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ESTRUTURA E COMPOSIÇÃO DA INFRACOMUNIDADE DE DÍPTEROS (STREBLIDAE E NYCTERIBIIDAE) ASSOCIADA A MORCEGOS (CHIROPTERA) EM DIFERENTES AMBIENTES AO LONGO DE UM GRADIENTE CLIMÁTICO E ECOLÓGICO NO ESTADO DE PERNAMBUCO, BRASIL

Recife
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Tese apresentada ao Programa de Pós-graduação em Biologia Animal, da Universidade Federal de Pernambuco, como parte dos requisitos parciais para obtenção do título de Doutor em Biologia Animal.

Área de concentração: Zoologia

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RESUMO

O estudo sobre as relações parasitos-hospedeiros é uma importante ferramenta para entendermos questões relacionadas às dinâmicas populacionais, especificidade parasitária, coevolução, entre outras. Morcegos pertencem ao segundo maior grupo de mamíferos terrestres, com maior abundância nas regiões tropicais, e podem albergar uma variedade de grupos parasitos. Devido a diversos fatores ecológicos como riqueza (183 espécies registradas no Brasil), diversidade trófica (e.g., frugívoros, insetívoros, carnívoros, nectarívoros) e comportamental (e.g., formação de grandes colônias), os morcegos representam um importante modelo para o estudo de suas relações com parasitos. Dos diversos grupos de artrópodes que podem parasitar esses mamíferos, as moscas das famílias Streblidae e Nycteribiidae são as mais conspícuas por apresentarem várias adaptações morfológicas (e.g., redução ou ausência de asas, olhos compostos reduzidos) e fisiológicas (e.g., viviparidade adenotrófica) alinhadas ao hábito parasitário no hospedeiro. Adicionalmente, moscas ectoparasitas de morcegos possuem alta especificidade pelo hospedeiro (majoritariamente são espécie-específicas) e, assim como os morcegos, são mais diversas nos trópicos. Este estudo objetivou (i) verificar se o ambiente e os hospedeiros influenciam a presença e distribuição de moscas ectoparasitas, (ii) entender como a carga parasitária de moscas ectoparasitas sobre morcegos é afetada em de um pronunciado gradiente de precipitação e vegetação, (iii) avaliar se existem diferenças nos índices parasitológicos entre morcegos cavernícolas e não-cavernícolas e (iv) se a concentração de morcegos dentro do ambiente cavernícola está correlacionada com a carga parasitária de moscas. Os morcegos e suas respectivas moscas foram mensalmente amostrados em três diferentes ambientes no estado de Pernambuco, Brasil, denominados “área úmida”, “área de transição” e “área semiárida”, e em uma caverna. Para verificar se haviam diferenças na carga parasitária entre os ambientes, foram utilizados os índices de prevalência, intensidade média e abundância média. Esses mesmos índices foram utilizados para testar a diferença na carga parasitária entre morcegos cavernícolas e não-cavernícolas e para verificar a correlação entre o número de morcegos no interior da caverna com sua carga de parasitos. Não houve diferença estatisticamente significativa na carga parasitária, nem dentro do mesmo ambiente ao longo do período amostrado, nem entre os ambientes estudados. Quando comparada a carga parasitária de morcegos capturados dentro e fora de caverna, não houve diferença entre a prevalência, mas a intensidade e a abundância médias dos ectoparasitos foram significativamente maiores no ambiente cavernícola. Não houve correlação da concentração de morcegos na caverna com a carga parasitária exibida por eles. Esses resultados indicam que ambientes cavernícolas podem favorecer uma maior carga parasitária em morcegos, provavelmente por propiciar um microclima ideal para o desenvolvimento das pupas das moscas. Além disso, a fidelidade de morcegos a ambientes cavernícolas beneficia as reinfestações por aquelas moscas recém emergidas. Todavia, a frequência com que os morcegos em ambientes cavernícolas são parasitados não difere de ambientes não-cavernícolas nem é afetada pela concentração dos indivíduos na caverna. Para os ambientes não-cavernícola, os resultados mostram que a prevalência e a carga parasitária das moscas independem do habitat no qual os morcegos estão inseridos e que, mesmo podendo haver influências bióticas e abióticas, suas relações parasito-hospedeiro não são significativamente alteradas.

Palavras-chave: Caatinga. Índices parasitológicos. Interação parasito-hospedeiro. Mata Atlântica.

ABSTRACT

Studying hot-parasite relationships is an important tool to understand issues related to population dynamics, parasitic specificity and coevolution, for example. Bats belong to the second largest group of terrestrial mammals, with greater abundance in tropical regions, and may harbor a variety of parasite groups. Due to diverse ecological factors such as richness (183 species registered in Brazil), trophic diversity (e.g., frugivorous, insectivorous, carnivorous, nectarivorous), and behavior (e.g., formation of large colonies), these mammals represent an important model for the study of their relationships with parasites. Of the various groups of arthropods that can parasitize bats (e.g., mites, ticks, fleas), the flies of the Streblidae and Nycteribiidae families are the most conspicuous because they have several morphological (e.g., reduction or absence of wings, reduced compound eyes), and physiological (e.g., adenotrophic viviparity) adaptations according to their parasitic habit. Additionally, bat ectoparasitic flies have high host specificity (mostly species-specific) and, like bats, are more diverse in the tropics. This study aimed to verify (i) if the environment and the hosts influence the presence and distribution of ectoparasitic flies, (ii) to understand how the parasitic load of bat ectoparasitic flies on bats is affected along a gradient of precipitation and vegetation, (iii) if there are differences in parasitological indices between cave bats and non-cave bats, and (iv) whether bats concentration within the cave environment is correlated with the flies parasitic load. Bats and their respective flies were monthly sampled in three different environments in the state of Pernambuco, Brazil, called "wet area", "transitional area" and "semiarid area", and in a cave. To verify if there were differences in the parasitic load among environments, the prevalence, mean intensity, and mean abundance indices were used. These same indices were used to test the difference in parasitic load between cave and non-cave bats and to verify the correlation between the bats concentration inside the cave with their parasitic load. There was no statistically significant difference in parasitic load, neither within the same environment during the sampled period, nor between the environments studied. When comparing the parasitic load of bats captured in and out of the cave, there was no difference between the prevalence, but the mean intensity and abundance were significantly higher in the cave environment. There was no correlation between the bats concentration in the cave and the parasitic load exhibited by them. These results indicate that cave environments may favor a greater parasitic load on bats, probably for providing an ideal microclimate for the development of pupae of flies. In addition, the fidelity of bats to cave environments benefits re-infestations by those newly emerged flies. However, the frequency in which bats in cave environments are parasitized does not differ from non-cave environments, nor is it affected by the concentration of individuals in the cave. For non-cave environments, the results show that the prevalence and parasitic load of flies is independent of the habitat in which bats are inserted and that, although there may be biotic and abiotic influences, their host-parasite relationships are not significantly altered.

Keywords: Atlantic Forest. Caatinga. Host-parasite interactions. Parasitological indices.

SUMÁRIO

1 INTRODUÇÃO

No Brasil, atualmente são reconhecidas 183 espécies de morcegos (Mammalia: Chiroptera) (NOGUEIRA et al., 2014; FEIJÓ; ROCHA; ALTHOFF, 2015; FISCHER et al., 2015; MORATELLI; DIAS, 2015; GREGORIN et al., 2016; ROCHA et al., 2016), representando cerca de 25% das espécies de mamíferos conhecidas no país (PAGLIA et al., 2012). Embora a maior parte do território brasileiro ainda esteja subamostrada para morcegos (BERNARD; AGUIAR; MACHADO, 2011), o Brasil é o segundo país com maior número de espécies deste grupo, abrigando aproximadamente 14% do total mundial, atrás apenas da Colômbia (FENTON; SIMMONS, 2014).

Morcegos são principalmente conhecidos por desempenharem importante papel na manutenção dos ecossistemas, devido à dispersão de sementes (quiropterocoria), polinização (quiropterofilia) e controle de populações animais (artropodofilia) (e.g., GARDNER, 1977; FENTON et al., 1992; COSSON; PONS; MASSON, 1999). Além disso, morcegos possuem uma diversidade de estratégias de forrageio, exploram inúmeros tipos de abrigos e podem formar colônias com centenas de milhar de indivíduos (e.g., GARDNER, 2008; FENTON; SIMMONS, 2014). Devido a essas características ecológicas e comportamentais, morcegos podem interagir com diversos grupos animais, incluindo artrópodos ectoparasitos (MARSHALL, 1982).

Entre os ectoparasitos de morcegos estão ácaros, carrapatos, pulgas, percevejos e moscas (WENZEL; TIPTON; KIEWLICZ, 1966; WENZEL, 1976; GRACIOLLI; CARVALHO, 2001; SILVA; VALIM; GRACIOLLI, 2017); entretanto, as moscas (Diptera: Streblidae e Nycteribiidae) são as mais frequentemente registradas (FRANK et al., 2014). Esses dípteros apresentam uma série de adaptações morfológicas (e.g., asas reduzidas ou ausentes) e fisiológicas (e.g., viviparidade adenotrófica) e são encontrados obrigatoriamente parasitando a pele ou a membrana das asas de morcegos (MARSHALL, 1982). As associações parasito-hospedeiro entre morcegos e moscas ectoparasitas datam de, pelo menos, 15-20 milhões de anos atrás (POINAR; BROWN, 2012) e apresentam interações espécie-específica na maioria dos casos (i.e., mais de 85% das espécies possuem comportamento monoxênico) (e.g., DICK; PATTERSON, 2007; BARBIER; GRACIOLLI, 2016; LOURENÇO; ALMEIDA; FAMADAS, 2016; BARBIER; BERNARD, 2017). As regiões tropicais abrigam a maior riqueza de espécies (DITTMAR et al., 2015) e no Brasil mais de 110 já foram registradas (GRACIOLLI; AUTINO; CLAPS, 2007; BEZERRA; VASCONCELOS; BOCCHIGLIERI, 2016; LOURENÇO; ALMEIDA; FAMADAS, 2016; BARBIER et al., 2018).

Do mesmo modo que ocorre com seus hospedeiros, ainda existem diversas lacunas no conhecimento sobre moscas das famílias Streblidae e Nycteribiidae, especialmente no que diz respeito às suas relações ecológicas com os morcegos e o ambiente em que ambos os grupos coexistem. Como a maioria dos estudos têm se concentrado principalmente em abordagens mais descritivas das interações parasito-hospedeiro, existe uma carência de informações que permitam entender de forma mais conclusiva como, por exemplo, fatores bióticos e abióticos afetam (e se afetam) esta relação. Neste sentido, a presente tese objetivou amostrar morcegos e suas respectivas moscas ectoparasitas em distintos ambientes, com marcada diferença na vegetação e precipitação, e testar se as relações parasitárias são afetadas ao longo deste gradiente ambiental.

2 APRESENTAÇÃO

A presente tese está organizada em três manuscritos. No primeiro manuscrito, “*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*”, foi realizada uma meta-análise abrangendo toda a região nordeste do Brasil, utilizando dados inéditos e disponíveis na literatura, com objetivo principal de verificar se o ambiente e as espécies de morcegos ali presentes exercem influência na presença e distribuição de moscas ectoparasitas. Este manuscrito foi previamente submetido e publicado no periódico *Parasitology Research* (volume 116, número 11, páginas 3043–3055, doi 10.1007/s00436-017-5615-7).

O segundo manuscrito, “*Structure and composition of Nycteribiidae and Streblidae flies on bats along an environmental gradient in Northeastern Brazil*”, teve como objetivo central analisar se a prevalência e a carga parasitária de moscas ectoparasitas sobre morcegos são afetadas de acordo com a precipitação ao longo do período amostrado e se há diferença significativa nos valores desses índices parasitológicos ao longo de um gradiente ambiental. Este manuscrito está estruturado seguindo as normas do periódico *Canadian Journal of Zoology* (ISSN: 0008-4301).

No terceiro e último manuscrito, “*Parasitic load and network of bat ectoparasitic flies in cave and non-cave environments in Northeastern Brazil*”, objetivou-se investigar e comparar a presença e carga parasitária de moscas ectoparasitas sobre morcegos entre ambiente cavernícola e não-cavernícola, além de verificar se a carga parasitária está correlacionada com a abundância de morcegos no ambiente cavernícola. Adicionalmente, foram extraídas métricas das redes de interações formadas entre os morcegos e as moscas para ambos os ambientes. Este manuscrito está formatado de acordo com as normas estabelecidas pelo periódico *Parasitology* (ISSN: 0031-1820).

3 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

Observação: Devido ao fato do primeiro manuscrito já ter sido publicado, optou-se por incluir o artigo resultante no Apêndice A.

4 STRUCTURE AND COMPOSITION OF NYCTERIBIIDAE AND STREBLIDAE FLIES ON BATS ALONG AN ENVIRONMENTAL GRADIENT IN NORTHEASTERN BRAZIL

Structure and composition of Nycteribiidae and Streblidae flies on bats along an environmental gradient in Northeastern Brazil

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Title: Structure and composition of Nycteribiidae and Streblidae flies on bats along an environmental gradient in Northeastern Brazil

Abstract: Bats can be parasitized by several arthropod groups, including ectoparasitic flies. The high host specificity is a common phenomenon between flies and bats. In recent years, more efforts have been employed to understand how environmental variables can influence richness and parasitic load (PL). However, many gaps still need to be filled in order to better understand this issue. We analyzed the PL of flies on bats sampled in three environments with different rain volume and vegetation types to verify if are correlated with the rainfall and if there are differences in the PL on bats within and between environments. There was no correlation between rainfall and PL in the same environment nor difference between in the three studied environments. We observed that the host-parasite interactions were driven by other factors rather than the amount of rainfall or vegetation alone. Our study reinforces such close relationship indicating that, in this case, host characteristics may be more important than environmental variables. Therefore, it is reasonable to say that richness and abundance of bat ectoparasitic flies are more strongly correlated with the number of species and concentration of bats in a given area rather than on abiotic factors, like rain and vegetation.

Key words: Atlantic Forest, bat ectoparasitic flies, Caatinga, Chiroptera, Diptera, host-parasite relationships, environmental variables, transitional areas

Introduction

Bats are the second largest group of mammals and can be parasitized by several groups of ectoparasites such as mites, ticks, bugs, fleas, and flies (Marshall 1981, 1982; Fenton and Simmons 2014). Among the ectoparasites of bats, especially in the tropics, the hematophagous flies of the families Streblidae and Nycteribiidae (Diptera: Hippoboscoidea) are the most frequently found on these hosts (see Frank et al. 2014).

Contrary to what would be expected, due to diverse ecological and behavioral characteristics of the host, bat ectoparasites are highly specialized and for streblid and nycteribiid, for example, there is a phylogenetic correlation with their hosts (Dittmar et al. 2006; Dick 2007). Although the high specificity of flies by bat hosts seems to be a unanimous and widespread issue among the vast majority of researchers (e.g., Wenzel et al. 1966; Wenzel 1976; Dick and Patterson 2007; Dittmar et al. 2015; Lourenço et al. 2016; Barbier et al. 2016), the structure and composition along the geographic distribution of species has been little explored (e.g., Barbier and Bernard 2017).

