Ministério da Agricultura, Pecuária e Abastecimento, 2020).

Bat foraging in cocoa areas is common in both South America and Africa (Faria, 2006; Atagana et al., 2021; Ferreira et al., 2023a,

10.3389/fevo.2025.1499475

Ferreira et al., 2023b). In the Amazon, however, studies in cocoa environments are limited, and comparisons between cocoa areas and other environments (urban and rural) regarding bat ecology and interaction networks remain understudied (Palheta et al., 2020). Bat sampling in the Amazon is among the lowest in Brazil, covering only 23% of the area (Bernard et al., 2012), which hampers the development of effective conservation strategies for Phyllostomidae bats (Cardoso et al., 2019).

This study aims to: (i) identify ectoparasitic fly species on bats from Cocoa, Natural Vegetation, and Urban areas in the Brazilian Amazon; and (ii) assess whether land-use changes impact the structure of interaction networks between ectoparasitic flies (Diptera: Streblidae, Nycteribiidae) and Phyllostomidae bats (Mammalia: Chiroptera). We analyze bat infracommunities, assemblage of parasite species cooccurring within individual host organisms (Bush et al., 1997), and predict that (i) cocoa area networks will show higher specialization and modularity, (ii) urban networks will be more vulnerable to extinction, and (iii) cocoa areas will have the lowest levels of network nesting. We also report four new occurrences of flies from Brazil and ten new occurrences for the state of Pará.

2 Material and methods

2.1 Study area

The study area includes ten municipalities in the state of Pará: Altamira, Anapú, Bragança, Brasil Novo, Medicilândia, Nova Timboteua, Placas, Rurópolis, Uruará, and Vitória do Xingu (Figure 1). Eight of these municipalities are in the region known as the 'arc of deforestation,' a phenomenon that began in 1974 with the opening of the Trans-Amazonian Highway and was intensified by the creation of the Belo Monte Hydroelectric Plant - UHBM, in the 2000s (Palheta et al., 2020). The predominant biome in Pará is the Amazon, with a tropical humid climate according to the Köppen-Geiger classification system (Peel et al., 2007). The average annual temperature ranges from 25.5°C to 27.1°C, and rainfall indices vary between 1900 mm and 3000 mm per year (SEMAS, 2021). Bats were sampled over 69 nights at 36 sites: 21 sites and 24 nights in vegetation areas (forest fragments), 5 sites and 25 nights in urban areas, and 10 sites and 20 nights in cocoa cultivation areas. For all analyses we use the nights as replicate.

The sampled areas included natural vegetation, consisting of forest fragments that have undergone anthropogenic modifications, primarily located in municipalities within the Trans-Amazonian region. The cocoa cultivation areas comprised conventional, nonintercropped plantations. The urban sites were sampled within the urban zone of the municipality of Altamira-PA.

2.2 Bats and bat flies sampling

The ChiroXingu research group (Center for Studies in Ecology and Conservation of Chiroptera) conducted bat collections between 2017 and 2022 under SISBIO license no. 57294-2. Collections were carried out during the dry season (between July and November) at sites selected for accessibility and spaced at least 5 km apart. At each sampling location, researchers deployed ten mist nets (9 m x 2.5 m) at sunset. The nets remained in place for six hours, with inspections conducted every 30 minutes (Bernard, 2001; Silva, 2012).

Captured bats were temporarily placed in 100% cotton fabric bags and for field sorting. For each individual, we recorded weight, sex, age, and forearm measurement. Bats not retained as specimens were marked with numbered bands and released. Voucher specimens were transported to the Laboratory of Chiroptera Studies (LABEQ) at the Laboratory of Ecology (LABECO) of the Federal University of Pará (UFPA), Altamira campus, there, we euthanized two individuals of each species from each locality, one male and one female. We recorded morphometric data, including total length, foot length, ear length, tragus length, forearm length, and weight. Following measurements, specimens were fixed in 10% formalin and subsequently preserved in 70% alcohol in the ChiroXingu Bat Collection.

In the field, we conducted thorough examinations of captured bats to collect ectoparasites. The process involved: 1. Active searches across the entire body of each bat including fur, wings, membranes, and ears. 2. Removal of ectoparasitic flies using tweezers and brushes moistened with 70% alcohol. Preservation of collected flies: placed in individual containers filled with 70% alcohol and labeled according to the host bat. Fly identification was carried out in the laboratory to the lowest taxonomic level, using identification keys proposed by Guerrero (1996), Wenzel (1976), and Graciolli and Carvalho (2001).

2.3 Data analysis

The lists of bat species and ectoparasitic flies were organized as follows: the flies were listed in alphabetical order and divided into the two sampled families, Nycteribiidae and Streblidae. The bats were categorized according to the flies captured in our study, those already recorded in the literature, and the total richness and abundance by genus (male and female) of the flies, as well as new occurrences for Brazil and the state of Pará. The interactions between fly and bat communities were described by constructing interaction networks, considering the abundance of flies on the bats as the frequency of interactions. This analysis was carried out for the entire dataset and for each environment investigated (Cocoa, Natural Vegetation, and Urban Area).

To characterize and analyze the structure of the networks, we calculated the degree of ectoparasites and hosts, as well as the metrics of Connectivity, Nesting, Specialization, and Modularity, along with parasites vulnerability, extinction slope, and species richness. The specification of each metric is described in the Supplementary Material. To assess the significance of the indices of Nesting (WNODF), Connectivity (C), Modularity (M), and Specialization (H₂) obtained from the interaction networks, we used the Monte Carlo procedure based on random matrices according to the null model (Dormann et al., 2008), with 10,000 randomizations. The analysis of network metrics (Interaction

Degree, Nesting, Connectivity, Specialization, Modularity, Parasite Vulnerability, Extinction Slope, and Species Richness) was conducted using the bipartite package (Dormann et al., 2008) in R (R Core Team, 2022).

Finally, for the description of the infracommunities, we considered only hosts that occurred in all environments and had an abundance of more than two individuals in each environment. For all infracommunities, we calculated the absolute number of occurrences and the relative frequency (the ratio between the absolute frequency of parasites and the total population of each host) of ectoparasites. We defined an infracommunity as the association of a host with two or more species of ectoparasitic flies (Bush et al., 1997).

3 Results

With 69 nights of sampling at 36 points (Figure 1), we achieved a sampling effort of 93,150 h.m², 32,400 h.m² in fragments, 33,750 h.m² in urban areas and 27,000 h.m² in cocoa plantation (Straube and Bianconi, 2002). A total of 1,091 bats were captured, with 774 individuals hosting ectoparasitic flies. We sampled 2,694 flies (see Supplementary Table S1). The bats belonged to six families and 42 species, with Phyllostomidae and Mormoopidae being the most abundant families (see Supplementary Table S1). The most abundant host species in the three environments were *Carollia perspicillata* (450 individuals), *Pteronotus rubiginosus* (50), *Artibeus lituratus* (44) and *Artibeus obscurus* (31) (Supplementary Table S1).

