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GUSTAVO LIMA URBIETA

MOSCAS ECTOPARASITAS (DIPTERA, STREBLIDAE) DE MORCEGOS (MAMMALIA, CHIROPTERA) EM CAVERNAS DO NORDESTE DO BRASIL, COM ÊNFASE NO BIOMA DA CAATINGA

JOÃO PESSOA (PARAÍBA)
2022

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Tese apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Zoologia) da Universidade Federal da Paraíba, como requisito parcial para a obtenção do título de Doutor em Ciências Biológicas.

Orientador: Profa. Dra. Valéria da Cunha Tavares

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Ata da 159ª Apresentação e Banca de Defesa de Doutorado de GUSTAVO LIMA URBIETA

Ao(s) vinte e nove dias do mês de setembro de dois mil e vinte e dois, às 08:30 horas, no(a) Ambiente Virtual, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a tese de doutorado de **GUSTAVO LIMA URBIETA**, candidato(a) ao grau de Doutor(a) em Ciências Biológicas. A banca examinadora foi composta pelos seguintes membros: **Dra. Valéria da Cunha Tavares (Orientadora - UFPB/PB); Dr. Alan Fredy Eriksson (UFMT/MT); Dra. Ana Carolina Pavan (MZUSP/SP); Dra. Karoline Ceron (UNICAMP/SP); Dra. Fabiana Rocha (UFPB/PB).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra ao(à) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **GUSTAVO LIMA URBIETA**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"Moscas ectoparasitas (Diptera, Streblidae) de morcegos (Mammalia, Chiroptera) em cavernas do Nordeste do Brasil, com ênfase no bioma da Caatinga".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito **aprovado**. Perante o resultado proclamado, os documentos da banca foram preparados para trâmites seguintes. Encerrados os trabalhos, nada mais havendo a tratar, eu, orientador(a), como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 29/09/2022.

Valeria C. Tavares
Orientador(a) Valeria da Cunha Tavares

Karoline Ceron
Examinador(a) Karoline Ceron

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SUMÁRIO

DEDICATÓRIA

Para minha mãe, que me ensinou cedo o ofício das palavras como agentes da “escrevivência” e para Elaine Anjos, que me colocou numa rota de colisão instigante com as moscas uma década atrás. Vejam onde chegamos.

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“[..] Quando ele chegou na gruta
ficou com a mente espantada
com as rochas estalagtites
no teto dependuradas
agradou-a da caverna
sem saber ser encantada [...]”

Abraão Batista
(Trecho do Cordel *“O pássaro encantado da Gruta do Ubajara”,* 3ª edição, 1978)

RESUMO

Cavidades subterrâneas oferecem aos morcegos abrigo, proteção e estabilidade de condições para reprodução e socialização. Dentre outros organismos associados aos morcegos, as moscas ectoparasitas também são favorecidas pelo ambiente das cavidades e estão intimamente associadas a esses mamíferos, embora aspectos biológicos sobre essa associação sejam pouco conhecidos. Em particular, há ausência de estudos comparativos sobre as associações de assembleias de morcegos cavernícolas e de suas moscas ectoparasitas em "cavernas quentes" ("hot caves" ou "cuevas calientes", cavidades com populações grandes de morcegos e condições únicas de temperatura e umidade, dentre outras características) e "cavernas frias" ("cold caves ou bat caves", cavidades com grandes populações de morcegos) incluindo possíveis efeitos da variação desses ambientes nessa relação parasitária. Portanto, o objetivo desse trabalho foi caracterizar as interações entre morcegos e moscas ectoparasitas em cavernas e avaliar se essas interações variam em diferentes tipos de cavidades na região Nordeste do Brasil. Assim, capturamos 700 morcegos em 16 cavernas pertencentes a 19 espécies de seis famílias, e um total de 1.412 moscas de morcego distribuídas em 29 espécies. No **Capítulo I**, investigamos informações publicadas sobre interação morcego-mosca em poleiros (i.e., cavernas, construções humanas) a nível global e avaliamos os padrões de coautoria para identificar tendências de novos estudos. No **Capítulo II**, testamos o efeito de variáveis microclimáticas e tipo de cavernas (i.e., "hot" e "cold caves") no parasitismo de estreblídeos em morcegos no Nordeste brasleiro. Por fim, no **Capítulo III**, descrevemos e avaliamos a estrutura das interações morcego-mosca em "hot" e "cold caves" na região Nordeste do Brasil.

Palavras-chave: Parasitismo, Poleiro, Hospedeiro, Especificidade, Redes de interação.

Bat flies (Diptera, Streblidae) of bats (Mammalia, Chiroptera) in caves from Northeastern Brazil, with an emphasis on the Caatinga biome

ABSTRACT

Cavities provide bats shelters, protection and stable conditions for reproduction and socialization. Among organisms associated with bats, bat flies are also favored by the cavity environment and are closely associated with these mammals, although biological aspects of this association are poorly understood. In particular, there is a lacune of comparative studies on the associations of cave bats assemblages and their bat flies in “hot caves” (“hot caves” or “cuevas calientes”, cavities with large populations of bats and unique conditions of temperature and humidity, among other characteristics) and “cold caves” (“cold caves or bat caves”, cavities with large populations of bats) including possible effects of the variation of these environments in these parasitic interactions. Therefore, the aim of this work was to characterize the interactions between bats and bat flies in caves and to assess whether they interactions vary in different types cavities in Northeast region of Brazil. Thus, we captured 700 bats in 16 caves belonging to 19 species six families, and a total of 1.412 bat flies distributed in 29 species. In **Chapter I**, we investigated published information on bat-fly interaction in roosts (i.e., caves, human constructions) at a global level and assessed patterns of co-authorship to identify trends in further studies. In **Chapter II**, we tested the effect of microclimatic variables and cave type (i.e., “hot” and “cold caves”) on streblids parasitism in bats in northeastern Brazil. Finally, in **Chapter III**, we describe and evaluate the structure of bat-fly interactions in “hot” and “cold caves” in the northeast region of Brazil.

Keywords: Parasitism, Roost, Host, Specificity, Interaction networks.

INTRODUÇÃO GERAL E JUSTIFICATIVA

As associações entre morcegos (Chiroptera) e moscas ectoparasitas (Streblidae) constituem excelentes modelos para estudos ecológicos em diferentes ambientes e escalas. A maior parte das espécies de moscas ectoparasitas associa-se exclusivamente a um número limitado de espécies de hospedeiros (Dittmar et al., 2015). Essas moscas apresentam adaptações como compressão lateral, compressão dorsoventral, ausência de asas e olhos reduzidos (Peterson e Wenzel, 1987; Meier et al., 1999; Dick e Patterson, 2006), devido a diferentes processos coevolutivos. São conhecidas no Brasil 181 espécies de morcegos distribuídas em 68 gêneros (Garbino et al., 2020). Essa elevada riqueza de espécies resulta em elevada riqueza de espécies de moscas ectoparasitas (Wenzel 1976; Dick e Gettinger, 2005). Assim, 96 espécies de moscas ectoparasitas (Streblidae) são registradas e distribuídas ao longo de 23 gêneros em todos os biomas do país (Graciolli, 2020).

Dentre os variados tipos de abrigos que os morcegos ocupam (e.g., folhagens, troncos de árvores) as cavernas se destacam por serem estruturas de natureza mais permanente e do ponto de vista evolutivo e ecológico por oferecerem aos morcegos estabilidade e permanência de um abrigo, proteção contra predadores, menor condições ambientais adversas, condições adequadas para hibernação e reprodução (Kunz, 1982; Tuttle e Moreno, 2005). Elas são amplamente variáveis quanto ao tamanho, geomorfologia e vários outros aspectos (e.g., cavernas, grutas, fendas em afloramentos rochosos) e são frequentemente são utilizados como abrigo por diversas espécies de morcegos (Kunz et al., 2012). Por exemplo, as condições microclimáticas (i.e., temperatura e umidade) e a estrutura interna das cavernas foram sugeridas como os principais fatores que influenciam a ocupação de cavernas por morcegos (Brunet e Medellín, 2001).

De modo geral, cavernas ocupadas por assembleias muito grandes de morcegos, podem ser discriminadas em dois grandes grupos quanto a regulação térmica e condições de umidade, se comparados ao meio externo na região Neotropical: “cavernas quentes” (“hot caves”, “cuevas calientes”) e “frias” (“cold caves”, “bat caves” – durante essa tese utilizaremos frequentemente a primeira denominação para contrastar com “hot caves”) (Silva-Taboada, 1979, Rocha, 2013; Medellin et al., 2017). As cavernas quentes são conhecidas por terem uma ou poucas entradas, agregarem milhares de morcegos, apresentarem baixa circulação de ar e, elevada umidade (>90%) e temperatura (28-40ºC) (Silva-Toboada, 1979; Rocha, 2013). Já as "cavernas frias" possuem várias entradas, maior circulação de ar, umidade variando de 60 a 80% e temperatura média de 25ºC (Silva-Taboada, 1979; Rocha, 2013; Medellin et al., 2017). Apesar das "cold caves" terem, aparentemente, maior influência do ambiente externo, ambas são diariamente e sazonalmente influenciadas pela posição geográfica e estrutura/composição de hospedeiros da caverna (Kunz et al., 2012).

Os morcegos cavernícolas são fundamentais para a manutenção desses ecossistemas únicos (Kunz, 1982; Kunz et al., 2012). Eles introduzem matéria orgânica nas cavernas por meio de suas fezes, ou guano, que por sua vez mantém outras comunidades de invertebrados nesses ambientes (Ferreira et al., 2010). Além disso, diferentes espécies de morcegos cavernícolas exercem funções importantes para a manutenção de serviços ecossistêmicos, como a polinização e dispersão de sementes de espécies vegetais ao longo da região neotropical (Lobova et al., 2009), e também auxiliam no controle de populações de invertebrados (i.e., preferencialmente insetos voadores) e pequenos vertebrados dentro e fora das cavernas (Kalka et al., 2008). Portanto, diferentes perturbações incidentais, extrativismo industrial e entrada descontroladas nas cavernas podem alterar ou extinguir essas e outras funcionalidades ecológicas exercidas pelos morcegos neste ecossistema (Furey e Racey, 2016).

Devido à alta especificidade entre morcegos e moscas ectoparasitas (Wenzel, 1976), o ambiente cavernícola exerce influência sobre as associações parasitárias. As moscas ectoparasitas apresentam desenvolvimento por viviparidade adenotrófica, ou seja, as larvas se desenvolvem no corpo da mãe e são subsequentemente depositadas em forma de pupa na parede dos abrigos dos morcegos (Dittmar et al., 2015). Como parte da vida das moscas é fora do morcego, evidências sugerem que essa oportunidade de menor contato com as moscas seja uma maneira dos morcegos controlarem suas cargas parasitárias (Lewis, 1995; ter Hofstede e Fenton, 2005). Quando os hospedeiros distinguem os sítios com maior carga de parasitas em relação a outros potenciais locais para nidificar, eles podem evitá-los introduzindo mudanças à adaptação de ciclos de nidificação (Moore, 2002; Reckardt e Kerth, 2007). Além disso, as disposições das pupas nas superfícies de cavernas afetam sua viabilidade e, consequentemente, as cargas parasitárias nos morcegos (ver Dittmar et al., 2009), na qual, morcegos que usam cavernas como abrigos são mais infestados (i.e., cargas parasitárias) e mais parasitados por várias espécies de moscas (Patterson et al., 2007), embora essa seja uma relação ainda pouco conhecida e testada.

Morcegos e moscas ectoparasitas são potenciais reservatórios de agentes patogênicos (e.g., *Bartonella* spp., *Hepatozoon* spp.) e o transbordamento desses patógenos para fora do ambiente cavernícola pode ser desencadeado por perturbações ambientais na estrutura da caverna ou no entorno. O uso de solo por expansão agrícola e pecuária desenfreada, é um dos principais fatores negativos sobre a biodiversidade, levando a extinções locais, perda de serviços ambientais, redução da diversidade genética de populações e da diversidade taxonômica e funcional das comunidades (Lino et al. 2019). A perda e a fragmentação de habitats podem impactar a dinâmica das interações entre parasitas e hospedeiros nas cavernas com efeitos ainda pouco conhecidos, mas relevantes do ponto de vista sanitário humano e da fauna doméstica e silvestre (Brook et al., 2015; Szentiványi et al., 2020).

Embora as cavernas tenham enorme importância para a conservação dos morcegos e suas interações ecológicas, ainda existem muitas regiões subamostradas quanto a esse ecossistema no Brasil (Guimarães e Ferreira, 2014). As principais lacunas se concentram nas porções Norte e Nordeste do país, nos biomas da Amazônia e Caatinga (Guimarães e Ferreira, 2014). Apesar disso, 72 espécies de morcegos têm sido registradas em cavernas no Brasil, utilizando-as como abrigo alternativo ou como abrigo principal em diferentes biomas, incluindo a Caatinga (Oliveira et al., 2018). A Caatinga compreende um bioma semi-árido endêmica do nordeste do Brasil (MMA/IBAMA, 2011), que vai desde o estado do Ceará e estende-se até ao norte da Bahia e norte de Minas Gerais (Leal et al., 2003). Apresenta em sua porção maior uma floresta tropical sazonal seca com vegetação de espinho, presença de pequenas folhas com características xerofíticas e florestas lenhosas com áreas arbustivas compostas por Bromeliaceae e Cactaceae (Leal et al., 2003; Santos et al., 2011). As folhas e flores aparecem na curta estação chuvosa e na seca as folhas estão ausentes na maior parte do ano (Leal et al., 2003). Além disso, apresenta características particulares como alta temperatura média anual, menores taxas de umidade relativa do ar, maior evapotranspiração e maior radiação solar (Prado, 2008). Ações antrópicas como o desmatamento e agricultura estão causando rápida e continua degradação e desertificação da Caatinga (Leal et al., 2003), com pouca atenção atribuída em termos de conservação de sua paisagem natural (Silva et al., 2004). Até 2009, 53,38% da cobertura natural da Caatinga permaneceu intacta (MMA/IBAMA, 2011) e apenas 7,4% de toda a sua extensão estava dentro de unidades de conversação e proteção integral e áreas protegidas de uso sustentável (MMA/IBAMA, 2011).

A Caatinga e a Mata Atlântica são biomas com diferentes níveis de estudo em relação a quiropterofauna. No domínio de Mata Atlântica (bioma mais estudado sobre morcegos) são conhecidas 98 espécies de morcegos distribuídas em oito famílias, performando aproximadamente 54% da riqueza de morcegos registra para o Brasil (Novaes et al., 2022). Esse bioma também possui algumas espécies ameaçadas de extinção e endêmicas (e.g., *Lasiurus ebenus*, *Dryadonycteris capixaba* e *Lonchophylla peracchii*) (Novaes et al., 2022). Por outro lado, a quiropterofauna da Caatinga é composta aproximadamente por 82 espécies (Rocha et al., 2019), sendo que pelo menos 39 espécies (47,5%) utilizam as cavernas como abrigo (Vargas-Mena et al., 2018), evidenciando a importância das cavidades para os morcegos que habitam a Caatinga (Cordero-Schmidt et al., 2017). Além disso, existem duas espécies, *Xeronycteris vieirai* Gregorin & Ditchfield, 2005 e *Lonchophylla inexpectata* Moratelli & Dias, 2015 e uma subespécie, *Chiroderma doriae vizottoi* Taddei & Lim, 2010 (revisado por Garbino et al., 2020) que são endêmicas desse bioma e ocupam cavernas. Entretanto, apenas recentemente foram realizados estudos com dados sobre moscas parasitas de morcegos cavernícolas dos sistemas da Caatinga (Cordero-Schmidt et al., 2017; Barbier e Bernard, 2017; Barbier et al., 2018; Silva et al., 2019) sendo registradas até o momento 26 espécies, pertencentes a nove gêneros (Barbier e Bernard, 2017). Em geral, a Caatinga representa uma enorme lacuna em termos do conhecimento de associações entre morcegos e moscas ectoparasitas (Barbier e Bernard, 2017). Dentre as abordagens, destaca-se a ausência de trabalhos mais simples com viés taxonômico, como inventários de espécies, até trabalhos mais ecológicos com comparações de associações faunísticas em diferentes cavernas quanto a atributos físicos e microclimáticos, como é o caso das cavernas “quentes” e “frias” do Nordeste brasileiro.

Assim, o estudo das relações entre morcegos e moscas ectoparasitas em cavernas quentes e frias na matriz composta de Caatinga e Mata Atlântica, conforme proposto no presente trabalho, permite: i- testar variações de composição da fauna desses organismos entre os biomas, ii- testar variações nas cargas parasitárias (e.g., abundância, especificidade parasitária, prevalência e intensidade média de infestação) entre cavernas, iii - construir hipóteses sobre a influência de fatores microclimáticos que possam interferir nessas relações, contribuindo assim para o preenchimento das lacunas acerca da interação entre morcegos e moscas ectoparasitas no Nordeste brasileiro..

OBJETIVOS

Objetivo geral

Caracterizar as composições e interações da fauna cavernícola de morcegos e moscas ectoparasitas em cavernas quentes e frias do Nordeste brasileiro contidas na matriz Caatinga - Mata Atlântica e testar características das cavernas que podem afetar as relações de parasitismo.

Objetivos específicos

- Inventariar a fauna de morcegos e suas moscas ectoparasitas em cavernas quentes e frias do nordeste brasileiro;
- Testar se a temperatura e umidade das cavernas afetam as abundâncias de moscas ectoparasitas e se as espécies se diferenciam entre os tipos de cavernas;
- Testar se a topologia e métricas de interações moscas-morcegos variam entre as cavernas e conjuntos de cavernas (i.e., "quentes" e "frias").

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OBSERVAÇÕES QUANTO A FORMATAÇÃO DOS CAPÍTULOS

Entendemos que é preciso respeitar as normas estabelecidas por cada revista quanto a formatação de suas publicações e ao mesmo tempo devemos facilitar a leitura dos avaliadores dessa tese. Neste sentido, o alinhamento a esquerda e especificações envolvendo numeração de linhas, por exemplo, foram desconsideradas com objetivo de manter uma padronização geral da tese. Os Capítulos I e II estão padronizados seguindo a revista *Parasitology Research* e o Capítulo III seguindo o padrão da *Acta Chiropterologica*. Nesse último, decidimos manter o corpo do texto em língua portuguesa, contudo, alguns elementos em língua inglesa foram mantidos (e.g., título, abstract e elementos nas figuras).

CHAPTER I

Published in Parasitology Research – Urbieta, G.L., Graciolli, G. & da Cunha Tavares, V. Review of studies about bat-fly interactions inside roosts, with observations on partnership patterns for publications. Parasitol Res (2022). https://doi.org/10.1007/s00436-022-07635-z

Review of studies about bat-fly interactions inside roosts, with observations on partnership patterns for publications

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Abstract

Pressures from anthropogenic disturbances have triggered a wealth of studies focusing on the assessment and mitigation of the negative impacts of these disturbances on inter and intraspecific ecological interactions, including bats and bat flies in their roosts. The heterogeneity of research methods employed for these studies and the scientific imbalance between countries may constrain advances and the consolidation of the knowledge on this subject. We reviewed the literature regarding bat and bat–ectoparasite interactions in roosts assessing global research trends and patterns of author collaborative work to be able to identify key questions for future studies and potential initiatives to improve the knowledge on this subject. Current information available have mostly come from the Americas and is predominantly focused on the recognition and description of parasite-host interactions between bats and bat flies. Our findings suggest the value of increasing collaboration for future research, as several countries with largely diverse environments and high organismal richness are disconnected from the countries that produce the most publications in this area, and/or have low records of publications. These regions are in the Global South, mostly in South American and African countries. We suggest that more collaborative networks may increase scientific production in the area, and that investing in local research development and enhancing partnerships for publications may strengthen the field. These research programs and collaborations are key for the development of conservation strategies for bats and bat flies, for their roosts, and for understanding bat and bat–ectoparasite interactions.

Key words: Parasitism, Cave, Streblidae, Nycteribiidae, Collaborative work.