Nevertheless, especially in recent years, studies have indicated some influence, even if indirect, of environmental variables on species richness and parasitic load of ectoparasitic flies occurring on bats (e.g., Stanko et al. 2006; Pilosof et al. 2012; Zarazúa-Carbajal et al. 2016). On the other hand, patterns for parasite communities are more complex to predict, since, in addition to environmental characteristics, host factors (e.g., morphology, evolutionary traits) also play an important role in such associations (e.g., Krasnov et al. 1998) and may vary between different biogeographical regions (e.g., Korallo et al. 2007; Poulin 2007; Krasnov et al. 2003, 2011, 2012). Thus, in order to increase the knowledge on these issues, it is essential investigate such associations in the most diverse scales and regions.

Here, we analyzed the parasitic load of ectoparasitic flies (Streblidae and Nycteribiidae) on bats (Chiroptera) sampled in three environments with different rain volumes and vegetation types in Northeastern Brazil to verify (i) whether the parasitological indices (prevalence, mean intensity, and mean abundance) are correlated with the seasonal rainfall; and (ii) whether there are differences in the parasitic load on the bats within and between environments. Our hypothesis was that the parasitological indices would be influenced by rainfall, both within and between environments and, considering vegetation is directly influenced by rainfall, we also predicted that the parasitological indices would be affected by the type of habitat sampled.

Materials and methods

Study area

In the state of Pernambuco, Northeastern Brazil, there is a remarkable climatic gradient in the east-west direction, from a more humid environment on the eastern coast, passing through a transition area (locally known as *agreste*), until the western semiarid (Andrade 1980, 1989; Lins 1989; Barbosa et al. 2002; Ferraz 2002; Andrade-Lima 2007; Lima 2007). Fieldwork was conducted in three environments along that gradient (Fig. 1), hereafter wet area (*WA*), transitional area (*TA*), and semiarid area (*SA*).

WA – The Saltinho Biological Station is a 562 ha Federal Reserve of Atlantic Forest, near Tamandaré city (ICMBio 2015). The climate is constantly hot (annual temperature averaging 25°C) and humid with a dry season in the summer and a rainy season (1,500–2,000 mm) along autumn-winter (Barbosa et al. 2002; Ferraz 2002). Composed mainly of secondary forest in advanced natural regeneration, Saltinho was created in 1983 and is currently one of the largest Atlantic Forest fragments of Pernambuco (Brasil 1983; ICMBio 2015). The samplings were carried out in four sites – 08°43'49.32" S, 35°10'34.95" W; 08°43'52.8" S, 35°10'41.4" W; 08°43'44.4" S, 35°10'36.8" W; and 08°43'49.5" S, 35°10'39.2" W.

TA – The *agreste* is a microregion of Northeastern Brazil extending from the state of Rio Grande do Norte to the southeast of the state of Bahia (Rizzini 1979). Characterized as a transitional area between the Atlantic Forest and Caatinga, the *agreste* has intermediate characteristics with humid sites such as the coast, and others dry as in semiarid area (Andrade 1980, 1989, Lins 1989). The region's climate is classified as BSh's, following Köpen, and the mean annual temperature is 25°C with an annual rainfall of 599 mm, marked by irregularity throughout the year. The captures were carried out in three sites – 08°11'55.8" S, 35°28'59.3" W; 08°12'34.5" S, 35°29'00.0" W; and 08°11'00.9" S, 35°27'30.7" W in the municipality of Chã Grande.

SA – The Catimbau National Park has 62,292 ha and located in the central region of the state of Pernambuco. Its area covers the municipalities of Buíque, Tupanatinga, and Ibimirim and it 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), and *Xeronycteris vieirai* Gregorin and Ditchfield, 2005 (Cordero-Schmidt et al. 2017; Delgado-Jaramillo et al. 2017). Rainfall to the region is concentrated from April to June, with an annual average ranging from 300 mm 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. Fieldwork was carried out in nine sites as follows — 08°34'16.2" S, 37°14'50.2" W; 08°32'04.1" S, 37°14'05.4" S; 08°34'02.4" S, 37°14'30.8" W; 08°28'42.8" S, 37°20'07.1" W; 08°32'17.8" S, 37°11'40.6" W; 08°25'41.4" S, 37°18'34.4" W; 08°28'44.8" S, 37°14'12.9" W; 08°24'41.8" S, 37°18'54.6" W; and 08°29'44.1" S, 37°13'50.2" W.

Data collection

From July 2014 to June 2015, bats were monthly sampled using 10 mist nets (12 m × 2.5 m), set at the ground level during six hours at the sunset; except in July 2014 and June 2015, there were no captures in the TA and SA respectively. Therefore, *WA* obtained 144 h of captures, *TA* 114 h, and *SA* 138 h. At the end of the captures period, we obtained an effort of 3,960 mist-net-hours (mnh) (one 12 m × 2.5 m net open for 1 h equals 1 mnh) (Table 1). The monthly precipitation in each area was obtained from INPE/SUDENE/CPTEC (2016) based on information from weather stations in the municipalities of Tamandaré (for *WA*), Chã Grande (for *TA*), and Buíque (for *SA*).

Each captured bat was individually placed in clean cotton bags, used only once in each night. The entire body surface and wing membranes of the hosts were checked to find possible ectoparasites. The ectoparasitic flies were collected with soft forceps and placed in properly labeled vials containing 70% ethanol for later identification in the laboratory. All specimens' manipulation, *in situ* or *ex situ*, was conducted in order to prevent contamination of the parasites through the hosts, following Barbier and Bernard's (2017) recommendations.

After screening, the bats were measured, sexed, and marked on the back with non-toxic ink to recapture control in the same sampling period and released. Recaptures were not considered for data analysis. Bats were handled according to Sikes et al. (2011) and fieldwork was authorized by MMA/ICMBio/SISBIO (permits #43816-1 and #43816-2) and Ethics Committee on Animal Care–UFPE (permit #23076.027916/2015-13).

Species identification

For bat species identification, we followed Gregorin and Taddei (2002), Gregorin and Ditchfield (2005), Gardner (2008), Díaz et al. (2011), Moratelli et al. (2011), Feijó et al. (2015), and Moratelli and Dias (2015). We followed Nogueira et al. (2014) for bat nomenclature. For flies, we followed the diagnoses and/or taxonomic keys available in Guimarães (1938), Guimarães and D'Andretta (1956), Wenzel et al. (1966), Wenzel (1976), and Guerrero (1998). We followed Graciolli and Dick (2008) and Dick and Graciolli (2008) for flies' nomenclature. Voucher specimens are deposited in the Mammal Collection (UFPE) and in the Entomological Collection (CE–UFPE) of Federal University of Pernambuco.

Data analysis

In order to quantitatively describe the parasite's populations, we used prevalence (number of infested hosts with a particular parasite species/number of examined hosts), mean intensity (number of parasites of a particular species/number of hosts infested with that parasite), and mean abundance (number of individuals of a particular parasite species on a particular host species/number of hosts of that species examined; including both infected and uninfected hosts) (*sensu* Bush et al. 1997). Non-primary associations were not considered in the analyzes (*sensu* Dick 2007). The parasitological indices were calculated with the program Quantitative Parasitology–QPweb 1.0.13 (Reiczigel et al. 2013).

We used Spearman's (r_s) correlation to test the relationship between rainfall and parasitic load (prevalence, mean intensity, and mean abundance) during the studied period, separately for each sampled area. To test whether parasitic load differs between environments and between host sexes, we used the Kruskal-Wallis (H) test. We chose to analyze such influence only for the host species that were more representative of each study area (≥ 30 captures; see Rózsa et al. 2000). Therefore, bats and species with no parasites were excluded from comparative statistical analyses. Data normality was verified with the Shapiro-Wilk test. We used the program PAST 3.16 for the analyses (Hammer et al. 2001), with the significant level at $P < 0.05$.

Results

In total, we captured 1,572 bats of 36 species and 28 genera of the families Phyllostomidae (26 species), Vespertilionidae (5 species), Molossidae (2 species), Emballonuridae (1 species), Mormoopidae (1 species), and Noctilionidae (1 species) (Table 2). Among the captured bats, 967 (61.5%) were parasitized by flies. *Artibeus lituratus* (Olfers, 1818), *A. planirostris* (Spix, 1823), *Carollia perspicillata* (Linnaeus, 1758), *Glossophaga soricina* (Pallas, 1766), *Lonchophylla mordax* Thomas, 1903, and *Myotis lavali* Moratelli, Peracchi, Dias & Oliveira, 2011 were the most infested species, accounting for 1,224 bats (~ 78%) and 2,565 flies (~ 70%) (Table 2).

The *WA* was the site with the highest number of bat captured (*n* = 921) and species (23 spp.), followed by the *SA* (*n* = 436; 21 spp.), and the *TA* (*n* = 215; 12 spp.) (Table 1). The top-three most abundant bat species were: *C. perspicillata* (*n* = 440; 48%), *M. lavali* (*n* = 168; 18%), and *A. planirostris* (*n* = 70; 8%), in the *WA*; *A. planirostris* (*n* = 81; 38%), *C. perspicillata* (*n* = 44; 20%), and *Sturnira lilium* (É. Geoffroy, 1810) (*n* = 25; 12%), in the *TA*; *A. planirostris* (*n* = 145; 33%), *L. mordax* (*n* = 72; 16.5%), and *G. soricina* (*n* = 62; 14%), in the *SA* (Table 2). *Dermanura cinerea* Gervais, 1856 (*n* = 73) and *Molossus molossus* (Pallas, 1766) (*n* = 44) were also abundant in the *WA*, but were not infested by flies and were excluded from all analyses.

We collected 3,688 flies of 39 species and 13 genera of the families Streblidae (37 species) and Nycteribiidae (2 species) (Table 3). The *WA* was the environment with the highest number of collected flies (*n* = 2,397 flies, on 583 bats), followed by *SA* (*n* = 927 flies, on 268 bats), and *TA* (*n* = 364, on 116 bats) (Tables 2 and 3). The top-three most abundant fly species were: *Trichobius joblingi* Wenzel, 1966 (*n* = 1,092), *Basilia travassosi* Guimarães, 1938 (*n* = 400), and *T. dugesioides dugesioides* Wenzel, 1966 (*n* = 227), in the *WA*; *T.*

joblingi (*n* = 93), *Megistopoda aranea* (Coquillett, 1899) (*n* = 66), and *B. travassosi* (*n* = 39), in the *TA*; *T. diphyllae* Wenzel, 1966 (*n* = 169), *T. lonchophyllae* Wenzel, 1966 (*n* = 143), and *Trichobius* sp. 3 (*n* = 107), in the *SA*.

Among the most captured bats (≥ 30), the prevalence of flies ranged from 3.2% (*Trichobius* sp. 1 on *A. lituratus*) to 79.3% (*T. joblingi* on *C. perspicillata*) in *WA*; from 11.1% (*A. phyllostomatis* on *A. planirostris*) to 75.0% (*T. joblingi* on *C. perspicillata*) in *TA*; and from 5.6% (*Strebla* sp.) to 66.7% (*T. lonchophyllae*) both on *L. mordax* (Supplementary material – Tables S1, S2, and S3).

There was no correlation between rainfall and parasitic load in the same environment throughout the study period (Table 4). There was no significant difference neither between the parasitological indices in the three studied environments (prevalence: $H = 1.617$, $P = 0.4454$; mean intensity: $H = 3.027$, $P = 0.2201$; mean abundance: $H = -0.0147$, $P = 1$) nor between the host sex (prevalence: $H = 0.0641$, $P = 0.9684$; mean intensity: $H = 0.5547$, $P = 0.4559$; mean abundance: $H = 0.1146$, $P = 0.7349$).

Discussion

When sampling along an ecological gradient from Atlantic Forest to the dry forest in Northeastern Brazil we observed that, contrary to our predictions, the prevalence, mean intensity, and mean abundance of bat ectoparasitic flies were not influenced by rainfall, and there was no significant difference of such indices between environments. Although environmental variables are often highlighted as one of the main influences on the host-parasite association (e.g., Morand and Poulin 1998; ter Hofstede and Fenton 2005; Bordes et al. 2008), in our study we observed that the host-parasite interactions were driven by other factors rather than the amount of rainfall or vegetation alone.

Environmental variables have recently been identified in some studies as a driver for parasitic load and host interactions. Pilosof et al. (2012), for instance, recently found an effect of temperature and precipitation on the abundance of bat ectoparasitic flies in Venezuela using a meta-analysis. However, as indicated by Pilosof et al. (2012), there is a need for an approach with local data at the time of capture. In a meta-analysis, many details are suppressed in favor of a more general examination, such as the existence and/or analysis of microenvironments, which could otherwise result in more detailed knowledge about host-parasite relationship (e.g., Lourenço et al. 2016). Our data, both from hosts and ectoparasitic flies, were obtained *in situ* and collected with rigorous methodology (see Materials and methods) and the information about rainfall was provided on a small scale (local data). This set of features can favor the obtaining of information that better represent the interactions between bats and their ectoparasitic flies along a climatic gradient.

Besides that, for host specificity, for example, small- and large-scale analysis is important because different responses in host-parasite relationships can be observed at the local or regional level (e.g., Krasnov et al. 2011). For fleas, links between their own communities, host communities, and habitat types appears to manifest differently across geographic regions. Among-habitat, differences in flea assemblages within a host species in temperate zones appear to be less pronounced than those in desert habitats (see Laudisoit et al. 2009). The greater the number of environments and regions sampled for streblids and nycteribiids, the greater our capacity to understand the interactions with their bat hosts.

Another factor that should be considered when studying the relationship between ectoparasites and their hosts is data robustness. Some studies analyzing the effect of seasonal and/or vegetation variation on bat ectoparasitic flies have used lower numbers of both individuals and species [e.g., Zarazúa-Carbajal et al. (2016) (145 bats, 246 flies); Rivera-García et al. (2017) (318 bats, 836 flies)]. We analyzed data from 1,153 infested bats of six species, parasitized with 2,265 flies of 12 species, considering only those most representative hosts in the sample (≥ 30). On the one hand, it is likely that the refinement of our data is showing in more detail the host-parasite relationship between environments with different vegetation and rainfall. On the other hand, it is important that similar studies investigate this association in distinct regions in Brazil to confirm whether there is a regional influence or if this pattern is the same regardless of location.

The species-specific response in both the ectoparasitic load and in the fly species richness we observed agree, in part, with those found by Salinas-Ramos et al. (2017) in a dry tropical forest in Mexico. Of the four bat species studied by these authors, some experienced a significant increase in the ectoparasitic load in the wet season (higher mean intensity and mean abundance), while other species had the highest parasitic load in the dry season. Apparently, there is no general pattern and each species is likely to respond in a particular way: the same species of host and parasite may present different traits in different locations and, when analyzed in a macroscale, no general patterns are found among parasite richness and some ecological variables (see Poulin 2007).

