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VARIAÇÕES SAZONAIS E SEXUAIS DO HOSPEDEIRO AFETAM AS REDES DE INTERAÇÃO ENTRE MOSCAS E MORCEGOS NAS SAVANAS DO AMAPÁ, NORDESTE DA AMAZÔNIA BRASILEIRA

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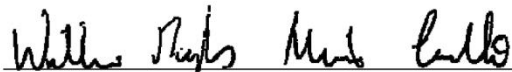
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SUMARIO

RESUMO

Mejía, Paulo Alejandro. VARIAÇÕES SAZONAIS E SEXUAIS DO HOSPEDEIRO AFETAM AS REDES DE INTERAÇÃO ENTRE MOSCAS E MORCEGOS NAS SAVANAS DO AMAPÁ, NORDESTE DA AMAZÔNIA BRASILEIRA. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação – Universidade Federal do Amapá.

Os morcegos interagem com uma ampla variedade de moscas ectoparasitas, e é por isso que é essencial determinar como os aspectos ambientais e biológicos afetam as interações das moscas de morcego, para entender a diversidade e a estrutura deste sistema parasita-hospedeiro. No presente estudo, analisamos como as redes de interação antagônicas entre morcego-mosca de morcego e a estrutura da assembleia das moscas de morcego são afetadas pela estação do ano, sexo e a idade dos morcegos nas Savanas do Amapá, nordeste da Amazônia brasileira. Estimamos a riqueza e composição de espécies de moscas de morcego e construímos redes de interação entre morcegos e moscas de morcego para testar o efeito da estação (chuvosa *versus* seca), sexo e idade do hospedeiro. Capturamos 1.221 morcegos de 27 espécies de 10 manchas de floresta dentro da savana e identificamos 1.583 moscas de 39 espécies parasitando 38% dos morcegos. O parasitismo foi maior na estação chuvosa (42%) do que na estação seca (32%) e foi maior para morcegos adultos (38%) em comparação com morcegos juvenis (37%). Além disso, as fêmeas adultas (42%) foram mais infestadas do que os machos adultos (32%), enquanto os machos juvenis (41%) foram mais parasitados do que as fêmeas jovens (39%). A riqueza de espécies de moscas e morcegos foi maior na estação chuvosa e a composição das moscas mudou entre as estações. A rede local morcego-mosca de morcego foi altamente especializada (0,88) e modular (0,70). A sub-rede da estação seca foi mais especializada (0,98) e modular (0,80) e a sub-rede de fêmeas adultas foi mais especializada (0,88) e modular (0,73). Quanto aos hospedeiros jovens, registramos sub-redes pequenas com menos espécies de morcegos e mosca de morcego. No geral, destacamos que a estação, o sexo e a idade dos hospedeiros contribuem para explicar a diversidade de variação e estrutura das redes de interação entre morcegos e moscas de morcego na savana amazônica.

Palavras-chave: bioma amazônico; Cerrado Amapá; Chiroptera; morcegos filostomídeos; Streblidae

ABSTRACT

Bats interact with a wide variety of ectoparasitic flies, and that is why determining how environmental and biological aspects affect the bat-bat fly interactions is essential to understand diversity and structure in this host-parasite system. In the present study, we analyzed how the antagonistic bat-bat fly interaction networks and the bat fly assemblage structure is affected by the season, host sex, and age of bats in the Savannahs of Amapá, northeast of the Brazilian Amazon. We estimated bat flies species richness, composition and we built interaction networks to test for the effect of the season (wet *versus* dry), host sex, and age. We captured 1221 bats of 27 species from 10 forest patches within the savannah and we identified 1583 bat flies from 39 species parasitizing 38% of the bats. Parasitism was higher in the rainy season (42%) than in the dry season (32%) and was higher for adult (38%) compared to the younger bats (37%). Also, adult females (42%) were more infested than adult males (32%) while young males (41%) were more parasitized than young females (39%). Bat and bat flies species richness was higher in the rainy season and bat flies composition changed between seasons. The overall bat-bat fly network was highly specialized (0.88) and modular (0.70). The dry season sub-network was more specialized (0.98) and modular (0.80) and the sub-network of adult females was more specialized (0.88) and modular (0.73). As for young hosts, we recorded small sub-networkss with fewer bat and bat fly species. Overall, we highlight that season, sex and age of the hosts contribute to explain the variation diversity and structure of bat-bat fly interaction networks in the Amazonian savannah.