The captured ectoparasitic flies belonged to the family Nycteribiidae, with 18 individuals from three species of the genus Basilia, and to the family Streblidae, with 2,676 individuals from 49 species and 14 genera (Table 1). The most abundant species were Trichobius joblingi (1,224), Speiseria ambígua (243), Trichobius johnsonae (153), Trichobius dugensioides (119), Strebla guajiro (113) e Nycterophilia parnelli (112) (Table 1). Four new occurrences of flies were observed in Brazil, and ten new occurrences were recorded for the state of Pará (Table 1). All sampled ectoparasite species presented new associations with hosts (Table 1), with particular emphasis on Speiseria ambigua, Strebla guajiro, and Trichobius joblingi, which were associated with Carollia perspicillata according to the literature and observed in numerous other host species, including non-Phyllostomidae, in our study (Table 1). Among the species with the highest number of associations, we observed Trichobius joblingi associated with 20 host species, Strebla guajiro with 12 hosts, Trichobius dugesioides and Speiseria ambigua with 11 hosts, and Aspidoptera falcata and Megistopoda aranea with eight hosts (Supplementary Table S2; Figure 2).

When analyzed by type of environment, we found that *Trichobius joblingi*, *Speiseria ambigua*, *Megistopoda aranea*, and *Aspidoptera falcata* had the lowest degree of interaction with bats in the cacao area (Supplementary Table S2; Figure 3) and the highest degree in the natural vegetation area (Supplementary Table S2; Figure 4), followed by the urban area (Supplementary Table S2; Figure 5). The hosts with

the highest degree of interaction (Supplementary Table S3) were *Carollia perspicillata* with 33 parasite species, *Artibeus lituratus* with 17 species, *Phyllostomus discolor* with 12 species, *Sturnira giannae* with 11 species, and *Pteronotus rubiginosus* with 10 parasite species (Supplementary Table S3; Figure 2). *Carollia perspicillata* showed high degrees of interaction across all three environments (Supplementary Table S3; Figures 3–5). *Artibeus lituratus* had the highest number of interactions in the Urban Area (Supplementary Table S3; Figure 5), *Phyllostomus discolor* in the Cacao areas (Supplementary Table S3; Figure 3), and *Pteronotus rubiginosus* and *Sturnira giannae* in Natural Vegetation (Supplementary Table S3; Figure 4).

The overall interaction networks, including all types of land use and cover sampled (Cacao, Natural Vegetation, and Urban Area), showed a richness of 42 host species and 52 ectoparasite species (Figure 2; Table 2). When constructing the networks by type of land use and cover (Figures 3–5; Table 2), we observed that the highest richness of ectoparasites was in the natural vegetation areas, with 47 species, followed by cacao and urban areas with 30 and 29 species, respectively. This same pattern of richness was observed in the hosts, with the highest richness in natural vegetation, followed by cacao and urban areas.

The general network exhibited high specialization, low Connectance, and moderate Modularity (Table 2; Figure 2). When evaluating the networks separately, the cocoa interaction network exhibited the predicted structural properties consistent with our initial hypotheses, showing high specialization, low connectance, and high modularity (Table 2; Figure 3). In the natural vegetation interaction network, we observed high specialization and low Connectance and Modularity (Table 2; Figure 4). Finally, in the urban areas interaction network, we observed low specialization, Connectance, and Modularity (Table 2; Figure 5). The extinction slope values for both hosts and parasites were proportional or mirrored (Table 2). Natural and urban areas had the highest extinction slopes, with cacao areas showing the lowest value and thus the highest risk (Table 2). For all networks, we observed nonsignificant values of nestedness (WNODF) and parasite vulnerability (Table 2). With these results we were able to answer our second and third hypotheses (ii) the network in urban areas will face greater risk of extinction with a shallower extinction slope; and (iii) cocoa areas will display the lowest levels of network nesting.

In all the environments investigated, bats infested with more than one species of ectoparasite were observed, characterizing infestations by parasitic infracommunities (assemblage of parasite species co-occurring within individual host organisms; Bush et al., 1997) (Supplementary Tables S4–S6). We observed five host species occurring in all land use and cover types studied, which were infested with infracommunities of ectoparasites: *Artibeus lituratus, Carollia perspicillata, Phyllostomus discolor, Pteronotus rubiginosus*, and *Sturnira giannae* (Supplementary Tables S4–S6). Natural Vegetation Areas exhibited the highest composition of infracommunities, with 38 infracommunities, followed by Urban Areas with 26 infracommunities, and Cacao Areas with 22 infracommunities (Table 3). Notably, a large number of



Spatial distribution of sampling sites across different environment types in the study area, 2017–2022. (A) shows the collection points in the municipalities of Uruará and Medicilândia, while (B) displays the collection points in the municipalities of Altamira, Anapu, and Vitória do Xingu.

associations were observed among the ectoparasite genera Speiseria, Strebla, and Trichobius (Table 3). With these results we were able to answer our first hypothesis (i) the network in cocoa areas will exhibit a higher degree of specialization and modularity.

Carollia perspicillata was the species with the highest number of interactions, with its association with Trichobius joblingi present in all three environments and showing the highest relative abundance (AR% = 54.1% in Natural Vegetation, 48.5% in Cacao areas, and 36.6% in Urban Areas). The second most significant association was with Speiseria ambigua (1.5%, 8.1%, and 17%, respectively). Regarding infracommunity associations, the highest relative

abundance was observed for the association between Speiseria ambigua and Trichobius joblingi (8.8%, 14.1%, and 6.3%) and between Strebla guajiro and Trichobius joblingi (4.4%, 4.4%, and 3.6%) (Table 3). For Artibeus lituratus, no infracommunities were observed in Cacao areas (Table 3).

4 Discussion

As expected, the fly family with the highest richness was Streblidae, which can be attributed to the widespread abundance

TABLE 1 Species list of bat flies (Diptera: Streblidae) identified in the study.