We did not find any influence of host sex on the relationship between ectoparasitic flies and bats. Recently, Frank et al. (2016) observed that tree cover was not a significant predictor of bat ectoparasitic flies abundance in Costa Rica. On the other hand, they found that parasite load on a particular bat host can be changed in a sex-specific way, through habitat change. Moura et al. (2003) and Presley (2007), for example, also found no correlation between the host sex and parasite community structure on the greater bulldog bat *Noctilio leporinus* (Linnaeus, 1758), a species with sex-based social system.

A high specific relationship

Streblid and nycteribiid are hematophagous flies found exclusively on bats and are one of the most specialized in Diptera, having an association with bats at least since the Miocene (15–20 million years ago), currently covering more than 500 described species worldwide (Marshall 1981; Dick and Patterson 2006; Poinar and Brown 2012). Additionally, streblid and nycteribiid present high host specificity, occurring on a single bat species or on congeners, in most cases (e.g., Marshall 1981; Dick and Patterson 2007; Barbier and Graciolli 2016; Barbier et al. 2016). Our study reinforces the close relationship, indicating that host characteristics may be more important than environmental variables. In fact, in Northeastern Brazil, bat ectoparasitic fly species richness are also correlated with the bat host species richness and distinct groups can be recognized among biomes, both for bat and fly species, showing that the occurrence of flies is dependent on their specific host (Barbier and Bernard 2017).

Due to the high host specificity, the abundance of bat ectoparasitic flies is likely to be affected mainly by host species density as recently suggested by Pilosof et al. (2012). Complementary, Arneberg et al. (1998) found a stronger positive association between host population density and average of parasite abundance within mammalian taxa. It is also the case of fleas on small mammals, where the host composition appears to better explain the variance in flea species composition than environmental variables, for example (Laudisoit et al. 2009). The more complex a system, the less likely we are to achieve quantitatively accurate predictions and to find general laws (Kauffman 1993). Parasite communities are complex systems and they exist in non-equilibrium conditions, a situation where contingencies should be predominant (see Rohde 2006). Thus, as presented here, it is reasonable to say that richness and abundance of bat ectoparasitic flies are more strongly correlated with the number of species and concentration of bats in a given area rather than on external factor surrounding them.

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Table 1. Sampled sites, annual rainfall, sampling effort, and bat captures in a study on the structure and composition of ectoparasitic flies on bats in different habitats in the state of Pernambuco, Northeastern Brazil, between July 2014 and June 2015.

Habitat	No. of sites	Annual rainfall (mm) *	No. of bat captures	No. of bat species	Effort (mnh) [a]	Capture ratio [b]	Species ratio [c]
Wet area	3	1,498.58	921	23	1,440	0.639	0.025
Transitional area	3	934.88	215	12	1,140	0.188	0.056
Semiarid area	9	608.93	436	21	1,440	0.303	0.048
Total	15	-	1572	-	4,020	-	-

[a] Mist-net-hours, [b] Number of bat captures divided by effort, [c] Number of bat species divided by number of bat captures, * Available from http://proclima.cptec.inpe.br/balanco_hidrico/balancohidrico.shtml.

Table 2. Bat species, abundance of bats (N), and number of infested hosts (IH) captured in three environments in the state of Pernambuco, Northeastern Brazil.

Species	Family code	Environments						Total
		WA		TA		SA		
		N	IH	N	IH	N	IH	
Carollia perspicillata	Phy	440	382	44	35	40	17	524
Artibeus planirostris	Phy	70	24	81	37	145	79	296
Myotis lavali	Ves	168	108	6	6	5	3	179
Glossophaga soricina	Phy	27	12	5	1	62	36	94
Dermanura cinerea	Phy	73	0	14	0	0	0	87
Lonchophylla mordax	Phy	0	0	0	0	72	51	72
Artibeus lituratus	Phy	31	11	22	12	6	3	59
Molossus molossus	Mol	44	0	2	0	1	0	47
Phyllostomus discolor	Phy	28	26	3	3	0	0	31
Sturnira lilium	Phy	3	1	25	16	2	2	30
Xeronycteris vieirai	Phy	0	0	0	0	27	24	27
Platyrrhinus lineatus	Phy	2	2	10	5	11	9	23
Micronycteris sanborni	Phy	0	0	0	0	21	18	21
Trachops cirrhosus	Phy	11	11	0	0	0	0	11
Anoura geoffroyi	Phy	0	0	0	0	8	6	8
Desmodus rotundus	Phy	3	0	0	0	5	4	8
Histiotus diaphanopterus	Ves	0	0	0	0	8	1	8
Diphylla ecaudata	Phy	0	0	0	0	7	7	7
Micronycteris sp.	Phy	0	0	0	0	6	0	6

Artibeus obscurus	Phy	5	1	0	0	0	0	5
Lonchorhina aurita	Phy	1	1	0	0	3	3	4
Platyrrhinus sp.	Phy	4	0	0	0	0	0	4
Rhogeessa sp.	Ves	0	0	0	0	3	3	3
Chiroderma doriae	Phy	2	0	0	0	0	0	2
Eptesicus brasiliensis	Ves	0	0	2	1	0	0	2
Lophostoma brasiliense	Phy	2	1	0	0	0	0	2
Pteronotus gymnonotus	Mor	0	0	0	0	2	2	2
Tonatia saurophila	Phy	2	2	0	0	0	0	2
Artibeus cf. *fimbriatus*	Phy	1	0	0	0	0	0	1
Chiroderma villosum	Phy	1	0	0	0	0	0	1
Lasiurus blossevillii	Ves	0	0	0	0	1	0	1
Molossus rufus	Mol	1	0	0	0	0	0	1
Noctilio leporinus	Noc	0	0	1	0	0	0	1
Peropteryx sp.	Emb	0	0	0	0	1	0	1
Phyllostomus elongatus	Phy	1	1	0	0	0	0	1
Rhinophylla pumilio	Phy	1	0	0	0	0	0	1
Total:		921	583	215	116	436	268	1,572
Richness: 36		23	-	12	-	21	-	-

Environments: WA, wet area; TA, transitional area; SA, semiarid area. Families: Emb, Emballonuridae; Mol, Molossidae; Mor, Mormoopidae; Noc, Noctilionidae; Phy, Phyllostomidae; Ves, Vespertilionidae.

Table 3. Number of bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) collected in three environments in the state of Pernambuco, Northeastern Brazil.

Family/Species	WA	TA	SA	Total
Nycteribiidae				
Basilia travassosi	400	39	15	454
Basilia sp.	0	0	2	2
Streblidae				
Trichobius joblingi	1,092	93	27	1,212
Speiseria ambigua	208	15	7	230
Trichobius dugesioides dugesioides	227	0	0	227
Megistopoda aranea	38	73	88	199
Trichobius sp. 3	0	0	180	180
Trichobius lonchophyllae	0	0	171	171
Trichobius diphyllae	0	0	169	169
Aspidoptera phyllostomatis	22	16	84	122
Trichobius costalimai	90	24	0	114
Strebla guajiro	88	12	2	102
Trichobioides perspicillatus	80	2	0	82
Trichobius anducei	76	0	0	76
Paratrichobius longicrus	18	31	19	68
Trichobius dugesii	16	1	30	47
Trichobius uniformis	4	4	29	37
Megistopoda proxima	1	26	3	30
Trichobius parasiticus	0	0	27	27

Aspidoptera falcata	0	23	0	23
Exastinion clovisi	0	0	18	18
Trichobius sp. 4	0	0	16	16
Trichobius flagellatus	7	0	7	14
Trichobius sp. 2	0	0	14	14
Strebla galindoi	10	0	0	10
Trichobius propinquus	0	0	6	6
Strebla hertigi	4	1	0	5
Strebla mirabilis	5	0	0	5
Strebla wiedemanni	0	0	5	5
Trichobius angulatus	1	4	0	5
Strebla sp.	0	0	4	4
Streblid *	0	0	3	3
Strebla altmani	2	0	0	2
Strebla cf. *carvalhoi*	2	0	0	2
Trichobius cf. *persimilis*	2	0	0	2
Trichobius sp. 1	2	0	0	2
Mastoptera minuta	1	0	0	1
Nycterophilia parnelli	0	0	1	1
Pseudostrebla greenwelli	1	0	0	1
Total:	2,397	364	927	3,688
Richness: 39	25	15	24	-

WA, wet area; TA, transitional area; SA, semiarid area; * undescribed genus.

Table 4. Spearman (r_s) correlation test between rainfall and parasitic load from July 2014 to June 2015 in three environments in the state of Pernambuco, Northeastern, Brazil.

Variables	Rainfall (mm) *	Prevalence		Mean intensity		Mean abundance	
		r_s	p	r_s	p	r_s	p
Rain_WA	1,498	0.1409	0.2341	-0.0542	0.6486	0.0713	0.5516
Rain_TA	934	0.2579	0.1472	0.0543	0.7638	0.2048	0.2527
Rain_SA	608	0.2061	0.1426	0.2061	0.1426	-0.2014	0.1745

WA, wet area; TA, transitional area; SA, semiarid area; * Available from http://proclima.cptec.inpe.br/balanco_hidrico/balancohidrico.shtml.

Figure legend

Fig. 1. Study sites for bats (Mammalia: Chiroptera) and their ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in the state of Pernambuco (PE), Northeastern Brazil. States – AL: Alagoas, CE: Ceará, PB: Paraíba, PI: Piauí, RN: Rio Grande do Norte, SE: Sergipe.

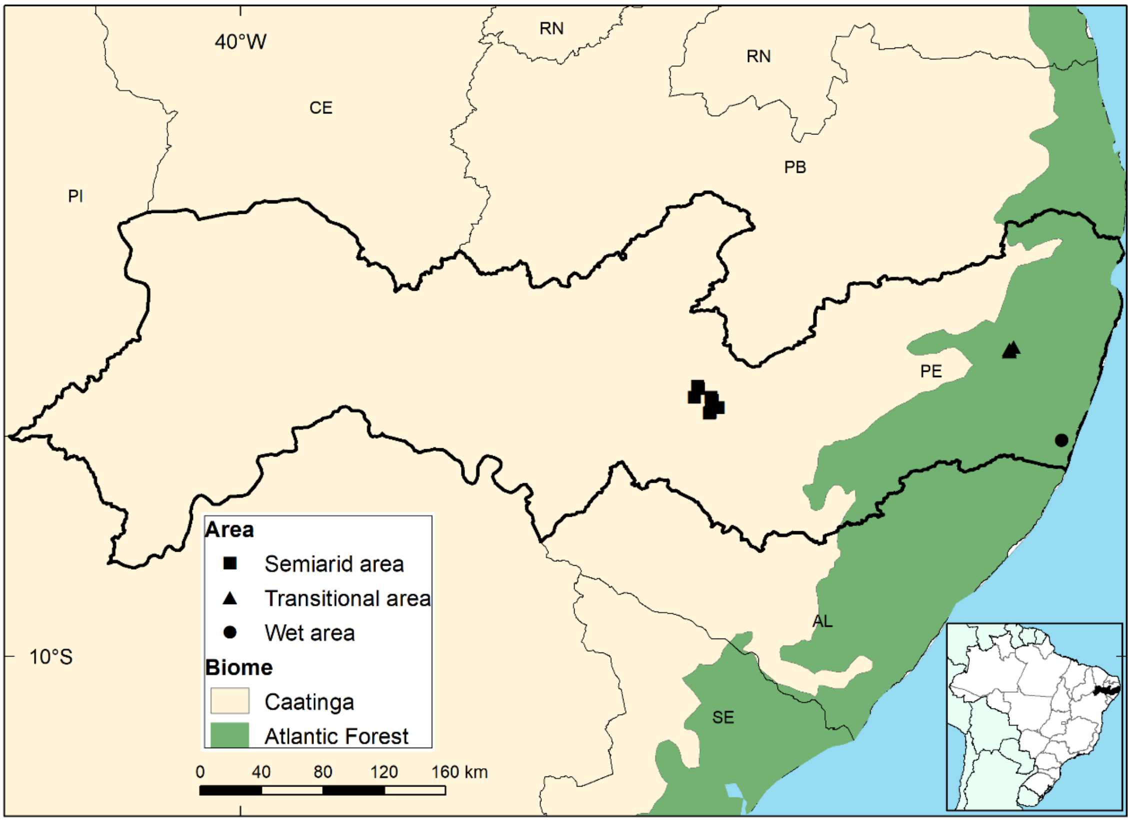
40°W
10°S
PI
CE
RN
RN
PB
PE
AL
SE
Area
■ Semiarid area
▲ Transitional area
● Wet area
Biome
Caatinga
Atlantic Forest
0
40
80
120
160 km

Fig. 1

Table S1. Parasitological indices of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in a wet area (*WA*), state of Pernambuco, Northeastern Brazil.

Host	EH	IH (%)	Parasite	N	P%	MI	MA
Artibeus cf. *fimbriatus*	1	0	-	-	-	-	-
Artibeus obscurus	5	1 (20)	*Trichobius* sp. 1	1	20 (0.5-71.6)	1 (NA)	0.2 (0-0.4)
Artibeus lituratus	31	11 (35.5)	*Aspidoptera phyllostomatis* *	1	3.2 (0.1-16.7)	1 (NA)	0.0323 (0-0.0968)
			Megistopoda aranea *	3	3.2 (0.1-16.7)	3 (NA)	0.0968 (0-0.29)
			Paratrichobius longicrus	15	29 (14.2-48.0)	1.67 (1.22-2)	0.484 (0.226-0.806)
			Trichobius sp. 1	1	3.2 (0.1-16.7)	1 (NA)	0.0323 (0-0.0968)

Artibeus planirostris	70	24 (34.3)	*Aspidoptera phyllostomatis*	21	18.6 (10.3-29.7)	1.62 (1.15-2.31)	0.3 (0.143-0.529)
			Megistopoda aranea	35	28.6 (18.4-40.6)	1.75 (1.35-2.45)	0.5 (0.3-0.771)
			Paratrichobius longicrus *	1	1.4 (0-0.77)	1.0 (NA)	0.0143 (0-0.0429)
Carollia perspicillata	440	383 (87)	*Speiseria ambigua*	204	30.5 (26.2-35.0)	1.52 (1.38-1.71)	0.464 (0.384-0.553)
			Strebla guajiro	88	14.8 (11.6-18.4)	1.35 (1.2-1.55)	0.2 (0.155-0.257)
			Trichobius anducei	76	13.6 (10.6-17.2)	1.27 (1.15-1.4)	0.173 (0.132-0.218)
			Trichobius costalimai *	6	0.2 (0-1.3)	6 (NA)	0.0136 (0-0.0409)
			Trichobius joblingi	1,092	79.3 (75.2-83.0)	3.12 (2.9-3.37)	2.48 (2.27-2.70)
Chiroderma doriae	2	0	-	-	-	-	-
Chiroderma villosum	1	0	-	-	-	-	-
Dermanura cinerea	73	0	-	-	-	-	-
Desmodus rotundus	3	0	-	-	-	-	-