Introduction

Anthropogenic disturbance interfere in ecological interactions, resulting in losses such as local extinction of species and degraded ecological functions (Cisneros et al. 2015; Carvalho et al. 2020; Ramírez-Mejía et al. 2020) as it has been observed for bat (Mammalia: Chiroptera) and bat fly (Diptera: Streblidae, Nycteribiidae) interactions (Ramalho et al. 2021). Negative effects to bat hosts, such as roost disruption and habitat fragmentation may affect in interspecific interactions and also local and/or regional ecosystems (Pilosof et al. 2012; Bolívar-Cimé et al. 2018). Effects of environmental impacts on bat-plant interactions for feeding and for roosting are apparently better understood than those between bats and their ectoparasites (Oliveira et al. 2019; Hemprich-Bennett et al. 2021; Tormanen and Garrie 2021). Although most studies about bat and bat-ectoparasite interactions are historically descriptive, they provide crucial data to understand the host-parasite dynamics across diverse environments (Patterson et al. 2007; Fagundes et al. 2017; Salinas-Ramos et al. 2018). Studies focusing on the ecology of bat-parasite relationships in their roosts are scarce event though they are essential to the knowledge of pathogenic cycles of bats and their bat flies (Morse et al. 2012c; Abundes-Gallegos et al. 2018).

Diurnal roosts offer climatic stability to bats, protection from predators, optimal conditions for the bat’s reproduction, and social interactions (Kunz 1982; Kunz, Murray and Fuller, 2012; Tuttle and Moreno, 2012). Roosts used by bats can be temporary (e.g., leaves, foliage) or permanent (e.g., caves, rock outcrops) (Voss et al. 2016; Garbino and Tavares 2018) and appear to be essential for the development of interactions of bat flies and their hosts. Several species of bats are gregarious, many of them forming groups or colonies roosting in caves (Vargas-Mena et al. 2020), which may facilitate the creation and maintenance of ideal conditions for the bat flies’ life cycle. Indeed, the development of the flies is limited by the microclimatic conditions of the shelter (Dittmar et al. 2009; Morse et al. 2012a), and by the bats’ ability to avoid the parasitism (Reckardt and Kerth 2007a). As part of its reproductive cycle, each female bat fly may deposit a prepupa in a roost wall surface, from which the pupa develops in approximately three weeks (Dick and Patterson 2007). As soon as the pupa hatches the young fly needs to find a host to be able to survive (Dittmar et al. 2009) as it will perish in a few hours away from their hosts (Overal 1980; Fritz 1983).

Studies focusing on bat and bat–fly interactions in their roosts can also play important roles for the conservation of the biodiversity associated to natural and artificial roosts. Some of the recent novelties about bats and bat-flies interactions include the study of fungal hyper parasitism on bat flies (Walker et al. 2018; Szentiványi et al. 2019a, 2020), the detection of new pathogens in bats and in the bat flies including viruses and bacteria (Jansen Van Vuren et al. 2017; Stuckey et al. 2017; Abundes-Gallegos et al. 2018; Sándor et al. 2018) and the description of patterns of interaction (Lourenço and Palmeirim 2004; Lourenço 2008; Teixeira and Ferreira 2010). Studies of diurnal roosts of bats are essential for bat conservation and to minimize impacts in cave ecosystems (Kunz 1982; Marshall 1982; Vargas-Mena et al. 2020; De Sousa Barros et al. 2021). On the other hand, most studies including bats and the bat and bat-ectoparasites data have been conducted in the open, outside bat roosts, when bats are out foraging. Over the course of a study on bat-ectoparasite ecological interactions in caves, we noticed a lacune for comparative data related to roosting ecology patterns associated to bats and bat–ectoparasite interactions. The scarcity of information on roosts, bat and bat fly dynamics poses limitations to our ability to understand the biological cycles of the hosts and their parasites, and the importance of the roosts for these interactions, and consequently limits conservation actions for these systems.

Economic and scientific inequality contributes to restrict science production (Adams 2012, 2013; Gui et al. 2019) and partnerships between researchers from different countries promote engagement to scientific development, enabling collaboration, problem-solving and to the visibility of results (Adams 2012, 2013; McManus et al. 2020). Programs improving the exchange among researchers have been developed worldwide (Adams 2012, 2013) but some countries are lagging behind, such as megadiverse countries from South America, Africa, and Asia, mostly lacking basic information regarding the biology of the bats and their interactions with ectoparasites (Phelps et al. 2019; Frick et al. 2020; Conenna et al. 2021; Mas et al. 2021). Thus, bibliometric information about studies of bat and bat-ectoparasite interactions in roosts, international partnership and co-authorship networks may offer a useful overview and can potentially help to identify ways to increase international collaborations.

Our aim in this study was to compile published data and analyze the state-of-the-art of the bat and bat–ecosystem interactions in roosts, investigating global patterns and trends for future studies and learning about patterns of collaborative networks using bibliometric analyzes. We were also interested in understanding the variation of the knowledge in the topic along time and spatially, considering the geopolitical distribution of the institutions of the lead authors. Based on our analyzes, we comment on practices for boosting the knowledge on bat and bat-ectoparasite interactions across the globe.

Materials and methods

Literature search

We performed a bibliographic search using the ISI Web of Science (WoS) database and performed a search with the terms ((cav* OR "hot cav*" OR "bat cav*" OR roost OR shelter) AND bat* AND ("bat fl*" OR "ectoparasitic fl*" OR Streblidae OR Nycteribiidae)). We then saved all articles retrieved, departing from 1945 until October 29th, 2021. We choose to use only WoS database to avoid redundancy (Calver *et al.*, 2017). We subsequently filtered the documents by examining each of them and saving every study containing records of bats and bat flies in our database.

After this first selection, we discriminated the distribution of bat and bat fly studies by roost types, separating in the categories: i) records exclusively in caves; ii) records in all types of roosts except caves (e.g., buildings, tunnels, bat boxes) and iii) records in caves and any other roost. We then excluded studies mistakenly selected because they were conducted outside roosts and studies based on secondary data or not including field data on bats and bat flies. We followed a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram to guide our revisionary work (Moher et al. 2009) (Supplementary Material S1).

Data analysis

We built interaction networks for the collaborations and keywords compiled from the bibliometric data analyses using the software *VOSviewer* version 1.6.15 (van Eck and Waltman 2010). For each network, the node size represents the number of publications or keywords, and the link is the connection between items (i.e., countries or keywords). The cluster was calculated by using the Association Strength Method (van Eck and Waltman 2010). For the construction of the collaboration network, we used the country of the lead author’s affiliation.

Previous to the analyses, we merged the following the terms ‘Cave’ and ‘Caves’; “Chiroptera” and “Bats”; “Parasite load” and “Prevalence”; ‘Ectoparasite’ and ‘Ectoparasites’, and “Bat flies” and “Bat fly” to avoid redundancy. We considered that the keyword “Parasite load” is a generic way to represent distinctly named parasitological indexes that all relate the number of parasites/hosts, such as “Prevalence”, “Mean Intensity”, “Mean Abundance”. We assumed that keywords cited at least three times in different studies may represent an incipient publication pattern and used these keywords to build the interaction network. We evaluated the relationships between the number of links, in this case, of partnerships and the number of publications through a linear regression in the R environment software (R Core Team 2020).

Results

We initially retrieved 116 studies and filtered to 66 (first year with study record) covering a 25-year interval (1996-2021) with an average number of publications of 3.5 studies/year, and peaks of publication between 2006 and 2021 (Fig. 1) (Supplementary Material Table S2). Most studies were published from 2015 on (n = 36; 54%) with a sharp drop in 2020 (n = 3; 4%). Approximately 2.5 studies/year were published in average from 1996 to 2014, and the rate of publications doubled up to 5.14 from 2015 on. A larger number of publications was concentrated in the years of 2017 and 2018 (Fig. 1). Studies carried out exclusively in caves were more frequent (n = 38; 57%), followed by studies in other type of roosts (n = 19; 29%) and in both caves and other type of roosts (n = 9; 14%).

Collaborative research led to the formation of 14 clusters composed of 36 countries (Fig. 2a) (Supplementary Data for *VOSviewer*). Only five clusters contained publications restricted to authors from the same country (Australia, India, Iran, Slovakia e Philippines), and except for Iran (n = 2 studies) these countries were represented by a single study each. The countries with larger number of publications were The United States of America (USA) (n = 25 studies), Mexico (n = 10 studies), Brazil (n = 9 studies), and Madagascar (n = 6 studies). Most studies published by researchers based in the USA and Brazil were published from 2014 and 2015, while publications of researchers based in Madagascar and Mexico were more recent, starting to appear in the literature database in 2016 and 2018, respectively (Fig. 2b). The USA, Mexico, Brazil, and Madagascar represent approximately 76% of all publications and the production led by USA based researchers accounted for the largest share of all global production (39%).

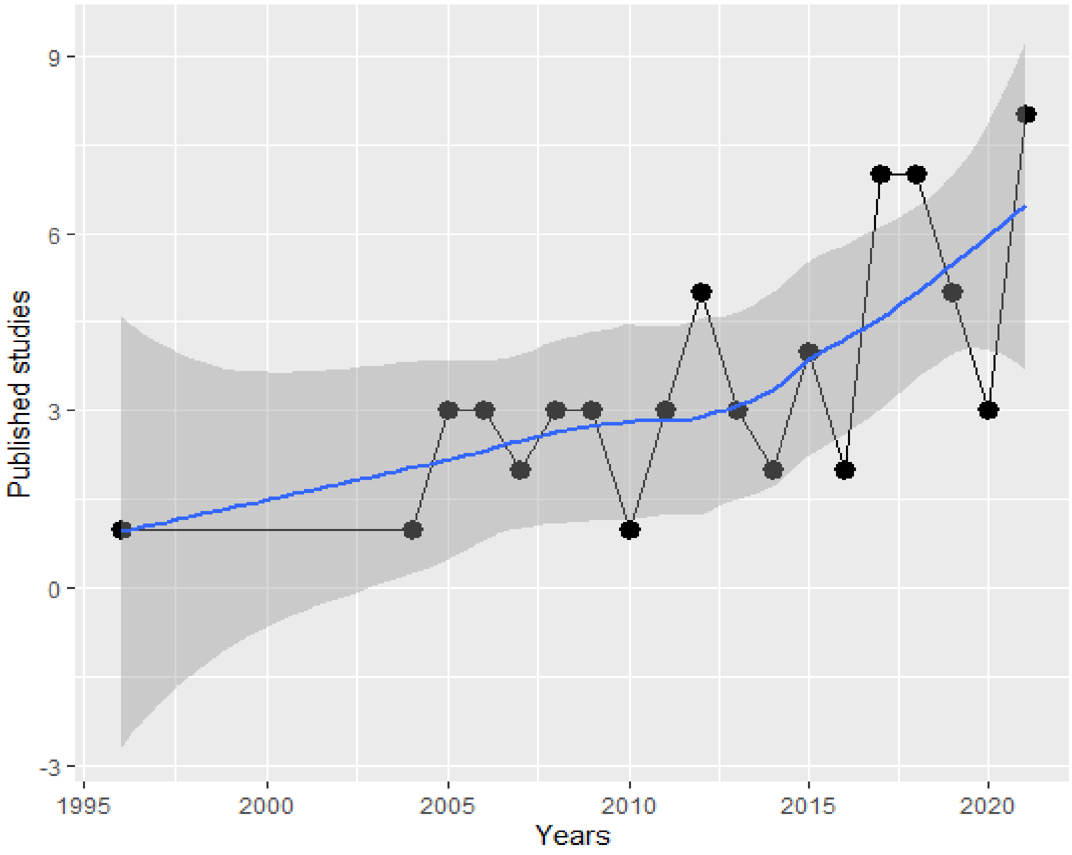

Fig. 1. Number of publications about bats and bat-flies in roosts per year (1996 to 2021). The blue line is the data trend curve.

Countries accounting for a larger number of publications tend to have more connections with other clusters ($R^2 = 0.70$; $P = <0.001$; $df = 34$) (Fig. 3a). The USA institutions have the highest international network, connecting with five clusters (36%) and with a total of 17 countries represented in their collaborative publications (47%) (Fig. 2a), and this substantial network appear to reinforce partnerships ($R^2 = 0.27$; $P = <0.001$; $df = 33$) (Fig. 3b). Following the USA, Mexico is the second in productions and connections, respectively ten studies and five connections to other clusters followed by Brazil and Madagascar, with nine and six publications, respectively and both with two connections. Some clusters are formed by two or three isolated countries, such as Poland and Turkey, which may indicate a trend to specific, regional partnerships (Fig. 2a). Furthermore, there appears to occur constant collaborations between researchers or study groups, e.g., Mexico, Costa Rica, Brazil, Argentina which, together with Russia, form a cluster. Another example is the cluster formed by France, Cambodia, and Gabon (Fig. 2a).

We identified 18 keywords distributed in five clusters, containing three main terms: ‘Bats’, ‘Ectoparasite’, and ‘Nycteribiidae’ (Fig. 4a). The cluster in blue centralized by ‘Bats’ connects most keywords that are restricted to caves (e.g., Caves, Diversity and *Bartonella*) and connects keywords related to the diversity and to the presence of microorganisms in bats and bat flies. The cluster in red, centered by ‘Ectoparasites’, connects most keywords related to general relationships between bats and ectoparasites found in the Neotropics, including several species of bats and parasites. The green cluster, centered by ‘Nycteribiidae,’ connects keywords relative to more specific host-parasite interactions between Madagascar (i.e., endemic fruit bat *Rousettus madagascariensis* G. Grandidier, 1928) and their bat flies. The keywords ‘Bats’ and ‘Nycteribiidae’ are strong connectors between clusters (46 and 30 links, respectively).

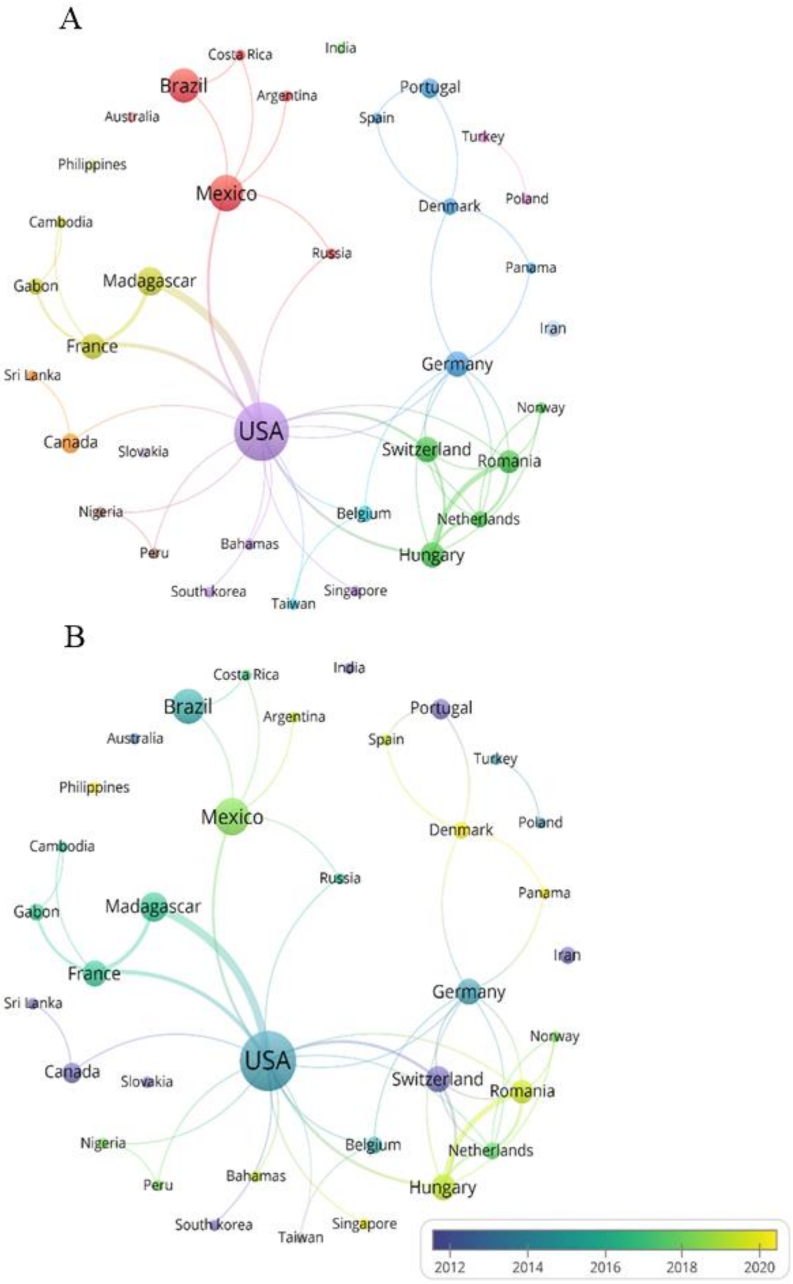

Fig. 2. Collaborative networks for the study of bats and bat–ectoparasites interaction in roosts, including studies primarily produced by researchers affiliated to institutions based in 34 countries, a) total number of publications b) number of publications along time. The size of the nodes represents the number of publications per country, and the lines indicate connections between countries. The scale of years refers to figure B with the darker color representing older publications in the last twenty years.

Classical parasitological descriptors and indexes (e.g., parasite load, prevalence) were the main topics studied in 2011 (Fig. 4b). Starting from 2012 onwards, studies include research on pathogens related to bat and bat fly life cycles as indicated by the appearance of '*Bartonella*' as a keyword. This period is also marked by studies about co-occurrence and interactions of bat flies and other bat ectoparasites and the terms 'Host specificity', 'Spinturnicidae', and 'Bat flies' were recurrent. In 2015, there appear the terms 'Roost' and 'Cave' in the publications. The most recent terms to emerge in the clusters are 'Diversity', 'Host-parasite interactions, 'Madagascar' and 'Hippoboscoidea', from 2017 onwards. (Fig. 4b).

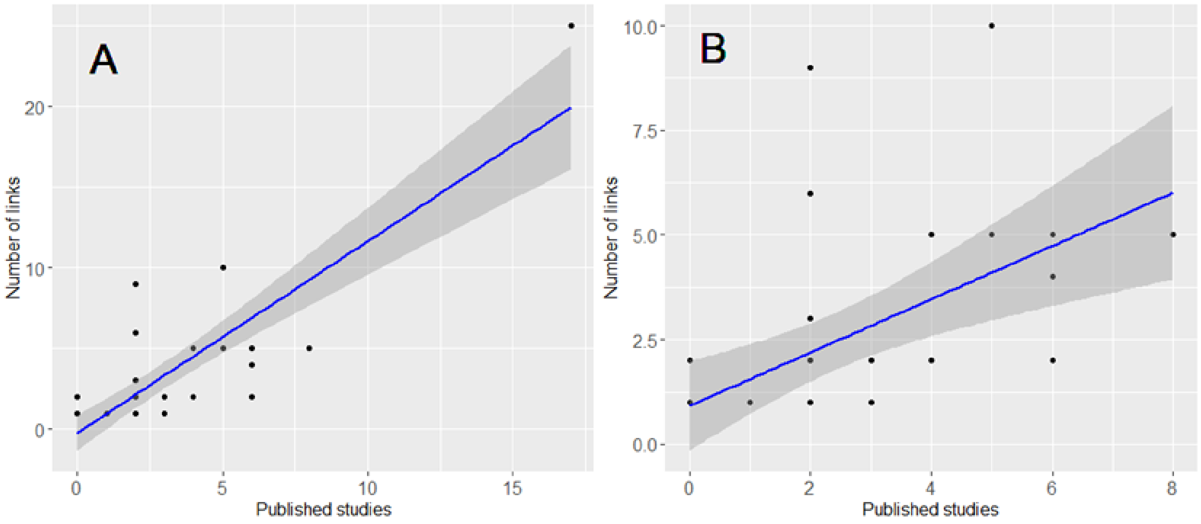

Fig. 3. Relationships between the number of collaborative research and published studies about bats and bat–ectoparasite interaction in roosts from 1996 to 2021. A) all countries; B) all countries except USA.

