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From the Atlantic Forest to the borders of Amazonia: species richness, distribution, and host association of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in northeastern Brazil

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Abstract Better knowledge of the geographical distribution of parasites and their hosts can contribute to clarifying aspects of host specificity, as well as on the interactions among hosts, parasites, and the environment in which both exist. Ectoparasitic flies of the Nycteribiidae and Streblidae families are highly specialized hematophagous parasites of bats, whose distributional patterns, species richness, and associations with hosts remain underexplored and poorly known in Brazil. Here, we used information available in the literature and unpublished data to verify if the occurrence of bat hosts in a given environment influences the occurrence and distribution of nycteribiid and streblid flies in different ecoregions in the northeastern Brazil. We evaluate species richness and similarity between ecoregions and tested correlations between species richness and the number of studies in each ecoregion and federative unit. We recorded 50 species and 15 genera of bat ectoparasitic flies on 36 species and 27 genera of bat hosts. The Atlantic Forest had the highest fly species richness (n = 31; 62%), followed by Caatinga (n = 27; 54%). We detected the formation of distinct groups, with low species overlap between ecoregions for both flies and bats. Fly species richness was correlated with host species richness and with the number of studies in each federative unit, but not with the number of studies by ecoregion. Due to the formation of distinct groups with low species overlap for both groups, host availability is likely to be one of the factors that most influence the occurrence of highly specific flies. We also discuss host specificity for some species, produced an updated list of species and distribution for both nycteribiid and streblid flies with information on interaction networks, and conclude by presenting recommendations for more effective inventories of bat ectoparasites in the future.

Keywords Bat fly · Brazilian ecoregions · Caatinga · Cerrado · Chiroptera · Host-parasite interactions

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Introduction

The study of the occurrence and distribution of parasites is an important tool to understand issues related to population dynamics, as well as the evolution of host-parasite interactions (Giorgi et al. 2004; Hawlena et al. 2005; Poulin 2007). The geographic distribution pattern of parasites can also help to elucidate questions about the selection pressures that act on the parasite itself, as well as their hosts (Gandon et al. 1998). Nevertheless, several factors may influence the distribution of a parasite, with host specificity and dispersion being issues frequently raised (e.g., Price 1990; Perlman and Jaenike 2003; Krasnov et al. 2005; Dick and Patterson 2007; Poulin 2007).

In general, most of the parasite groups are highly specific to a host species and occur in a limited number of species (Giorgi et al. 2004). Thus, the degree of host specificity may reflect the coevolutionary history between a particular parasite

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species and a particular host species (Krasnov et al. 2003; Poulin 2007). Nycteribiidae Westwood, 1835 and Streblidae Kolenati, 1863 (bat ectoparasitic flies) are two families of obligate hematophagous flies; parasites exclusively associate with bats (Wenzel et al. 1966; Marshall 1982). These parasites have an evolutionary history associated with their hosts (Poinar and Brown 2012), resulting in several adaptations at morphological and physiological levels, such as reduction of compound eyes, some brachypterous species (nycteribiids are wingless), and adenotrophic viviparity (Dick and Patterson 2007; Dick and Dittmar 2014).

Bat ectoparasitic flies are distributed worldwide, but they present some endemism and greater species richness in the tropics region (Dittmar et al. 2015). In Brazil, 26 species and two genera of Nycteribiidae, and 84 species and 24 genera of Streblidae are currently recognized (Graciolli et al. 2007; Bezerra et al. 2016; Lourenço et al. 2016). Knowledge about bat flies in Brazil has increased in recent years (e.g., Graciolli et al. 2010; Eriksson et al. 2011; Santos et al. 2013; Soares et al. 2013; Figueiredo et al. 2015; Barbier and Graciolli 2016; Barbier et al. 2016; Bezerra et al. 2016; Lourenço et al. 2016; Vasconcelos et al. 2016), but several states and regions still remain poorly sampled or without any information. The ecoregions with the highest number of recorded species are, respectively, Cerrado (mostly in the central region of Brazil), Amazonia, and Atlantic Forest (especially in the southeast region of Brazil) (see Lourenço et al. 2016). One of the greatest gaps in knowledge on the occurrence, richness, and distribution of the bat ectoparasitic flies in Brazil is in the northeast region, particularly in the Caatinga (seasonally dry tropical forest). Nevertheless, recent studies have indicated that this region has high species richness (Barbier et al. 2016; Bezerra et al. 2016; Soares et al. 2016), although still sub-sampled.

Although there is a stronger relationship in the bat-fly association (Dick and Patterson 2006), several environment factors such as temperature, humidity, rainfall, quality, and availability of roosts for the host can affect the occurrence and/or abundance of the parasite (e.g., Morand and Poulin 1998; ter Hofstede and Fenton 2005; Bordes et al. 2008). Furthermore, the presence and distribution of the host in a given environment are factors that directly influence the occurrence of a particular parasite, especially for monoxenous species (e.g., Wenzel et al. 1966; Wenzel 1976; Dick and Patterson 2006; Poulin et al. 2011). However, studies that correlate the occurrence and distribution of bat flies with any of the mentioned variables remain incipient.

In order to verify if the environment and its hosts influence the presence and distribution of bat ectoparasitic flies, we performed a systematic literature review, as well as using unpublished data on Nycteribiidae, Streblidae and their bat hosts occurring in the different ecoregions in the northeastern Brazil. For this, we (i) evaluated the similarity between the ecoregions according to the fly and bat species richness present, (ii) analyzed the correlation between the fly species richness and the bat species richness with the number of studies performed, and (iii) showed species geographic distribution among the different ecoregions and by federative unit. Due to the frequently reported host specificity and influence of abiotic factors on the host-parasite relationships, as mentioned above, we predict that the presence and interaction of bat ectoparasitic flies will be different between ecoregions and will be related to the presence of their specific host. Additionally, we build host-parasite interaction networks, update the list of fly-host species and distribution, discuss some host specificity, and elaborate a series of recommendations for future studies on bat ectoparasites.