Glossophaga soricina	27	12 (44.44)	*Speiseria ambigua* *	1	3.7 (0.1-19.0)	1.0 (NA)	0.037 (0-0.111)
			Strebla cf. *carvalhoi*	2	3.7 (0.1-19.0)	2.0 (NA)	0.0741 (0-0.222)
			Trichobius dugesii	16	44.4 (25.5-64.7)	1.33 (1-1.75)	0.593 (0.333-0.889)
			Trichobius uniformis	4	11.1 (2.4-29.2)	1.33 (1-1.67)	0.148 (0-0.37)
Lonchorhina aurita	1	1 (100)	*Strebla altmani*	2	100 (2.5-100)	2 (NA)	(NA)
			Trichobioides perspicillatus *	1	100 (2.5-100)	1 (NA)	(NA)
			Trichobius flagellatus	7	100 (2.5-100)	7 (NA)	(NA)

Lophostoma brasiliense	2	1 (50)	*Mastoptera minuta*	1	50 (1.3-98.7)	1 (NA)	0.5 (0-0.5)
			Pseudostrebla greenwelli	1	50 (1.3-98.7)	1 (NA)	0.5 (0-0.5)
Molossus molossus	44	0	-	-	-	-	-
Molossus rufus	1	0	-	-	-	-	-
Myotis lavali	168	108 (64.3)	*Basilia travassosi*	400	65.5 (57.8-72.6)	3.64 (3.16-4.3)	2.38 (1.99-2.9)
Phyllostomus discolor	28	26 (92.85)	*Strebla hertigi*	4	14.3 (4.0-32.7)	1.0 (NA)	0.143 (0-0.25)
			Trichobioides perspicillatus	79	75.0 (55.1-89.3)	3.76 (2.43-6)	2.82 (1.68-4.64)
			Trichobius costalimai	84	82.1 (63.1-93.9)	3.65 (2.71-4.78)	3 (2.04-4.14)

Phyllostomus elongatus	1	1 (100)	*Trichobius* cf. *persimilis*	2	100 (2.5-100)	2 (NA)	(NA)
Platyrrhinus sp.	4	0	-	-	-	-	-
Platyrrhinus lineatus	2	1 (50)	*Paratrichobius longicrus*	1	50 (1.3-98.7)	1 (NA)	(NA)
			Trichobius angulatus	2	50 (1.3-98.7)	2 (NA)	1 (0-1)
Rhinophylla pumilio	1	0	-	-	-	-	-
Sturnira lilium	3	1 (33.33)	*Megistopoda proxima*	1	33.3 (0.8-90.6)	1 (NA)	0.333 (0-0.667)
			Speiseria ambigua *	3	33.3 (0.8-90.6)	3 (NA)	1 (0-2)
Tonatia saurophila	2	2 (100)	*Strebla galindoi*	10	100 (15.8-100)	5.0 (3-5)	5 (3-5)

Trachops cirrhosus	11	11 (100)	*Strebla mirabilis*	5	27.3 (6.0-61.0)	1.67 (1-2)	0.455 (0-0.909)
			Trichobius dugesioides dugesioides	227	100 (71.5-100)	20.64 (12.1-33.5)	20.6 (11.4-34.2)
Total: 921; 23 species			**2,397; 24 species**				

EH, examined host; IH, infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; * Non-primary infestation.

Table S2. Parasitological indices of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in a transitional area (*TA*), state of Pernambuco, Northeastern Brazil.

Host	**EH**	**IH (%)**	**Parasite**	**N**	**P%**	**MI**	**MA**
Artibeus lituratus	22	12 (60)	*Megistopoda aranea* *	1	4.5 (0.1-22.8)	1.0 (NA)	0.0455 (0-0.136)
			Paratrichobius longicrus	22	50 (28.2-71.8)	2.0 (1.35-2.91)	1 (0.5-1.68)
Artibeus planirostris	81	37 (45.7)	*Aspidoptera phyllostomatis*	16	11.1 (5.2-20)	1.78 (1.22-2.44)	0.198 (0.0864-0.395)
			Megistopoda aranea	66	42 (31.1-53.5)	1.94 (1.59-2.35)	0.815 (0.58-1.11)
			Paratrichobius longicrus *	3	1.2 (0-6.7)	3.0 (NA)	0.037 (0-0.111)

Carollia perspicillata	44	35 (79.5)	*Speiseria ambigua*	15	22.7 (11.5-37.8)	1.5 (1.1-1.9)	0.341 (0.159-0.591)
			Strebla guajiro	12	25 (13.2-40.3)	1.09 (1-1.27)	0.273 (0.136-0.413)
			Trichobius joblingi	93	75 (59.7-86.8)	2.82 (2.21-4.09)	2.11 (1.55-3.07)
			Trichobius uniformis *	1	2.3 (0.1-12)	1.0 (NA)	0.0227 (0-0.0682)
Dermanura cinerea	14	0	-	-	-	-	-
Eptesicus brasiliensis	2	1 (50)	*Basilia travassosi*	1	50 (1.3-98.7)	1.0 (NA)	0.5 (0-0.5)
Glossophaga soricina	5	1 (20)	*Trichobius dugesii*	1	20 (0.5-71.6)	1.0 (NA)	0.2 (0-0.4)
			Trichobius uniformis	3	20 (0.5-71.6)	3.0 (NA)	0.6 (0-1.2)

Molossus molossus	2	0	-	-	-	-	-
Myotis lavali	6	6 (100)	*Basilia travassosi*	38	100 (54.1-100)	6.33 (3.67-8.83)	6.33 (3.5-9.17)
Noctilio leporinus	1	0	-	-	-	-	-
Phyllostomus discolor	3	3 (100)	*Strebla hertigi*	1	33.3 (0.8-90.6)	1 (NA)	0.333 (0-0.667)
			Trichobioides perspicillatus	2	33.3 (0.8-90.6)	2 (NA)	0.667 (0-1.33)
			Trichobius costalimai	24	100 (29.2-100)	8.0 (6-9.67)	8 (6-9.67)
Platyrrhinus lineatus	10	5 (50)	*Paratrichobius longicrus*	6	40 (12.2-73.8)	1.5 (1-2)	0.6 (0.1-1.3)
			Trichobius angulatus	4	20 (2.5-55.6)	2.0 (1-2)	0.4 (0-1.2)

Sturnira lilium	25	16 (64)	*Aspidoptera falcata*	23	36 (18-57.5)	2.56 (1.56-3.89)	0.92 (0.4-1.68)
			Megistopoda aranea *	6	8 (1-26)	3.0 (1-3)	0.24 (0-1.04)
			Megistopoda proxima	26	44 (24.4-65.1)	2.36 (1.64-3.09)	1.04 (0.56-1.68)
Total: 215; 12 species			**364; 15 species**				

EH, examined host; IH, infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; * Non-primary infestation.

Table S3. Parasitological indices of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in a semiarid area (*SA*), state of Pernambuco, Northeastern Brazil.

Host	**EH**	**IH (%)**	**Parasite**	**N**	**P%**	**MI**	**MA**
Anoura geoffroyi	8	6 (75)	*Exastinion clovisi*	18	75.0 (34.9-96.8)	3.00 (1.83-4.5)	2.25 (1-3.75)
			Trichobius propinquus	4	25.0 (32-65.1)	2.00 (1-2)	0.5 (0-1.5)
Artibeus lituratus	6	3 (50)	*Paratrichobius longicrus*	15	50.0 (11.8-88.2)	5.00 (1-9)	2.5 (0.167-7)
Artibeus planirostris	145	79 (54.5)	*Aspidoptera phyllostomatis*	84	32.4 (24.9-40.7)	1.79 (1.47-2.13)	0.579 (0.414-0.766)
			Megistopoda aranea	88	35.2 (27.4-43.5)	1.73 (1.43-2.1)	0.607 (0.448-0.807)
Carollia perspicillata	40	17 (42.5)	*Speiseria ambigua*	4	7.5 (1.5-20.4)	1.33 (1-1.67)	0.1 (0-0.263)

			Trichobius joblingi	27	37.5 (22.7-54.2)	1.80 (1.33-2.47)	0.675 (0.375-1.08)
Desmodus rotundus	5	4 (80)	*Strebla wiedemanni*	5	60.0 (14.7-97.4)	1.67 (1-2)	1 (0-1.6)
			Trichobius parasiticus	27	80.0 28.4-99.5)	6.75 (5.25-8)	5.4 (2-7.2)
Diphylla ecaudata	7	7 (100)	*Trichobius diphyllae*	169	100.0 (59-100)	24.14 (16.3-30.7)	24.1 (16.5-30.4)
Glossophaga soricina	62	36 (58)	*Speiseria ambigua* *	2	3.2 (0.4-11.2)	1.00 (NA)	0.0323 (0-0.0806)
			Strebla guajiro *	2	3.2 (0.4-11.2)	1.00 (NA)	0.0323 (0-0.0806)
			Trichobius dugesii	30	29.0 (18.2-41.9)	1.67 (1.22-2.29)	0.484 (0.29-0.806)
			Trichobius uniformis	57	46.8 (34.0-59.9)	1.97 (1.59-2.38)	0.919 (0.613-1.24)

Histiotus diaphanopterus	8	1 (12.5)	*Basilia* sp.	2	12.5 0.3-52.7)	2.00 (NA)	0.25 (0-0.75)
Lasiurus blossevillii	1	0	-	-	-	-	-
Lonchophylla mordax	72	51 (70.8)	*Speiseria ambigua* *	1	1.4 (0-7.5)	1.00 (NA)	0.0139 (0-0.0417)
			Strebla sp.	4	5.6 (1.5-13.6)	1.00 (NA)	0.0556 (0.0139-0.111)
			Trichobius lonchophyllae	143	66.7 (54.6-77.3)	2.98 (2.38-3.83)	1.99 (1.49-2.65)
Lonchorhina aurita	3	3 (100)	*Trichobius flagellatus*	9	100.0 (29.2-100)	3.00 (2-4)	3 (2-4)
Micronycteris sanborni	21	18 (85.7)	Streblid **	3	9.5 (1.2-30.4)	1.50 (1-1.50)	0.143 (0-0.429)
			Trichobius sp. 2	64	85.7 (63.7-97.0)	3.56 (2.39-5.28)	3.05 (2-4.67)

Micronycteris sp.	6	0	-	-	-	-	-
Molossus molossus	1	0	-	-	-	-	-
Myotis lavali	5	3 (60)	*Basilia travassosi*	15	60.0 (14.7-94.7)	5.00 (4-5.67)	3 (0-4.8)
Peropteryx sp.	1	0	-	-	-	-	-
Platyrrhinus lineatus	11	9 (81.8)	*Paratrichobius longicrus*	4	36.4 (10.9-69.2)	1.00 (NA)	0.364 (0.0909-0.545)
			Trichobius angulatus	29	81.8 (48.2-97.7)	3.22 (2-4.11)	2.64 (1.55-3.73)
Pteronotus gymnonotus	2	2 (100)	*Nycterophilia parnelli*	1	50.0 (1.3-98.7)	1.00 (NA)	0.5 (0-0.5)
			Trichobius sp. 4	16	100.0 (15.8-100)	8.00 (NA)	8 (1-8)

Rhogeessa sp.	3	0	-	-	-	-	-
Sturnira lilium	2	2 (100)	*Megistopoda proxima*	3	100.0 (15.8-100)	1.50 (1-1.50)	1.5 (1-1.5)
Xeronycteris vieirai	27	24 (88.9)	*Trichobius* sp. 3	107	88.9 (70.8-97.6)	4.46 (3.38-7.15)	3.96 (2.89-6.25)
Total: 436; 21 species			**936; 24 species**				

EH, examined host; IH, infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; * Non-primary infestation; ** Undescribed genus.

5 PARASITIC LOAD AND NETWORK OF BAT ECTOPARASITIC FLIES IN CAVE AND NON-CAVE ENVIRONMENTS IN NORTHEASTERN BRAZIL

Parasitic load and network of bat ectoparasitic flies in cave and non-cave environments in Northeastern Brazil

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Running title: Parasitic load and network of bat ectoparasitic flies

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SUMMARY

Biotic and/or abiotic variables are considered as possible influencers in the ecological relationship between hosts and ectoparasites. Although there has been an increase in the studies correlating parasitological indices on bats and such variables, this topic is poorly explored in Brazil. Here, we analyzed and compared parasitological indices of bat ectoparasitic flies on bats in cave and non-cave environments in Northeastern Brazil. We also tested possible correlations between the number of bats sheltered in the cave and their parasitological indices. Interaction networks were built for each environment. Bats in the cave were more infested than outside based both on the mean intensity and mean abundance; however, there was no difference in the parasite prevalence. There was no correlation between the abundance of bats in the cave and their parasitological indices. Flies were highly specific to a host species and the interaction networks were very modular. Our study demonstrated that the environment did not affect infestation prevalence but bats living in cave have a higher parasitic load when compared to non-cave environment. Additionally, this study reinforces the high species-specificity in the bat-fly association and shows that this interaction is not dependent on the environment in which both coexist.

Key words: Chiroptera, day roost, Diptera, ectoparasite, host-parasite interactions, nycteribiid, parasitological indices, streblid.

KEY FINDINGS

Bats in the cave environment were more infested than outside;

There was no correlation between the abundance of bats in the cave and the prevalence or load of flies;

Ectoparasitic flies were highly specific to a host species in both cave and non-cave environments;

In both environments, the interaction networks were modular formed by several subgroups.

INTRODUCTION

Bat ectoparasitic flies of the families Nycteribiidae and Streblidae are highly adapted dipterans that feed exclusively on the blood of their hosts (Marshall, 1982). Like their bat hosts, such flies are distributed worldwide – except in the polar regions – and have high host specificity (Marshall, 1982; Dick and Patterson, 2006). Despite the wide distribution, bat ectoparasitic flies present species endemism in different regions and are more species-rich in the Tropics (Dittmar *et al*. 2015). In the Neotropics, Streblidae has more species richness and abundance and is mainly associated with bats of the families Phyllostomidae, Mormoopidae, Natalidae, and Noctilionidae (e.g., Guerrero, 1997; Graciolli and Carvalho, 2001*a*; Lourenço *et al*. 2016; Barbier and Bernard, 2017). In contrast, Nycteribiidae is less recorded and known for only two genera associated with Vespertilionidae and Thyropteridae families (Guimarães and D'Andretta, 1956; Graciolli *et al*. 2007). However, much of the knowledge gap on this fly family is a result of a sample bias – vespertilionids and thyropterids are frequently underrepresented in studies using mist nets as the main capture method (e.g., Sampaio *et al*. 2003; Bernard *et al*. 2011).