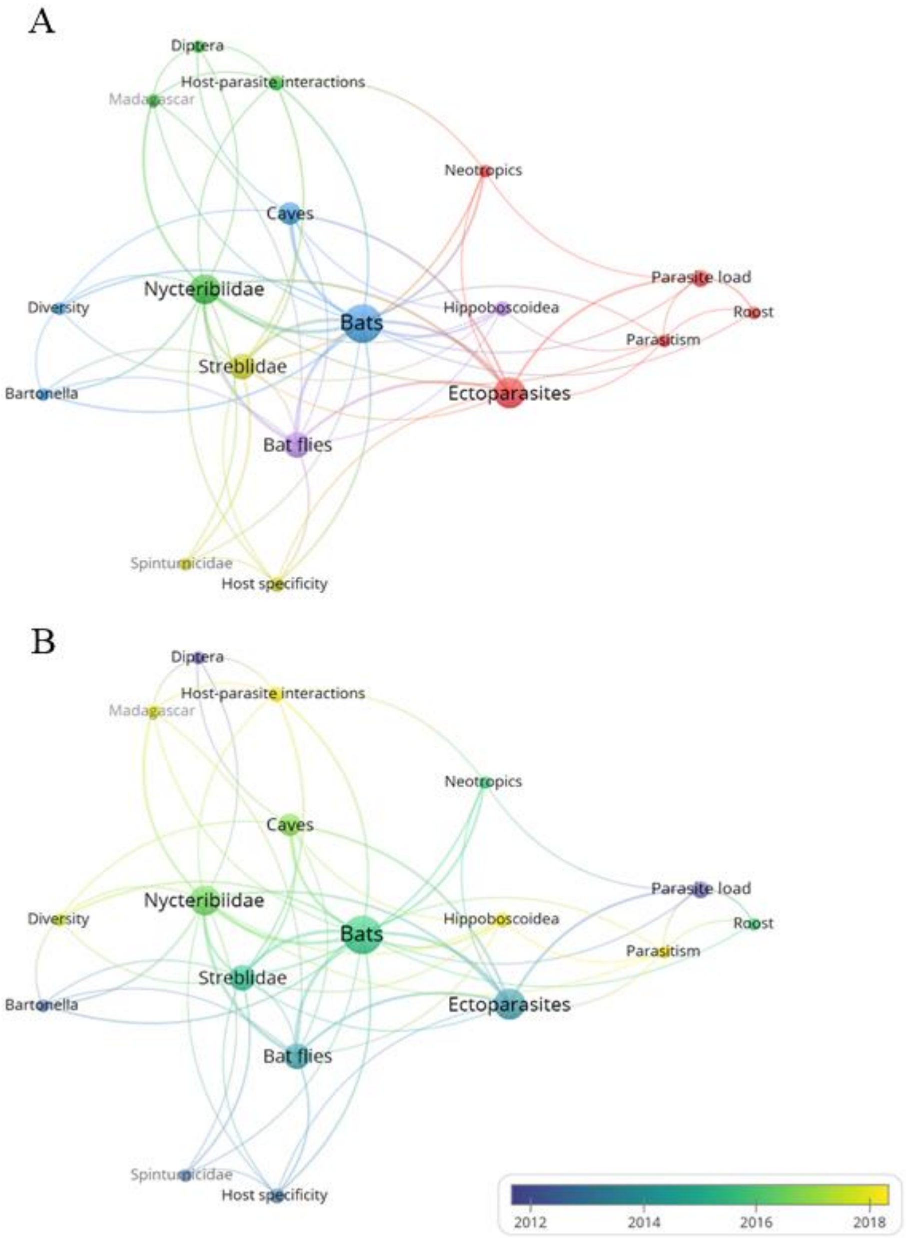

Fig. 4. Keywords network of studies of bat and bat–ectoparasite interactions in diurnal roosts, considering keywords cited at least 3 times displaced as a) clusters colors and b) over time. The size of the node represents the number of occurrences of keywords, and the links indicate the connections among them. The scale of years refers to figure B, and goes from the dark green, older publications to yellow, recent publications.

Discussion

Research about ecology of roosting bats and their parasites has progressed slowly, and increased recently (Zarazúa-Carbajal et al. 2016; Tlapaya-Romero et al. 2021). Early considerations about the importance of the roosts to the bat and bat-ectoparasite ecological interactions, with detailed descriptions about the reproduction and parasitism of bat flies appear in the studies of Wenzel and Tipton (1966) and Wenzel (1976). Stringer and Meyer-Rochow (1996) also contributed with data on bat and bat–ectoparasite interactions in roosts. Almost a decade after, there appear in the literature data on cave bats' ecology, bat roosting preferences, estimates of ectoparasite densities, and reproduction of the bat flies (Reeves et al. 2005; Ter Hofstede and Fenton 2005), about stable isotopes and bat and bat–ectoparasite relationships (Voigt and Kelm 2006), tests of variables potentially constraining the circulation of bat flies among bats (Lourenço and Palmeirim 2008), and on parasite's specificity (Seneviratne et al. 2009). In this period, key findings and hypotheses concerning the bat, bat–ectoparasite and roost interactions were consolidated, such as the high parasite specificity hypothesis, the recurrent findings of bat flies as hosts of pathogens, and the patterns of reproduction of bat flies in caves (Dittmar et al. 2009; Seneviratne et al. 2009).

Significant advances in the study of bat–ectoparasite interactions in their roosts have been made in the last 12 years, including data on the evolutionary history of bat flies (Lack et al. 2011), spatial and temporal effects on bat–fly reproduction (Dittmar et al. 2011), newly proposed parasitological indexes (Esbérard et al. 2012), and endosymbiosis (Morse et al. 2012a). In the second half of the 2010's decade, the use of interaction networks contributed to an alternative way to study the bat and bat-ectoparasite ecological interactions helping to build a broader understanding to studies including eco-epidemiology, endosymbiosis, and hyperparasitism (Fagundes et al. 2017; Sándor et al. 2018; Jensen et al. 2019). From 2020 onwards new data are added to the description of interactions within caves and to the reports of viruses found in bat-flies and in bats (Bennett et al. 2020; Hiller et al. 2021; Tlapaya-Romero et al. 2021).

The growth in number of publications along time was halted in the surge of the pandemics of the new coronavirus, SARS-CoV-2, which in a first view appear to have had overall negative effects in the scientific, non-medical production (Huh 2021). This scenario was complicated because of the limited access to research facilities and universities and of the constraints to fieldwork. On the other hand, perhaps the home-based work enabled to the writing and submission of more manuscripts (Aubry et al. 2021) as suggested by the peak of publications in 2021.

The global concern for detecting and studying pathogens (e.g., '*Bartonella*', 'Ebola') and understanding their life cycles has contributed to increase the number of research groups working with these biological systems (Morse et al. 2012c; Stuckey et al. 2017). Most of these studies included few bat and ectoparasite individuals (<50) for genetic and molecular analysis (Sándor et al. 2018). Apparently, caves have been the preferred study sites of researchers working with zoonoses because they may concentrate many bats, ectoparasites, and guano. The term 'Diversity' in roosts appears indirectly contemplated based on molecular studies (Jansen Van Vuren et al. 2017; Abundes-Gallegos et al. 2018) and directly, in species inventories (Barbier et al. 2018; Tlapaya-Romero et al. 2019). The publication of inventories of bats and their bat-ectoparasites is essential because they can indicate whether each roost should be viewed as a research target, depending on the focus of the research. The remarkable presence of the item ‘Streblidae’ in the red cluster reinforces the dominance of studies in American countries where the family reaches its higher diversity (Dick et al. 2016), and reinforces that this group as more specific to their host than are the nycteribiids.

Parasitological descriptors have been the starting point for studies of bat–ectoparasites interactions in roosts, which seems to coincide with the standardization of several parasitological and statistical terms used in this field (Bush et al. 1997). In the late 1990's the use of several of these indices became popular in bat studies, and the further development of software to calculate them, and new indexes has expanded the use of these descriptors in different contexts (Reiczigel et al. 2019). However, we only found the use of indexes describing parasite loading for bat roosting ecology studies starting in the late 2000's, and mostly beginning in the 2010's decade. Prevalence, mean intensity infestation, and specificity have been the main metrics recorded in roosting bats (Teixeira and Ferreira 2010; Aguiar and Antonini 2011, 2016; Tlapaya-Romero, L., A. Horváth, S. Gallina-Tessaro, E. J. Naranjo 2015), and provide basic information about interspecific interactions between ectoparasites and bats, infracommunities, and ectoparasite populations. However the absence of standardization for the use of these indexes, i.e., the minimum number of hosts, reliability of values, among others, generates misinterpretations about host-parasite relationships (Reiczigel et al. 2019). Although common in other studies (Lourenço et al. 2016) the use of these descriptors in roosting ecology is still incipient and may be useful to disentangle parasitic patterns and help setting methodological standardization for further research.

The expansion of the bat (green) cluster is a result of the exploration of new regions, hosts, and decentralization of studies. *Rousettus madagascariensis* is probably among the most studied bats in Madagascar, including ecological, and epidemiological studies (Andrianaivoarivelo et al. 2012; Cardiff et al. 2012; Obame-Nkoghe et al. 2016; Ramanantsalama et al. 2019). The number of studies in roosts of Madagascar has increased in the last 10 years, most of them conducted in caves (Cardiff et al. 2012). The study of bat flies has then followed, and Madagascar is one of the countries that most publish about the theme.

The centralization of the cluster of 'Nycteribiidae' highlights the focus of studies and diversity of this family in the Old World (Graciolli and Dick 2018), and the study of ectoparasite flies may favor the establishment of other lines of research. In this case, the term ‘Diptera’ had been registered five years before the appearance of the term ‘Nycteribiidae’, and posteriorly, ‘cave’ studies and ‘*Rousettus madagascariensis*’ were recorded.

The inequality of collaboration between countries makes it difficult to consolidate and expand research on bat interactions in their roosts. In the Americas, the larger part of these studies was led by researchers based in the US, Brazil, and Mexico. Our findings may indicate a positive effect of developing local research and promoting international collaboration i.e. boosting the ability to study the roosts and interaction as a consequence of the partnership. The USA has the greatest weight in interactions and connects the main clusters. Several advances in the research of bat and batflies in this country, between 1960 and 1970, with emphasis on entomologists Dr. Vernon J. Tipton, and Dr. Rupert L. Wenzel (Wenzel and Tipton 1966; Wenzel 1976). In this period, several new species and genera were described, and the first partnerships between researchers and institutions emerged. Since then, publications follow in a constant pace from the USA research groups, highlighting the contributions of researchers Dr. Carl W. Dick, Dr. Katharina Dittmar, and Dr. Bruce Patterson. Similarly, the establishment of research in Central and South American countries has been strengthened with research groups from Mexico (e.g., Dr. Juan B. Morales-Malacara), Venezuela (e.g., Dr. Ricardo Guerrero), Brazil (e.g, Dr. Gustavo Graciolli) and Argentina (e.g., Dra. Analía G. Autino). A possible strategy to stimulate research in this topic is to promote partnerships between geographically close countries, e.g., Belgium, Germany, Hungary. Countries far from the Americas and lacking partnerships, according to our data, lag in publications. Another constant scenario is the lack of collaboration between researchers of a same country. In all cases, it appears that collaboration connecting researchers and countries with the potential for studies of bats and their parasites in their roosts is beneficial to advance more rapidly the knowledge on the theme and to help avoiding lacunes leading to the crisis of the biodiversity (Bini et al. 2005).

For that matter we emphasize that countries with more publications tend to form more partnerships with researchers from other countries independently of the research time (years) invested previously. Researchers (herein represented by countries) that started early with this theme of research – bat and bat-ectoparasite interactions in caves and other roosts – (e.g., Brazil) have similar contributions compared to researchers that began working later in the subject (e.g., Mexico). The USA, for example, had its first publication in this theme registered approximately in 2009, similarly to Brazil. Similarly, research conducted in Madagascar date as late as 2016 and counted with an expressive international collaborative network.

International partnership may help preventing local researchers from countries with less resources to perish or publishing only occasionally in the subject (Adams 2012, 2013). However, financial resource limitation to scientific research impair the emergence and development of technological innovations (Wagner et al. 2015; Whitley et al. 2018) and regardless of the willingness of the countries to collaborate, the lack of funding contributes to the countries' distance from a “well-connected world” (Adams 2015).

The overview of the collaborative patterns for the studies on bat and bat–ectoparasite interactions in roosts reveals heterogeneity, often concurrently with differences in terms of country development (Valente-Neto et al. 2021). In Brazil, for example, resources for research were severely cut over the last years, accounting for 92% of budget originally destinated to Science and Technology (De Moura and De Camargo Junior 2017; Santos et al. 2019). Access to resources and misuse of this advantage can contribute for the so-called ‘helicopter surveys’ (Rochmyaningsih 2018; Valente-Neto et al. 2021).

Mexico and Brazil have a high concentration of karstic areas still relatively little studied (Kunz 1982; Lewis 1995; Rodríguez-Durán and Soto-Centeno 2003; Medellin et al. 2017; de Oliveira et al. 2018; Téllez et al. 2018; De Sousa Barros et al. 2021). Parallel to natural roosts, urban spaces offer a variety of artificial roosts for different studies involving bat and bat–fly interactions. Creating a global database on roosts, bats and bat flies could also help to facilitate international collaboration and enhance the study of macroecological patterns for the interaction between bat and their bat flies in their roosts.

Conclusion

The recent use of bibliometric analyzes has made it possible to identify patterns and trends in studies in different contexts considering collaborations between researchers over the globe. Here, we focus on understanding international collaboration patterns and trends in studies of bat and bat-ectoparasite interactions in roosts. Our results showed that studies on this area mainly involve cave roosts and mostly are carried out by the USA, Mexican, and Brazilian researchers, and institutions. In general, countries with more publications make more partnerships with other countries. We suggest that local research development and international collaboration can promote research improvement in countries that are disconnected in networks.

Abbreviations

Not applicable.

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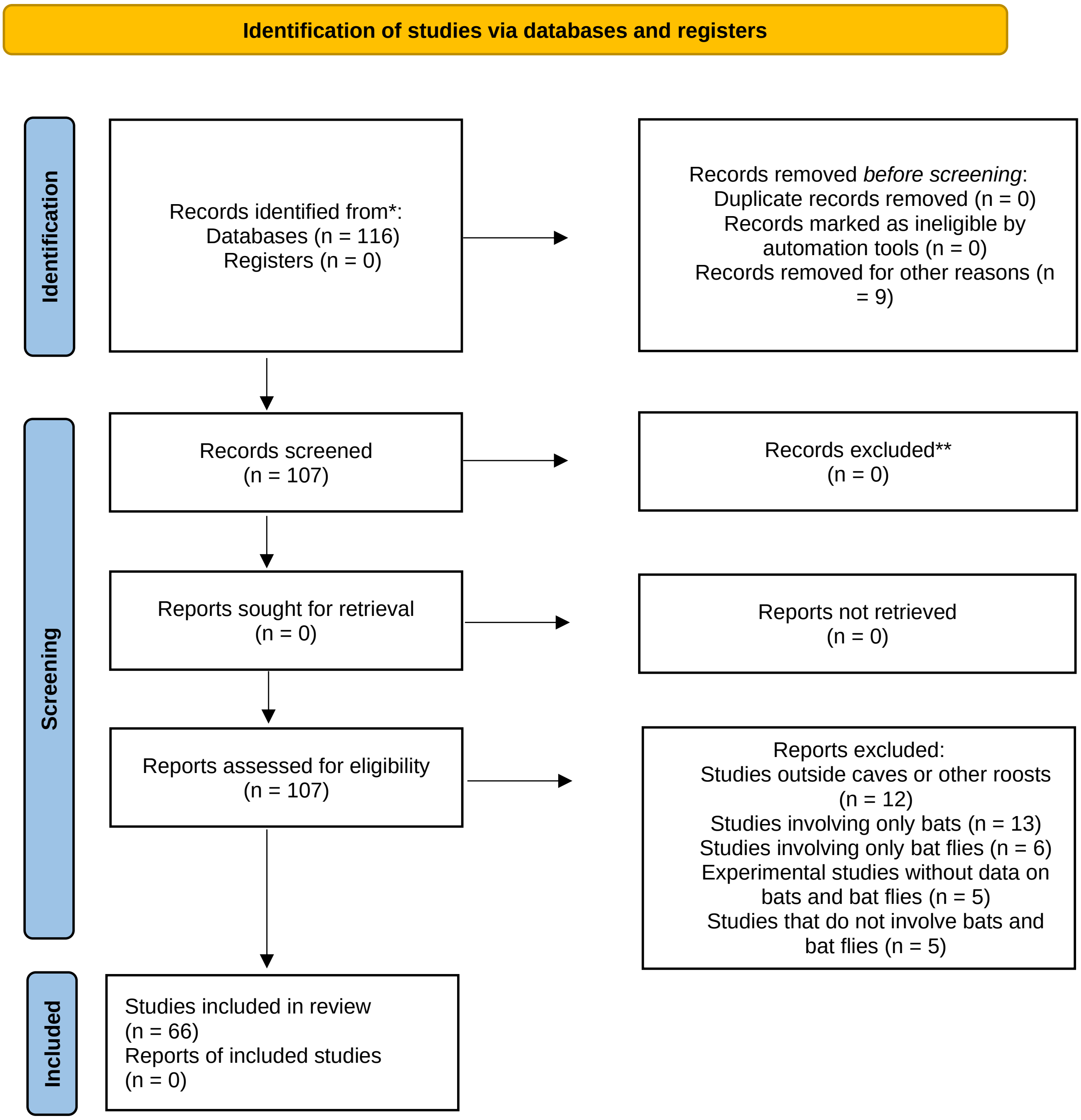
Supplementary Material S1



*Consider, if feasible to do so, reporting the number of records identified from each database or register searched (rather than the total number across all databases/registers).
**If automation tools were used, indicate how many records were excluded by a human and how many were excluded by automation tools.
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CHAPTER II

How does cave microclimate affect bat fly parasitism?

Abstract

Caves offer shelter, protection from predators, and environmental stability that may facilitate reproduction and social interaction among bats. Bat flies (Streblidae) may have also acquired cave roosting habits, given their high specificities and tight associations with their hosts. Streblids are hematophagous flies, obligatory parasites of bats distributed throughout the Neotropical region and often associated with cave-roosting bats. A crescent amount of data have been gathered on Neotropical bats and their ectoparasites in their roosts, but investigations on abiotic factors constraining bat-fly interactions are incipient. In order to estimate the potential influence of the the microclimate of caves in the bat and bat-streblids interaction we tested for the influence of this effect in two sets of caves, namely “hot caves” and “cold caves”, in the interface between Caatingas and Atlantic Forest, in northeastern Brazil. Although both sets of hot and cold caves share the characteristic presence of hundreds to millions of bats, the “hot caves” have unique combinations of extremely high temperature and humidity. A total of 700 cave roosting bats recorded in 16 caves belonging to 19 species five families, we recorded a total of 1.412 bat flies distributed in 29 species. Our findings revealed that temperature and humidity can predict whether a bat is parasitized, and that each of these variables alone do not affect parasitism. Also, larger abundances coupled with high temperatures may decay the potential of parasitism. Seen this, the hot/cold cave systems may constitute excellent models for study of controlling mechanisms for the parasitism, and perhaps experimental models to investigate the effects of climate change mirroring strict host-parasite interactions elsewhere.

Key Words: Streblidae, Chiroptera, host-parasite interaction, cave bats, ectoparasite, hot cave, Caatinga, Atlantic Forest

Introduction

Caves are permanent roosts providing advantages to cave bats, including protection against predators and climatic stability that may be crucial for their life cycle activities, such as reproduction, social interactions, and hibernation (Kunz 1982; Tuttle and Moreno 2005; Altringham 2011; Neil M. Furey and Racey 2016). Microclimatic variation, size, and structural compartmentalization of caves have been suggested as important factors to influence the occupation of caves by bats (Brunet and Medellín 2001; Vargas-Mena et al. 2020). Accordingly, the occupation of the inner space of caves by different bat species is often not random (Kunz 1982; Tejedor et al. 2005; Kunz et al. 2012; Barros et al. 2020), and organisms closely associated with the bats, such as the adult forms of the ectoparasitic flies from the Strebilidae family may follow that distribution.

Streblidae Kolenati,1863 includes approximately 100 species of bat flies broadly distributed in the Neotropical region (Dick and Miller 2010; Alcantara et al. 2019; Guerrero 2019). Bat flies have several morphological adaptations related to bat parasitism, such as the lateral compression of their bodies, their reduced eyes, curved claws, and elongated legs (Peterson and Wenzel 1987; Meier et al. 1999; Dick and Patterson 2006). These flies are highly dependent on their hosts, and consequently on their hosts' roosts also because they may deposit their larvae in the form of pulps in the bat roosts walls (Dittmar et al. 2009, 2015). Previous studies have shown that cave sheltering bats usually have high parasitic loads (Patterson et al.

2007) and that the viability of the pups is correlated to the surface where it is deposited (Dittmar *et al*., 2009). Nonetheless, bats seem to avoid places with high concentrations of pups and flies, shifting their life cycle related activities to other parts of the cave, to avoid parasitism (Reckardt and Kerth 2007a).