Materials and methods

Literature review

We carried out a bibliographic review aiming at the compilation of studies on bat ectoparasitic flies to northeastern (hereafter NE) Brazil. We searched for published papers until April 2017 in online databases using "Nycteribiidae," "Streblidae," "bat flies," and "*moscas ectoparasitas de morcegos*" as keywords. The databases consulted were Web of Science (www.webofknowledge.com), Scopus (www.scopus.com), Google Scholar (scholar.google.com.br), Periódicos CAPES (www.periodicos.capes.gov.br), and SciELO (www.scielo.br). Additionally, we consulted literature not available in the previously mentioned databases: Guimarães (1937, 1938, 1941, 1944, 1946), Pessôa and Galvão (1937), Guimarães and D'Andretta (1956), and Guerrero (1994). For this compilation, we consider the all nine states of the NE region: Alagoas (AL), Bahia (BA), Ceará (CE), Maranhão (MA), Paraíba (PB), Pernambuco (PE), Piauí (PI), Rio Grande do Norte (RN), and Sergipe (SE). These states correspond to an area of 1,554,291.744 km^2 (IBGE 2016).

New data

In addition to information obtained through the literature review, we added unpublished data from bat ectoparasitic flies collected on bats in the states of BA, PE, and RN. Each sampled site and information about data collection is described below:

> *Raso da Catarina Ecological Station (RCES)*—with 104,842 ha, the RCES (09°39′S, 38°28′W) is located in the Caatinga ecoregion in the state of BA, covering the municipalities of Paulo Afonso, Rodelas, and Jeremoabo (Paes and Dias 2008; ICMBio 2016). This region has very sandy soils, with altitudes ranging from 400 to 600 m. The climate is semi-arid, hot, and dry, with average rainfall 650 mm per year concentrated between December and

July. Vegetation is predominantly of arboreal caatinga and shrub caatinga (Velloso et al. 2002; Paes and Dias 2008). Bats were captured using six to ten mist nets (12 m × 2.5 m) from 6 to 10 September 2012, totaling 2568 h m^2 of sampling effort [calculated according to Straube and Bianconi (2002) by multiplying mist net area (m^2), number of mist nets, and hours of exposure (h)].

Seridó Ecological Station (SES)—the SES region (06°34′55″S, 37°15′09″W) is considered one of the critical centers of desertification in Brazil (MMA 2004). Located in the state of RN, with 1166 ha, this area of Caatinga presents stony soils and altitude ranging from 100 to 400 m (Brasil 1982). Rainfall in the region is concentrated between February and May, with up to 10 months of drought per year. The climate is semi-arid, very hot, and with a rainy season in the summer (BSh, according to Köppen) (MMA 2004). SES has vegetation of arboreal caatinga and shrub caatinga (Brasil 1982; Ferreira et al. 2009). Sampling occurred in July 2012 and March 2013, using five to 10 mist nets (12 m × 2.5 m) totaling 12,705 h m^2 (sensu Straube and Bianconi 2002).

Catimbau National Park (CNP)—with 62,292 ha and located in the central region of the state of PE, CNP (8°32′S, 37°11′W; 08°30′S, 37°20′W) covers the municipalities of Buíque, Tupanatinga, and Ibimirim and is identified as a priority area for conservation of Caatinga, mainly because it harbors rare and endemic species (MMA 2002). The park also houses at least three species of nationally threatened bats in the Vulnerable category (MMA 2014)—*Lonchorhina aurita* Tomes, 1863, *Natalus macrourus* (Gervais, 1856) (Delgado-Jaramillo et al. 2017), and *Xeronycteris vieirai* Gregorin and Ditchfield, 2005 (Cordero-Schmidt et al. 2017). Rainfall to the region is concentrated from April to June, with an annual average ranging from 300 to 500 mm (SUDENE 1990; Rodal et al. 1998). Like other regions of Caatinga, rainfall is historically very irregular, and there may be long periods of drought. Captures occurred between July 2014 and June 2015 with 10 mist nets (12 m × 2.5 m), totaling 43,200 h m^2 of sampling effort (sensu Straube and Bianconi 2002).

Saltinho Biological Reserve (SBR)—SBR (08°43′49″S, 35°10′34″W) has 562,57 ha, divided into the municipalities of Rio Formoso and Tamandaré, and is one of the largest and most important remnants of the Atlantic Forest in the state of PE, harboring cryptic and endangered species (MMA 2008; ICMBio 2015; Hintze et al. 2016). With an average temperature of 25 °C and average annual rainfall range between 1500 and 2000 mm, the climate of the region is hot and humid (As, according to Köppen) (Brasil 1983; Ferraz 2002; ICMBio 2015). Fieldwork period, methodology, and sampling effort in the SBR were the same one used in the CNP.

We also added occasional records of bat ectoparasitic flies collected in the states of CE, in the Chapada do Araripe Environmental Protection Area (07°16′55″S, 39°26′23″W; with predominant Caatinga vegetation–Brasil 1997; ICMBio 2016) and in the state of RN, at the Federal University of Rio Grande do Norte, UFRN *campus* (05°50′17″S, 35°12′05″W; Atlantic Forest), and in the municipality of João Câmara (05°24′38″S, 35°51′17″W; Caatinga). Captures were carried out in the state of CE on 22 May 2016 and 4 June 2016. Bats were captured using one mist net and one harp trap at the entrance of bat diurnal roost. In RN, flies were collected on bats in the UFRN *campus* in October 2013 and January 2014 and in the municipality of João Câmara in November 2016. Marília A. S. Barros donated these fly specimens.

In each sampled environments described above, the bat hosts were individually placed in clean cloth bags (used only once each night) for further inspection to locate ectoparasites. The bat specimens were handled according to Sikes et al. (2011). Bat ectoparasitic flies were collected on the host with featherweight forceps and deposited in labeled vials with 70% ethanol.