FAMILY		Abundance			
Species	Literature	Female	Male	Total	
NYCTERIBIIDAE					
Basilia hughscotti Guimarães, 1946*		Artibeus lituratus; Myotis nigricans	0	1	3
Basilia manu Guerrero, 1996**		Myotis nigricans	0	0	13
<i>Basilia</i> sp.		Gardnerycteris crenulatum	2	0	2
STREBLIDAE					
Aspidoptera delatorrei Wenzel et al, 1966	Sturnira giannae; Artibeus planirostris	Artibeus lituratus; Artibeus planirostris; Sturnira giannae; Sturnira tildae	2	1	10
Aspidoptera falcata Wenzel, 1976	Sturnira tildae	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Lophostoma silvicola; Phyllostomus hastatus; Sturnira giannae; Sturnira tildae; Uroderma bilobatum	15	12	31
Aspidoptera phyllostomatis (Perty, 1833)	Artibeus fimbriatus; Artibeus planirostris	Artibeus lituratus; Carollia perspicillata; Desmodus rotundus	3	2	5
Mastoptera guimaraesi Wenzel, 1966**		Lophostoma silvicola; Phyllostomus hastatus; Tonatia bidens; Tonatia maresi			22
Mastoptera minuta (Costa Lima, 1921)	Mimon crenulatum; Lophostoma brasiliense; Lophostoma silvicola; Pteronotus parnellii; Phyllostomus elongatus; Phyllostomus hastatus	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Glossophaga soricina; Lophostoma carrikeri; Phyllostomus hastatus; Tonatia bidens		6	17
Megistopoda aranea (Coquillett, 1899)	Artibeus fimbriatus; Artibeus planirostris	Artibeus lituratus; Artibeus obscurus; Artibeus planirostris; Carollia perspicillata; Phyllostomus hastatus; Sturnira giannae; Sturnira tildae	10	22	57
Megistopoda proxima (Séguy, 1926)	Sturnira lilium; Sturnira tildae	Artibeus lituratus; Carollia perspicillata; Glossophaga soricina; Phyllostomus hastatus; Sturnira giannae; Sturnira tildae	12	13	41
<i>Neotrichobius delicatus</i> (Machado- Allison, 1966)	Rhinophylla pumilio	Rhinophylla fischerae; Tonatia maresi		0	2
<i>Noctiliostrebla guerreroi</i> Alcantara, Graciolli & Nihei, 2019	Noctilio albiventris	octilio albiventris Carollia perspicillata; Desmodus rotundus; Noctilio albiventris; Sturnira giannae		11	19
Nycterophilia fairchildi Wenzel, 1966	Pteronotus gymnonotus; Pteronotus personatus	Pteronotus rubiginosus	0	0	13
Nycterophilia parnelli Wenzel, 1966	Pteronotus gymnonotus	Artibeus lituratus; Artibeus obscurus; Pteronotus rubiginosus	24	20	112
Paradyschiria parvula Falcoz, 1931		Carollia perspicillata; Desmodus rotundus; Noctilio albiventris	0	2	7
Parastrebla handleyi Wenzel, 1966	Trinycteris nicefori	Rhinophylla fischerae	0	0	1
Paratrichobius dunni (Curran, 1935)	Artibeus planirostris; Uroderma bilobatum	Artibeus lituratus; Uroderma bilobatum	0	0	7
<i>Paratrichobius longicrus</i> (Miranda Ribeiro, 1907)	Artibeus lituratus	Artibeus lituratus; Carollia perspicillata; Lophostoma silvicola; Saccopteryx leptura	10	11	38
Pseudostrebla riberoi Costa Lima, 1921	Lophostoma silvícola	Carollia perspicillata; Noctilio leporinus; Tonatia bidens	1	1	3
Speiseria ambigua Kessel, 1925	Carollia perspicillata	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Dermanura anderseni; Desmodus rotundus; Lophostoma silvicola; Noctilio leporinus; Phyllostomus discolor; Rhinophylla fischerae; Sturnira giannae; Trachops cirrhosus	60	64	243

(Continued)

TABLE 1 Continued

FAMILY		Abundance			
Species	Literature	Female	Male	Total	
STREBLIDAE					
Speiseria peytoni Wenzel, 1976**	Carollia brevicauda	Carollia perspicillata	0	0	2
Strebla altmani Wenzel, 1966*		Carollia perspicillata; Lonchorhina aurita	0	4	5
Strebla consocia Wenzel, 1976	Phyllostomus elongatus	Phyllostomus hastatus	1	0	1
Strebla diaemi Wenzel, 1966*	Diaemus youngii	Phyllostomus elongatus	1	3	6
Strebla galindoi Wenzel, 1966	Tonatia saurophila	0	0	30	
Strebla guajiro (García and Casal, 1965)	Carollia perspicillata	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Glossophaga soricina; Noctilio albiventris; Noctilio leporinus; Phyllostomus discolor; Phyllostomus hastatus; Pteronotus rubiginosus; Rhinophylla fischerae; Sturnira giannae; Sturnira tildae	37	29	113
Strebla hertigi Wenzel, 1966	Phyllostomus discolor	Phyllostomus discolor Carollia perspicillata; Desmodus rotundus; Phyllostomus discolor; Tonatia maresi; Trachops cirrhosus			
Strebla kohlsi Wenzel, 1966*		Carollia perspicillata	0	1	1
Strebla matsoni Wenzel, 1976*	Macrophyllum macrophyllum	Carollia perspicillata	0	0	1
Strebla mirabilis (Waterhouse, 1879)	Trachops cirrhosus	Anoura caudifer; Carollia perspicillata; Lophostoma carrikeri; Phyllostomus elongatus; Trinycteris nicefori	2	1	8
Strebla proxima Wenzel, 1976	Peropteryx kappleri; Peropteryx trinitatis	Myotis nigricans; Peropteryx kappleri; Peropteryx trinitatis	0	0	36
<i>Strebla</i> sp.		Artibeus obscurus; Carollia perspicillata; Desmodus rotundus; Pteronotus rubiginosus	6	13	20
Strebla wiedemanni Kolenati, 1856	Desmodus rotundus	Carollia perspicillata; Desmodus rotundus; Phyllostomus discolor; Rhinophylla fischerae	4	3	20
<i>Trichobioides perspicillatus</i> (Pessôa and Galvão, 1976)*	Phyllostomus discolor	Artibeus obscurus; Carollia perspicillata; Glossophaga soricina; Phyllostomus discolor; Pteronotus rubiginosus; Sturnira giannae	4	8	29
Trichobius affinis Wenzel, 1976	Lophostoma brasiliense	Lophostoma brasiliense Lophostoma brasiliense; Lophostoma silvicola; Tonatia maresi		5	9
Trichobius anducei Guerrero, 1998	Carollia perspicillata	Artibeus lituratus	1	1	2
Trichobius caecus Edwards, 1918	Pteronotus gymnonotus; Pteronotus personatus	Carollia perspicillata; Phyllostomus discolor; Pteronotus gymnonotus; Pteronotus rubiginosus	2	7	44
Trichobius cf. etophallus		Cynomops abrasus; Platyrrhinus brachycephalus	0	6	6
Trichobius costalimai Guimarães, 1938	Phyllostomus discolor	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Phyllostomus discolor	6	13	50
Trichobius dugesii Townsend, 1891*	Glossophaga soricina, Trachops cirrhosus	Artibeus obscurus; Carollia perspicillata; Dermanura cinerea; Glossophaga soricina; Lophostoma carrikeri; Phyllostomus discolor; Phyllostomus elongatus	7	9	20
Trichobius dugesioides Wenzel, 1966	Mimon bennettii; Phyllostomus elongatus; Trachops cirrhosus; Chrotopterus auritus; Phyllostomus discolor	Artibeus lituratus; Artibeus obscurus; Carollia perspicillata; Hsunycteris thomasi; Noctilio leporinus; Phyllostomus discolor; Phyllostomus elongatus; Phyllostomus hastatus; Pteronotus rubiginosus; Tonatia bidens; Trachops cirrhosus; Trinycteris nicefori; Vampyressa thyone	32	21	119
Trichobius flagellatus Wenzel, 1976*	Lonchorhina aurita	Lonchorhina aurita	0	0	2
Trichobius handleyi Wenzel, 1976*		Carollia perspicillata	2	5	13