Neotropical cave systems are heterogeneous in terms of abiotic and biotic elements, including bat composition and abundance (Ladle et al. 2012; Luo et al. 2013; Medellin et al. 2017), and likely for the associated bat fly composition. Whilst most Neotropical caves have stable microclimate patterns set at values close to the average external, local temperature (cold caves), the so-called hot caves, or “cuevas calientes” stabilize at very high combined values of temperature and humidity compared to the average outside temperature (Iskali and Zhang 2015; Medellin et al. 2017; Pimentel et al. 2022). Hot caves are characterized by possessing a small unique entrance, low inner air circulation, high temperatures year-round (28-40ºC), nearly constant, high humidity (over 90%), and the presence of large gregarious bat populations. This gregarious amount of bats, contains thousands of individuals (e.g. *Pteronotus* species, *Phyllonycteris poeyi*) (Taboada 1979; Da Rocha et al. 2011), which may segregate in different parts of the cave, such as chambers with different temperatures (Taboada 1979; De La Cruz 1992; Tejedor et al. 2005). Hot caves are a unique, diverse and poorly known system composed of a strict combination of these abiotic and biotic characteristics (Taboada 1979; De La Cruz 1992; Tejedor et al. 2005; Pimentel et al. 2022).

Studies of bat communities occupying hot caves have been conducted in Venezuela, Mexico, and in the Caribbean karst (Bateman and Vaughan 1974; Taboada 1979; Bornaccorso et al. 1992; De La Cruz 1992) and cold caves globally (Iskali and Zhang 2015; Medellin et al. 2017; Pimentel et al. 2022). Only recently has the phenomenon of hot caves have been recorded in Brazil, as it was recorded in Caatinga lands of Northeastern Brazil interspersed with patches of Atlantic Forest (Da Rocha et al. 2011; Rocha 2013; Pimentel et al. 2022). The semi-arid Caatinga is a biome exclusively found in Eastern Brazil that includes mosaics with karstic landscapes with several caves. The Caatinga harbors approximately 96 species of bats (da Silva et al. 2018; Garbino et al. 2022) some of them caatinga endemics species of cave dwelling bats, such as *Xeronycteris vieirai* Gregorin & Ditchfield, 2005 and *Lonchophylla inexpectata* Moratelli & Dias, 2015 (Vargas-Mena et al. 2018; Otálora-Ardila et al. 2020).

Herein, we evaluate the effects of extreme microclimate differences on the parasitism of ectoparasitic bat flies considering “hot caves” and “cold caves”. Our expectations were (i) that higher temperatures in caves would limit the parasitism, given that bat flies depend on specific conditions for reproduction (Dittmar et al., 2009); (ii) that the high humidity would favour bat flies interactions due to fly dependence on moist substrates that prevent their pupae from dehydration (Dittmar et al. 2009; Szentiványi et al. 2019b; Tlapaya-Romero et al. 2021); (iii) that the cave type (hot or cold cave) may constrain parasitism, given that they have different internal characteristics that could affect occupancy by bats including airflow, chamber structure, and cave entrance, temperature, and humidity (De La Cruz 1992; Dittmar et al. 2009; Tlapaya-Romero et al. 2021); and iv) that hot caves may help selecting for a lower richness and abundance of bats and their ectoparasitic bat flies due to higher temperatures and humidity (De La Cruz 1992; Tlapaya-Romero et al. 2021).

Material and Methods

Study Area

We sampled bats and their ectoparasites in 16 caves distributed in eastern South America, in the Northeastern Brazilian states of Ceará, Rio Grande do Norte and Sergipe (Fig.1). The caves are distributed in mosaics along the Brazilian Northeastern landscapes, where predominates the semi-arid Caatinga and there also are, in a lesser extent, ecosystems related to the Atlantic Forest biome (Table 1). The semi-arid Caatinga vegetation includes deciduous xerophytic Caatinga, forests with thorny shrubs and open dry forested vegetation (Lemos and Meguro 2010; Ipece 2012; Bento et al. 2013). The Atlantic Forest sites have xeromorphic tropical semideciduous forests – the "Cerrado do Araripe" interspersed with typical Atlantic forest vegetation, and it is the landscape surrounding the caves (Figueira 1989; Costa et al. 2004). Semi-arid locations can be classified as BSh (Köppen), with hot and semi-arid climate and a rainy autumn and the Atlantic Forest sites as Aw (Köppen) with a humid tropical climate with, dry winters and humid summers (Peel et al. 2007). We characterized six of these caves as hot caves, according to the parameters defined by (Taboada 1979; De La Cruz 1992) and ten other caves as "cold caves or bat caves", as described by (Medellin et al. 2017) (Table 1).

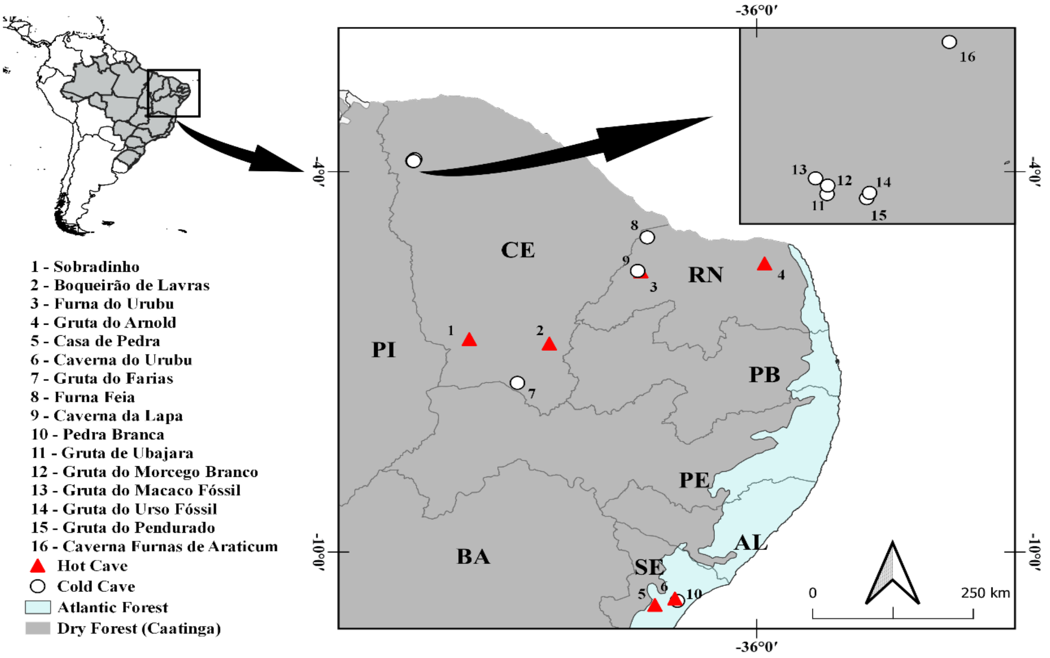

Fig. 1. Hot and cold caves sampled for bats and their bat flies in Eastern South America, northeastern Brazil. Abbreviations are Brazilian states PI = Piauí; CE = Ceará; RN = Rio Grande do Norte; PB = Paraíba; PE = Pernambuco; AL = Alagoas; SE = Sergipe; BA = Bahia).

Table 1. General physical characteristics with location and biome of caves sampled for bats and their bat flies Eastern South America, northeastern Brazil.

Cave	**Coordinates**		**Biome**	**System type**	**Lithology**	**Length (m)**
	Latitude	**Longitude**				
Sobradinho	6°38'35.53"S	40° 5'57.08"W	Caatinga	Hot cave	Sandstone	-
Boqueirão de Lavras	6°42'44.65"S	38°57'27.63"W	Caatinga	Hot cave	Sandstone	200
Furna do Urubu	5°34'22.97"S	37°39'8.71"W	Caatinga	Hot cave	Limestone	250
Gruta do Arnold	5°26'54.96"S	35°53'12.85"W	Caatinga	Hot cave	Limestone	87
Casa de Pedra	10°50'3.08"S	37°27'3.56"W	Atlantic Forest	Hot cave	Sandstone	210
Caverna do Urubu	10°43'58.47"S	37° 9'56.12"W	Atlantic Forest	Hot cave	Sandstone	195
Gruta do Farias	7°19'59.15"S	39°24'46.47"W	Atlantic Forest	Cold cave	Sandstone	150
Furna Feia	5°2'12.76"S	37°33'36.64"W	Caatinga	Cold cave	Limestone	739.1
Caverna da Lapa	5°33'58.58"S	37°41'51.74"W	Caatinga	Cold cave	Limestone	-
Pedra Branca	10°46'18.37"S	37° 7'53.49"W	Atlantic Forest	Cold cave	Limestone	100
Gruta de Ubajara	3°49'59.60"S	40°54'0.52"W	Atlantic Forest	Cold cave	Limestone	1,120
Gruta do Morcego Branco	3°49'53.68"S	40°54'0.10"W	Atlantic Forest	Cold cave	Limestone	274
Gruta do Macaco Fóssil	3°49'48.64"S	40°54'7.74"W	Atlantic Forest	Cold cave	Limestone	50
Gruta do Urso Fóssil	3°49'58.74"S	40°53'33.81"W	Atlantic Forest	Cold cave	Limestone	195
Gruta do Pendurado	3°50'2.46"S	40°53'35.60"W	Atlantic Forest	Cold cave	Limestone	194
Caverna Furnas de Araticum	3°48'13.84"S	40°52'43.65"W	Atlantic Forest	Cold cave	Limestone	200

Data Collection

We captured cave bats and their bat flies during three expeditions conducted in July, October 2019, and February 2022. Before each capture, we entered each cave with a metric tape, KG100 data logger (±1°C -10 to 50°C) and an AK28 thermo-hygrometer (±1°C -10 to 50°C) to make observations and took notes on: i) location of places used as roosts in each cave, ii) distribution of roosting bats (species and individuals) along the cave, iii) microclimate parameters (temperature and humidity), and iv) distribution of bat flies and pupae in the environment inside the cave. These observations were conducted in absolute silence and carefully to avoid disturbance and stress to the colonies, using slow movements and low lighting. After taking notes of all observations, we started the capturing session using hand nets inside the caves, strategically positioned and carefully supervised mist nets (3.0m x 1.5m), and harp traps set at the entrance of each cave. We placed each captured bat in a separate cloth bag to avoid contamination between them (i.e., flies in unusual hosts). As captures occurred at different periods of the day (e.g., night, afternoon), we used the average temperature and humidity of each roost for further analysis.

Bats were identified following the identification keys and specialized bibliography for some taxa individually (Gardner 2008; Díaz et al. 2021). Each bat was carefully examined for bat flies, which were collected with entomological forceps, and kept in microtubules pre-filled with 70% ethanol. Each bat was then identified, weighted, had the forearm measured, and was released often in the same place it was captured. We posteriorly identified the flies in the lab using a stereomicroscope (40x), following the dichotomous keys provided by several authors (Wenzel and Tipton 1966; Wenzel 1976; Guerrero 1994, 1995, 1996). All flies collected were deposited in the Entomological Collection of Federal University of Paraíba (UFPB). This research has been authorized by the Chico Mendes Institute for Biodiversity Conservation under the licenses ICMBio / SISBIO, number of processes: # 10,566; request: 72,660, 72,678 and 52,492-3 and ABIO #45, 2021).

Data analysis

Initially, to assess differences in the composition of bats and flies (dependent variable - abundance) in hot and cold caves (predictor variable) and, we performed a principal coordinate analysis (PCoA) using Bray-Curtis distance matrix method to standardize the data in *vegan* package (Oksanen et al. 2022). Additionally, we tested the normality and homogeneity of the variance of richness and abundance of bats and bat flies using the QQ-plot, Shapiro-Wilk, and Levene's test. Subsequently, we performed a t-test to compare the averages of these data between the two types of systems using the *vegan* package (Oksanen et al. 2022).

For all ectoparasite data, we tested the residues for the presence of zero-inflation and overdispersion using *performance* package (Lüdecke et al. 2021). We used a Hurdle distribution model with a truncated negative binomial (hurNB) to all model structures, i.e., disregarding zeros, and two zero-inflated models using negative binomial distribution (ZINB) and Poisson (ZIP), as implemented in the *glmmTMB* package to standardize the data (Brooks et al. 2017). Data were divided into two sets according to the Hurdle models (or zero-altered models): i) data greater than 1 were transformed in presence-absence (e.g. binomial distribution) and ii) considering only positive values with no zero (e.g., Poisson or truncated negative binomial) (Brooks et al. 2017; Da Silva et al. 2022). The truncated distribution assumes that both, ecology and sampling errors, indistinguishably generate zeros (Blasco-Moreno et al. 2019; Da Silva et al. 2022), so these zeros are excluded from the distribution with count data.

The ZINB and ZIP models operate similarly but allow the presence of zeros from the Poisson distribution. In these models, zeros are considered the result of ecological pattern, e.g., the absence of specific habitat (Blasco-Moreno et al. 2019; Da Silva et al. 2022). The interpretation of these results must be performed contrasting with both the conditional and zero-inflated model (Brooks et al. 2017). The use of zero-inflated models in the analysis of the bat-fly interaction allows to account for the differentiation of absence (zero) errors versus the real absence of flies in the study area (Pilosof et al. 2012).

We used a series of five generalized linear models (GLMs) using different distributions (*Poisson* and *Negative binomial*) to verify the influence of abiotic variables on the prevalence of bat flies parasites and choose the best model under the criterion dAICc (< 2) and Akaike Weights (Table 3). Models were set to not discriminate among host species, as we wanted to investigate the response of general fly abundance in the cave. We also tested the predictor variables to avoid higher collinearity (<0.7). We considered the effects of temperature (Temp), humidity (Humi), type of cave (Type), and interactions among these variables. As the dAICc values isolated cannot serve to define parameters for a good fited model, we performed diagnoses using the *DHARMa* package as an additional test of models' adequacy in terms of variance homogeneity, outliers, and overdispersion (Hartig 2017). All analyzes were performed in the R environment 4.2.1 (R Core Team 2022).

Results

We captured a total of 700 bats of 19 species, belonging to the families Phyllostomidae (13 sp.; n = 475), Mormoopidae (3 sp.; n = 209), Furipteridae (1 sp.; n = 1) Emballonuridae (1 sp.; n = 1), and Natalidae (1 sp.; n = 1) (Supplementary Material S1). The most abundant bat species were *Pteronotus gymnonotus* (n = 184), followed by *Phyllostomus discolor* (n = 175). We collected 1,412 bat flies (Streblidae) from 29 species. The most abundant fly species were

Nycterophilia fairchildi (n = 223; 15.7% of total), and *Trichobius johnsonae* (n = 204; 14.4% of total). The richness and abundance of bats (17 sp.; n = 482) and ectoparasitic flies (27 sp.; n = 857) were larger in cold caves. However, the richness (t_{14} = 1.04; p-value = 0.31) and abundance (t_{14} = 0.69; p-value = 0.50) of bats were not significantly different between hot and cold caves. Similarly, for the richness (t_{14} = 1.67; p-value = 0.11) and abundance (t_{14} = 0.05; p-value = 0.95) of bat flies. A total of 615 individuals (87.8%) from 17 species of bats recorded were parasitized by at least one species of bat fly, except for *Furipterus horrens* and *Peropteryx macrotis*. Bat species most parasitized were *Pteronotus gymnonotus* (n = 170; 92.3%) and *Phyllostomus discolor* (n = 175; 100%). We recorded the formation of two consistent groups of bat and fly species distributed according to the type of cave system (Fig. 2).

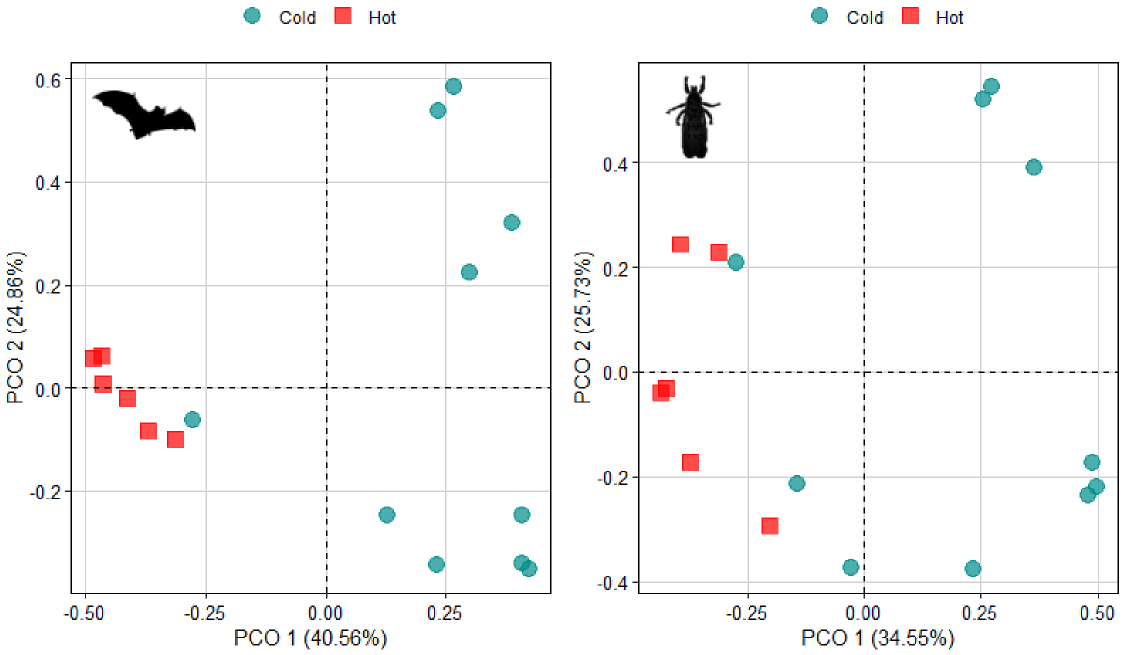

Fig. 2. PCoA plot sorting bat and fly species sampled in hot and cold caves between 2019 and 2022 in the Caatinga and Atlantic Forest, northeastern Brazil.

Bats were distributed along photic and aphotic zones of the caves. Colonies of the hematophagous bat *Desmodus rotundus* (Desmodontinae) usually used the transition between photic and aphotic, tending to displace toward the entrance and distant from it by approximately three to 10 m, with the proximity of the entrance for this species more evident in hot caves. Several other bat species roosted closer to the entrances of the caves, such as the fish-eating bat *Noctilio leporinus* (Noctilionidae), which preferentially occupied crevices (e.g., Boqueirão de Lavras), the nectar-feeding bat *Anoura geoffroyi* (Glossophaginae) (e.g., "Sobradinho" cave) and the small insect feeder *Furipterus horrens* (Furipteridae) (e.g., "Gruta de Ubajara"). *Pteronotus* bats occupied only the aphotic areas in all caves, forming large colonies distributed in one to three small chambers in the caves (e.g., > 2,000 individuals).

Most bat species did not segregate inside the caves, often roosting closely in contact with other species (e.g., *A. geoffroy*, *C. perspicillata* and *P. gymnonotus* in "Gruta do Farias" cave). On the other hand, we observed that colonies of the omnivorous foliage gleaner *Phyllostomus discolor* kept roosting markedly segregated from other species in cold caves such as a colony (> 200 individuals) found in the "Furna Feia" cave, another found in "Gruta de Ubajara" (> 3,000) and another one in the "Furnas de Araticum" cave (1,000 individuals), far from other species.

In the cold caves, the puparium was located on average three meters from the bat roost (e.g., Gruta do Farias Cave, Pedra Branca Cave) and few flies were found flying in the surroundings. On the other hand, in hot caves, the puparium and flies were placed together and close to the colony of *Pteronotus* (e.g., in the "Boqueirão de Lavras" cave, "Casa de Pedra" cave). We observed the flies *N. fairchild* and *T. johnsonae* constantly flying an trying to hit bats on their way to leave or to enter the chamber (Fig. 3).

The best model to fit our data was Hurdle distribution (Table 2). The coefficients for the variables temperature and humidity were significant for the excess of zeros (i.e., presence-absence of the fly) (Table 3). Therefore, temperature and humidity only determine whether the bat will be or not be parasitized in a cave environment (Fig. 3). The positive contrast of the variables in the conditional part of the model suggests that the higher the temperature and humidity, the lower is the chance of parasitism. The interaction between temperature and humidity is significant only to the excess of zeros (Table 3). Thus, the incidence of parasitism depends on the interaction between temperature and humidity of the roosting place (Fig. 4). As for the type of cave, the contrast of values is negative for hot caves, i.e., in this environment there is a greater chance of a bat be parasitized than in cold caves. The values of the estimated coefficients for the types of caves are different between the models. Values are low for the abundance of flies, which in cold caves is slightly higher (Table 2).