A given species of bat may interact with several ectoparasitic flies; however, for most of cases the interactions are species-specific (monoxenic) (e.g., Graciolli and Carvalho, 2001*a*; ter Hofstede *et al*. 2004). In the last decades, special attention has been given to the study on the interactions between bats and their ectoparasitic flies (e.g., Guerrero, 1994, 1995, 1996; Graciolli and Carvalho 2001*a*, *b*). However, most of them were focused strictly on the description of which species were found on their hosts. In recent years, there has been an increase of studies focused on the description of parasitological indices, parasite load, and on the host specificity (e.g., Santos *et al*. 2009, 2013; Eriksson *et al*. 2011; Bezerra *et al*. 2016; Barbier and Graciolli 2016; Vasconcelos *et al*. 2016). Other approaches, especially involving factors such as precipitation, temperature, and host traits are important for a better understanding on which variables may or may not influence the parasite load in the host-parasite system (e.g., ter Hofstede and Fenton, 2005; Patterson *et al*. 2008; Pilosof *et al*. 2012; Bolívar-Cimé *et al*. 2018). For bats, daytime shelter is also an important factor shaping the relations between then and their ectoparasites and some studies have indicated that these host-parasite interactions may change depending on the type of roost, host richness, and host concentration (ter Hofstede and Fenton, 2005; Dittmar *et al*. 2009; Fagundes *et al*. 2017). The variety of roosts and the roosting behavior adopted by bats – from single individuals roosting in the foliage to millions of bats living in caves (Kunz, 1982) – affect the way ectoparasitic flies interact with their hosts (e.g., ter Hofstede and Fenton, 2005). But most of the details of such interactions remain poorly understood or unknown.

Brazil is a continental-sized, biodiversity-rich country harboring more than 180 species of bats (Nogueira *et al*. 2014; Feijó *et al*. 2015; Fischer *et al*. 2015; Moratelli and Dias, 2015; Gregorin *et al*. 2016; Rocha *et al*. 2016), the second highest bat species richness in the world (Fenton and Simmons, 2014; Nogueira *et al*. 2014). However, research on bat parasites using parasitological indices and some of the mentioned environmental variables still remain scarce in the country (e.g., Moura *et al*. 2003; Esbérard *et al*. 2012; Fagundes *et al*. 2017). In the present study, we analyzed and compared the difference of parasitic load (prevalence, mean intensity, and mean abundance) of ectoparasitic flies on bats in cave and non-cave environments in a seasonally dry tropical forest region in Northeastern Brazil. Additionally, in the cave, we analyzed whether the parasitological load correlates with the number of bats sheltered in that environment. We hypothesized that there will be differences between the parasitological indices for each site and that the parasitic load in the cave will be positively correlated with the abundance of bats. We also verified host-parasite relationships by building interaction networks separately for each environment.

MATERIALS AND METHODS

Study area

The Catimbau National Park (CNP), in Pernambuco state, Northeastern Brazil (8°32' S, 37°11' W; 08°30' S, 37°20' W; Fig. 1), is part of the Caatinga ecological region, a seasonally dry tropical forest (MMA, 2002; Silva *et al*. 2004). The Caatinga presents a vegetation mosaic ranging from non-thorny arboreal to xeric environments, where spiny shrubs predominate (Rodal *et al*. 1998; Andrade *et al*. 2004). Rainfall in the region is concentrated between April and June, with an annual average of 300-500 mm (SUDENE, 1990; Rodal *et al*. 1998); however, annual rainfall in the Caatinga varies widely in time and space (Silva *et al*. 2017). For more details on CNP, see Barbier and Bernard (2017) and Cordero-Schmidt *et al.* (2017).

The park has a high cave potential, where valleys and mountain ranges mark the relief with altitude ranging from 400 m to 1,000 m (SNE, 2002; Azevedo and Bernard, 2015). Located at CNP, the “Meu Rei” cave (08°29'14.1" S, 37°16'48.8" W) is a natural cavity of sandstone formation with about 160 m of horizontal projection, 4,100 m^3 volume, and is classified with the status of "Maximum Relevance" which grants it full protection (Azevedo and Bernard, 2015). The cave houses bats of at least three families (Natalidae, Mormoopidae, and Phyllostomidae), including *Natalus macrourus* (Gervais, 1856) and *Lonchorhina aurita* Tomes, 1863, nationally threatened species — Vulnerable category (MMA, 2014; Delgado-Jaramillo *et al*. 2017).

Samplings

Between July 2014 and June 2015, bats were captured at CNP using 10 mist nets (12 m × 2.5 m), monthly, during two nights each month [= 12 h/month; total effort of 43,200 h.m^2, *sensu* Straube and Bianconi (2002)]. Each captured bat was individually placed in a clean cotton bag for subsequent screening. The bats were sexed, weighed and had the reproductive stage, age, and forearm size length checked. Ectoparasites were collected with soft forceps and preserved in labeled vials containing 70% ethanol. Hosts and parasites were handled carefully to prevent possible contamination among the samples, following Barbier and Bernard (2017).

From July 2014 to December 2016, bats were captured monthly in the "Meu Rei" cave with a hand-net, always between 16:00 h and 16:30 h, totaling 1,050 min of searching, following the methodology previously described.

Counting cave bats

To determine the number of bats roosted in the cave during the captures period, the bat's emergence time was filmed using a FLIR® E60 thermal imaging camera, with a thermal sensitivity lower than 0.05 °C and temperature range of -20 °C to 650 °C. The exit of bats (emergence flights) from the cave was monitored for two consecutive days, monthly, from October 2014 to December 2016. For recordings, the camera was positioned perpendicular to the entrance of the cave, initiating the recording between 17:30 h and 17:45 h until there was no more outflow of bats. In the laboratory, the images were analyzed and the bats counted automatically (Supplementary Material S1) using an algorithm specially designed to track and count bats in video (Rodrigues *et al*. 2016).

Species identification

Bats were identified according to Gregorin and Taddei (2002), Gregorin and Ditchfield (2005), Gardner (2008), Díaz *et al*. (2011), Moratelli *et al*. (2011), Feijó *et al*. (2015), and Moratelli and Dias (2015), and nomenclature followed Nogueira *et al*. (2014). For fly species identification, we followed Guimarães and D'Andretta (1956), Wenzel *et al*. (1966), and

Wenzel (1976); and Dick and Graciolli (2008) and Graciolli and Dick (2008) for nomenclature. Voucher specimens for both bats and flies were deposited, respectively, in the Mammal Collection (UFPE) and Entomological Collection (CE-UFPE) of Universidade Federal de Pernambuco. Bats were handled according to Sikes *et al*. (2011) and fieldwork was authorized by MMA/ICMBio/SISBIO (permits #43816-1 and #43816-2) and by Ethics Committee on Animal Care – UFPE (permit #23076.027916/2015-13).

Data analysis

We calculated parasitological indices (prevalence, mean intensity, and mean abundance), according to Bush *et al*. (1997), for the ectoparasites collected on the most representative bats (≥ 30) in each of the environments. This first step allowed the comparison between the hosts captured in and outside the cave. We used Chi-square test (χ^2) to compare prevalence and Mann-Whitney test (U) to compare both mean intensity and mean abundance between the two environments.

We tested for possible correlations between the parasitological indices calculated for cave bats and the number of bats (the average for the two sampled days) roosting in the cave. To verify if the fly parasitic load on bats in a cave environment was correlated with the number of roosted bats, we used the Spearman test (r_s). The normality of the data distribution was tested *a priori* with the Shapiro-Wilk test. Parasitological indices were calculated using Quantitative Parasitology – QPweb 1.0.13 (Reiczigel *et al*. 2013). All other analyses were conducted in the PAST 3.16 program (Hammer *et al*. 2001), with the significant level at $p < 0.05$.

Using all host and parasite data, we built interaction networks separately for each environment. We used 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. In addition, we extracted the following metrics: (i) connectance (i.e., proportion of interactions performed in relation to the total of possible interactions), ranging from zero (no interactions) to 1 (all species connected); (ii) average degree (i.e., average of the degree values of all vertices); and (iii) degrees of centralization (i.e., relative importance of each vertex to the network structure as a whole) (Jordano, 1987; Nooy *et al*. 2011; Mello *et al*. 2016). Non-primary associations were not considered (*sensu* Dick, 2007). For this step, we use the Pajek 5.01 program (Nooy *et al*. 2011; http://mrvar.fdv.uni-lj.si/pajek/).

RESULTS

Non-cave environment

We captured 436 bats from 21 species of the families Emballonuridae, Phyllostomidae, Mormoopidae, Molossidae, and Vespertilionidae (Table 1). *Artibeus planirostris* (Spix, 1823) (n = 145), *Lonchophylla mordax* Thomas, 1903 (n = 72), *Glossophaga soricina* (Pallas, 1766) (n = 62), and *Carollia perspicillata* (Linnaeus, 1758) (n = 40) were the most captured hosts. Seventeen species were discarded because of their low representativeness (Table 1). Among the most representative bats (n ≥ 30), *L. mordax* was parasitized with higher prevalence (71%; 51/72).

We collected 927 ectoparasitic flies of 26 species of the families Streblidae (24 species) and Nycteribiidae (2 species). Of the nine genera of flies we recorded, *Trichobius* Gervais, 1844 was the richest (13 species), followed by *Strebla* Wiedemann, 1824 (3 species) (Table 1). The most abundant fly species were *Trichobius diphyllae* Wenzel, 1966 (n = 169), *T. lonchophyllae* Wenzel, 1966 (n = 143), and *Megistopoda aranea* (Coquillett, 1899) (n = 88). We collected two undescribed species of *Trichobius* and one of *Strebla*. Additionally, we collected an undescribed genus of Streblidae parasitizing *Micronycteris sanborni* Simmons, 1996 (Table 1). *Speiseria ambigua* Kessel, 1925 and *Strebla guajiro* (García & Casal, 1965) occurred on non-primary hosts and were considered a non-primary association (Table 1).

Cave environment

In the cave environment, we captured 354 bats of nine species, from the families Phyllostomidae, Mormoopidae, and Natalidae (Table 2). *Pteronotus gymnonotus* (Wagner, 1843) (n = 170), *Carollia perspicillata* (n = 66), and *Diphylla ecaudata* Spix, 1823 (n = 60) were the most captured species. Six species were discarded because of their low representativeness (Table 2). Among the most abundant species (n ≥ 30), *D. ecaudata* had the highest parasite prevalence (96.7%; 58/60).

We collected 2,724 ectoparasitic flies of 18 species and six genera, belonging to Streblidae. *Trichobius diphyllae* (n = 1,511), *Trichobius* sp. 4 (n = 724; undescribed species), and *Nycterophilia parnelli* Wenzel, 1966 (n = 238) were the most abundant fly species (Table 2). *Trichobius joblingi* Wenzel, 1966 and *N. parnelli* occurred on non-primary hosts but also were considered as contamination or transitional association (Table 2).

Parasitic load between environments

When comparing the parasitological indices between the environments, there was no difference between the prevalence ($\chi^2 = 18.667$; df = 21; $p = 0.6065$). On the other hand, there was a notable difference between the mean intensities ($U = -3.1783$; $p = 0.0014$) and mean abundances ($U = -3.3208$; $p = 0.0008$), being higher in the cave environment.

Parasitic load versus *cave bat abundance*

The average number of bats sheltering in the cave ranged from 85.5 in November 2016 to 107,809 individuals in August 2015 (Supplementary Material S2). There was no statistically significant correlation between the number of bats roosted in the cave and the prevalence ($r_s = -0.0843$; $p = 0.3856$), mean intensity ($r_s = -0.0760$; $p = 0.4349$) or mean abundance of parasites ($r_s = -0.1073$; $p = 0.3223$).

Host-parasite network

In both environments, cave and non-cave, the flies presented a high host specificity, being 100% (18/18) and 92% (23/25) species-specific, respectively (Fig. 2). In both environments, interactions networks were quite modular, as expected for networks involving highly specific parasites (Fig. 2). Details on the metrics extracted from the networks are shown in Table 3.

DISCUSSION

Our results indicate that bats in a cave environment have a higher parasite load (intensity and mean abundance of infestation) than those in a non-cave environment but, conversely, the frequency (prevalence) in which bats are parasitized do not differ between the two environments. We also demonstrate that neither the number of infested bats nor the intensity of the parasite load they present are directly influenced by the abundance of bats in a cave roost. Moreover, the relationship between flies and bats is highly specific, with strong modular interaction networks.

Caves are known to confer important advantages not only for vertebrates roosting inside them (including bats) but also for invertebrate fauna (including bat ectoparasites) (Kunz, 1982; Dittmar *et al*. 2009). Such importance lies on the stable environment caves provide (e.g., temperature, humidity) when compared to the outside (Kunz, 1982; Dittmar *et al*. 2011; Furey and Racey, 2016). Thus, the higher parasite load we observed on the bats roosting in the studied cave may be explained because caves are favorable environments for the maturation of flies' pupae (Dittmar *et al*. 2009). Moreover, in a situation where hosts converge to single roost and present site fidelity – like bats in a cave – newly emerged flies may have higher success in locating new hosts (e.g., Lewis, 1995; Dittmar *et al*. 2009, 2011).

Another important factor with regard to the parasite load on bats (especially when comparing bats in a cave and non-cave environments) is the fact that there is a synchronization between the bat foraging period and the fly larviposition rhythm. Female flies ready to larviposit tend to leave the host at the beginning of the foraging activity of bats; and the immature ones emerge during the period of return of the bats to the cave (Dittmar *et al*. 2011). These authors also found a difference in the parasitic load on bats captured inside and outside the cave environment; being the former more parasitized. So, at least for the studied species and conditions, the roost environment influenced more on the number of ectoparasitic flies on each bat (intensity and abundance) than on the frequency those bats were parasitized (prevalence).

Fagundes *et al*. (2017) observed that roost fidelity by cave bats does not explain the number of ectoparasitic interactions in which bats are involved, but positively affects the number of ectoparasites per bat. In our study, bats showed fidelity to the cave during the entire monitoring period, which may have contributed to their higher parasite load. Contrary to our results, Fagundes *et al*. (2017) verified that the abundance of bats also correlates positively with the number of parasites in each infested bat. Although there was no correlation between fly load (mean intensity and mean abundance) and bat colony size in our study, cave bats, in general, have higher rates of parasites when compared with non-cave environment (e.g., ter Hofstede and Fenton, 2005). Interestingly, in our study, the most parasitized species were *Pteronotus gymnonotus* and *Diphylla ecaudata*, species known for gregarious behavior, forming large – for the former – or very socially cohesive colonies – for the latter (Kwon and Gardner, 2008; Patton and Gardner, 2008). Frequent contact between individuals favors the exchange of parasites and may function as a dilution effect among hosts. In fact, some studies have indicated that cavity-roosting bats are more likely to share ectoparasites than foliage-roosting ones, for example (e.g., ter Hofstede *et al*. 2004; ter Hofstede and Fenton, 2005; Patterson *et al*. 2007).