Species identification and taxonomic nomenclature

In the laboratory, bat ectoparasitic flies were identified according to the diagnoses and/or taxonomic keys available in Guimarães (1938), Guimarães and D'Andretta (1956), Wenzel et al. (1966), Wenzel (1976), and Guerrero (1998). For flies nomenclature, we follow Graciolli and Dick (2008) for Nycteribiidae and Dick and Graciolli (2008) for Streblidae. We consider *Trichobius dugesioides* on *Carollia perspicillata* (Linnaeus, 1758) in Bezerra et al. (2016) as *Trichobius dugesioides dugesioides* Wenzel, 1966 (but see Guerrero 1998). Voucher specimens are deposited in the Entomological Collection of Federal University of Pernambuco (CE-UFPE). For bats, we adopted the nomenclature proposed by Hurtado and Pacheco (2014) and Nogueira et al. (2014). In this way, we consider *Lonchophylla thomasi* in Santos et al. (2013) as *Hsunycteris thomasi* (J.A. Allen, 1904) and *Mimon crenulatum* in Dias et al. (2009) and Santos et al. (2013) as *Gardnerycteris crenulatum* (É. Geoffroy, 1803).

Data analysis

The geographic coordinates available in the consulted literature, as well as for the new records, were extracted, and a map with the occurrence sites was produced in ArcGIS 10.2.2. In the absence of this information, we added the generic coordinates to those places where the specimen was collected (e.g., "municipality of Aracati, CE"), based on Google Maps (www.google.com.br/maps). Records which showed very superficial information about the location of the species (e.g., "state of

Pernambuco") did not have the point included in the map, but were included in the species compilation and attributed to their respective state of occurrence. The ecoregions Atlantic Forest, Caatinga, Cerrado, and a portion of Amazonia, in the state of Maranhão, occur in NE Brazil. Information on which ecoregion species occurred was obtained in the respective articles or consulting the map of Brazilian ecoregions of the Brazilian Institute of Geography and Statistics (IBGE; www.ibge.gov.br). Flies that were not identified at species level were not added to the total species for each state or ecoregion, but they were added to the number of genera (e.g., "*Hershkovitzia* sp.").

Based on both fly and host species data for each ecoregion, we separately evaluated the similarity of ecoregions using cluster analysis (Bray-Curtis index). To statistically verify the dissimilarity in species composition between ecoregions, for both fly and bat species, we performed an analysis of similarity (ANOSIM) with 9999 permutations. ANOSIM is a test based on comparing distances within groups with distances between groups, and the result varies from 0 to 1 (*R* value) (Clarke 1993; Hammer 2016). Values from 0 to 0.25 indicate that there are no distinct groups in the sample; values from 0.25 to 0.5 indicate distinct groups in the sample, but with a high percentage of overlap in the species composition; and values above 0.5 indicate that there are distinct groups in the sample, with a low percentage of overlap in the species composition (Sosa et al. 2008; Zarazúa-Carbajal et al. 2016). Pairwise ANOSIMs between all pairs of groups are provided as a post hoc test (significance level at $P < 0.05$).

We used the Spearman's correlation coefficient (*rs*) to test the relationship between fly species richness and bat parasitized species richness in each study; and the relationship between the fly species richness and the number of studies conducted in each ecoregion. For this test, we did not consider isolated/occasional fly records. In addition, we used non-parametric species richness estimators (Jackknife 1 and 2) to determine the expected richness of flies in each ecoregion (except for the Cerrado, where there is only one inventory). Analyses were performed using PAST 3.15 (Hammer et al. 2001; https://folk.uio.no/ohammer/past/). In order to visually demonstrate the host-parasite relationships, we built interaction networks using Pajek 5.01 (Nooy et al. 2011; http://mrvar.fdv.uni-lj.si/pajek/). We use a presence-absence matrix data for the links (i.e., the presence of a given ectoparasite on a given host) and data on the number of connections that each species of ectoparasite and host presented in the network, reflected in the vertices' size.

Results

Species richness and distribution

Including known and new records, 13 genera and 47 species of Streblidae and two genera and three species of Nycteribiidae were recorded in the NE Brazil (Table 1). Two genera (*Exastinion* Wenzel, 1966 and *Nycterophilia* Ferris, 1916) and seven species (*Exastinion clovisi* (Pessôa & Guimarães 1937), *Nycterophilia parnelli* Wenzel, 1966, *Trichobius anducei* Guerrero 1998, *T. angulatus* Wenzel 1976, *T. flagellatus* Wenzel 1976, *T. lonchophyllae* Wenzel, 1966, and *T. propinquus* Wenzel 1976) were recorded for the first time in the NE (Table 1). First records also included both Nycteribiidae and Streblidae families in the state of Rio Grande do Norte. Twenty-four other new species records for the ecoregions and/or federative units were also recorded (see Tables 1 and 2 for details). The states of Alagoas and Piauí do not have any information about bat ectoparasitic flies. Most of the sites studied are concentrated in the coastal region, leaving much of the Caatinga and practically the whole of the Cerrado without any information (Fig. 1).

The Atlantic Forest was the ecoregion with the highest number of bat ectoparasitic fly species (*n* = 31; 62%; Jackknife 1, 2 = 46, 50), followed by Caatinga (*n* = 27; 54%; Jackknife 1, 2 = 47, 59), Cerrado (*n* = 23; 46%), and Amazonia (*n* = 22; 44%; Jackknife 1, 2 = 31, 31) (Fig. 1; Table 2). *Aspidoptera phyllostomatis* (Perty, 1833), *Megistopoda aranea* (Coquillett, 1899), *Speiseria ambigua* Kessel 1925, *Strebla guajiro* (García & Casal, 1965), *S. hertigi* Wenzel, 1966, *Trichobioides perspicillatus* (Pessôa and Galvão 1937), *Trichobius costalimai* Guimarães 1938, *T. dugesii* Townsend, 1891, *T. joblingi* Wenzel, 1966, *T. longipes* (Rudow, 1871), and *T. parasiticus* Gervais, 1844 occurred in all ecoregions, representing 22% of the species. On the other hand, 21 species (42%) occurred exclusively in a single ecoregion (Table 2). Pernambuco is the state with largest species richness (*n* = 34; 68%), followed by the state of Maranhão (*n* = 28; 56%) (Table 1).