(Continued)

TABLE 1 Continued

FAMILY		Abundance			
Species	Literature	Female	Male	Total	
STREBLIDAE					
Trichobius joblingi Wenzel, 1966	Carollia perspicillata	Ametrida centurio; Artibeus lituratus; Artibeus obscurus; Carollia brevicauda; Carollia perspicillata; Dermanura anderseni; Desmodus rotundus; Diphylla ecaudata; Glossophaga soricina; Hsunycteris thomasi; Lophostoma silvicola; Noctilio leporinus; Phyllostomus discolor; Phyllostomus elongatus; Phyllostomus hastatus; Platyrrhinus infuscus; Pteronotus personatus; Pteronotus rubiginosus; Sturnira giannae; Uroderma magnirostrum	341	391	1224
Trichobius johnsonae Wenzel, 1966	Pteronotus personatus	Artibeus lituratus; Carollia perspicillata; Glossophaga soricina; Lophostoma silvicola; Pteronotus personatus; Pteronotus rubiginosus	56	84	153
Trichobius longipes (Rudow, 1871)	Phyllostomus elongatus; Phyllostomus hastatus	Carollia perspicillata; Lophostoma silvicola; Phyllostomus discolor; Phyllostomus elongatus; Phyllostomus hastatus; Sturnira tildae; Uroderma bilobatum	12	17	60
Trichobius parasiticus Gervais, 1844	Desmodus rotundus	Carollia perspicillata; Desmodus rotundus; Lophostoma silvicola; Phyllostomus discolor; Rhinophylla fischerae	10	10	28
Trichobius silvicolae Wenzel, 1976*	Lophostoma brasiliense	Carollia perspicillata; Lophostoma carrikeri; Sturnira giannae; Sturnira giannae; Tonatia bidens	2	1	8
Trichobius sp		Carollia perspicillata; Pteronotus rubiginosus; Vampyressa thyone	2	3	9
Trichobius tiptoni Wenzel, 1976*		Carollia perspicillata	1	0	1
Trichobius tuttlei Wenzel, 1976**		Carollia perspicillata	5	1	6
Trichobius uniformis Curran, 1935	Glossophaga soricina	Glossophaga soricina; Trinycteris nicefori	2	1	3
Total			705	821	2694

The fly species are categorized by family and listed alphabetically within each family. Under Hosts, the table presents the bat species described in the literature as hosts for the parasite species (Literature) and the species recorded in our study (Study). * Indicates a new species occurrence in the state of Pará; ** indicates a new species occurrence in Brazil. The new occurrences and the hosts listed in the literature are based on the Taxonomic Catalogue of the Brazilian Fauna (Graciolli, 2024).

of Phyllostomidae bats, as these two families are strongly correlated (Dick and Graciolli, 2006; Barbier et al., 2019; Hrycyna et al., 2019). The genera Trichobius and Speiseria were the most common in this study, with Trichobius joblingi being the species with the highest abundance and degree of interaction within the overall network, followed by Speiseria ambigua. This pattern has also been observed in other regions of Brazil (Bertola et al., 2005; Eriksson et al., 2011; Aguiar and Antonini 2016; Urbieta et al., 2018; Palheta et al., 2020; Júnior et al., 2020; Urbieta et al., 2021; Falcão et al., 2022; Alcantara et al., 2023). This pattern observed in these flies can be attributed to their broad generality in parasitizing various hosts, consistent with the findings of Wenzel et al. (1966), Dick et al. (2009), and Trujillo-Pahua and Ibáñez-Bernal (2020). Despite T. joblingi and S. ambigua being found on various other bat hosts, their overall abundances were related to Carollia perspicillata, with this interaction being a primary association that has been recorded in other studies (Aguiar and Antonini 2016; Soares et al., 2016; Torres et al., 2019; Vasconcelos et al., 2016; Bezerra and Bocchiglieri, 2023).

The species *Carollia perspicillata* is frequently recorded throughout the Amazon region (Costa et al., 2018; Verde et al., 2018) and across the country (Bianconi et al., 2006; Aguiar and Marinho-Filho 2007; Barreto, 2020) due to its significant ecological

plasticity and widespread distribution in the Neotropical region (Gardner, 2008). Additionally, *C. perspicillata* exhibits high adaptability to human-altered environments, such as secondary vegetation or areas with a high abundance of pioneer species. It is found across the country in habitats where *Piper* species, its primary food source, thrive. The widespread presence of *Piper* in disturbed and secondary habitats plays a crucial role in sustaining the high abundance of *C. perspicillata* in these environments (Aguiar and Marinho-Filho 2007; Silva et al., 2024).

Cacao plantations support a high abundance of *Carollia perspicillata*, a species that feeds on pioneer plants like *Solanum* spp. and various *Cecropia* species commonly found in these areas (Silva, 2024). The proximity of cacao to natural or regenerating vegetation also enhances food availability for *Carollia* and other frugivores, such as *Sturnira guianensis*, *Sturnira tildae*, and *Artibeus lituratus*, which rely on pioneer plants. Additionally, cacao environments provide access to nectar, insects, and pollen, further supporting these bat species (Silva, 2024).

The cacao environment exhibited the second highest richness of flies and bats, and the difference compared to the natural area was not as pronounced. This is because cacao cultivation combines agriculture with the planting of fruit trees, and the shade provided by the cover and height of these trees contributes to increased diversity, abundance, and richness of frugivorous, insectivorous, and nectarivorous bats. Consequently, agroforestry processes are an important and viable technique for maintaining biodiversity (França et al., 2023; Ferreira et al., 2023a; Palheta et al., 2020; Russo et al., 2023).