Interaction networks

The interaction networks in both environments we studied were modular. The specificity observed was so intense that few species formed truly or complex networks. Of the 30 different interactions observed in both environments, only two fly species – *Paratrichobius* *longicrus* and *Trichobius propinquus*, both in the non-cave environment – had linked with more than one host species. Nesting in interaction networks has been observed in both mutualistic and antagonistic networks, but in host-parasite networks involving high host-specific parasites few links are expected since a small number of species interact with many species (e.g., Jordano *et al*. 2003; Krasnov *et al*. 2012). In other words, host-parasite interaction networks tend to be more specialized and compartmentalized when compared to others such as seed-dispersal (Poulin, 2010; Krasnov *et al*. 2012; Mello *et al*. 2015). Besides that, nestedness is related to generalism and opportunism in host-parasite networks (Bellay *et al*. 2013; Fagundes *et al*. 2017). Rivera-García *et al*. (2017), for example, observed a decrease in the bat ectoparasitic fly specialization among seasons in a cave in Mexico. Nonetheless, this change in host-parasite relationships recorded by these authors was also accompanied by changes in host species composition (but see Luna *et al*. 2017).

In a modular host-parasite network, closely related hosts tend to cluster and therefore be infested by the same group of ectoparasites (Krasnov *et al*. 2012). Indeed, in our study, the hosts exploited by *P. longicrus* and *T. propinquus* belonged to the same subfamilies – *Artibeus lituratus* and *Platyrrhinus lineatus* (Stenodermatinae) and *Anoura geoffroyi* and *Glossophaga soricina* (Glossophaginae). It is likely that phylogenetic and ecological affinity between these host species favors an interaction/exchange of their bat ectoparasitic flies. In a host-parasite network, the number of links is determined by the parasite’s host specificity (Poulin, 2010). In this way, the more species of generalist parasites in the interactions, the more links will exist in the network and it will be less modular.

Because most bat ectoparasitic flies are highly host specific (e.g., Wenzel *et al*. 1966; Marshall, 1982; Dick and Patterson, 2006), fewer connections within- and among-modules were expected. On the other hand, to the extent more host species – and consequently more parasite species – are included in a network analysis, it is possible that the number of connections (links) between them is increased. Future studies investigating bat-fly ecological networks at different scales and species richness may expand our knowledge about these relationships. However, it is important to mention that factors related to data robustness (see Luna *et al*. 2017) and methodological rigor (see Barbier and Bernard, 2017) interfere in the results, which can lead us to biased conclusions. Thus, such issues should always be observed and taken into account in studies on parasite-host interactions.

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Table 1. Bats (Chiroptera) and their ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) sampled in the Catimbau National Park, state of Pernambuco, Brazil, from July 2014 to June 2015.

Family/Bat species	N	IH (%)	Fly species	N
Emballonuridae				
Peropteryx sp.	1	0	-	-
Phyllostomidae				
Anoura geoffroyi	8	6 (75.0)	*Exastinion clovisi*	18
			Trichobius propinquus	3
			Trichobius sp. 1	1
Artibeus lituratus	6	3 (50.0)	*Paratrichobius longicrus*	15
Artibeus planirostris	145	79 (54.5)	*Aspidoptera phyllostomatis*	84
			Megistopoda aranea	88
Carollia perspicillata	40	17 (42.5)	*Speiseria ambigua*	4
			Trichobius joblingi	27
Desmodus rotundus	5	4 (80.0)	*Strebla wiedemanni*	5
			Trichobius parasiticus	27
Diphyllae ecaudata	7	7 (100.0)	*Trichobius diphyllae*	169
Glossophaga soricina	62	36 (58.1)	*Speiseria ambigua**	2
			*Strebla guajiro**	2
			Trichobius dugesii	30
			Trichobius propinquus	3
			Trichobius uniformis	57
Lonchophylla mordax	72	51 (71.0)	*Speiseria ambigua**	1
			Strebla sp.**	4

			Trichobius lonchophyllae	143
Lonchorhina aurita	3	3 (100.0)	*Trichobius flagellatus*	9
Micronycteris sanborni	21	18 (85.7)	Streblid***	3
			Trichobius sp. 2	64
Micronycteris sp.	6	0	-	-
Platyrrhinus lineatus	11	9 (81.8)	*Paratrichobius longicrus*	4
			Trichobius angulatus	29
Sturnira lilium	2	2 (100.0)	*Megistopoda proxima*	3
Xeronycteris vieirai	27	24 (88.9)	*Trichobius* sp. 3**	98
Mormoopidae				
Pteronotus gymnonotus	2	2 (100.0)	*Nycterophilia parnelli*	1
			Trichobius sp. 4**	16
Molossidae				
Molossus molossus	1	0	-	-
Vespertilionidae				
Histiotus diaphanopterus	8	1 (12.5)	*Basilia* sp.	2
Lasiurus blossevillii	1	0	-	-
Myotis lavali	5	3 (60.0)	*Basilia travassosi*	15
Rhogeessa sp.	3	0	-	-
Total: 21 species	436	265 (60.8)	26 species	927

IH: infested host; N: number of individuals; * non-primary association; ** undescribed species; *** undescribed genus.

Table 2. Bats (Chiroptera) and their ectoparasitic flies (Diptera: Streblidae) sampled in the "Meu Rei" cave, Catimbau National Park, state of Pernambuco, Brazil, from July 2014 to December 2016.

Family/Bat species	N	IH (%)	Fly species	N
Phyllostomidae				
Anoura geoffroyi	19	17 (89.5)	*Anastrebla modestini*	2
			Exastinion clovisi	46
			*Nycterophilia parnelli**	1
			Trichobius propinquus	13
			Trichobius sp. 1	1
Carollia perspicillata	66	20 (30.3)	*Speiseria ambigua*	1
			Strebla guajiro	4
			Trichobius joblingi	26
Desmodus rotundus	4	3 (75.0)	*Strebla wiedemanni*	9
			Trichobius parasiticus	10
Diphylla ecaudata	60	58 (96.7)	*Trichobius diphyllae*	1,511
Glossophaga soricina	5	4 (80.0)	*Trichobius dugesii*	2
			*Trichobius joblingi**	1
			Trichobius tiptoni	2
			Trichobius uniformis	1
Lonchorhina aurita	20	13 (65.0)	*Strebla altmani*	10
			Trichobius flagellatus	17
Tonatia sp.	1	0	-	-
Mormoopidae				
Pteronotus gymnonotus	170	149 (87.6)	*Nycterophilia parnelli*	238

			Nycterophilia sp.	103
			*Trichobius joblingi**	2
			Trichobius sp. 4**	724
Natalidae				
Natalus macrourus	9	0	-	-
Total: 9 species	354	264 (74.6)	18 species	2,724

IH: infested host; N: number of individuals; * non-primary association; ** undescribed species.

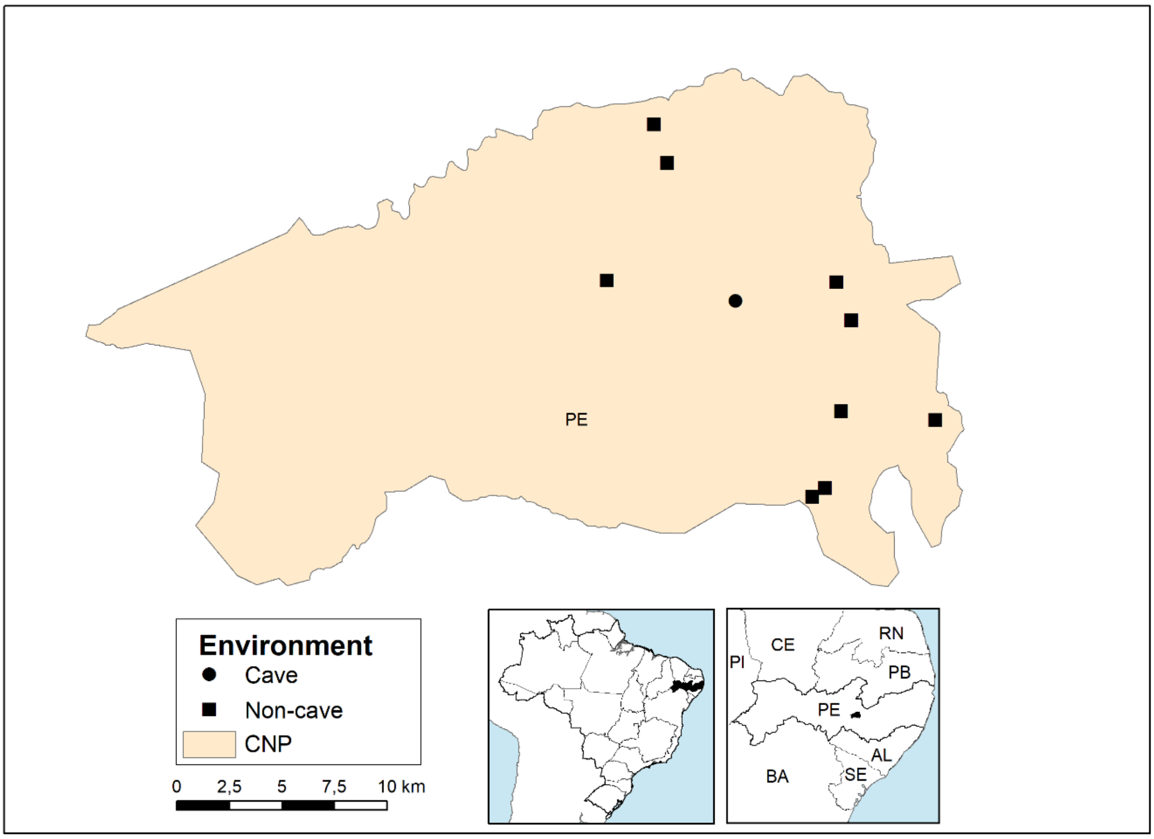
Table 3. Metrics of interaction networks between bats (Mammalia: Chiroptera) and ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in two environments at Catimbau National Park, Northeastern Brazil.

Parameter	Environment	
	Cave	Non-cave
Number of vertices	27	46
Number of arcs	18	27
Connectance	0.02469	0.01222
Average degree	1.33333	1.14893
Input degree centralization	0.13313	0.05387
Output degree centralization	0.01331	0.03166

FIGURE LEGENDS

Fig. 1. Sites sampled for bats (Mammalia: Chiroptera) and their ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in cave (black circle) and non-cave (black squares) environments at Catimbau National Park (CNP), state of Pernambuco (PE), Northeastern Brazil. States – AL: Alagoas, BA: Bahia, CE: Ceará, PB: Paraíba, PI: Piauí, RN: Rio Grande do Norte, SE: Sergipe.

Fig. 2. Interaction networks between bats (Mammalia: Chiroptera; green circles) and ectoparasitic flies (Diptera: Nycteribiidae and Streblidae; red circles) in cave (A) and non-cave (B) environments at Catimbau National Park, Northeastern Brazil. Fly species — Ana.mode: *Anastrebla modestini*, Asp.phyl: *Aspidoptera phyllostomatis*, Bas.sp.: *Basilia* sp., Bas.trav: *B. travassosi*, Exa.clov: *Exastinion clovisi*, Meg.aran: *Megistopoda aranea*, Meg.prox: *M. proxima*, Nyc.parn: *Nycterophilia parnelli*, Nyc.sp.: *Nycterophilia* sp., Par.long: *Paratrichobius longicrus*, Spe.ambi: *Speiseria ambigua*, Str.guaj: *Strebla guajiro*, Str.sp.: *Strebla* sp., Str.wied: *S. wiedemanni*, Streblid: undescribed genus, Tri.angu: *Trichobius angulatus*, Tri.diph: *T. diphyllae*, Tri.duge: *T. dugesii*, Tri.flag: *T. flagellatus*, Tri.jobl: *T. joblingi*, Tri.lonc: *T. lonchophyllae*, Tri.para: *T. parasiticus*, Tri.prop: *T. propinquus*, Tri.sp.1: *Trichobius* sp. 1, Tri.sp.2: *Trichobius* sp. 2, Tri.sp.3: *Trichobius* sp. 3, Tri.sp.4: *Trichobius* sp. 4, Tri.tipt: *T. tiptoni*, Tri.unif: *T. uniformis*. Bat species — Ano.geof: *Anoura geoffroyi*, Art.litu: *Artibeus lituratus*, Art.plan: *A. planirostris*, Car.pers: *Carollia perspicillata*, Des.rotu: *Desmodus rotundus*, Dip.ecau: *Diphylla ecaudata*, Glo.sori: *Glossophaga soricina*, His.diap: *Histiotus diaphanopterus*, Lon.auri: *Lonchorhina aurita*, Lon.mord: *Lonchophylla mordax*, Mic.sanb: *Micronycteris sanborni*, Myo.lava: *Myotis lavali*, Pla.line: *Platyrrhinus lineatus*, Pte.gymn: *Pteronotus gymnonotus*, Stu.lili: *Sturnira lilium*, Xer.viei: *Xeronycteris vieirai*.


PE
Environment
● Cave
■ Non-cave
CNP
0
2,5
5
7,5
10 km
PI
CE
RN
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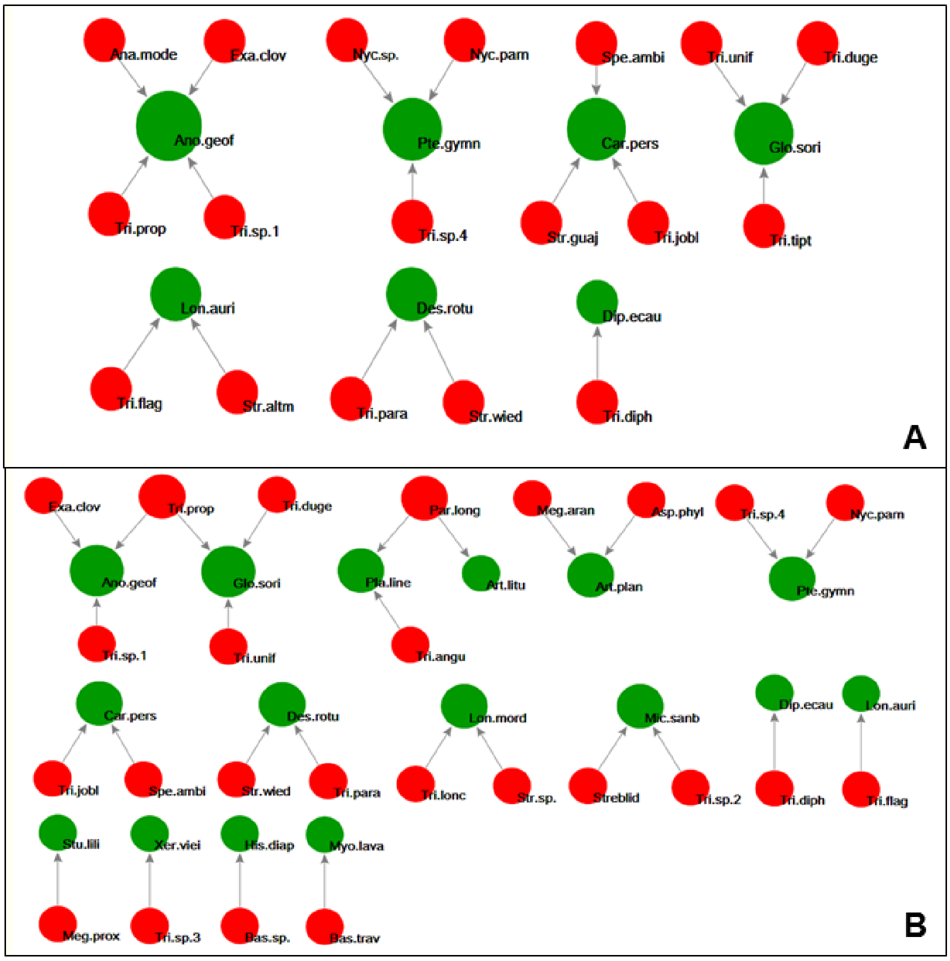
PE
AL
SE
BA