Cluster analysis showed greater similarity in the fly species composition between the Amazonia and Cerrado ecoregions (Fig. 2a) and a greater similarity between Amazonia and Cerrado and between Caatinga and Atlantic Forest, according to bat host species (Fig. 2b). Nevertheless, fly species composition differs significantly between all ecoregions ($R = 1$; $P = 0.0098$), indicating the formation of distinct groups with a low percentage of species overlap. The formation of distinct groups was also statistically significant in relation to the bat species sampled in each ecoregion ($R = 1$; $P = 0.0096$). Fly species richness in each ecoregion was correlated with the host species richness ($N = 14$; $rs = 0.9777$; $P = 0.0014$). There was also a correlation between the fly species richness and the number of studies carried out in each federative unit ($N = 7$; $rs = 0.5609$; $P = 0.0312$). Only between fly species richness and the number of studies in each ecoregion, there was no correlation ($N = 5$; $rs = 0.6155$; $P = 0.0625$); however, the *P* value was marginally significant.

Table 1 Bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) recorded in the northeastern Brazil

Family/species	Federative unit							Source
	BA	CE	MA	PB	PE	RN	SE	
Nycteribiidae								
Basilia hughscotti					X			19
Basilia mimoni			X					11, 14
Basilia sp.	X		X				X	10, 11, 16
Basilia travassosi	X[a]	X		X	X	X[b]		4, 8, 17, PS
Hershkovitzia sp.			X					14
Streblidae								
Aspidoptera delatorrei							X	16
Aspidoptera falcata			X		X		X	11, 12, 14–16, PS
Aspidoptera phyllostomatis			X		X[a]		X	11, 12, 14, 16, PS
Exastinion clovisi[c]	X[a]	X[a]			X[a]			PS
Mastoptera minuta			X		X			11, 12, 14, 15, 18, PS
Megistopoda aranea			X	X	X[a]		X	11, 12, 14, 16, 17, PS
Megistopoda proxima			X		X		X	11, 12, 14–16, PS
Nycterophilia parnelli[c]					X[a]			PS
Paradyschiria fusca	X							6
Paradyschiria parvula			X					11
Paratrichobius longicrus			X		X		X	11, 15, 16, 18, PS
Pseudostrebla greenwelli			X		X[a]			14, PS
Pseudostrebla ribeiroi			X					14
Pseudostrebla sparsisetis			X					14
Speiseria ambigua		X[a]	X	X	X		X	1, 5, 11, 12, 14–18, PS
Speiseria sp.	X							13
Stizostrebla longirostris			X					11, 12, 14
Strebla altmani					X			15, PS
Strebla curvata							X	16
Strebla diaemi			X					11
Strebla galindoi			X		X[a]			11, 14, PS
Strebla guajiro	X	X[a]	X		X		X	11–16, PS
Strebla hertigi			X		X[a]	X[b]	X	11, 12, 14, 16, PS
Strebla hoogstraali			X					14
Strebla mirabilis					X[a]		X	16, PS
Strebla sp.			X					11
Strebla tonatiae			X		X			11, 14, 15
Strebla wiedemanni	X			X	X		X	9, 10, 16–18, PS
Trichobioides perspicillatus	X		X		X	X[b]	X	3, 11, 12, 14–16, PS
Trichobius affinis					X			15
Trichobius anducei[c]					X[a]			PS
Trichobius angulatus[c]					X[a]			PS
Trichobius caecus		X						7
Trichobius costalimai			X		X	X[b]	X	2, 11, 12, 14–16, 18, PS
Trichobius diaemi			X					11
Trichobius diphyllae				X	X[a]			17, PS

Table 1 (continued)

Family/species	Federative unit							Source
	BA	CE	MA	PB	PE	RN	SE	
Trichobius dugesii	X[a]		X	X	X			2, 11, 12, 14, 17, PS
Trchobius dugesioides dugesioides				X	X		X	15–17, PS
Trichobius dugesioides phyllostomus			X					11, 12
Trichobius flagellatus[c]					X[a]			PS
Trichobius galei				X				17
Trichobius joblingi	X	X[a]	X		X		X	11–16, 18, PS
Trichobius lonchophyllae[c]					X[a]			PS
Trichobius longipes		X	X		X			2, 7, 11, 12, 14, 15
Trichobius pallidus				X				17
Trichobius parasiticus	X		X	X	X			2, 10, 11, 14, 15, 17, PS
Trichobius propinquus[c]					X[a]			PS
Trichobius silvicolae			X					14
Trichobius sp.			X	X				14, 15
Trichobius uniformis	X[a]				X			2, 18, PS
Total: 50 species/15 genera	10/7	7/5	28/13	10/5	34/12	4/4	16/8	

Data from studies published until April 2017 plus new data from the present study. 1: Kessel (1925); 2: Guimarães (1937); 3: Pessôa and Galvão (1937); 4: Guimarães (1938); 5: Jobling (1939); 6: Guimarães (1941); 7: Guimarães (1944); 8: Guimarães (1946); 9: Wenzel et al. (1966); 10: Rios et al. (2008); 11: Dias et al. (2009); 12: Santos et al. (2009); 13: Esbérard et al. (2012); 14: Santos et al. (2013); 15: Soares et al. (2013); 16: Bezerra et al. (2016); 17: Barbier et al. (2016); 18: Soares et al. (2016); 19: Barbier et al. (2017)

PS present study, *BA* Bahia, *CE* Ceará, *MA* Maranhão, *PB* Paraíba, *PE* Pernambuco, *RN* Rio Grande do Norte, *SE* Sergipe

[a] First record of the species in the state

[b] First record of the family and/or species in the state

[c] First record of the genus and/or species in northeastern Brazil

Host-fly interactions

Twenty-six fly species (52%) were collected on only one host species (Fig. 3). *Trichobius* Gervais, 1844 was the genus with most species ($n = 20$; 40%), followed by *Strebla* Wiedemann, 1824 ($n = 10$; 20%) (Table 1). *Trichobius joblingi* was the species that parasitized the largest number of host species ($n = 11$), followed by *Mastoptera minuta* (Costa Lima, 1921) ($n = 8$) (Fig. 3). Thirty-six bat species, 27 genera and eight families (Emballonuridae, Furipteridae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae, Thyropteridae, and Vespertilionidae) were recorded as hosts. The Phyllostomidae family represents about 71% of all host species confirmed in the NE. *Carollia perspicillata* and *Glossophaga soricina* (Pallas, 1766) were the species that most harbored bat ectoparasitic fly species (12 and 11, respectively), followed by *Lophostoma brasiliense* Peters, 1866 with eight bat ectoparasitic fly species (Fig. 3). The entire list of the host and their ectoparasitic fly species, with the respective source, is available as supplementary material (Online Resources 1 and 2).