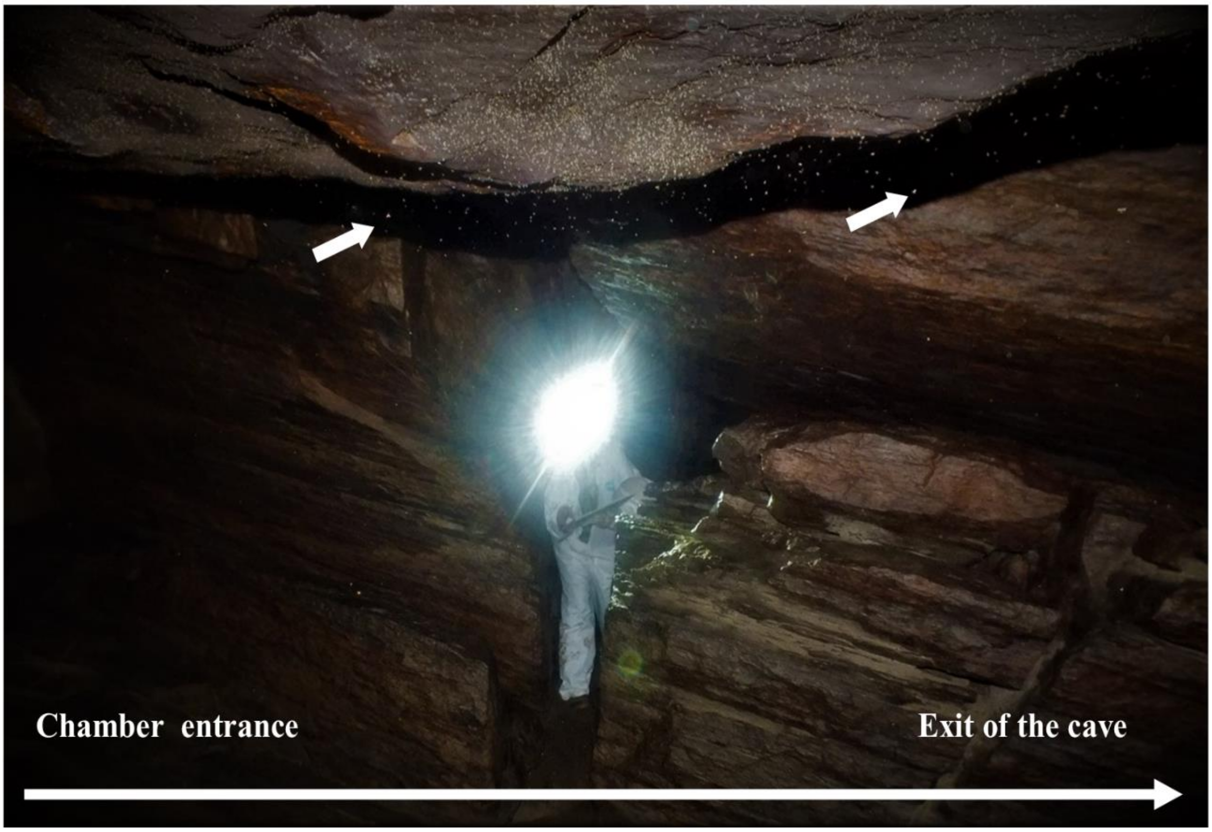

Fig. 3. Bat flies at the entrance to *Pteronotus gymnonotus* bat shelter in hot cave Boqueirão de Lavras. The arrows indicate the "target shooting" behavior. Note the cave wall with individuals of *Nycterophilia fairchildi* and *Trichobius johnsonae* (Photographed by Raquel Soares).

Discussion

Cave microclimate affects the abundance of ectoparasitic flies in bats and appears to affect their behavioral revealing different patterns of parasitism, and our results may provide a basis for understanding bat-fly relationships in cave environments. Notwithstanding the climatic stability of caves is an advantage offered to bats and ectoparasitic flies (Dittmar et al. 2009; Kunz et al. 2012), and this variation the distinct composition of hosts and flies between the extreme cave types (hot and cold caves) seems to be a limiting factor for hosts and parasites in combination with the structure of the cave. Microclimate is apparently a determining factor in the probability of parasitizing a bat and for the survival of the flies in the cave.

Table 2. Comparison between models used to test the effect of microclimatic variables and cave types in the abundance of streblids in cave bats of the Caatinga and Atlantic Forest of northeastern Brazil.

Model ranks	**Structure models**	**Type of model**	**dAICc**	***df***	**weight**
1º	A~Temp*Humi+Type	Hurdle models	52	11	<0.001
2º	A~Temp+Humi+Type	Zero-inflated	58.4	9	<0.001
3º	A~Temp+Humi	Zero-inflated	60.1	7	<0.001
4º	A~Humi	Hurdle models	70.5	5	<0.001
5º	A~Temp	Hurdle models	70.9	7	<0.001

Table 3. Parameters obtained from the GLM for the best model (1st in Table 1) describing the effect of microclimatic variables and cave type on the abundance of streblids in cave bats collected in the Caatinga and Atlantic Forest, northeastern Brazil.

	Parameter estimate	**SE**	**Z**	***P value***
Conditional model				
Intercept	-9.50	8.52	-1.11	0.26
Temp	0.42	0.31	1.33	0.18
Humi	0.10	0.09	1.11	0.26
TypeHot	0.14	0.28	0.50	0.61
Temp:Humi	-0.00	0.00	-1.29	0.19
Zero-inflation model				
Intercept	-37.38	8.30	-4.49	**<0.001**
Temp	1.37	0.31	4.42	**<0.001**
Humi	0.41	0.09	4.33	**<0.001**
TypeHot	-0.75	0.25	-2.94	**0.01**
Temp:Humi	-0.01	0.00	-4.28	**<0.001**

Thus, the composition of bat flies is correlated with hosts found in caves and with the microclimate of caves (Dick and Gettinger 2005; Eriksson et al. 2019). There is a high percentage of bat fly species recorded during our study that also occur along the mosaic of Caatinga and Atlantic Forest biomes from northeastern Brazil (86.2%, 25 species) (Barbier and Bernard 2017; Barbier et al. 2019a, c, b; da Silva et al. 2021). This faunal similarity may be related to the presence of some species frequently registered outside caves influenced by the regional pool of species (e.g., *A. phyllostomatis*, *T. costalimai*, *S. ambigua*) occurring in different Brazilian biomes (Lourenço et al. 2016; Graciolli 2022). The proportion of species commonly found in caves (e.g., *T. parasiticus*, *N. fairchildi*, *T. johnsonae*) in our study is similar to that of other studies carried out in caves throughout the Neotropical region (Fagundes et al. 2017; Rivera-García et al. 2017; Cuxim-Koyoc et al. 2018; Tlapaya-Romero et al. 2019). However, tt is noteworthy that the species *Anastrebla modestini*, *N. fairchildi*, *Strebla alvarezi* e *Trichobius handleyi* were recorded for the first time, in our study in the Caatinga.

The success of streblids to parasitize bats is microclimate-related according to our results and also to the host's fidelity to the roost (Patterson et al. 2007). This may be explained by the placement of pupae, which are deposited directly on the wall of the hosts' roosts (Dittmar et al. 2009) facilitating vertical parasitism, and by the ideal microclimate temperature and humidity gradients (Marshall 1982; Dittmar et al. 2009). In the absence of stability in these variables the pupal development may be inviable, decaying the abundance of flies in contact with the host (Dittmar et al. 2009; Szentiványi et al. 2019b). Moreover, fluctuations in temperature have negative effects on the prevalence and average abundance of flies in caves (Tlapaya-Romero et al. 2021). Streblids and pupae are difficult to find out of their hosts and in the cave walls due to their placement, often high and out of sight, and because of the types of substrates (Dittmar et al., 2009). The height of the roost and the puparium can vary, staying placed from a few meters to many meters above ground (e.g., at approximately one meter in Gruta do Farias Cave and approximately eight meters in Sobradinho Cave). This implies that although temperature, humidity and roost fidelity (of hosts) interfere in parasitism, the idiosyncrasies of roosts must be considered to elucidate how the microclimate modulates these relationships.

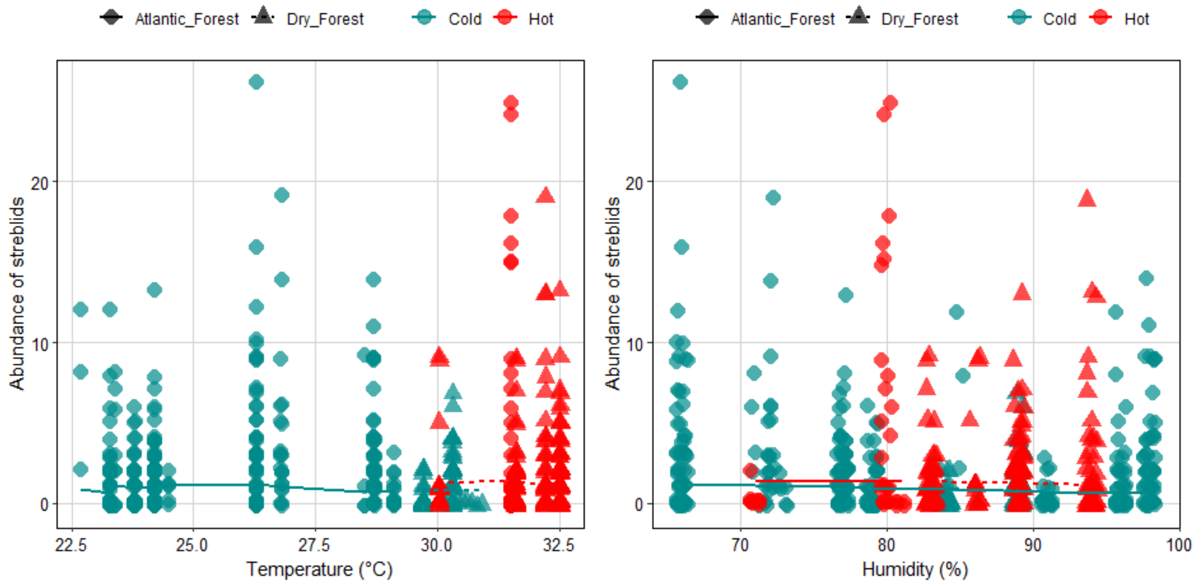

Fig. 4. Bat fly abundance in bats predicted from GLM (Hurdle model) across the range of temperature and humidity in hot and cold caves in Caatinga and Atlantic Forest locations in the northeastern Brazil.

The lower probability of parasitism in extreme microclimatic conditions could be a result of a trade-off between the costs of permanence of flies in this scenario and the possibility of parasitism (Reckardt and Kerth 2007b). The aggregation of bats (i.e., *Pteronotus*) in nursery chambers promotes high temperatures that push the flies out of the chamber, which is similar to the behavior of bats to avoid roosts with many flies (Patterson et al. 2007; Dittmar et al. 2009), maybe an “antiparasitic strategy” specific to this host genus, *Pteronotus*. In contrast, the higher probability of parasitism in hot caves may be related to responses of flies to the antiparasitic strategy. The dynamics of the flies might include remaining strategically away from the warmest parts of the cave, and performing “target shootings”, i.e., the flies make short flights to arrive at the host (Fig. 3). The behavior of flies and the different patterns of cave occupation of are still poorly studied and this understanding may be crucial to elucidate the delicate balance between extreme microclimate variation, roost structure, host choice and fitness of bat flies, perhaps helping to the identification of exclusive bats and bat flies associations for hot caves (e.g., symbionts) (Morse et al. 2012b).

The roosting behavior of the bat species and the structure of the cave can interfere with the probability of parasitism and the distribution of flies. It appears that some hosts' behaviors can induce parasitism patterns (Patterson et al. 2007). The low tolerance of *D. rotundus* to high temperatures (Wilkinson 1986) may explain its avoidance of deeper regions in hot caves. Thus, its presence closer to the cave entrances inflates the abundance of *T. parasiticus*, an associated streblid parasite, and makes fly prevalence higher when compared to previous data, e.g., from cold caves in the Cerrado neotropical savanna (Aguiar and Antonini 2011, 2016).

The distances between colonies and host social organization of bats in cold caves may lower the accidental association of the flies with unusual hosts (van Schaik and Kerth 2017). The specificity tends to be high in cold caves as also observed in other studies (Dick and Gettinger 2005; Dick 2007; Santos et al. 2013; de Vasconcelos et al. 2016; Barbier et al. 2019c) and it is related to the lower survival rates of flies in a unusually hot cave (Fritz 1983). Hot caves, conversely, tend to shelter patterns of low specificity, which is related to the host compositions. In Brazilian hot cave systems predominate the species *P. gymnonotus, P. personatus* e *P. rubiginosus* (approximately 86%) mainly parasitized by the flies *N. fairchildi, N. parneli* e *T. johnsonae*. Due to the high temperatures and humidity in this system, these flies may be unable to remain on the bats' roost for longer periods.

The structural (i.e., chambers, tunnels) and microclimatic variability of cold caves provide optimal conditions to roost for several bat species. This seems to be the main reason for the greater richness and abundance of bats in this type of cave. In addition, it is common for the presence of non-cave specialists (e.g., *Artibeus planirostris*) that use the cave only as a temporary roost (Barros et al. 2020).

Regardless of host richness and abundance, hot and cold caves are key habitats for bat conservation strategies in Brazil. The presence of large bat assemblages associated with both caves systems, and the vulnerability of cave bats species according to the Brazilian red list assessments (ICMBio 2021) (*F. horrens* and *N. macrourus*) reinforces the importance of caves, for conservation. The unicity of these complex systems, including a large assemblage of bats, reaches a maximum of specialty in hot caves, which are rare and poorly known (Ladle et al. 2012; Pimentel et al. 2022).

Several threats to cave systems have been recognized (i.e., mining, extractive activities and, agribusiness) (Bernard et al. 2012; Ladle et al. 2012) with habitat loss and cave destruction being the major problems (ICMBio 2021). It has been estimated for example that approximately 54% of the natural habitat of the cave specialist *N. macrourus* had been lost (Delgado-Jaramillo et al. 2017). Notably, as the bats are threatened there are consequences for the cave systems, and associations of bats and bat fly, specially to vulnerable species as *F. horrens* and *N. macrourus* (Barbier et al. 2016).

Conclusion

Our study confirms that the presence of both cave systems is relevant to bat-fly associations and it may be key to understanding roosting patterns of this exclusive semi-arid biome from Brazil. Our findings also suggest the presence of a microclimatic threshold for this parasitism to occur and that intrinsic factors of caves and hosts may influence interactions. Thus, research is needed to assess how the behavior, thermal tolerance, and landscape matrix influence the parasitism of flies in bats.

Abbreviations

Not applicable.

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The authors have no conflicts of interest to declare.

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Supplementary Material S1

List of species of bats (Chiroptera) and bat flies (Streblidae) in hot caves and bat (“cold”) caves, northeastern Brazil, collected between July of 2019 and February of 2022. * = non-primary association.

Hot Caves	
Boqueirão de Lavras	
Host (n)	**Bat flies (n)**
Big Naked-backed Bat, *Pteronotus gymnonotus* (38)	*Trichobius johnsonae* (32)
	Nycterophilia fairchildi (56)
	Nycterophilia parnelli (5)
Wagner’s Mustached Bat, *Pteronotus personatus* (13)	*Nycterophilia fairchildi* (16)
	Trichobius johnsonae (4)
Furna do Urubu	
Big Naked-backed Bat, *Pteronotus gymnonotus* (47)	*Trichobius johnsonae* (38)
	Nycterophilia parnelli (10)
	Nycterophilia fairchildi (4)
Vampire bat, *Desmodus rotundus* (3)	*Trichobius parasiticus* (26)
Gruta do Arnold	
Big Naked-backed Bat, *Pteronotus gymnonotus* (52)	*Nycterophilia fairchildi* (116)
	Nycterophilia parnelli (3)
	Trichobius johnsonae (1)
Sobradinho	

Big Naked-backed Bat, *Pteronotus gymnonotus* (12)	*Trichobius johnsonae* (7) *Nycterophilia fairchildi* (16) *Nycterophilia parnelli* (3)
Funnel-eared Bat, *Natalus macrourus* (7)	*Trichobius* sp. (3)
Geoffroy’s tailless bat, *Anoura geoffroyi* (3)	-
Vampire bat, *Desmodus rotundus* (2)	*Trichobius parasiticus* (14) *Strebla wiedmani* (3)
Wagner’s Mustached Bat, *Pteronotus personatus* (1)	-
Common mustached bat, *Pteronotus* cf. *rubiginosus* (1)	*Trichobius johnsonae* (2) *Nycterophilia parnelli* (2) *Nycterophilia fairchildi* (1)
Casa de Pedra	
Vampire bat, *Desmodus rotundus* (10)	*Trichobius parasiticus* (2)
Funnel-eared Bat, *Natalus macrourus* (2)	-
Big Naked-backed Bat, *Pteronotus gymnonotus* (2)	-
Geoffroy’s tailless bat, *Anoura geoffroyi* (1)	-
Urubu	
Vampire bat, *Desmodus rotundus* (10)	*Trichobius parasiticus* (139)
Wagner’s Mustached Bat, *Pteronotus personatus* (10)	*Trichobius johnsonae* (4) *Nycterophilia fairchildi* (1) *Trichobius parasiticus* (1)*
Big Naked-backed Bat, *Pteronotus gymnonotus* (4)	*Nycterophilia fairchildi* (10) *Trichobius johnsonae* (3)
Cold Caves	
Gruta do Farias	
Big Naked-backed Bat, *Pteronotus gymnonotus* (29)	*Trichobius johnsonae* (112) *Nycterophilia fairchildi* (3) *Nycterophilia parnelli* (12) *Exastinion clovisi* (1)* *Trichobius propinquus* (2)*
Geoffroy’s tailless bat, *Anoura geoffroyi* (21)	*Exastinion clovisi* (11)

	Anastrebla modestini (3)
	Trichobius propinquus (14)
	Trichobius johnsonae (1)*
Seba’s short-tailed bat, *Carollia perspicillata* (3)	*Speiseria ambigua* (4)
	Trichobius tiptoni (5)*
Pallas’s long-tongued bat, *Glossophaga soricina* (1)	*Speiseria ambigua* (1)*
Furna Feia	
Pale spear-nosed bat, *Phyllostomus discolor* (53)	*Trichobius costalimai* (69)
	Trichobioides perspicillatus (8)
Thumbless Bat, *Furipterus horrens* (1)	-
Lapa	
Flat-faced fruit-eating bat, *Artibeus planirostris* (35)	*Aspidoptera phyllostomatis* (1)
Pale spear-nosed bat, *Phyllostomus discolor* (17)	*Trichobius costalimai* (9)
Lesser Dog-like Bat, *Peropteryx macrotis* (2)	-
Pedra Branca	
Vampire bat, *Desmodus rotundus* (12)	*Trichobius parasiticus* (3)
Tomes’s sword-nosed bat, *Lonchorhina aurita* (7)	*Strebla altmani* (5)
	Trichobius flagellatus (2)
Seba’s short-tailed bat, *Carollia perspicillata* (4)	-
Gruta de Ubajara	
Pale spear-nosed bat, *Phyllostomus discolor* (84)	*Trichobius costalimai* (115)
	Trichobioides perspicillatus (23)
	Mastoptera minuta (15)
	Strebla hertigi (5)
	Strebla mirabilis (3)
	Trichobius longipes (1)
	Trichobius uniformis (1)*
Greater spear-nosed bats, *Phyllostomus hastatus* (32)	*Mastoptera minuta* (7)
	Trichobius longipes (9)
	Strebla mirabilis (5)
	Strebla hertigi (1)