Fig. 1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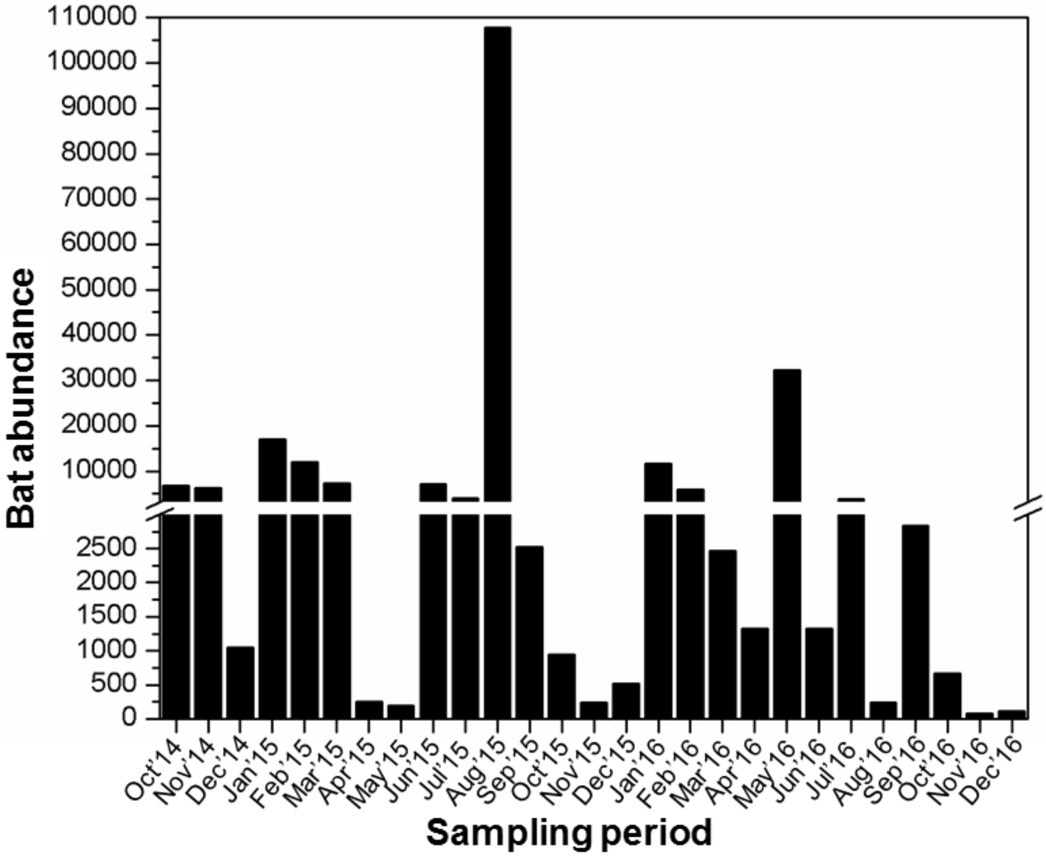
Bas.trav
B

Fig. 2

SUPPLEMENTARY MATERIAL



Supplementary Material S1. Monthly abundance of bats roosted in the "Meu Rei" cave, in the Catimbau National Park, Northeastern Brazil, between October 2014 and December 2016.

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APÊNDICE A – MANUSCRITO 1

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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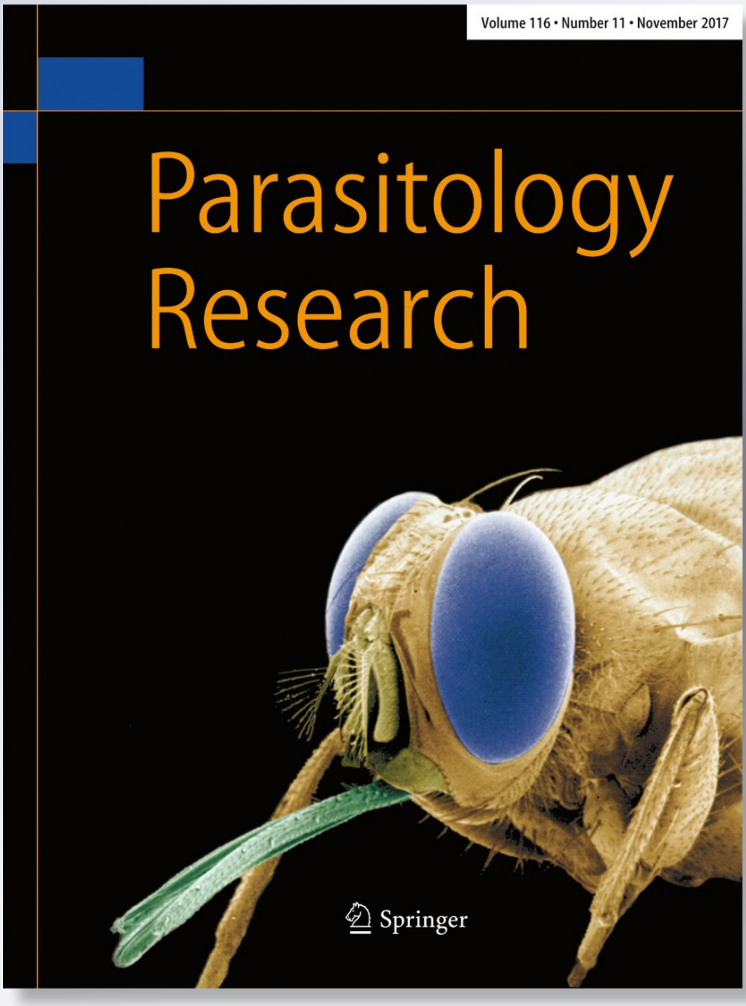

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ORIGINAL PAPER

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

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

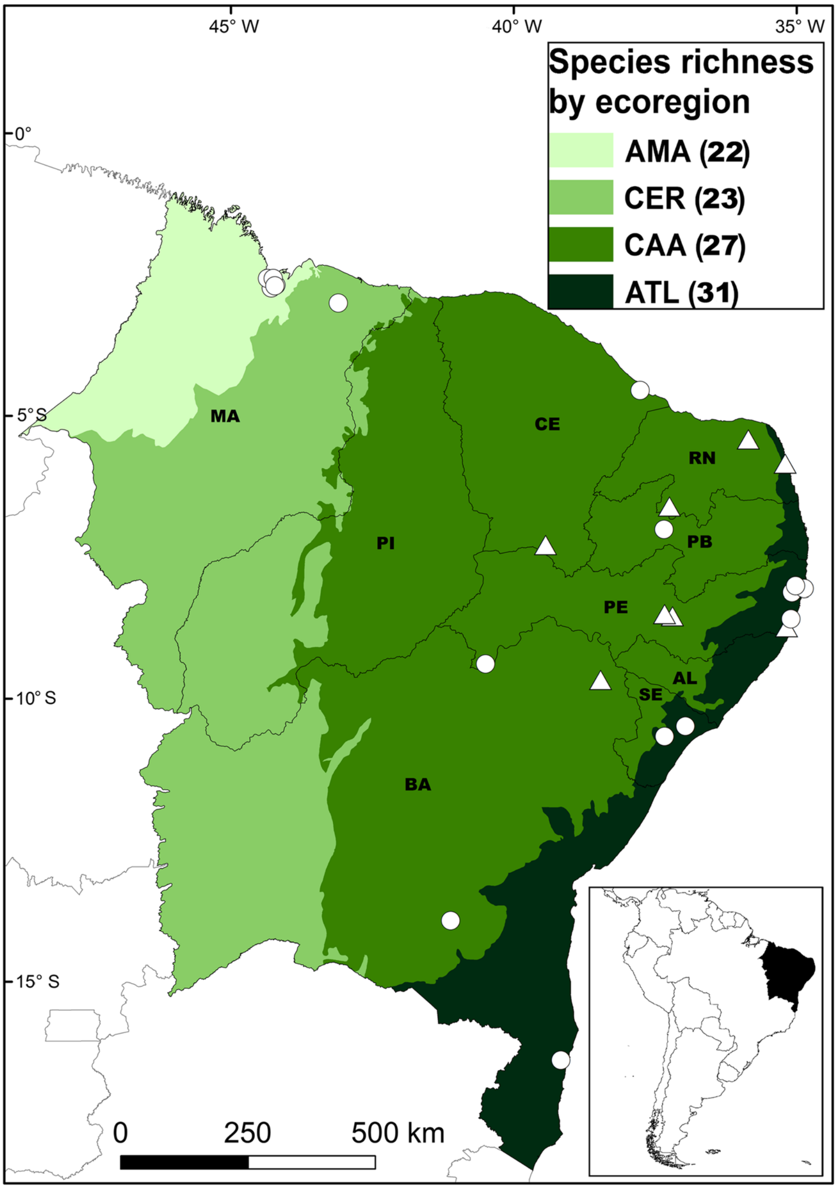

Fig. 1 Study sites and richness of bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) by ecoregion in northeastern Brazil. Data from studies published until April 2017 (white circles) plus new data from the present study (white triangles). Ecoregion: *AMA* Amazonia, *ATL* Atlantic Forest, *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.

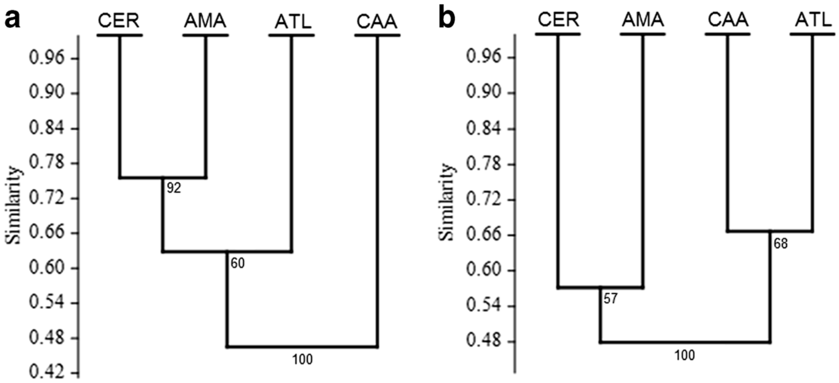

Fig. 2 Cluster analysis (Bray-Curtis with 9999 permutations) evaluating the similarity between ecoregions in northeastern Brazil with data on **a** fly species richness (Diptera: Nycteribiidae and Streblidae) and **b** host species richness (Chiroptera). *AMA* Amazonia, *ATL* Atlantic Forest, *CAA* Caatinga,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

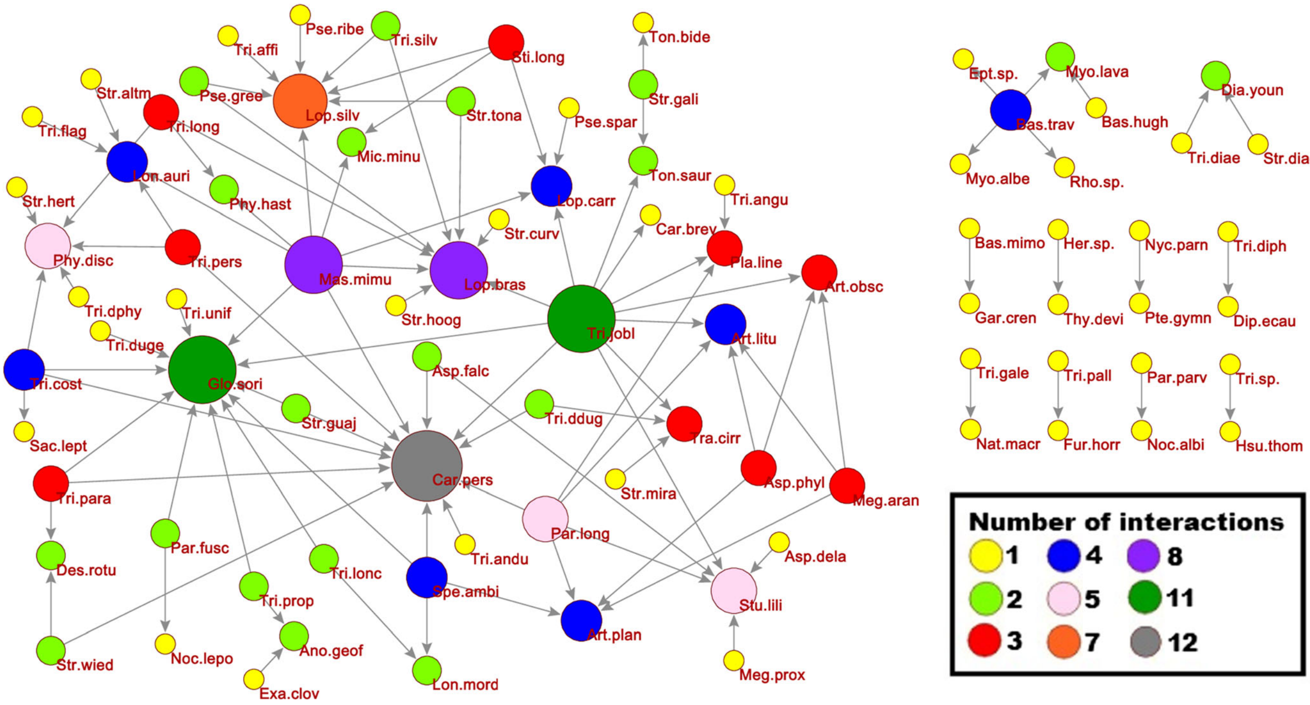

Fig. 3 Interaction networks between bat ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) and their bat hosts (Chiroptera) in northeastern Brazil. The lines correspond to the interactions and the arrows are indicating the hosts. Fly species— Bas.hugh: *Basilia hughscotti*; Bas.mimo: *B. mimoni*, 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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From the Atlantic Forest to the borders of Amazonia: species richness, distribution, and host association of ectoparasitic flies (Diptera: Streblidae and Nycteribiidae) in Northeastern Brazil

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Parasitology Research

Electronic Supplementary Material

ESM 1 Ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) and their respective hosts (Chiroptera) recorded in northeastern Brazil. Data from studies published until April 2017 plus new data from the present study. Source – **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