Discussion

Species richness and distribution

Our results reveal a rich fauna of bat ectoparasitic flies in the northeastern Brazil and corroborate our predictions, indicating that there is a low overlap of species among ecoregions formed by distinct groups and a positive association with the presence of bat hosts. Besides that, we expanded the number of known bat fly species for the Caatinga from 11 to 27. Unlike previously believed (Rios et al. 2008), the Caatinga has high species richness of bat ectoparasitic flies, and this number (27 species) is underestimated as indicated by species richness estimators. Recently, Vasconcelos et al. (2016) also recorded a rich fauna of streblids in a transitional Cerrado-Caatinga ecotone in southeastern Brazil. This reinforces the potential for the development of research in contact regions between the Caatinga and other environments. We also increase the known bat ectoparasitic fly species for the northeastern portion of the Atlantic Forest from 24 to 31, but as in

Table 2 Bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) recorded in different ecoregions in the northeastern Brazil

Family/species	Ecoregion			
	AMA	ATL	CAA	CER
Nycteribiidae				
Basilia hughscotti		X		
Basilia mimoni	X			X
Basilia sp.	X		X	
Basilia travassosi		X	X	
Hershkovitzia sp.				X
Streblidae				
Aspidoptera delatorrei		X		
Aspidoptera falcata	X	X		X
Aspidoptera phyllostomatis	X	X	X[b]	X
Exastinion clovisi			X[b]	
Mastoptera minuta	X	X		X
Megistopoda aranea	X	X	X	X
Megistopoda proxima		X	X[b]	X
Nycterophilia parnelli			X[b]	
Paradyschiria fusca[c]				
Paradyschiria parvula	X			
Paratrichobius longicrus	X	X	X[b]	
Pseudostrebla greenwelli		X[a]		X
Pseudostrebla ribeiroi				X
Pseudostrebla sparsisetis				X
Speiseria ambigua	X	X	X	X
Speiseria sp.		X		
Stizostrebla longirostris	X			X
Strebla altmani		X		
Strebla curvata		X		
Strebla diaemi	X			
Strebla galindoi	X	X[a]		X
Strebla guajiro	X	X	X[b]	X
Strebla hertigi	X	X	X[b]	X
Strebla hoogstraali				X
Strebla mirabilis		X		
Strebla sp.	X			
Strebla tonatiae	X	X		X
Strebla wiedemanni		X	X	
Trichobioides perspicillatus	X	X	X[b]	X
Trichobius affinis		X		
Trichobius anducei		X[a]		
Trichobius angulatus		X[a]	X[b]	
Trichobius caecus			X	
Trichobius costalimai	X	X	X[b]	X
Trichobius diaemi	X			
Trichobius diphyllae			X	
Trichobius dugesii	X	X[a]	X	X
Trichobius dugesioides dugesioides		X	X	
Trichobius dugesioides phyllostomus	X			
Trichobius flagellatus		X[a]	X[b]	
Trichobius galei			X	
Trichobius joblingi	X	X	X[b]	X
Trichobius lonchophyllae			X[b]	
Trichobius longipes	X	X	X	X
Trichobius pallidus			X	
Trichobius parasiticus	X	X	X	X
Trichobius propinquus			X[b]	
Trichobius silvicolae				X
Trichobius sp.		X		X
Trichobius uniformis		X	X[b]	
Total (species/genus):	22/11	31/10	27/10	23/11

Data from studies published until April 2017 plus new data from the present study

AMA Amazonia, *ATL* Atlantic Forest, *CAA* Caatinga, *CER* Cerrado

[a] First record for the Atlantic Forest in its northeastern portion

[b] First record for the Caatinga

[c] No information about the sampled ecoregion

the other ecoregions, the richness is still underestimated. Currently, in Brazil, the Atlantic Forest is the third in streblid species richness (53 species), behind the Cerrado (65) and Amazonia (56) (Lourenço et al. 2016).

Despite recent studies and data presented here, the NE region still has several gaps in the knowledge of bat ectoparasites in Brazil. When compared, for example, to the Federal District (in Central Brazil) and the state of Minas Gerais (Southeastern) with 44 and 39 Streblidae species (Lourenço et al. 2016), respectively, there is a clear sampling bias in the NE (50 species, ~ 45% of the bat ectoparasitic fly species in Brazil). Only the state of Pernambuco and the coastal regions of the states of Maranhão and Sergipe can be considered reasonably sampled. In this perspective, species richness and known distribution will certainly be increased as more studies are developed.