Hairy-legged vampire bat, *Diphylla ecaudata* (2)	*Trichobius diphyllae* (2)
Pallas's long-tongued bat, *Glossophaga soricina* (7)	*Trichobius uniformis* (2)
	Trichobius dugesii (10)
	Trichobius tiptoni (2)
	Trichobius lonchophyllae (1)*
Common Vampire bat, *Desmodus rotundus* (1)	*Trichobioides perspicillatus* (5)*
Round-eared bat, *Tonatia bidens* (1)	*Trichobius handleyi* (5)
	Strebla alvarezi (3)
Seba's short-tailed bat, *Carollia perspicillata* (10)	-
Thumbless Bat, *Furipterus horrens* (3)	-
Gruta do Morcego Branco	
Seba's short-tailed bat, *Carollia perspicillata* (36)	*Trichobius joblingi* (29)
	Strebla guajiro (3)
	Speiseria ambigua (1)
Common Vampire bat, *Desmodus rotundus* (13)	*Trichobius parasiticus* (11)
	Strebla wiedmani (1)
Round-eared bat, *Tonatia bidens* (3)	*Trichobius handleyi* (6)
	Strebla alvarezi (3)
Brazilian funnel-eared bat, *Natalus macrourus* (1)	-
Gruta do Macaco Fóssil	
Goldman's nectar bat, *Lonchophylla* cf. *mordax* (1)	*Trichobius lonchophyllae* (2)
Round-eared bat, *Tonatia bidens* (1)	*Trichobius handleyi* (9)
	Strebla alvarezi (3)
Seba's short-tailed bat, *Carollia perspicillata* (1)	*Trichobius joblingi* (8)
Gruta do Urso Fóssil	
Goldman's nectar bat, *Lonchophylla* cf. *mordax* (15)	*Trichobius lonchophyllae* (40)
	Speiseria ambigua (1)*
Round-eared bat, *Tonatia bidens* (5)	*Trichobius handleyi* (35)
	Strebla alvarezi (16)
Seba's short-tailed bat, *Carollia perspicillata* (3)	*Trichobius joblingi* (4)
Pallas's long-tongued bat, *Glossophaga soricina* (2)	*Trichobius dugesii* (1)

Hairy-legged vampire bat, *Diphylla ecaudata* (1)	-
Gruta do Pendurado	
Seba’s short-tailed bat, *Carollia perspicillata* (2)	*Trichobius joblingi* (1)
	Strebla guajiro (1)
Round-eared bat, *Tonatia bidens* (3)	*Trichobius handleyi* (12)
	Strebla alvarezi (5)
Caverna Furnas de Araticum	
Pale spear-nosed bat, *Phyllostomus discolor* (21)	*Trichobius costalimai* (57)
	Trichobioides perspicillatus (25)
	Mastoptera minuta (14)
	Trichobius longipes (7)
Greater spear-nosed bats, *Phyllostomus hastatus* (26)	*Mastoptera minuta* (36)
	Trichobius longipes (9)
Common Vampire bat, *Desmodus rotundus* (7)	*Trichobius parasiticus* (44)
	Strebla wiedmani (8)
Seba’s short-tailed bat, *Carollia perspicillata* (7)	*Trichobius joblingi* (5)
	Strebla guajiro (4)
	Trichobius longipes (1)*
Little yellow-shouldered bat, *Sturnira lilium* (4)	*Megistopoda proxima* (5)
	Aspidoptera falcata (2)
Hairy-legged vampire bat, *Diphylla ecaudata* (5)	-
TOTAL = 700 bats	**1,412 bat flies**

CAPÍTULO III

My cave, my rules: specialization, modularity and topology of bat-fly interactions in hot and cold caves from Eastern South America

Abstract

Caves are relatively stable and mostly advantageous roosts for bats that however promote a confined space for interactions with their ectoparasites, which directly influence in the biology of their hosts. Understanding the structure of interactions between bats, as hosts, and bat-flies, as parasites in cave ecosystems is a fundamental step to unravel the role of each species in the networks formed in the unique subterraneous ecosystems. Here we describe and evaluate the network structure of interactions bat and bat-fly in two different cave systems, the hot caves and the cold caves that occur in the Atlantic Forest and caatinga mosaics of Eastern South America, northeastern Brazil. Based on the records of 700 bats from 16 species and 1,412 bat flies from 29 species we uncovered highly distinct topologies comparing hot and cold caves, with differences also in interactions, specializations and modularity. The combination of a high species turnover and high specialization in this interaction resulted in distinct topologies and modules containing specific interactions in each network. We found relatively lesser specialization and modularity in hot caves in comparison to the cold caves, which may be associated to the bat composition and cave microclimate. The bat flies were highly species-specific to their bat hosts and consequently, dependent on the bats in both hot and cold caves systems and the higher weights of bat fly and bat species were recorded in hot caves and cold caves, respectively. The differences in network structure and at the species level between the hot and bat caves systems suggest that the bat and bat fly interaction are shaped by hosts' composition and cave system type. In this sense, changes are related to the constraints of each species of bats to roost in extreme microclimate conditions of caves and likely to species-specific roosting behaviors.

Keywords: Subterranean ecosystems, Caatinga, Atlantic Forest, Ectoparasite, Species interaction, Streblidae, network.

INTRODUÇÃO

Redes de interação ecológica oferecem importantes ferramentas para o estudo de interações parasito-hospedeiro pois representam como cada espécie se relaciona a outras num sistema e como o sistema/a comunidade se comporta em diferentes níveis (Poulin, 2010; Pilosof *et al.*, 2017). O uso de redes de interação auxilia na identificação de espécies chaves no sistema, de forma a subsidiar ações preventivas quanto ao desequilíbrio do mesmo caso essas espécies desapareçam (Tylianakis *et al.*, 2010). Com respeito à natureza da relação parasita/hospedeiro, quanto mais intrincada essa interação antagonista (Pires and Guimarães, 2013) melhor o entendimento de funcionalidades ecológicas dos parasitas na manutenção de populações de hospedeiros (Frainer *et al.*, 2018) e a influência biológica da comunidade na estruturação das interações em diferentes ambientes (Lewis *et al.*, 2002; Durán *et al.*, 2019).

As moscas ectoparasitas de morcegos (Streblidae) têm sido amplamente utilizadas para investigar padrões de estruturação de interações parasita-hospedeiro e como estas podem ser afetadas pela composição das comunidades de morcegos, por variações ambientais, em termos de paisagens, por graus de antropização e por variações sazonais (Zarazúa-Carbajal *et al.*, 2016; Rivera-García *et al.*, 2017; Durán *et al.*, 2019; Hiller *et al.*, 2021; Ramalho *et al.*, 2021; Urbieta *et al.*, 2021). As moscas são amplamente distribuídas na região neotropical e adaptadas morfologicamente a seus hospedeiros, i.e., compressão lateral do corpo, olhos reduzidos e pernas alongadas (Dick and Patterson, 2006; Alcantara *et al.*, 2019; Guerrero, 2019). Contudo, o entendimento sobre como essas interações são estruturadas em abrigos ainda é incipiente (Fagundes *et al.*, 2017; Saldaña-Vázquez *et al.*, 2019) e basal pelo limitado conhecimento do ciclo biológico das moscas Streblidae, havendo poucos dados ecológicos e de história de vida disponíveis sobre o grupo nesses ambientes (Urbieta *et al.*, 2022).

As moscas ectoparasitas de morcegos depositam larvas em forma de pupa na parede dos abrigos para que elas possam completar o seu desenvolvimento sendo, portanto, dependentes desses abrigos (Marshall, 1982; Dittmar *et al.*, 2009). No caso das moscas ectoparasitas de morcegos cavernícolas, essas estão sujeitas às dinâmicas ocorrentes nos ecossistemas subterrâneos, destacando-se a interação com os morcegos nesses ambientes, onde ambos passam grande parte dos seus ciclos de vida. Em cavernas, observa-se a tendência dos morcegos de preterir sítios com abundância de moscas (Reckardt and Kerth, 2007) e de evitar altas cargas parasitárias (Patterson *et al.*, 2007). Adicionalmente, o compartilhamento da caverna com outras espécies de hospedeiro e as variações microclimáticas podem alterar a topologia da rede em nível de comunidades e de espécies (Tlapaya-Romero *et al.*, 2021; Vidal *et al.*, 2021).

Moscas e morcegos são beneficiados pela heterogeneidade ambiental encontrada em cavernas (Ladle *et al.*, 2012; Medellin *et al.*, 2017). Contudo, pouco se sabe sobre possíveis variações dessas interações ao longo dos diferentes sistemas cavernícolas encontrados na região Neotropical. Um exemplo de sistemas subterrâneos diferentes devido às condições físicas, estruturais e bióticas é o caso das “bat caves”, também denominadas, por vezes, de “cold caves” em contrapartida às “hot caves”. Ambos os sistemas tem em comum abrigarem grandes populações de morcegos (Iskali and Zhang, 2015; Medellin *et al.*, 2017) mas oferecem cenários distintos para essa interação uma vez que “hot caves” apresentam temperatura e umidade constantemente altas (de 28-40ºC, umidade > 90%), baixa circulação de ar, e outras características que favorecem a manutenção dessas condições de microclima, como terem uma única entrada, câmaras pequenas e conterem milhares de morcegos muitas vezes segregados em compartimentos com características específicas em termos de composição de espécies e parâmetros climáticos (Taboada, 1979; De La Cruz, 1992; Tejedor *et al.*, 2005).

“Hot caves” ou “cuevas calientes” são, portanto, sistemas únicos mais conhecidos e estudados na região do Caribe, nas grandes Antilhas e na América central (Taboada, 1979; Bornaccorso *et al.*, 1992; Tejedor *et al.*, 2005). No Brasil foram encontradas apenas recentemente cavidades com características parecidas às “hot caves”, salvo que a composição das espécies é totalmente distinta, em mosaicos de Mata Atlântica e Caatinga, na região Nordeste brasileira, extremo leste da América do sul (Da Rocha *et al.*, 2011; Vargas-Mena *et al.*, 2018; Otálora-Ardila *et al.*, 2020; Pimentel *et al.*, 2022). Essas descobertas sugerem que o fenômeno das “hot caves” pode estar representado em ambos biomas, os quais também tem registro de muitas “cold caves”. Além disso, essas cavidades estão amplamente distribuídas na região Nordeste brasileira, que registra também espécies de morcegos endêmicas que habitam abrigos rochosos, sendo essa uma excelente oportunidade para o estudo de possíveis interações morcego-mosca ectoparasita específicas (Vargas-Mena *et al.*, 2018; Otálora-Ardila *et al.*, 2020).

Descrever padrões de interações ecológicas em diferentes escalas espaciais é um desafio para a ecologia (Levin, 1992; Dáttilo *et al.*, 2019; Cordeiro *et al.*, 2020) pois as diferenças entre escalas espaciais de estudo revela processos ecológicos únicos que influenciam essas interações (Vizentin-Bugoni *et al.*, 2019; Cordeiro *et al.*, 2020; Ceron *et al.*, 2022). Nesse sentido, estudos recentes demonstram que a conectividade das redes morcego-mosca ectoparasita está correlacionada com a variação de escalas em nível global, entretanto, como possível efeito da diversidade local de hospedeiros (Júnior *et al.*, 2020). Em ambientes antropizados as interações são marcadamente consistentes em escala local e regional com variações na topologia das redes (Ramalho *et al.*, 2021; Urbieta *et al.*, 2021). Os resultados dos ainda escassos estudos realizados em diferentes escalas são divergentes e, via de regra, não exploraram os abrigos.

Aqui, nós descrevemos e avaliamos as diferentes características associadas nas interações morcego-mosca ectoparasita a partir de dois sistemas cavernícolas em mosaicos Caatinga/Mata Atlântica no nordeste brasileiro, extremo leste da América do sul. O objetivo principal foi testar variações das interações morcego/mosca ectoparasita dentro de cavernas com microclimas divergentes, as “hot-caves” e as “cold-caves”, no que tange à comunidade (i) descrever a topologia das redes locais e regional, considerando ambos os sistemas subterrâneos, (ii) analisar a riquezas de hospedeiros, especializações complementares e modularidade; e a nível de espécie em cada rede: (iii) descrever o papel, a força e a especialização de cada espécie em cada rede. Esperamos encontrar, de forma geral, uma baixa especialização, a ocorrência de espécies funcionalmente diferentes nas redes entre as escalas locais devido às diferentes estruturas das cavidades e também ao microclima. Além disso, devido à concentração de muitos hospedeiros das diferentes espécies nessas cavernas (ambas, “hot” e “cold caves”) uma grande incidência de parasitismo acidental e sobreposição de nicho, levando a alterações na topologia das redes.

MATERIAL E MÉTODOS

Área de estudo

Nós coletamos os dados em 16 cavernas no nordeste do Brasil distribuídas em mosaicos de ecossistemas de Caatinga e Mata Atlântica ao longo dos estados do Ceará, Rio Grande do Norte e Sergipe. Identificamos e caracterizamos seis “hot caves” de acordo com os parâmetros específicos (Taboada, 1979; De La Cruz, 1992; Tejedor *et al.*, 2005) e dez “cold caves”(Iskali and Zhang, 2015; Medellin *et al.*, 2017) (Tabela 1). A vegetação semiárida da Caatinga inclui caatinga xerofítica decídua, matas com arbustos espinhosos e vegetação de floresta seca aberta (Lemos and Meguro, 2010; Ipece, 2012; Bento *et al.*, 2013) e os sítios de Mata Atlântica possuem florestas semidecíduas tropicais xeromórficas – o “Cerrado do Araripe” intercalado com vegetação típica da Mata Atlântica (Figueira, 1989; Costa *et al.*, 2004) (Tabela 1). As localidades semiáridas podem ser classificadas, climaticamente, como BSh (Köppen), apresentando clima quente e semiárido e outono chuvoso e os sítios da Mata Atlântica podem ser classificadas como Aw (Köppen), com clima tropical úmido com invernos secos e verões úmidos (Peel *et al.*, 2007).

Coleta de dados

Nós coletamos morcegos e moscas em três expedições conduzidas nos meses de julho e outubro (2019) e fevereiro (2022). Antes de cada captura, entramos nas cavernas com uma fita métrica, data logger KG100 (±1°C -10 a 50°C) e um termo-higrômetro AK28 (±1°C -10 a 50°C), e fizemos observações sobre: i) localização dos poleiros (concentrações de morcegos) em cada caverna, ii) distribuição dos morcegos (espécies e indivíduos) empoleirados ao longo da caverna, iii) temperatura e umidade (microclima), iv) distribuição de moscas ectoparasitas (quando fora dos morcegos) e pupas nas paredes do poleiro. Esses procedimentos foram conduzidos com cuidado para evitar perturbações e estresse às colônias, utilizando movimentos lentos e pouca iluminação. Em seguida, capturamos os morcegos usando redes de mão (i.e., puçá), redes de neblina (3,0 a 12 x 1,5m) e armadilhas de harpa nos poleiros. Todas as armadilhas foram posicionadas ou utilizadas nas saídas de cada poleiro (i.e., túneis, entradas de câmaras, cúpulas) para que fossem capturados indivíduos exclusivamente daquele local. Colocamos cada morcego capturado em um saco de pano separado para evitar contaminação entre eles.

Posteriormente, identificamos os morcegos fora da caverna utilizando chaves com caracteres e bibliografia especializada (Gardner, 2008; Díaz *et al.*, 2021). Cada indivíduo foi examinado cuidadosamente em busca de moscas ectoparasitas. Nós coletamos as moscas com pinça entomológica e individualizamos em microtúbulos com etanol 70%. Em laboratório, nós identificamos as moscas com o esteromicroscópio usando chaves dicotômicas (Wenzel and Tipton, 1966; Wenzel, 1976; Guerrero, 1994, 1995, 1996). Depositamos as moscas na coleção Entomológica da Universidade Federal da Paraíba (UFPB) e todos os procedimentos, incluindo a entrada em cavernas, foram autorizadas pelo Instituto Chico Mendes para a Conservação da Biodiversidade (ICMBio / SISBIO, número do processo: # 10,566 (solicitação: 72,660, 72,678 e 52,492-3) e ABIO #45, 2021).

Análises de dados

Construímos redes separadas para “hot caves” e “cold caves” (escala local) e meta-rede (escala regional). A meta-rede compreende todo o conjunto de espécies e interações encontradas nessas duas comunidades locais de cavernas. Cada rede é representada por uma matriz onde cada linha corresponde a uma espécie de morcego *i*, cada coluna corresponde a uma espécie de mosca *j* e as interseções correspondem à frequência de interações *aij*, que é o número de amostras de um morcego *i* em que um mosca *j* estava presente. Para cada rede, primeiro calculamos as métricas de rede: riqueza de morcegos, riqueza de moscas ectoparasitas, número de links, número de interações (N de moscas), especialização (H_2' índice) e modularidade (*Q*). O H_2' pode ser interpretado como uma medida de especialização complementar, ou seja, como as espécies dividem suas interações (Blüthgen *et al.*, 2006), e varia de 0 a 1 que indica generalização extrema ou especialização, respectivamente. Para a modularidade, nós usamos a métrica *Q* e o algoritmo DIRTLPAwb+, que procura a divisão ótima da matriz em subconjuntos de espécies altamente conectadas (Beckett 2016). Assim, a rede é modular quando subconjuntos de espécies interagem mais com elas mesmas que com outros membros da comunidade (Durán *et al.*, 2019; Urbieta *et al.*, 2021). Devido o DIRTLPAwb+ ser um algoritmo de otimização, nós selecionamos o maior valor detectado a partir de 10 repetições pois pode haver variações nos resultados entre as rodadas. Finalmente, usamos modelos nulos para estimar a significância das métricas a nível de rede (H_2', *Q*), considerados estatisticamente significativos quando superiores aos intervalos de confiança de 95% gerados pelo modelo *vaznull* null (Vázquez *et al.*, 2007). Esse modelo reorganiza as interações, preservando o total marginal (ou seja, a soma das linhas e colunas) e a conectividade como a rede observada.

Tabela 1. Características gerais físicas com localização e bioma de cavernas amostradas para morcegos e moscas ectoparasitas entre 2019 e 2022 na Caatinga e Mata Atlântica, nordeste do Brasil.