Family / Fly species	Host species (source)
Nycteribiidae	
Basilia hughscotti	*Myotis lavali* (19)
Basilia mimoni	*Gardnerycteris crenulatum* (11, 12)
Basilia sp.	*Myotis albescens* (11), *Myotis lavali* (16), *Myotis nigricans* (10), *Myotis riparius* (11)
Basilia travassosi	*Eptesicus* sp. (PS), *Myotis albescens* (8), *Myotis lavali* (17, PS), *Rhogeessa* sp. (PS), Undetermined bat (4, 8)
Hershkovitzia sp.	*Thyroptera devivoi* (14)
Streblidae	
Aspidoptera delatorrei	*Sturnira lilium* (16)
Aspidoptera falcata	*Carollia perspicillata* (11, 12), *Sturnira lilium* (11, 12, 14-16, PS)
Aspidoptera phyllostomatis	*Artibeus lituratus* (11, 12, PS), *Artibeus obscurus* (11, 12), *Artibeus planirostris* (14, 16, PS)
Exastinion clovisi	*Anoura geoffroyi* (PS)
Mastoptera minuta	*Carollia perspicillata* (11), *Glossophaga soricina* (11, 12), *Lonchorhina aurita* (15), *Lophostoma brasiliense* (11, 14, 15, 18, PS), *Lophostoma*

	carrikeri (11, 12, 14), *Lophostoma silvicola* (11, 14), *Micronycteris minuta* (11, 12), *Phyllostomus hastatus* (11, 12, 14)
Megistopoda aranea	*Artibeus lituratus* (11, 12, 16, PS), *Artibeus obscurus* (11, 12), *Artibeus planirostris* (14, 16, 17, PS)
Megistopoda proxima	*Sturnira lilium* (11, 12, 14-16, PS)
Nycterophilia parnelli	*Pteronotus gymnonotus* (PS)
Paradyschiria fusca	*Glossophaga soricina* (6), *Noctilio leporinus* (6)
Paradyschiria parvula	*Noctilio albiventris* (11)
Paratrichobius longicrus	*Artibeus lituratus* (15, 16, 18, PS), *Artibeus planirostris* (11, 16, PS), *Carollia perspicillata* (16), *Platyrrhinus lineatus* (15, 18, PS), *Sturnira lilium* (16)
Pseudostrebla greenwelli	*Lophostoma silvicola* (14), *Lophostoma brasiliense* (PS)
Pseudostrebla ribeiroi	*Lophostoma silvicola* (14)
Pseudostrebla sparsisetis	*Lophostoma carrikeri* (14)
Speiseria ambigua	*Artibeus planirostris* (16), *Carollia perspicillata* (11, 12, 14-16, 18, PS), *Glossophaga soricina* (11, 17, PS), *Lonchophylla mordax* (PS), Undetermined bat (1, 5)
Speiseria sp.	*Carollia perspicillata* (13)
Stizostrebla longirostris	*Lophostoma carrikeri* (11, 12, 14), *Lophostoma silvicola* (14), *Micronycteris minuta* (11, 12)
Strebla altmani	*Lonchorhina aurita* (15, PS)
Strebla curvata	*Lophostoma brasiliense* (16)
Strebla diaemi	*Diaemus youngi* (11)
Strebla galindoi	*Tonatia bidens* (14), *Tonatia saurophila* (11, PS)
Strebla guajiro	*Carollia perspicillata* (11-16, PS), *Glossophaga soricina* (PS)
Strebla hertigi	*Phyllostomus discolor* (11, 12, 14, 16, PS)
Strebla hoogstraali	*Lophostoma brasiliense* (14)
Strebla mirabilis	*Trachops cirrhosus* (16, PS)
Strebla sp.	*Micronycteris minuta* (11)
Strebla tonatiae	*Lophostoma brasiliense* (11), *Lophostoma silvicola* (14, 15)
Strebla wiedemanni	*Carollia perspicillata* (10, 16), *Desmodus rotundus* (9, 10, 17, 18, PS)
Trichobioides perspicillatus	*Carollia perspicillata* (3), *Lonchorhina aurita* (PS), *Phyllostomus discolor* (11, 12, 14-16, PS)
Trichobius affinis	*Lophostoma silvicola* (15)
Trichobius anducei	*Carollia perspicillata* (PS)
Trichobius angulatus	*Platyrrhinus lineatus* (PS)
Trichobius caecus	Undetermined bat (7)
Trichobius costalimai	*Carollia perspicillata* (11, PS), *Glossophaga soricina* (18), *Phyllostomus discolor* (11, 12, 14-16, 18, PS), *Saccopteryx leptura* (11), Undetermined bat (2)
Trichobius diaemi	*Diaemus youngi* (11)

Trichobius diphyllae	*Diphylla ecaudata* (17, PS)
Trichobius dugesii	*Glossophaga soricina* (11, 12, 14, 17, PS), Undetermined bat (2)
Trichobius dugesioides dugesioides	*Carollia perspicillata* (16), *Trachops cirrhosus* (15-17, PS)
Trichobius dugesioides phyllostomus	*Phyllostomus discolor* (11, 12)
Trichobius flagellatus	*Lonchorhina aurita* (PS)
Trichobius galei	*Natalus macrourus* (17)
Trichobius joblingi	*Artibeus lituratus* (16), *Artibeus obscurus* (11), *Carollia brevicauda* (11), *Carollia perspicillata* (11-16, 18, PS), *Glossophaga soricina* (11), *Lophostoma brasiliense* (16), *Lophostoma carrikeri* (14), *Platyrrhinus lineatus* (16, 18), *Sturnira lilium* (11, 12), *Tonatia saurophila* (16), *Trachops cirrhosus* (16)
Trichobius lonchophyllae	*Glossophaga soricina* (PS), *Lonchophylla mordax* (PS)
Trichobius longipes	*Lophostoma brasiliense* (15), *Phyllostomus discolor* (15), *Phyllostomus hastatus* (2, 11, 12, 14), Undetermined bat (7)
Trichobius pallidus	*Furipterus horrens* (17)
Trichobius parasiticus	*Carollia perspicillata* (10), *Desmodus rotundus* (10, 11, 14, 15, 17, PS), *Glossophaga soricina* (10), Undetermined bat (2)
Trichobius propinquus	*Anoura geoffroyi* (PS), *Glossophaga soricina* (PS)
Trichobius silvicolae	*Lophostoma brasiliense* (14), *Lophostoma silvicola* (14)
Trichobius sp.	*Hsunycteris thomasi* (14), *Lonchophylla mordax* (14), *Platyrrhinus lineatus* (15)
Trichobius uniformis	*Glossophaga soricina* (18, PS), Undetermined bat (2)

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

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Parasitology Research

Electronic Supplementary Material

ESM 2 Hosts (Chiroptera) and their respective ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) recorded in northeastern Brazil. Data from studies published until April 2017 plus new data from the present study. Source – **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

Host species	Fly species (source)
Anoura geoffroyi	*Exastinion clovisi* (PS), *Trichobius propinquus* (PS)
Artibeus lituratus	*Aspidoptera phyllostomatis* (11, 12, PS), *Megistopoda aranea* (11, 12, 16, PS), *Paratrichobius longicrus* (15, 16, 18, PS), *Trichobius joblingi* (16)
Artibeus obscurus	*Aspidoptera phyllostomatis* (11, 12), *Megistopoda aranea* (11, 12), *Trichobius joblingi* (11)
Artibeus planirostris	*Aspidoptera phyllostomatis* (14, 16, PS), *Megistopoda aranea* (14, 16, 17, PS), *Paratrichobius longicrus* (11, 16, PS), *Speiseria ambigua* (16)
Carollia brevicauda	*Trichobius joblingi* (11)
Carollia perspicillata	*Aspidoptera falcata* (11, 12), *Mastoptera minuta* (11), *Paratrichobius longicrus* (16), *Speiseria ambigua* (11, 12, 14-16, 18, PS), *Speiseria* sp. (13), *Strebla guajiro* (11-16, PS), *Strebla wiedemanni* (10, 16), *Trichobioides perspicillatus* (3), *Trichobius anducei* (PS), *Trichobius costalimai* (11, PS), *Trichobius dugesioides dugesioides* (16), *Trichobius joblingi* (11-16, 18, PS), *Trichobius parasiticus* (10)
Desmodus rotundus	*Strebla wiedemanni* (9, 10, 17, 18, PS), *Trichobius parasiticus* (10, 11, 14, 15, 17, PS)
Diaemus youngi	*Strebla diaemi* (11), *Trichobius diaemi* (11)
Diphylla ecaudata	*Trichobius diphyllae* (17, PS)
Eptesicus sp.	*Basilia travassosi* (PS)

Furipterus horrens	*Trichobius pallidus* (17)
Gardnerycteris crenulatum	*Basilia mimoni* (11, 14)
Glossophaga soricina	*Mastoptera minuta* (11, 12), *Paradyschiria fusca* (6), *Speiseria ambigua* (11, 17, PS), *Strebla guajiro* (PS), *Trichobius costalimai* (18), *Trichobius dugesii* (11, 12, 14, 17, PS), *Trichobius joblingi* (11, PS), *Trichobius lonchophyllae* (PS), *Trichobius parasiticus* (10), *Trichobius propinquus* (PS), *Trichobius uniformis* (18, PS)
Hsunycteris thomasi	*Trichobius* sp. (14)
Lonchophylla mordax	*Speiseria ambigua* (PS), *Trichobius lonchophyllae* (PS), *Trichobius* sp. (14)
Lonchorhina aurita	*Mastoptera minuta* (15), *Strebla altmani* (15, PS), *Trichobioides perspicillatus* (PS), *Trichobius flagellatus* (PS)
Lophostoma brasiliense	*Mastoptera minuta* (11, 14, 15, 18), *Pseudostrebla greenwelli* (PS), *Strebla curvata* (16), *Strebla hoogstraali* (14), *Strebla tonatiae* (11), *Trichobius joblingi* (16), *Trichobius longipes* (15), *Trichobius silvicolae* (14)
Lophostoma carrikeri	*Mastoptera minuta* (11, 12, 14), *Pseudostrebla sparsisetis* (14), *Stizostrebla longirostris* (11, 12, 14), *Trichobius joblingi* (14)
Lophostoma silvicola	*Mastoptera minuta* (11, 14), *Pseudostrebla greenwelli* (14), *Pseudostrebla ribeiroi* (14), *Stizostrebla longirostris* (14), *Strebla tonatiae* (14, 15), *Trichobius affinis* (15), *Trichobius silvicolae* (14)
Micronycteris minuta	*Mastoptera minuta* (11, 12), *Stizostrebla longirostris* (11, 12), *Strebla* sp. (11)
Myotis albescens	*Basilia* sp. (11), *Basilia travassosi* (8)
Myotis lavali	*Basilia* sp. (16), *Basilia travassosi* (17, PS), *Basilia hughscotti* (19)
Myotis nigricans	*Basilia* sp. (10)
Myotis riparius	*Basilia* sp. (11)
Natalus macrourus	*Trichobius galei* (17)
Noctilio albiventris	*Paradyschiria parvula* (11)
Noctilio leporinus	*Paradyschiria fusca* (6)
Phyllostomus discolor	*Strebla hertigi* (11, 12, 14, 16, PS), *Trichobioides perspicillatus* (11, 12, 14-16, PS), *Trichobius costalimai* (11, 12, 14-16, 18, PS), *Trichobius dugesioides phyllostomus* (11, 12), *Trichobius longipes* (15)
Phyllostomus hastatus	*Mastoptera minuta* (11, 12, 143), *Trichobius longipes* (2, 11, 12, 14)
Platyrrhinus lineatus	*Paratrichobius longicrus* (15, 18, PS), *Trichobius angulatus* (PS), *Trichobius joblingi* (16, 18), *Trichobius* sp. (15)
Pteronotus gymnonotus	*Nycterophilia parnelli* (PS)
Rhogeessa sp.	*Basilia travassosi* (PS)
Saccopteryx leptura	*Trichobius costalimai* (11)
Sturnira lilium	*Aspidoptera delatorrei* (16), *Aspidoptera falcata* (11, 12, 14-16, PS), *Megistopoda proxima* (11, 12, 14-16, PS), *Paratrichobius longicrus* (16), *Trichobius joblingi* (11, 12)
Thyroptera devivoi	*Hershkovitzia* sp. (14)
Tonatia bidens	*Strebla galindoi* (14)
Tonatia saurophila	*Strebla galindoi* (11, PS), *Trichobius joblingi* (16)

Trachops cirrhosus	*Strebla mirabilis* (16, PS), *Trichobius dugesioides dugesioides* (15-17, PS), *Trichobius joblingi* (16)
Undetermined bat	*Basilia travassosi* (4, 8), *Speiseria ambigua* (1, 5), *Trichobius caecus* (7), *Trichobius costalimai* (2), *Trichobius dugesii* (2), *Trichobius longipes* (7), *Trichobius parasiticus* (2), *Trichobius uniformis* (2)

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Parasitology Research

Electronic Supplementary Material

ESM 3 Key methodological recommendations for more effective studies on bat ectoparasites

- Mist nets should be inspected at short intervals and bats must be quickly removed to mitigate possible transfers by disturbance or escape of some parasites;
- The cotton bags where bats are kept must be clean, used only once each night, inspected after bat release to detect possible remaining parasites, and washed before new use;
- The entire bat body surface and wing membranes should be carefully inspected to locate all the ectoparasites. Especially for flies, gently blowing and/or moving the bat fur with the forceps makes it easy to find the parasite. Nevertheless, some mite species are not detectable without magnification, making it difficult to collect them in live host specimens in the field. For details on collecting these mite groups see Whitaker et al. (2009);
- Parasites should be collected from the host with agility to avoid evasion, especially for easily excitable and good flying species, like *Paratrichobius longicrus* (Miranda Ribeiro, 1907);
- Parasite collection should preferably be performed by the same researcher, previously trained, so the detection accuracy and sampling standardization are maintained across all individuals analyzed. When more than one researcher will collect the ectoparasites, all must be pre-trained together;
- Wherever possible, ectoparasites should be removed with soft forceps (e.g., featherweight forceps) to avoid damaging and compromising their identification. Nonetheless, nycteribiid flies usually attach strongly to the host fur, making it difficult to remove those using soft forceps. Hard forceps can then be carefully used to avoid damaging any morphological characters. For mites, wet brushes in ethanol and/or gently fine-tipped forceps (e.g., watchmaker forceps) can be used;
- Before release, each bat should be marked for recapture control (even if not permanent marking), avoiding the miscalculation of parasitological indices;
- As with cloth bags, gloves should be inspected after each host screening to avoid ectoparasite transfer;
- Vials, where the parasites are deposited, must be individual and properly labeled with information corresponding to the host, and label placed inside the vial to prevent damage and/or loss;

- Parasites can be preserved in 70-95 % ethanol for taxonomic identification based on morphological characters. However, for the identification at the species level of some fly species, it is necessary to mount them on slides, including the dissection of the male reproductive structures (see Wenzel et al. 1966). For mites, the mounting plate is essential for species-level identification (see Wenzel et al. 1966);
- The collection of ectoparasites should be performed out first so the possibility of parasite dispersion is reduced. Other procedures with the bat should be done after that (e.g., measurements and marking);
- The maximum information about general host conditions (e.g., sex, age, reproductive status) should be also collected since that information are fundamental for inferences and a better understanding of host-parasite relationships (see Whitaker et al. 2009).

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