There was a correlation between fly species richness and bat species richness in each ecoregion. Bat ectoparasites are mostly species-specific (Marshall 1981; Dick 2007), and the observed positive correlation contributes to what is expected for highly specific parasites, where its occurrence in a given region is restricted to the host occurrence (e.g., Poulin 2007). Our data corroborate those of Dick and Gettinger (2005), in Paraguay, where the geographic distribution of streblids closely followed that of the bat hosts. Besides that, the degree of specialization and the size of the geographical area of a given parasite are correlated (Krasnov et al. 2005). Thus, likely the geographical distribution of bat hosts is one of the main factors affecting the distribution of their highly specific

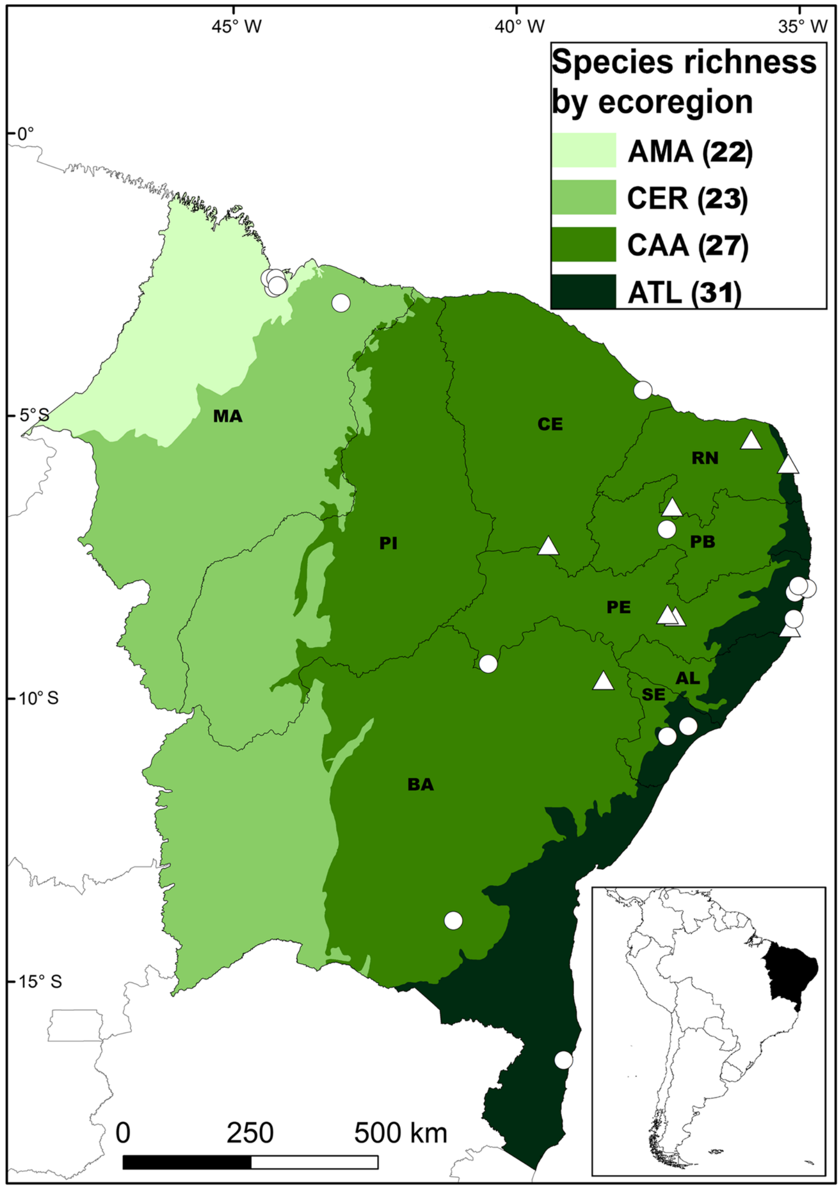

Fig. 1 Study sites and richness of bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) by ecoregion in northeastern Brazil. Data from studies published until April 2017 (white circles) plus new data from the present study (white triangles). Ecoregion: *AMA* Amazonia, *ATL* Atlantic Forest, *CAA* Caatinga, *CER* Cerrado. Federative unit: *AL* Alagoas, *BA* Bahia, *CE* Ceará, *MA* Maranhão, *PB* Paraíba, *PE* Pernambuco, *PI* Piauí, *RN* Rio Grande do Norte, *SE* Sergipe

ectoparasitic flies. Our results are also in agreement with those of Zarazúa-Carbajal et al. (2016), who found differences in host-fly interactions between dry forest and riparian forest in Mexico.

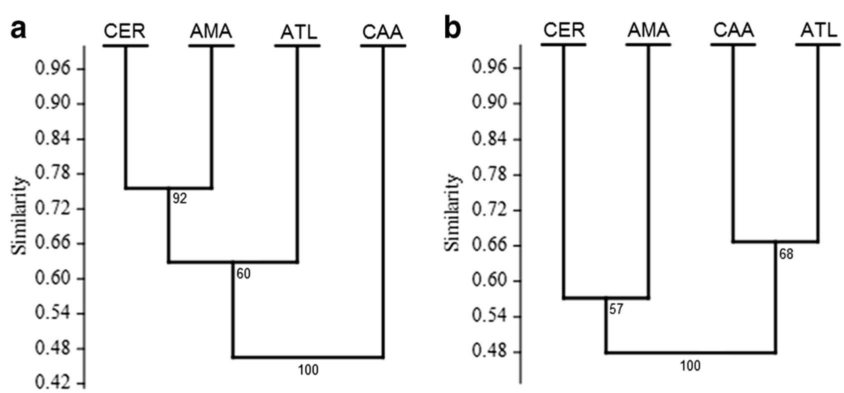

Fig. 2 Cluster analysis (Bray-Curtis with 9999 permutations) evaluating the similarity between ecoregions in northeastern Brazil with data on **a** fly species richness (Diptera: Nycteribiidae and Streblidae) and **b** host species richness (Chiroptera). *AMA* Amazonia, *ATL* Atlantic Forest, *CAA* Caatinga, *CER* Cerrado