However, the highest richness of both fly and bat species was recorded in areas of natural vegetation. This result can be explained by the greater availability of food resources, foraging opportunities, and shelter (Galindo-González, 1998; Kerches-Rogeri et al., 2020; Vieira et al., 2024) typically found in denser vegetation. These findings underscore the importance of natural vegetation areas and forest fragments for the conservation of species and their antagonistic interaction networks. In urban environments, *Carollia perspicillata* and *Artibeus lituratus* were abundant, likely due to the availability of pioneer plants and insects attracted by artificial lighting (Palheta et al., 2020; Alencastre-Santos et al., 2024; Vieira et al., 2021). Both species show high tolerance to urban conditions (Silveira et al., 2024).

We recorded infracommunity associations involving up to four dipteran species in different bats from the Phyllostomidae family. Notably, *Carollia perspicillata* is parasitized by various species of flies and appears to play a central role in the parasite–host interaction network (Aguiar and Antonini 2016). The high abundance of *C. perspicillata* observed in this study can be explained by its ability to roost in a variety of shelters, such as caves, culverts, storm drains, and abandoned buildings (Trajano and Gimenez, 1998; Bredt et al., 1999), which increases the opportunities for interaction between different bat species and their parasites (Fagundes et al., 2017).

The species Artibeus lituratus and Pteronotus rubiginosus had primary associations with flies of the genus Trichobius. No infracommunity was found for A. lituratus in the cacao area, and in the natural vegetation area, we observed a low presence of infracommunities. This is due to the heterogeneity of these environments and the greater abundance of bats due to higher vegetation cover (Purificação et al., 2020). In the urban area, we observed a higher presence of infracommunities with both primary and secondary associations. Pteronotus rubiginosus showed infestations by infracommunities in all environments, with particular emphasis on the natural vegetation area, where associations such as (Nycterophilia parnelli + T. johnsonae and Nycterophilia parnelli + Trichobius caecus) were noted. These primary associations have been recorded in other studies (Hrycyna et al., 2019).

The species *Sturnira guiannae* and *Phyllostomus discolor* presented infracommunities with up to four species of dipterans. *S. guiannae* showed a higher incidence of infracommunities in natural vegetation areas. From this study, we can infer that the infracommunity formed by *Aspidoptera delatorrei* + *Megistopoda próxima* may be considered a primary association for *S. guiannae*. The main association found in *P. discolor* was the infracommunity formed by *Trichobioides perspicillatus* + *Trichobius costalimai*. It is worth noting that *T. perspicillatus* represents a new occurrence in the state of Pará; the species had been previously described in the North region, specifically in the state of Amapá (Hrycyna et al., 2019).

Several previous studies suggest the broad distribution of this species in the Amazon region (Barbier and Bernard, 2017) and many other yet-uncatalogued species in this biome, demonstrating that a significant portion of ectoparasitic fly diversity remains unknown to science (Graciolli and Linardi, 2002; Graciolli and Bernard, 2002; Vasconcelos, 2016). Specific studies aimed at filling knowledge gaps for the Amazon region, including the identification, biology, and ecology of bat ectoparasites and their interaction networks, are extremely necessary and important. They contribute to identifying the best strategies for the conservation of fruit-eating Phyllostomidae bats, a key group for ecosystem recovery and conservation.

Although we recorded new bat-parasite associations, determining host specificity is complex, as it involves multiple anatomical, physiological, evolutionary, and behavioral factors (Esbérard et al., 2005; Aguiar and Antonini, 2011). For instance, some Neotropical *Strebla* species, typically associated with Phyllostomidae bats (Guerrero, 1996; Wenzel, 1966; Guerrero 1994; Graciolli and Carvalho, 2001b), were found on non-phyllostomid hosts in our study. Such associations are likely accidental or transient, possibly resulting from shelter-sharing among different bat species (Aguiar and Antonini, 2011; Bejec et al., 2023; Ospina-Pérez et al., 2023; Silva Almeida et al., 2024; Barbier et al., 2024; López-Rivera et al., 2024). Further studies are needed to explore host preference and better understand the drivers of host specificity (Amarga and Phelps, 2021; da Silva Reis et al., 2022; Orlova et al., 2022).

The study region faces rapid land-use changes due to deforestation and wildfires, with about 16.05% of the Amazon biome losing conditions necessary for bat-provided ecosystem services (Silva et al., 2016; Velasco Gomez et al., 2015; Brasileiro et al., 2022). Currently, 17% of the biome has been converted to pastures and short-cycle crops (MapBiomas, 2020), potentially impacting ectoparasite-host dynamics, such as reproduction and mortality rates of ectoparasitic insects (Hrycyna et al., 2019; Trujillo-Pahua and Ibáñez-Bernal, 2020; Amarga and Phelps, 2021; da Silva Reis et al., 2022; Orlova et al., 2022).

In all networks, we observed non-significant values for Nestedness (WNODF), which does not support our third hypothesis that cacao areas would exhibit the lowest nestedness. All networks showed a poorly nested structure, similar to findings in other studies on interactions between flies and bats (Fagundes et al., 2017; Vieira et al., 2024; Patterson et al., 2008), as well as in interactions between bats and plants (Cordero-Schmidt et al., 2021; Silva, 2024) and plants with frugivorous animals (Paixão et al., 2023). According to Patterson et al (2008), nested networks are more common in host-parasite relationships involving long-term infestations, that is, species with a long evolutionary association. Thus, the presence of accidental or opportunistic associations in our study may have influenced the low nestedness values.

Nestedness describes how species with fewer interactions to associate with subset of the partners of more connected species (Almeida-Neto and Ulrich, 2011), enhancing network robustness by increasing resilience to disturbances or species loss (Menezes and Fernandez, 2013). Although our networks, did not show significant nestedness, its typically inverse relationship with specialization and



Network of ectoparasites (Diptera: Nycteribiidae and Streblidae) and host bats (Chiroptera: Phyllostomidae) observed as the sum of all sampled areas across the 10 municipalities in the study from 2017 to 2022. Species are arranged from most to least abundant. The darker sections on the host and parasite sides represent the abundances of each species, while the middle (gray part) illustrates the interaction network. The thickness of the lines is adjusted according to the number of interactions between the species.

modularity supports our results. These metrics, associated with species co-evolution (Krasnov et al., 2012), followed and anthropization gradient – lower specialization and modularity, alongside higher nestedness, were observed in the most disturbed (urban) environments.

According to our data, the network with a somewhat more nested structure compared to the others was the urban network.