Cavernas	**Coordenadas**		**Bioma**	**Tipo de sistema**	**Litologia**	**Comprimento (m)**
	Latitude	**Longitude**				
Caverna Sobradinho	6°38'35.53"S	40° 5'57.08"W	Caatinga	Hot cave	Arenito	-
Boqueirão de Lavras	6°42'44.65"S	38°57'27.63"W	Caatinga	Hot cave	Arenito	200
Furna do Urubu	5°34'22.97"S	37°39'8.71"W	Caatinga	Hot cave	Calcário	250
Gruta do Arnold	5°26'54.96"S	35°53'12.85"W	Caatinga	Hot cave	Calcário	87
Casa de Pedra	10°50'3.08"S	37°27'3.56"W	Mata Atlântica	Hot cave	Arenito	210
Caverna do Urubu	10°43'58.47"S	37° 9'56.12"W	Mata Atlântica	Hot cave	Arenito	195
Gruta do Farias	7°19'59.15"S	39°24'46.47"W	Mata Atlântica	Cold cave	Arenito	150
Furna Feia	5°2'12.76"S	37°33'36.64"W	Caatinga	Cold cave	Calcário	739.1
Caverna da Lapa	5°33'58.58"S	37°41'51.74"W	Caatinga	Cold cave	Calcário	-
Pedra Branca	10°46'18.37"S	37° 7'53.49"W	Mata Atlântica	Cold cave	Calcário	100
Gruta de Ubajara	3°49'59.60"S	40°54'0.52"W	Mata Atlântica	Cold cave	Calcário	1,120
Gruta do Morcego Branco	3°49'53.68"S	40°54'0.10"W	Mata Atlântica	Cold cave	Calcário	274
Gruta do Macaco Fóssil	3°49'48.64"S	40°54'7.74"W	Mata Atlântica	Cold cave	Calcário	50
Gruta do Urso Fóssil	3°49'58.74"S	40°53'33.81"W	Mata Atlântica	Cold cave	Calcário	195
Gruta do Pendurado	3°50'2.46"S	40°53'35.60"W	Mata Atlântica	Cold cave	Calcário	194
Caverna Furnas de Araticum	3°48'13.84"S	40°52'43.65"W	Mata Atlântica	Cold cave	Calcário	200

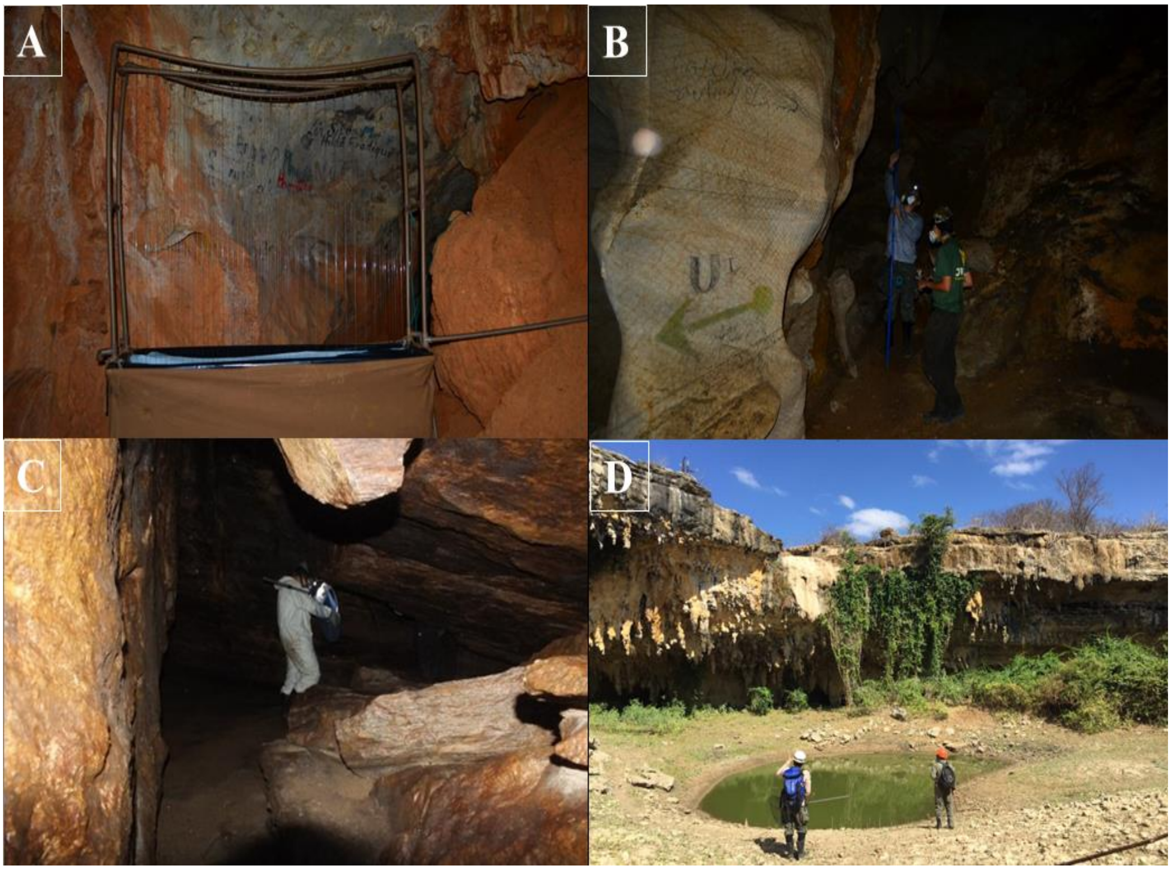

Fig. 1. Metodologias utilizadas para a captura de morcegos e coleta de moscas ectoparasitas em hot e cold caves entre 2019 e 2022 na Caatinga e Mata Atlântica, nordeste do Brasil. A = armadilha de harpa (“harp trap”) na saída de um poleiro na caverna Gruta de Ubajara (Fotografado por Werther Ramalho); B = rede de neblina aberta na saída de um poleiro na caverna Gruta de Ubajara (Fotografado por Werther Ramalho); C = captura por puçá em poleiros na caverna Boqueirão de Lavras (Fotografado por Raquel Soares) e D = busca ativa de entradas de cavernas na Caatinga (Fotografado por Juan Carlos Vargas-Mena).

Em seguida, obtivemos métricas considerando as espécies em cada rede: especialização em nível de *species strength* e interação *push-pull* (IPP). O *d'* pode ser interpretado como uma medida que avalia a especialização de uma espécie comparando as ligações realizadas entre uma espécie e seus parceiros de interação com o padrão de ligação esperado com base nas abundâncias de todos os parceiros de interação disponíveis (Blüthgen *et al.*, 2006). Similar a H_2*'*, varia de 0 a 1, o que indica extrema generalização ou especialização, respectivamente. O *species strength* (SS) é uma medida que avalia a importância de uma espécie para toda a rede, ou seja, a soma das dependências de todos os parceiros de interação dessa espécie (Barrat *et al.*, 2004; Bascompte *et al.*, 2006). A interação *push-pull* (IPP) é uma medida de assimetria de interação e equilíbrio de dependências de interação de uma espécie da rede com base nas frequências de interação com seus parceiros (Vázquez *et al.*, 2007), e varia de –1 a 1. Neste caso, as espécies "pullers" (IPP < 0) dependem mais de seus parceiros de interação nas outras classes de nós da rede do que seus parceiros dependem deles, enquanto os "pushers" (IPP > 0) fornecem mais para seus parceiros do que os recíprocos (Novella-Fernandez *et al.*, 2019; Diniz *et al.*, 2022). Por outro lado, fortes espécies "pushers" (IPP → 1) interagem com várias espécies que tendem a ter alta dependência delas, enquanto fortes "pullers" (IPP → − 1) são periféricos e interagem com espécies prolíficas que possuem dependências difusas (Novella-Fernandez *et al.*, 2019; Diniz *et al.*, 2022). Todas as análises foram realizadas usando o pacote *bipartite* (Dormann *et al.*, 2009) no software R (R Core Team, 2022).

RESULTADOS

Estrutura da rede

Capturamos 700 morcegos distribuídos em 16 espécies e 1,412 moscas ectoparasitas distribuídas em 29 espécies (estreblídeos) (Tabela 2; Fig. 1). A topologia e similaridade de espécies em hot caves foi drasticamente distinta de cold caves, promovendo menor número de links, de interações, módulos, especialização e modularidade (Tabela 2). Todas as redes foram significativamente especializadas (> 0.80) e modulares (0.43-0.73). A união dos sistemas de cavernas gerou uma meta-network com 16 espécies de morcegos e 30 espécies de moscas, gerando uma rede consistente com elevada especialização (0.93), modularidade (0.75) e apresentando 14 módulos (Tabela 2).

Tabela 2. Estrutura e métricas de topologia de interações morcego-mosca em hot e cold caves entre 2019 e 2022 na Caatinga e Mata Atlântica, nordeste do Brasil. Negrito indica resultados estatisticamente significativos, ou seja, quando o valor observado é superior ao intervalo de confiança de 95% (apresentado entre parênteses).

Métricas	**Hot caves**	**Cold caves**	**Meta-network**
Espécies de morcegos	5	13	16
Espécies de moscas	13	29	30
Links	12	43	50

Número de interações (N de indivíduos de moscas)	522	890	1.412
Número de módulos	3	13	14
Especialização (H_2’)	**0.80 (0.04-0.37)**	**0.92 (0.31-0.66)**	**0.93 (0.29-0.58)**
Modularidade (Q)	**0.46 (0.03-0.24)**	**0.73 (0.22-0.52)**	**0.75 (0.21-0.47)**

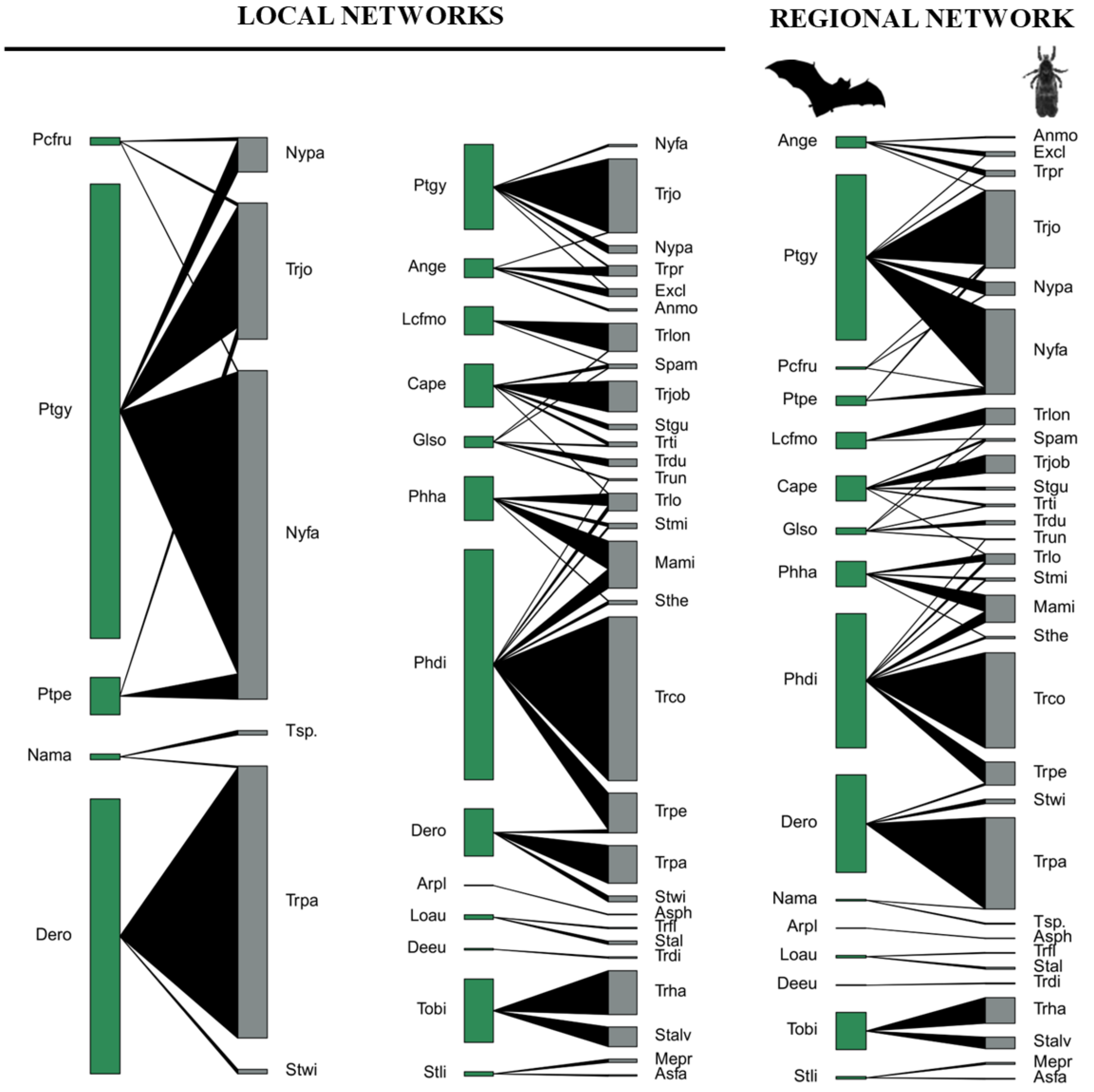

Fig. 2. Redes de interações morcego-mosca, uma meta-rede regional composta por todos os dois sítios agrupados e suas métricas de topologia em hot e cold caves entre 2019 e 2022 na Caatinga e Mata Atlântica, nordeste do Brasil. Cores distintas representam hospedeiro e mosca, com ligações pretas representando interações entre espécies e espessura de linha indica frequências de interação. Negrito indica resultados estatisticamente significativos, ou seja, quando o valor observado é superior ao intervalo de confiança de 95% (apresentado entre parênteses). Acrônimos dos morcegos: Ptgy – *Pteronotus gymnonotus*; Pcfru – *Pteronotus* cf. *rubiginosus*; Ptpe – *Pteronotus personatus*; Nama – *Natalus macrourus*; Dero – *Desmodus rotundus*; Phdi – *Phyllostomus discolor*; Ange – *Anoura geoffroyi*; Arpl – *Artibeus planirostris*; Loau – *Lonchorhina aurita*; Cape – *Carollia perspicillata*; Glso – *Glossophaga soricina*; Phha – *Phyllostomus hastatus*; Deeu – *Diphylla ecaudata*; Tobi – *Tonatia bidens*; Lcfmo – *Lonchophylla mordax*; Stli – *Sturnira lilium*. Acrônimos das moscas ectoparasitas (Streblidae): Nyfa – *Nycterophilia fairchildi*; Trjo - *Trichobius johnsonae*; Nypa - *Nycterophilia parnelli*; Tsp. – *Trichobius* sp.; Trpa – *Trichobius parasiticus*; Stwi - *Strebla wiedemanni*; Trco – *Trichobius costalimai*; Trpe – *Trichobioides perspicillatus*; Trpr - *Trichobius propinquus*; Excl – *Exastinion clovisi*; Anmo – *Anastrebla modestini*; Asph – *Aspidoptera phyllostomatis*; Trfl – *Trichobius flagellatus*; Stal – *Strebla altimani*; Spam – *Speiseria ambigua*; Trti – *Trichobius tiptoni*; Mami – *Mastoptera minuta*; Sthe – *Strebla hertigi*; Stmi – *Strebla mirabilis*; Trlo – *Trichobius longipes*; Trun – *Trichobius uniformis*; Trdi - *Trichobius diphyllae*; Trdu – *Trichobius dugesii*; Trlon - *Trichobius lonchophyllae*; Trha – *Trichobius handleyi*; Stalv – *Strebla alvarezi*; Trjob – *Trichobius joblingi*; Stgu – *Strebla guajiro*; Mepr – *Megistopoda proxima* and Asfa – *Aspidoptera falcata*.

Função individual das espécies

Todas as espécies de moscas ectoparasitas apresentaram tendência de alta especialização (d'> 0.50) quando consideramos a média de cada sistema: em "hot caves" ($d' = \bar{x}$ 0.51), "cold caves" ($d' = \bar{x}$ 0.64) e meta-network ($d' = \bar{x}$ 0.67) (Material Suplementar S1). A média de "species strength" das moscas foi maior em "hot caves" ($\bar{x}$ 0.83) e de morcegos em "cold caves" ($\bar{x}$ 2.23). Individualmente, em "hot caves" o maior valor de hospedeiro foi registrado para o morcego *Pteronotus gymnonotus* (2.72; $\bar{x}$ = 1.20) e para a mosca *Nycterophilia fairchildi* (1.54; $\bar{x}$ = 0.83). Em “cold caves”, os representantes foram *Phyllostomus discolor* (4.15; $\bar{x}$ = 2.23) e *Trichobius lonchophyllae* (1.03; $\bar{x}$ = 0.45). Por fim, regionalmente a espécie de morcego com maior valor foi *Phyllostomus discolor* (4.15; $\bar{x}$ = 1.87) e a mosca *Nycterophilia fairchildi* (1.35; $\bar{x}$ = 0.52). Quanto a *interaction push-pull* (IPP), em geral as espécies de moscas em “hot caves” ($\bar{x}$ = -0.20) e “cold caves” ($\bar{x}$ = -0.42) podem ser consideradas “pullers” (IPP < 0) e por isso, dependem mais da interação dos seus parceiros. Em contrapartida, os morcegos são considerados “pushers” (IPP > 0) em “hot caves” ($\bar{x}$ = 0.07) e “cold caves” ($\bar{x}$ = 0.33), exercendo maior força de dependência dos seus parceiros do que o recíproco. Logo, o padrão regional é representado de forma similar a escala local para moscas ectoparasitas ($\bar{x}$ = -0.34) e morcegos ($\bar{x}$ = 0.21).

DISCUSSÃO

Nosso trabalho é pioneiro em termos de análise comparativa de interações morcego-mosca em sistemas de cavernas quentes (“hot caves”) e frias (“cold caves”), sistemas esses que tem sido pouco estudado comparativamente (Rocha, 2013; Otálora-Ardila *et al.*, 2020; Pimentel *et al.*, 2022). Contrariando a predição inicial, nossos resultados confirmam que as interações entre morcegos e moscas ectoparasitas são altamente especializadas em ambos os sistemas e escalas. A distinta composição de morcegos e moscas entre os sistemas parece ter influenciado no sentido de delinear diferentes topologias em todas as redes, gerando métricas marcadamente distintas entre os sistemas. Por outro lado, confirmamos nossa expectativa em relação a importância e funcionalidade das espécies ao longo dos sistemas. Em “hot caves”, apenas as espécies de moscas ectoparasitas exerceram maior força, i.e., a soma das dependências dessas espécies nas interações, em comparação às demais redes. Em contraste, as moscas foram mais especializadas em “cold caves”. Em resumo, nossos resultados sugerem que, apesar da especialização nas interações, os sistemas cavernícolas geram padrões específicos que incidem nas topologias das redes, o que torna esses ambientes fundamentais para manter subgrupos específicos interagindo.

Interações morcego-mosca são consistentemente especializadas e modulares em diferentes escalas e tipos de caverna. A riqueza e a composição de hospedeiros locais têm sido registradas como as principais influenciadoras da alta especialização nas redes devido a dependência das moscas a esses hospedeiros, i.e., especificidade parasitária (Eriksson *et al.*, 2019; Júnior *et al.*, 2020). Neste sentido, as variações de composição e similaridade de moscas entre os tipos de cavernas depende da composição de hospedeiros que frequentam o poleiro (Urbieta *et al.*, 2021). Morcegos que permanecem mais tempo em cavernas tendem a ter mais moscas associadas (i.e., abundância), enquanto morcegos que visitam outras cavernas tendem a aumentar o contato com diferentes espécies de moscas e apresentar maior riqueza em termos de espécies (Fagundes *et al.*, 2017), aumentando as chances de desbalanço nas interações devido ao compartilhamento desses ectoparasitas.

O microclima das “hot caves” parece limitar a presença de estreblídeos a poucas espécies de hospedeiros e delimitar algumas maiores concentração de moscas em poucos sítios nas cavernas. Em contrapartida, maior riqueza de moscas é registrada em “cold caves” que oferecem mais poleiros dentro das cavernas e maior estabilidade microclimática, além de um clima menos extremo. Apesar da dificuldade em explicar como ocorre o parasitismo acidental de moscas em distintos hospedeiros (Hiller *et al.*, 2021), a topologia das redes pode ser alterada por essas associações (Luna *et al.*, 2017). Por exemplo, a mosca *Trichobius parasiticus* é ectoparasita de *Desmodus rotundus* (Aguiar and Antonini, 2011; Fagundes *et al.*, 2017), mas foi registrada em *Natalus macrourus*, espécie encontrada coabitando com *Desmodus rotundus* em hot caves (Fig. 1). A alta modularidade aqui é produto da alta especialização (Cordeiro *et al.*, 2020), associada ao comportamento e a tolerância dos morcegos ao microclima nas cavernas, levando a padrões globalmente semelhantes na interação morcego-mosca em ambientes antrópicos, cavernícolas e florestais (Fagundes *et al.*, 2017; Durán *et al.*, 2019; Júnior *et al.*, 2020; Hiller *et al.*, 2021; Urbieta *et al.*, 2021).

As espécies de moscas foram menos especializadas em “hot caves” devido a sua mobilidade e das condições microclimáticas do sistema cavernícola. O cenário criado pelas colônias de *Pteronotus* e a estrutura da caverna, i.e., câmaras com altas temperaturas, tornaram o ambiente seletivo quanto as espécies e a disposição segregada em poucos sítios (Otálora-Ardila *et al.*, 2020; Pimentel *et al.*, 2022). Aqui a mobilidade das moscas aparece como fator importante na especificidade parasitária (Wenzel, 1976; Marshall, 1982). Moscas com maior mobilidade (e.g., com asas desenvolvidas) tem maior facilidade em voar para outros hospedeiros dentro do poleiro, levando a menor especificidade. Esse salto entre hospedeiros talvez seja uma estratégia para encontrar seu hospedeiro primário, mas acaba por alterar as métricas das interações (Hiller *et al.*, 2021). De fato, todas as espécies de moscas registradas em hot caves possuem asas desenvolvidas, e foram observadas sobrevoando os poleiros em voos curtos (i.e., tiro ao alvo; ver capítulo II). Por outro lado, a competição interespecífica (i.e., presença ou ausência) pode ajudar a explicar os menores valores de especialização *d'* devido as idiossincrasias nas interações (Komeno and Linhares, 1999; Durán *et al.*, 2019). Por exemplo, *Nycterophilia fairchildi* (*d'* = 0.52) e *Trichobius johnsonae* (*d'* = 0.25) parasitaram três hospedeiros do gênero *Pteronotus*, mas exploram nichos distintos no morcego devido as suas morfologias, i.e., a primeira parasita principalmente áreas de pelagem se concentrando no pescoço e a segunda parasita áreas de membranas das (Hiller *et al.*, 2018), gerando padrões específicos de especialização e menor sobreposição de nicho no hospedeiro. A especialização das espécies também está intimamente ligada a modularidade e as características do poleiro, pois os módulos estão associados a escolha dos morcegos por poleiros persistentes e que são compostos por espécies que compartilham a estrutura desse poleiro (Hiller *et al.*, 2021).