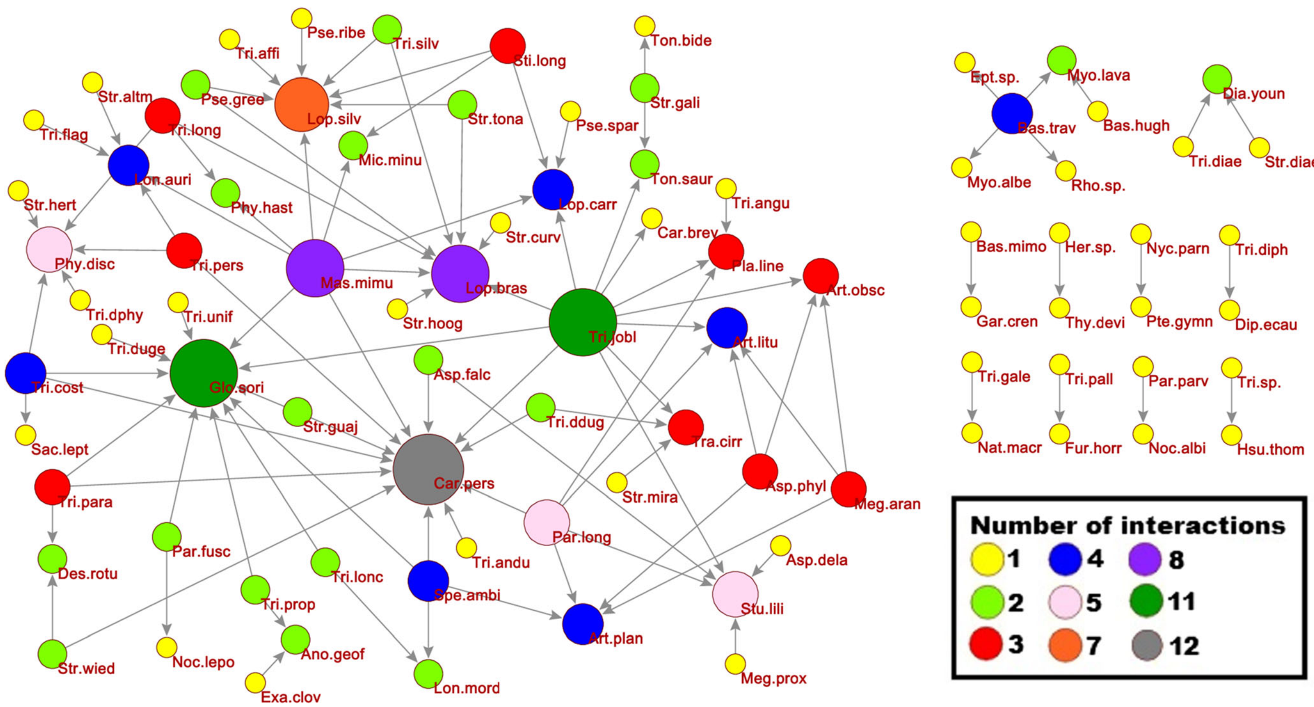

Fig. 3 Interaction networks between bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) and their bat hosts (Chiroptera) in northeastern Brazil. The lines correspond to the interactions and the arrows are indicating the hosts. Fly species— Bas.hugh: *Basilia hughscotti*; Bas.mimo: *B. mimoni*, Bas.trav: *B. travassosi*, Her.sp.: *Hershkovitzia* sp., Asp.dela: *Aspidoptera delatorrei*, Asp.falc: *A. falcata*, A.phyl: *A. phyllostomatis*, Exa.clov: *Exastinion clovisi*, Mas.minu: *M. minuta*, Meg.aran: *Megistopoda aranea*, Meg.prox: *M. proxima*, Nyc.parn: *Nycterophilia parnelli*, Par.fusc: *Paradyschiria fusca*, Par.parv: *P. parvula*, Par.long: *Paratrichobius longicrus*, Pse.gree: *Pseudostrebla greenwelli*, Pse.ribe: *P. ribeiroi*, Pse.spar: *P. sparsisetis*, Spe.ambi: *Speiseria ambigua*, Sti.long: *Stizostrebla longirostris*, Str.altm: *Strebla altmani*, Str.curv: *S. curvata*, Str.diae: *S. diaemi*, Str.gali: *S. galindoi*, Str.guaj: *S. guajiro*, Str.hert: *S. hertigi*, Str.hoog: *S. hoogstraali*, Str.mira: *S. mirabilis*, Str.tona: *S. tonatiae*, Str.wied: *S. wiedemanni*, Tri.pers: *Trichobioides perspicillatus*, Tri.affi: *Trichobius affinis*, Tri.andu: *T. anducei*, Tri.angu: *T. angulatus*, Tri.cost: *T. costalimai*, Tri.diae: *T. diaemi*, Tri.diph: *T. diphyllae*, Tri.duge: *T. dugesii*, Tri.ddug: *T. dugesioides dugesioides*, Tri.dphy: *T. dugesioides phyllostomus*, Tri.flag: *T. flagellatus*, Tri.gale: *T. galei*, Tri.jobl: *T. joblingi*, Tri.lonc: *T. lonchophyllae*, Tri.long: *T. longipes*, Tri.pall: *T. pallidus*, Tri.para: *T. parasiticus*, Tri.prop: *T. propinquus*, Tri.silv: *T. silvicolae*, Tri.sp.: *Trichobius* sp., Tri.unif: *T. uniformis*. Bat species— Ano.geof: *Anoura geoffroyi*, Art.litu: *Artibeus lituratus*, Art.obsc: *A. obscurus*, Art.plan: *A. planirostris*, Car.brev: *Carollia brevicauda*, Car.pers: *C. perspicillata*, Des.rotu: *Desmodus rotundus*, Dia.youn: *Diaemus youngi*, Dip.ecau: *Diphylla ecaudata*, Ept.sp.: *Eptesicus* sp., Fur.horr: *Furipterus horrens*, Gar.cren: *Gardnerycteris crenulatum*, Glo.sori: *Glossophaga soricina*, Hsu.thom: *Hsunycteris thomasi*, Lon.mord: *Lonchophylla mordax*, Lon.auri: *Lonchorhina aurita*, Lop.bras: *Lophostoma brasiliense*, Lop.carr: *L. carrikeri*, Lop.silv: *L. silvicola*, Mic.minu: *Micronycteris minuta*, Myo.albe: *Myotis albescens*, Myo.lava: *M. lavali*, Myo.nigr: *M. nigricans*, Myo.ripa: *M. riparius*, Nat.macr: *Natalus macrourus*, Noc.albi: *Noctilio albiventris*, Noc.lepo: *N. leporinus*, Phy.disc: *Phyllostomus discolor*, Phy.hast: *P. hastatus*, Pla.line: *Platyrrhinus lineatus*, Pte.gymn: *Pteronotus gymnonotus*, Rho.sp.: *Rhogeessa* sp., Sac.lept: *Saccopteryx leptura*, Stu.lili: *Sturnira lilium*, Thy.devi: *Thyroptera devivoi*, Ton.bide: *Tonatia bidens,* Ton.saur: *T. saurophila*, Tra.cirr: *Trachops cirrhosus*

As in the present study, Lourenço et al. (2016) also found a correlation between the richness of Streblidae and number of publications, comparing between federative units. On the other hand, Shapiro et al. (2016) found no correlation when analyzing the species richness of the genus *Raymondia* Frauenfeld, 1855 (Streblidae) and publications among African countries. More research is needed in the NE region to prove if there is a correlation between the fly species richness and the number of studies by ecoregion.