This nestedness may arise from various anthropogenic processes in the urban environment and could be due to the generalist interactions of the species, which allows connections between different bat species and the various flies present in this network. Overall, this location exhibited the lowest diversity (both parasites and hosts) and the lowest specialization (H_2). Nested patterns generated by processes such as extinction in fragmented or



Network of ectoparasites (Diptera: Nycteribiidae and Streblidae) and host bats (Chiroptera: Phyllostomidae) observed in cocoa plantation areas of the municipalities of Altamira, Anapú, Medicilândia, Rurópolis, Uruará, and Vitória do Xingu, sampled from 2021 to 2022. Species are arranged from most to least abundant. The darker sections on the host and parasite sides represent the abundances of each species, while the middle (gray part) illustrates the interaction network. The thickness of the lines is adjusted according to the number of interactions between the species.

anthropized landscapes are of particular interest for conservation because they imply a predictable order of species loss (Ganzhorn and Eisenbeiss, 2001; Martinez-Morales, 2005).

Connectivity Connectivity indices did not differ significantly among Cocoa, Natural, and Urban areas, with consistently low values across all networks. This reflects a dominance of generalist species, which reduces interspecific competition (Blüthgen, 2010). The uniformity in connectivity likely stems from the similar richness and composition of bats and flies across environments, as well as the ecological plasticity of bats in adapting to disturbed habitats. Similar patterns have been observed in mutualistic bat-plant networks (Almeida and Mikich, 2018). Despite low connectivity, modularity enhances network robustness by containing disturbances, such as disease spread or species loss, within isolated modules (Robinson and Strauss, 2020). Preserving key species within modules is thus vital for sustaining both the network structure and its associated ecosystem services (Messeder et al., 2020).

The overall network showed a high specialization index, with cacao areas exhibiting the highest values, followed by natural vegetation. Specialization reflects the exclusivity of interactions



Network of ectoparasites (Diptera: Nycteribiidae and Streblidae) and host bats (Chiroptera: Phyllostomidae) observed in natural areas of the municipalities of Altamira, Bragança, Brasil Novo, Medicilândia, Nova Timboteua, Placas, and Vitória do Xingu, sampled from 2017 to 2022. Species are arranged from most to least abundant. The darker sections on the host and parasite sides represent the abundances of each species, while the middle (gray part) illustrates the interaction network. The thickness of the lines is adjusted according to the number of interactions between the species.

(Sebastián-González et al., 2015), and elevated values may result from reduced resource diversity, even in areas with greater vegetation cover (Zhang et al., 2023). In cacao landscapes, ongoing anthropogenic disturbances likely contribute to this pattern by simplifying network structures. Additionally, specialization may be shaped by the phylogenetic relationships between parasites and their hosts (Poulin et al., 2011; Palheta et al., 2020). Although specialization can signal co-evolution,

high values indicate stronger interdependence, making specialist species more susceptible to extinction (Kaiser-Bunbury and Blüthgen, 2015).

The values of specialization and modularity in the Cocoa and Natural vegetation networks were high, not supporting our initial hypothesis that these metrics would be higher only in the Cocoa area. Regarding modularity, we observed that in the networks of all three environments, small modules were formed groups with more



Network of ectoparasites (Diptera: Nycteribiidae and Streblidae) and host bats (Chiroptera: Phyllostomidae) observed in urban areas of Altamira, sampled from 2017 to 2022. Species are arranged from most to least abundant. The darker sections on the host and parasite sides represent the abundances of each species, while the middle (gray part) illustrates the interaction network. The thickness of the lines is adjusted according to the number of interactions between the species.

interactions among themselves due to preferential interactions between specific bat and fly species. The Cocoa area recorded the highest modularity index, followed by the Natural vegetation environment, indicating low nesting and low connectivity in these networks. The urban area exhibited a low specialization index, which aligns with findings from other studies (Ramalho et al., 2021), indicating that this network primarily consists of generalist species. Although this trend is often attributed to the limited availability of shelters and resources in urban settings, leading to reduced selectivity among parasites (Urbieta et al., 2018), Ramalho et al. (2021) observed that, even in urban environments with relatively abundant roosting sites – due to various tree species and building features like expansion joints – the level of specialization in parasite–host interactions remains low. Their study suggests that anthropogenic changes may shape the TABLE 2 Description of interaction network indices between parasites, bat flies (Diptera: Nycteribiidae and Streblidae), and hosts, bats (Chiroptera: Phyllostomidae).

Network metric		General		Сосоа		Natural		Urban		
		Index	р	Index	р	Index	р	Index	р	
Connectance (C)		0.09	< 0.01	0.09	< 0.01	0.08	< 0.01	0.15	< 0.01	
Modularity Q (M)	0.41	< 0.01	0.59	< 0.01	0.43	< 0.01	0.32	< 0.01	
Weighted NODF (WNODF)		17.49	1.00	10.05	1.00	11.03	1.00	28.15	1.00	
Specialization (H ₂₎		0.52	< 0.01	0.78	< 0.01	0.62	< 0.01	0.37	< 0.01	
Vulnerability parasites (V)		2.47	1.00	1.62	1.00	2.01	1.00	2.65	1.00	
Host		2.54	0.06	1.59	0.05	2.12	0.01	2.08	0.20	
Extinction slope	Parasites	2.58	0.07	1.86	0.01	2.56	0.01	2.33	0.42	
Dishassa	Host	42	20			33		17		
Richness	Parasites	52		30		47		29		

p, Probability of Type I Error.

TABLE 3 Bat species with their respective infracommunities observed in cocoa, natural vegetation and urban areas of Altamira, sampled from 2017 to 2022.

Infracomunities								
Сосоа		AR%	Natural		AR%	Urban		AR%
Artibeus lituratus (N 5)			Artibeus lituratus (N 5)			Artibeus lituratus (N 34)		
Aspidoptera delatorrei	3	60.0%	Mastoptera minuta + Trichobius joblingi	1	20.0%	Aspidoptera falcata	2	5.9%
Paratrichobius dunni	1	20.0%	Megistopoda proxima + Strebla guajiro	1	20.0%	Aspidoptera falcata + Megistopoda aranea	1	2.9%
Paratrichobius longicrus	1	20.0%	Paratrichobius longicrus	1	20.0%	Aspidoptera phyllostomatis	1	2.9%
			Trichobius joblingi	2	40.0%	Basilia hughscotti	1	2.9%
						Megistopoda aranea	1	2.9%
						Megistopoda aranea + Speiseria ambigua + Trichobius joblingi	1	2.9%
						Nycterophilia parnelli	2	5.9%
						Nycterophilia parnelli + Trichobius joblingi	1	2.9%
						Paratrichobius longicrus	8	23.5%
						Paratrichobius longicrus + Strebla guajiro	1	2.9%
						Speiseria ambigua	1	2.9%
						Speiseria ambigua + Trichobius dugesioides	1	2.9%
						Trichobius anducei	1	2.9%
						Trichobius costalimai	1	2.9%
						Trichobius joblingi	10	29.4%
						Trichobius johnsonae	1	2.9%
Carollia perspicillata (N 68)			Carollia perspicillata (N 270)			Carollia perspicillata (N 112)		
Paratrichobius longicrus + Strebla guajiro + Trichobius joblingi	1	1.5%	Aspidoptera phyllostomatis + Megistopoda aranea + Speiseria ambigua + Trichobius joblingi	1	0.4%	Aspidoptera falcata	1	0.9%
Pseudostrebla riberoi	1	1.5%	Aspidoptera phyllostomatis + Trichobius silvicolae	1	0.4%	Aspidoptera falcata + Megistopoda proxima + Trichobius joblingi	1	0.9%
Speiseria ambigua	1	1.5%	Mastoptera minuta + Noctiliostrebla guerreroi + Trichobius longipes	1	0.4%	Aspidoptera falcata + Trichobius joblingi	2	1.8%
Speiseria ambigua + Strebla guajiro	1	1.5%	Mastoptera minuta + Trichobius longipes	1	0.4%	Aspidoptera phyllostomatis	2	1.8%