A importância das espécies para a rede inteira, i.e., *species strength*, parece estar ligada ao tipo de sistema cavernícola e a composição de espécies da rede. A heterogeneidade das comunidades, a especificidade das moscas e a vulnerabilidade dos hospedeiros promovem padrões quantitativos distintos nas espécies da rede (Bellay *et al.*, 2015). Assim, esses padrões podem refletir como uma medida de dependência mútua entre hospedeiro e parasita em uma rede, i.e., a força da espécie (Bascompte *et al.*, 2006; Cardoso *et al.*, 2021). Neste sentido, em "hot caves" as espécies formam módulos específicos de interações, mas que diluem a força das espécies ao longo da rede devido a capacidade das moscas de parasitarem mais de duas espécies de morcegos (Fig. 1). A elevada abundância de hospedeiros aumenta os encontros com moscas que ocorrem em baixas e altas densidades nos poleiros da caverna (Morand *et al.*, 2015; Dallas *et al.*, 2019, 2020) e contribuem mais para o deslocamento dessas moscas do que populações menores de hospedeiros (Johnson *et al.*, 2020). Essa dinâmica resulta em alteração no número de interações e interferência na força das espécies. Em contrapartida, poucas espécies de moscas parasitam mais de dois hospedeiros em "cold caves", formando mais módulos de interações independentes e aumentando a força das espécies ("*species strengh*"). Além disso, o compartilhamento de poleiros por diferentes hospedeiros não tem sido sinônimo de compartilhamento de moscas em "cold caves", gerando dependência das moscas a seus hospedeiros primários para sobreviverem (Pejić *et al.*, 2021). Deste modo, a representatividade de ambos os sistemas aparece na meta-network representadas pelas espécies *Phyllostomus* *discolor* e *Nycterophilia fairchildi*, fundamentais para a estruturação das interações em escala regional.

Em “hot caves”, moscas ectoparasitas são menos dependentes de seus hospedeiros, i.e., “pullers”, mas os morcegos são fracos “empurradores”, i.e., “weak pushers”. Curiosamente, aqui as espécies consideradas “strong pullers” (i.e., *Strebla wiedemanni*, *Nycterophilia fairchildi* e *Nycterophilia parnelli*) parasitam uma ou duas espécies de morcegos. Com exceção de *S. wiedemanni*, as outras espécies possuem morfologias idênticas e são ectoparasitas específicos de morcegos do gênero *Pteronotus* (Wenzel, 1976). A menor abundância de *Nycterophilia parnelli* pode sinalizar competição interespecífica com *Nycterophilia fairchildi* ou que essa espécie é menos abundante localmente. Neste sentido, padrões de similaridade fenotípica dos hospedeiros e suas relações filogenéticas podem influenciar os padrões de interações e alterar o papel das espécies na rede (Urbieta *et al.*, 2021). Similar a “força das espécies”, a capacidade das moscas de parasitarem múltiplos hospedeiros diminui a dependência delas a uma única espécie o, que, em certo ponto, fortalece o argumento de maior sobreposição de nicho de moscas em redes menores provenientes de cavernas (Saldaña-Vázquez *et al.*, 2019). Diferentemente de “cold caves”, nas quais os hospedeiros “empurram” mais as moscas causando uma assimetria acentuada nas interações e por isso elas se tornam mais dependentes dos seus hospedeiros. Logo, o papel das espécies nas interações morcego-mosca são bem definidos em ambas escalas, mas em escala local variam drasticamente em “hot caves”, o que provavelmente é derivado dos processos que moldaram os fenótipos e a ecologia das espécies ao longo do tempo evolutivo em conjunto ao microclima adverso das cavernas (Saldaña-Vázquez *et al.*, 2019; Tlapaya-Romero *et al.*, 2021; Urbieta *et al.*, 2021).

Em conclusão, nosso estudo tem mostrado que além da composição e riqueza de espécies, as estruturas das interações morcego-mosca podem sofrer alterações induzidas pelas condições ambientais (Fagundes *et al.*, 2017; Tylianakis and Morris, 2017; Saldaña-Vázquez *et al.*, 2019). O *turnover* de espécies entre os sistemas mostra a importância de cada sistema em escala regional. Contudo, em “hot caves” encontramos padrões específicos em nível de comunidade e de funções das espécies na rede, que torna esse tipo de caverna importante para a conservação de morcegos e moscas ectoparasitas. A paisagem, i.e., matriz das cavernas, possivelmente afeta as interações dentro desses abrigos e futuros estudos que avaliem o efeito de variáveis externas nas interações de sistemas subterrâneos podem trazer mais luz as interações morcego-mosca em matrizes cársticas.

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Material Suplementar S1

Métricas em nível de espécie nas interações morcego-mosca oriundas de hot e cold caves amostradas entre 2019 e 2022 na Caatinga e Mata Atlântica, nordeste do Brasil.

		Interaction push-pull (IPP)			
Hot cave		**Cold cave**		**Regional**	
Bat fly species		Bat fly species		Bat fly species	
Nycterophilia fairchildi	0.18	*Nycterophilia fairchildi*	-0.98	*Nycterophilia fairchildi*	0.11
Trichobius johnsonae	0	*Trichobius johnsonae*	-0.05	*Trichobius johnsonae*	0.04
Nycterophilia parnelli	-0.26	*Nycterophilia parnelli*	-0.91	*Nycterophilia parnelli*	-0.26
Trichobius sp.	-0.25	*Trichobius parasiticus*	-0.19	*Trichobius parasiticus*	0.09
Trichobius parasiticus	0.11	*Trichobius costalimai*	-0.29	*Trichobius costalimai*	-0.28
Strebla wiedemanni	-0.98	*Trichobioides perspicillatus*	-0.39	*Trichobioides perspicillatus*	-0.41
-	-	*Trichobius propinquus*	-0.25	*Trichobius propinquus*	-0.25
-	-	*Exastinion clovisi*	-0.31	*Exastinion clovisi*	-0.3
-	-	*Anastrebla modestini*	-0.90	*Anastrebla modestini*	-0.89
-	-	*Aspidoptera phyllostomatis*	0	*Aspidoptera phyllostomatis*	0
-	-	*Trichobius flagellatus*	-0.71	*Trichobius flagellatus*	-0.71
-	-	*Strebla altimani*	-0.29	*Strebla altimani*	-0.28
-	-	*Speiseria ambigua*	-0.28	*Speiseria ambigua*	-0.28
-	-	*Trichobius tiptoni*	-0.40	*Trichobius tiptoni*	-0.4
-	-	*Mastoptera minuta*	-0.14	*Mastoptera minuta*	-0.13
-	-	*Strebla hertigi*	-0.49	*Strebla hertigi*	-0.48
-	-	*Strebla mirabilis*	-0.46	*Strebla mirabilis*	-0.45
-	-	*Trichobius longipes*	-0.23	*Trichobius longipes*	-0.23
-	-	*Trichobius uniformis*	-0.44	*Trichobius uniformis*	-0.43
-	-	*Trichobius diphyllae*	0	*Trichobius diphyllae*	0
-	-	*Trichobius dugesii*	-0.35	*Trichobius dugesii*	-0.35
-	-	*Trichobius lonchophyllae*	0.02	*Trichobius lonchophyllae*	0.01

-	-	*Trichobius handleyi*	-0.31	*Trichobius handleyi*	-0.3
-	-	*Strebla alvarezi*	-0.69	*Strebla alvarezi*	-0.69
-	-	*Trichobius joblingi*	-0.29	*Trichobius joblingi*	-0.28
-	-	*Strebla guajiro*	-0.88	*Strebla guajiro*	-0.87
-	-	*Megistopoda proxima*	-0.88	*Megistopoda proxima*	-0.95
-	-	*Strebla wiedemanni*	-0.29	*Strebla wiedemanni*	-0.28
-	-	*Aspidoptera falcata*	-0.71	*Aspidoptera falcata*	-0.71
-	-	-	-	*Trichobius* sp.	-0.25
$\bar{x}$	**-0.20**	$\bar{x}$	**-0.42**	$\bar{x}$	**-0.34**
Bat species		Bat species		Bat species	
Pteronotus gymnonotus	0.57	*Pteronotus gymnonotus*	0.44	*Pteronotus gymnonotus*	0.4
Pteronotus cf. *rubiginosus*	-0.29	*Desmodus rotundus*	0.36	*Desmodus rotundus*	0.35
Pteronotus personatus	-0.41	*Phyllostomus discolor*	0.45	*Phyllostomus discolor*	0.45
Natalus macrourus	0	*Anoura geoffroyi*	0.45	*Anoura geoffroyi*	0.44
Desmodus rotundus	0.49	*Artibeus planirostris*	0	*Artibeus planirostris*	0
-	-	*Lonchophylla aurita*	0.50	*Lonchophylla aurita*	0.5
-	-	*Carollia perspicillata*	0.49	*Carollia perspicillata*	0.49
-	-	*Glossophaga soricina*	0.22	*Glossophaga soricina*	0.22
-	-	*Phyllostomus hastatus*	0.26	*Phyllostomus hastatus*	0.26
-	-	*Diphylla ecaudata*	0	*Diphylla ecaudata*	0
-	-	*Tonatia bidens*	0.50	*Tonatia bidens*	0.5
-	-	*Lonchophylla mordax*	0.06	*Lonchophylla mordax*	0.05
-	-	*Sturnira lilium*	0.50	*Sturnira lilium*	0.5
-	**-**	-	-	*Pteronotus* cf. *rubiginosus*	-0.03
-	-	-	-	*Pteronotus personatus*	-0.44
-	-	-	-	*Natalus macrourus*	0
$\bar{x}$	**0.07**	$\bar{x}$	**0.33**	$\bar{x}$	**0.21**

Species strength (SS)

Hot cave		**Cold cave**		**Regional**	
Bat fly species		Bat fly species		Bat fly species	

Nycterophilia fairchildi	1.54	*Nycterophilia fairchildi*	0.02	*Nycterophilia fairchildi*	1.35
Trichobius johnsonae	0.98	*Trichobius johnsonae*	0.89	*Trichobius johnsonae*	1.19
Nycterophilia parnelli	0.46	*Nycterophilia parnelli*	0.09	*Nycterophilia parnelli*	0.47
Trichobius sp.	0.75	*Trichobius parasiticus*	0.81	*Trichobius parasiticus*	1.18
Trichobius parasiticus	1.23	*Trichobius costalimai*	0.71	*Trichobius costalimai*	0.71
Strebla wiedemanni	0.01	*Trichobioides perspicillatus*	0.23	*Trichobioides perspicillatus*	0.17
-		*Trichobius propinquus*	0.50	*Trichobius propinquus*	0.48
-		*Exastinion clovisi*	0.39	*Exastinion clovisi*	0.38
-		*Anastrebla modestini*	0.10	*Anastrebla modestini*	0.1
-		*Aspidoptera phyllostomatis*	1	*Aspidoptera phyllostomatis*	1
-		*Trichobius flagellatus*	0.29	*Trichobius flagellatus*	0.28
-		*Strebla altimani*	0.71	*Strebla altimani*	0.71
-		*Speiseria ambigua*	0.16	*Speiseria ambigua*	0.15
-		*Trichobius tiptoni*	0.19	*Trichobius tiptoni*	0.19
-		*Mastoptera minuta*	0.72	*Mastoptera minuta*	0.72
-		*Strebla hertigi*	0.03	*Strebla hertigi*	0.02
-		*Strebla mirabilis*	0.08	*Strebla mirabilis*	0.08
-		*Trichobius longipes*	0.31	*Trichobius longipes*	0.3
-		*Trichobius uniformis*	0.12	*Trichobius uniformis*	0.12
-		*Trichobius diphyllae*	1	*Trichobius diphyllae*	1
-		*Trichobius dugesii*	0.65	*Trichobius dugesii*	0.64
-		*Trichobius lonchophyllae*	1.03	*Trichobius lonchophyllae*	1.03
-		*Trichobius handleyi*	0.69	*Trichobius handleyi*	0.69
-		*Strebla alvarezi*	0.31	*Strebla alvarezi*	0.3
-		*Trichobius joblingi*	0.71	*Trichobius joblingi*	0.71
-		*Strebla guajiro*	0.12	*Strebla guajiro*	0.12
-		*Megistopoda proxima*	0.71	*Megistopoda proxima*	0.71
-		*Strebla wiedemanni*	0.13	*Strebla wiedemanni*	0.04
-		*Aspidoptera falcata*	0.29	*Aspidoptera falcata*	0.28
-		-	-	*Trichobius* sp.	0.75
$\bar{x}$	**0.83**	**$\bar{x}$**	**0.45**	**$\bar{x}$**	**0.52**

Bat species		Bat species		Bat species	
Pteronotus gymnonotus	2.72	*Pteronotus gymnonotus*	3.19	*Pteronotus gymnonotus*	3.01
Pteronotus cf. *rubiginosus*	0.11	*Desmodus rotundus*	2.08	*Desmodus rotundus*	2.07
Pteronotus personatus	0.16	*Phyllostomus discolor*	4.15	*Phyllostomus discolor*	4.15
Natalus macrourus	1	*Anoura geoffroyi*	2.80	*Anoura geoffroyi*	2.79
Desmodus rotundus	1.99	*Artibeus planirostris*	1	*Artibeus planirostris*	1
-		*Lonchophylla aurita*	2	*Lonchophylla aurita*	2
-		*Carollia perspicillata*	3.46	*Carollia perspicillata*	3.46
-		*Glossophaga soricina*	2.11	*Glossophaga soricina*	2.11
-		*Phyllostomus hastatus*	2.05	*Phyllostomus hastatus*	2.05
-		*Diphylla ecaudata*	1	*Diphylla ecaudata*	1
-		*Tonatia bidens*	2	*Tonatia bidens*	2
-		*Lonchophylla mordax*	1.11	*Lonchophylla mordax*	1.11
-		*Sturnira lilium*	2	*Sturnira lilium*	2
-		-	-	*Pteronotus* cf. *rubiginosus*	0.07
-		-	-	*Pteronotus personatus*	0.11
-		-	-	*Natalus macrourus*	1
$\boldsymbol{\bar{x}}$	**1.20**	$\boldsymbol{\bar{x}}$	**2.23**	$\boldsymbol{\bar{x}}$	**1.87**

Specialization (*d’*)

Hot cave		**Cold cave**		**Regional**	
Bat fly species		Bat fly species		Bat fly species	
Nycterophilia fairchildi	0.52	*Nycterophilia fairchildi*	0.02	*Nycterophilia fairchildi*	0.61
Trichobius johnsonae	0.25	*Trichobius johnsonae*	0.89	*Trichobius johnsonae*	0.57
Nycterophilia parnelli	0.18	*Nycterophilia parnelli*	0.09	*Nycterophilia parnelli*	0.32
Trichobius sp.	0.94	*Trichobius parasiticus*	0.81	*Trichobius parasiticus*	0.96
Trichobius parasiticus	0.97	*Trichobius costalimai*	0.71	*Trichobius costalimai*	0.80
Strebla wiedemanni	0.19	*Trichobioides perspicillatus*	0.23	*Trichobioides perspicillatus*	0.36
-		*Trichobius propinquus*	0.50	*Trichobius propinquus*	0.70
-		*Exastinion clovisi*	0.39	*Exastinion clovisi*	0.70
-		*Anastrebla modestini*	0.10	*Anastrebla modestini*	0.61
-		*Aspidoptera phyllostomatis*	1	*Aspidoptera phyllostomatis*	1

-		*Trichobius flagellatus*	0.29	*Trichobius flagellatus*	0.79
-		*Strebla altimani*	0.71	*Strebla altimani*	0.94
-		*Speiseria ambigua*	0.16	*Speiseria ambigua*	0.45
-		*Trichobius tiptoni*	0.19	*Trichobius tiptoni*	0.52
-		*Mastoptera minuta*	0.72	*Mastoptera minuta*	0.57
-		*Strebla hertigi*	0.03	*Strebla hertigi*	0.18
-		*Strebla mirabilis*	0.08	*Strebla mirabilis*	0.31
-		*Trichobius longipes*	0.31	*Trichobius longipes*	0.45
-		*Trichobius uniformis*	0.12	*Trichobius uniformis*	0.42
-		*Trichobius diphyllae*	1	*Trichobius diphyllae*	1
-		*Trichobius dugesii*	0.65	*Trichobius dugesii*	0.91
-		*Trichobius lonchophyllae*	1.03	*Trichobius lonchophyllae*	0.97
-		*Trichobius handleyi*	0.69	*Trichobius handleyi*	0.88
-		*Strebla alvarezi*	0.31	*Strebla alvarezi*	0.69
-		*Trichobius joblingi*	0.71	*Trichobius joblingi*	0.90
-		*Strebla guajiro*	0.12	*Strebla guajiro*	0.57
-		*Megistopoda proxima*	0.71	*Megistopoda proxima*	0.94
-		*Strebla wiedemanni*	0.13	*Strebla wiedemanni*	0.34
-		*Aspidoptera falcata*	0.29	*Aspidoptera falcata*	0.79
-		-	-	*Trichobius* sp.	0.95
$\bar{x}$	**0.51**	$\bar{x}$	**0.64**	$\bar{x}$	**0.67**
Bat species		Bat species		Bat species	
Pteronotus gymnonotus	0.82	*Pteronotus gymnonotus*	0.96	*Pteronotus gymnonotus*	0.93
Pteronotus cf. *rubiginosus*	0.21	*Desmodus rotundus*	0.92	*Desmodus rotundus*	0.97
Pteronotus personatus	0.16	*Phyllostomus discolor*	0.85	*Phyllostomus discolor*	0.91
Natalus macrourus	0.72	*Anoura geoffroyi*	0.92	*Anoura geoffroyi*	0.93
Desmodus rotundus	0.99	*Artibeus planirostris*	1	*Artibeus planirostris*	1
-	-	*Lonchophylla aurita*	1	*Lonchophylla aurita*	1
-	-	*Carollia perspicillata*	0.96	*Carollia perspicillata*	0.97
-	-	*Glossophaga soricina*	0.85	*Glossophaga soricina*	0.88
-	-	*Phyllostomus hastatus*	0.80	*Phyllostomus hastatus*	0.83

-	-	*Diphylla ecaudata*	1	*Diphylla ecaudata*	1
-	-	*Tonatia bidens*	1	*Tonatia bidens*	1
-	-	*Lonchophylla mordax*	0.97	*Lonchophylla mordax*	0.98
-	-	*Sturnira lilium*	1	*Sturnira lilium*	1
-	-	-		*Pteronotus* cf. *rubiginosus*	0.22
-	-	-		*Pteronotus personatus*	0.29
-	-	-		*Natalus macrourus*	0.75
$\bar{x}$	**0.58**	**$\bar{x}$**	**0.94**	**$\bar{x}$**	**0.85**

CONSIDERAÇÕES FINAIS

Em resumo, a presente tese buscou sanar essa lacuna persistente envolvendo o estudo das interações morcego-mosca em abrigos/poleiros no Brasil. Sobretudo, nas cavernas que são poleiros abundantes na região nordeste. Neste sentido, nossas descobertas oferecem visões da problemática em duas escalas principais. A **primeira**, em escala global, mostra que o estudo de interações morcego-mosca em abrigos tem se concentrado na descrição de interações parasito-hospedeiro com avanço na última década focado em cavernas. Contudo, países com maior diversidade (e.g., animais, cavernas, ecorregiões) estão desconectados da rede de parceria de pesquisa nesse tema. Neste ponto, nós sugerimos alguns movimentos importantes para que pesquisadores oriundos de países do Sul Global conectem suas pesquisas com países próximos geograficamente explorando melhor o estudo dessas interações em cavernas e outros abrigos. A **segunda**, em uma escala regional, que busca oferecer uma visão geral – como uma “grande fotografia” – de como o microclima das cavernas afeta o parasitismo de moscas em morcegos oriundos de cavernas quentes e frias do nordeste brasileiro. Evidenciamos a importância do estudo dessas cavernas, principalmente em cavernas quentes (“hot caves”) onde são encontradas espécies e interações ecológicas únicas. Além disso, essas cavernas são fundamentais para mitigar projetos de conservação de morcegos e moscas cavernícolas. E por fim, uma **subdivisão da segunda escala**, que oferece uma visão a nível de interação ecológica. Neste caso, as estruturas das redes de interação morcego-mosca são totalmente distintas em cavernas quentes, moldadas principalmente pela composição de morcegos e pelo microclima da caverna. Como resultado, as espécies possuem pesos e funções distintas entre os tipos de cavernas e escalas espaciais.