We observed phyllostomid bats as the most species-rich hosts (~ 71%), which is in agreement with the number of species in this family (~ 52% of all bat species in Brazil; Nogueira et al. 2014). This is likely influenced by the easy to capture those bats using mist nets at ground level. Although abundant in many sites, high-flyer insectivorous species are able to detect and avoid nest more easily (e.g., Handley 1967), such as Mormoopidae and Vespertilionidae species, which remain with no information or undersampled.

Host-fly interactions

Although 52% of fly species were monoxenous (i.e., parasitizing only one host species), this result is lower when compared to some sites in Brazil or some sites in other countries (e.g., Wenzel et al. 1966; Wenzel 1976; Komeno and Linhares 1999; ter Hofstede et al. 2004; Dick and Gettinger 2005; Dick 2007). However, when analyzed separately, some studies in the NE region showed higher specificity—80% in the Atlantic Forest (Soares et al. 2013), 88% in the Cerrado (Santos et al. 2013), and 100% in the Caatinga (Barbier et al. 2016). On the one hand, these results may indicate that there is an inequality in host specificity among ecoregions. That is, it is likely that some fly species are more species-specific when analyzed on a local scale, but more generalists when analyzed on a regional scale. According to Krasnov et al. (2011), it is important that the parasite specificity is viewed from smaller scales (α-diversity) to more comprehensive scales (γ-diversity). This may be even more recommended for parasites of hosts as mobile as bats. On the other hand, the use of a non-rigorous methodology (i.e., lack of care to prevent contamination between samples) can bias results about host specificity. In fact, several records of fly parasitizing bats in the NE are from old and isolated records (e.g., Kessel 1925; Pessôa and Galvão 1937; Guimarães 1937, 1938, 1944, 1946; Jobling 1939), and many of them lack information on the care taken during manipulation of specimens to avoid contamination; or they are resulting of specimens deposited in collections, often without source information. Such combination may hinder the true understanding of host-parasite interaction or may lead to wrong conclusions.

Among the more generalist fly species found here, *T. joblingi* and *M. minuta* were those that parasitized most bat species, 12 and eight, respectively. *Mastoptera* Wenzel, 1966 can be one of the few exceptions in Streblidae, with low host specificity when parasitizing phyllostomids, especially of the subfamily Phyllostominae (e.g., ter Hofstede et al. 2004; Dick 2013). Of the eight bat species parasitized by *M. minuta*, only *C. perspicillata* and *G. soricina* belong to another subfamily, which may represent contamination or transient infestation. Conversely, *T. joblingi* is a primary parasite of *Carollia* species, and its occurrence in other bats may be considered a transitory association, transfer by disturbance, or contamination (Wenzel 1976), especially when it is recorded in the presence of the primary host (see Dick 2007). It is likely that some of the previously discussed factors have influenced these non-primary associations. The fact that *C. perspicillata* is the most abundant phyllostomid bat in tropical forests, present in almost all studies of bats in Brazil, increases the possibilities of contamination and transfer disturbance. Additionally, at least five of the hosts recorded for *T. joblingi* have the habit of roosting in cavities, some together with *C. perspicillata*. Although not frequent, roosts sharing by different host species can facilitate accidental or transient transfers of ectoparasites (ter Hofstede et al. 2004). Another possibility is the erroneous identification of the flies since *T. joblingi* belongs to a species complex which parasites several subfamilies of phyllostomid bats and are of difficult taxonomic distinction (see Wenzel et al. 1966).

Recommendations for future studies

Given the host species richness, ecoregion diversity, and lack of studies, the NE is a priority region for research on bat ectoparasites in Brazil. The region presents a large potential for species description, endemism, new records, expanding knowledge about distribution patterns, and parasitic associations. Therefore, future studies should focus on optimizing sampling methods, such as the association of mist nets and hand-net capture in diurnal roosts, as well as investing in the capture of little-inventoried host species such as emballonurids, mormoopids, and thyropterids. In addition, sampling in different ecoregions or in transitional areas (e.g., Atlantic Forest-Caatinga and Caatinga-Cerrado) and environments such as mangroves and caves may contribute to the advancement of studies with bat ectoparasites.

Few are the medium- and long-term studies in each ecoregion in the NE which allow a more robust analysis on host-parasite interactions; therefore, more studies with rigorous and systematized methodologies focused directly on bat ectoparasites should be developed. Additionally, comparisons of parasitological indices (e.g., abundance, infestation intensity, prevalence) between different ecoregions may highlight possible association patterns since environmental factors like temperature, precipitation, and humidity may interfere on local host-parasite interactions (e.g., Morand and Poulin 1998; ter Hofstede and Fenton 2005; Bordes et al. 2008).

Due to the possibility of contamination in a parasite survey, a strictly standardized methodology must be applied from the very first handling of bats and parasites in the field to the laboratory screening and identification. In this sense, we list some preventive measures that we consider fundamental for more effective studies on bat ectoparasites (available as supplementary material; Online Resource 3). Together, these recommendations can contribute greatly to the better knowledge of biology, ecology, and coevolution in this host-parasite system.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Fieldwork was authorized by MMA/IBAMA/ICMBio (permits #33353-1, #33353-2, #43816-1, and #43816-2) and Ethics Committee on Animal Care-UFPE (permit #23076.027916/2015-13).

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