(Continued)

TABLE 3 Continued

Infracomunities								
Сосоа		AR%	Natural		AR%	Urban		AR%
Carollia perspicillata (N 68)			Carollia perspicillata (N 270)			Carollia perspicillata (N 112)		
Speiseria ambigua + Strebla guajiro + Trichobius joblingi	1	1.5%	Megistopoda aranea	1	0.4%	Megistopoda aranea	4	3.6%
Speiseria ambigua + Strebla matsoni + Trichobius dugesioides	1	1.5%	Megistopoda aranea + Strebla wiedemanni + Trichobioides perspicillatus + Trichobius sp.	1	0.4%	Megistopoda aranea + Megistopoda proxima	1	0.9%
Speiseria ambigua + Trichobius dugesii	1	1.5%	Megistopoda proxima	1	0.4%	Megistopoda aranea + Strebla guajiro	1	0.9%
Speiseria ambigua + Trichobius dugesioides	1	1.5%	Megistopoda proxima + Strebla guajiro + Trichobius joblingi	1	0.4%	Megistopoda aranea + Trichobius joblingi	1	0.9%
Speiseria ambigua + Trichobius joblingi	6	8.8%	Noctiliostrebla guerreroi + Paradyschiria parvula + Trichobius joblingi	1	0.4%	Megistopoda proxima	3	2.7%
Speiseria ambigua + Trichobius joblingi + Trichobius tutlei	1	1.5%	Paratrichobius longicrus	1	0.4%	Megistopoda proxima + Trichobius joblingi	1	0.9%
Speiseria ambigua + Trichobius sp.	1	1.5%	Speiseria ambigua	22	8.1%	Paratrichobius longicrus	2	1.8%
Speiseria ambigua + Trichobius tiptoni	1	1.5%	Speiseria ambigua + Strebla guajiro	1	0.4%	Paratrichobius longicrus + Trichobius parasiticus + Trichobius sp.	1	0.9%
Speiseria peytoni	1	1.5%	Speiseria ambigua + Strebla guajiro + Trichobius dugesioides + Trichobius joblingi	1	0.4%	Speiseria ambigua	19	17.0%
Strebla guajiro	2	2.9%	Speiseria ambigua + Strebla guajiro + Trichobius joblingi	11	4.1%	Speiseria ambigua + Strebla guajiro	2	1.8%
Strebla guajiro + Trichobius dugesii	1	1.5%	Speiseria ambigua + Strebla guajiro + Trichobius joblingi + Trichobius tutlei	1	0.4%	Speiseria ambigua + Strebla wiedemanni	1	0.9%
Strebla guajiro + Trichobius dugesioides + Trichobius joblingi	1	1.5%	Speiseria ambigua + Strebla sp + Trichobius joblingi	1	0.4%	Speiseria ambigua + Trichobius dugesioides	3	2.7%
Strebla guajiro + Trichobius joblingi	3	4.4%	Speiseria ambigua + Trichobius caecus	1	0.4%	Speiseria ambigua + Trichobius joblingi	7	6.3%
Trichobius dugesioides	1	1.5%	Speiseria ambigua + Trichobius dugesioides + Trichobius joblingi	2	0.7%	Strebla altmani	1	0.9%
Trichobius dugesioides + Trichobius joblingi	5	7.4%	Speiseria ambigua + Trichobius joblingi	38	14.1%	Strebla guajiro	1	0.9%
Trichobius handleyi	2	2.9%	Speiseria ambigua + Trichobius johnsonae	1	0.4%	Strebla guajiro + Trichobius joblingi	4	3.6%
Trichobius handleyi + Trichobius longipes	1	1.5%	Speiseria peytoni + Trichobius joblingi	1	0.4%	Strebla kohlsi	1	0.9%
Trichobius joblingi	33	48.5%	Strebla guajiro	3	1.1%	Strebla mirabilis + Trichobius dugesioides	1	0.9%
Trichobius joblingi + Trichobius tutlei	1	1.5%	Strebla guajiro + Trichobius dugesioides + Trichobius joblingi	4	1.5%	Strebla wiedemanni	2	1.8%
			Strebla guajiro + Trichobius joblingi	12	4.4%	Trichobioides perspicillatus	1	0.9%
			Strebla guajiro + Trichobius joblingi + Trichobius tutlei	1	0.4%	Trichobius caecus + Trichobius joblingi	1	0.9%
			Strebla hertigi	1	0.4%	Trichobius costalimai	2	1.8%
			Trichobius caecus	1	0.4%	Trichobius dugesioides	1	0.9%
			Trichobius costalimai	1	0.4%	Trichobius joblingi	41	36.6%
			Trichobius dugesii + Trichobius joblingi	1	0.4%	Trichobius johnsonae	2	1.8%
			Trichobius dugesii + Trichobius tutlei	1	0.4%	Trichobius longipes	2	1.8%
			Trichobius dugesioides	2	0.7%			
			Trichobius dugesioides + Trichobius joblingi	1	0.4%			
			Trichobius dugesioides + Trichobius joblingi + Trichobius sp.	1	0.4%			
			Trichobius handleyi	2	0.7%			
			Trichobius joblingi	146	54.1%			
			Trichobius joblingi + Trichobius johnsonae	1	0.4%			
			Trichobius joblingi + Trichobius tutlei	1	0.4%			

(Continued)

TABLE 3 Continued

Infracomunities								
Сосоа		AR%	Natural		AR%	Urban		AR%
Carollia perspicillata (N 68)			Carollia perspicillata (N 270)			Carollia perspicillata (N 112)		
			Trichobius silvicolae	1	0.4%			
Phyllostomus discolor (N 4)			Phyllostomus discolor (N 3)			Phyllostomus discolor (N 7)		
Strebla guajiro + Trichobioides perspicillatus + Trichobius costalimai + Trichobius dugesii	1	25.0%	Trichobioides perspicillatus	1	33.3%	Speiseria ambigua + Strebla wiedemanni + Trichobius caecus + Trichobius joblingi	1	14.3%
Strebla hertigi + Trichobius dugesioides	1	25.0%	Trichobioides perspicillatus + Trichobius costalimai	1	33.3%	Strebla hertigi + Trichobioides perspicillatus + Trichobius costalimai	1	14.3%
Trichobioides perspicillatus + Trichobius longipes	1	25.0%	Trichobius longipes	1	33.3%	Strebla hertigi + Trichobius costalimai	1	14.3%
Trichobius parasiticus	1	25.0%				Trichobioides perspicillatus + Trichobius costalimai	2	28.6%
						Trichobius costalimai	1	14.3%
						Trichobius joblingi	1	14.3%
Pteronotus rubiginosus (N 17)			Pteronotus rubiginosus (N 31)			Pteronotus rubiginosus (N 2)		
Nycterophilia parnelli + Trichobius johnsonae	3	17.6%	Nycterophilia fairchildi + Nycterophilia parnelli	1	3.2%	Nycterophilia parnelli + Strebla sp	1	50.0%
Trichobius dugesioides	1	5.9%	Nycterophilia parnelli	6	19.4%	Strebla guajiro + Trichobius joblingi	1	50.0%
Trichobius joblingi + Trichobius johnsonae	1	5.9%	Nycterophilia parnelli + Trichobioides perspicillatus	1	3.2%			
Trichobius johnsonae	12	70.6%	Nycterophilia parnelli + Trichobius caecus	6	19.4%			
			Nycterophilia parnelli + Trichobius johnsonae	5	16.1%			
			Trichobius caecus	2	6.5%			
			Trichobius joblingi	1	3.2%			
			Trichobius johnsonae	8	25.8%			
			Trichobius sp.	1	3.2%			
Sturnira giannae (N 3)			Sturnira giannae (N 8)			Sturnira giannae (N 8)		
Aspidoptera delatorrei	1	33.3%	Aspidoptera delatorrei + Megistopoda proxima	1	12.5%	Aspidoptera delatorrei + Megistopoda proxima	1	12.5%
Aspidoptera falcata + Trichobius joblingi	1	33.3%	Aspidoptera falcata + Megistopoda proxima	1	12.5%	Megistopoda proxima	1	12.5%
Megistopoda aranea	1	33.3%	Megistopoda aranea	1	12.5%	Strebla guajiro	1	12.5%
			Megistopoda proxima	1	12.5%	Trichobius joblingi	3	37.5%
			Megistopoda proxima + Trichobius joblingi	1	12.5%			
			Noctiliostrebla guerreroi + Trichobius joblingi	1	12.5%			
			Speiseria ambigua + Trichobius joblingi + Trichobius silvicolae	1	12.5%			
			Trichobioides perspicillatus	1	12.5%			

N, Absolute number of occurrences; AR%, Relative abundance values.

structure of bat-bat fly interaction networks, resulting in a more hierarchical arrangement where parasites become less specialized and interact with a broader range of host species. This reduced specialization could impact parasite fitness and potentially increase the transmission of pathogens across different bat populations.

Contrary to our second hypothesis, extinction risk was highest in the cacao area, while natural and urban areas showed lower values. This suggests that, although urbanization acts as an environmental filter for bats and ectoparasitic flies (Palheta et al., 2020), it does not necessarily result in the highest extinction risk. Some bat species may persist or even thrive in urban environments, while others decline due to habitat loss - responses that are highly species-specific (Palheta et al., 2020; Bernard et al., 2023). Notably, the urban network exhibited the highest parasite vulnerability index, highlighting the complex and contextdependent effects of urbanization.

The loss of fly diversity in urban areas may be related to the reduction in the number and diversity of bats (Dick and Gettingert, 2005), supporting the idea that the network is fragile and at risk of local extinction of ectoparasitic dipterans due to the loss of bat species from anthropogenic factors. The cacao and natural vegetation areas had low vulnerability indices, with no significant differences between them. Indeed, bat and fly communities are more diverse in rural

environments than in urban ones. Additionally, since these species are correlated, they seem to respond differently to the two environments, resulting in heterogeneity in rural areas (which contributes to the low parasite vulnerability index) and homogeneity in urban areas (which contributes to increased parasite vulnerability).

Changes in land use and cover likely influenced the structure of bat-fly networks. Host and parasite diversity are closely linked to environmental shifts, which affect ectoparasite reproduction and survival (Tlapaya-Romero et al., 2021; Biz et al., 2023). Vegetated areas, with their environmental heterogeneity and greater resource availability, supported higher diversity of both bats and flies. In contrast, urban areas, characterized by homogeneity and limited resources, showed reduced bat diversity and, consequently, lower fly diversity (Dick and Gettingert, 2005; Palheta et al., 2020). Our results reflect this gradient, with urban networks exhibiting lower specialization and diversity, but higher nestedness and vulnerability. This suggests that fewer bat species are hosting a broader array of ectoparasites, forming asymmetric networks where generalist hosts support specialist parasites (Mello et al., 2016; Ramalho et al., 2021).

We also highlight the discovery of four new occurrences of bat flies for Brazil and ten new species for the state of Pará. Additionally, all 51 parasite species identified in this study presented new host associations, emphasizing the need for increased investment in research focused on primary data collection and the documentation of parasite-host interactions. This knowledge gap regarding the geographical distribution of ectoparasitic flies is not unique and is also observed in bats, especially in the Amazon (Vieira et al., 2024). This indicates that the Brazilian Amazon remains understudied in terms of its chiropterofauna, with great potential for the discovery of new species (Aguiar et al., 2021). Furthermore, the conservation of bats is directly linked to human health, as their population decline could lead to an increase in infant mortality rates, due to the intensified use of pesticides for pest insect control in agricultural fields (Frank, 2024). The decline in bat populations also destabilizes production chains and compromises food security, as crop losses caused by pest insect attacks are exacerbated (Frank, 2024).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by Sistema de Autorização e Informação em Biodiversidade (SISBIO) license no. 57294-2. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

SD: Formal analysis, Methodology, Writing – original draft. RA: Writing – review & editing. LC: Data curation, Writing – review & editing. LA: Writing – review & editing. GG: Writing – review & editing. DA: Writing – review & editing. TV: Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1499475/ full#supplementary-material

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