Keywords: amazon biome; Cerrado Amapá; Chiroptera; phyllostomid bats; Streblidae

1. INTRODUÇÃO GERAL

1.1 Parasitismo em morcegos

Os morcegos são parasitados por uma grande variedade de endoparasitas e ectoparasitas (Nogueira et al. 2004, Añez et al. 2009, Whitaker et al. 2009). Os endoparasitas comumente se alojam em órgãos ou tecidos, enquanto os ectoparasitas habitam a superfície externa do hospedeiro (Martin 2007). Os endoparasitas de morcegos podem ser de vários tipos, principalmente helmintos e protozoários, além de bactérias. A maioria dos registros de helmintos menciona os gêneros Capillaria e Hymenolepis, com parasitas deste último gênero sendo os mais importantes como agentes zoonóticos em animais domésticos e humanos (Kobayashi et al. 1995, Malheiros et al. 2014, Santos and Gibson 2016). Outros protozoários do Filo Apicomplexa são parasitas típicos de morcegos, incluindo os gêneros Polychromophilus e Babesia (Lord and Brooks 2016). Além desses, é possível encontrar diferentes espécies do gênero Trypanosoma, causadoras de diversas doenças em animais silvestres, domésticos e humanos, como a doença de Chagas e a Leismaniose (Lima et al. 2008). Os morcegos também são hospedeiros de bactérias e suas relações com esses microrganismos ainda são pouco conhecidas, especialmente nos Neotrópicos (Muhldorfer 2013). Muhldofer (2013) menciona principalmente dados da Europa em sua revisão, na qual ele lista bactérias patogênicas de diferentes gêneros que causam doenças em humanos (por exemplo, Clostridium, Salmonella e Vibrio). Alguns desses parasitas causam sintomas em morcegos, então é possível que sejam adquiridos acidentalmente, enquanto outros parecem apenas permanecer dormentes nos hospedeiros (Lord and Brooks 2016). Diferentes bactérias também podem ser encontradas em ectoparasitas de morcegos, como Bartonella em moscas da família Streblidae (Diptera: Hippoboscoidea) (Morse et al. 2012a, 2012b) e Bartonella e Rickettsia em carrapatos da família Argasidae (Hornok et al. 2012, 2019, Judson et al. 2015, Luz et al. 2019), com um registro particular em Ornithodoros hasei (Acari: Argasidae) no estado do Amapá, nordesde da Amazônia brasileira (Luz et al. 2019).

Por outro lado, os ectoparasitas dos morcegos podem ser ácaros, carrapatos, hemípteros e moscas (Whitaker et al. 2009), que por sua vez podem ser reservatórios para outros tipos de infecções. Os carrapatos e ácaros (Subclasse Acari) que parasitam morcegos podem pertencer a uma ampla variedade de famílias (Whitaker et al. 2009), das

quais cinco são as mais comuns nos Neotrópicos: Chirodiscidae, Spinturnicidae, Macronissidae, Ixodidae e Argasidae (Dick and Patterson 2007, Presley and Willig 2008, Whitaker et al. 2009). Indivíduos da família Chirodiscidae são ácaros cilíndricos que comumente parasitam morcegos da família Molossidae e possivelmente se alimentam de secreções sebáceas (Presley and Willig 2008, Whitaker et al. 2009, Gomes et al. 2012). Spinturnicidae é uma família que agrupa os ácaros parasitas obrigatórios de morcegos, comumente encontrados nas membranas das asas (Whitaker et al. 2009, Beron 2020), principalmente das famílias Phyllostomidae e Vespertilionidae (Presley and Willig 2008, Dantas-Torres et al. 2009). No Brasil existem registros em morcegos das famílias Phyllostomidae, Mormopidae, Natalidae e Vespertilionidae (Gettinger and Gribel 1989, Dantas-Torres et al. 2009, Silva and Graciolli 2013, Almeida et al. 2016). Ácaros da família Macronissidae podem parasitar vários grupos de vertebrados, como pássaros e mamíferos (Radovsky and Furman 1969, Radovsky and Estebanes-Gonzales 2001) e há registros desses ácaros parasitando morcegos das famílias Vespertilionidae, Thyropteridae e Phyllostomidae ao longo de todo o Neotrópico (Radovsky and Furman 1969, Radovsky et al. 1971, Presley and Willig 2008). Carrapatos da família Ixodidae parasitam morcegos do velho mundo, onde comumente transmitem bactérias patogênicas entre morcegos (Whitaker et al. 2009, Buettner et al. 2013, Hornok et al. 2019), enquanto Argasidae são carrapatos comuns em morcegos em todo o mundo (Dick et al. 2007, Presley and Willig 2008, Whitaker et al. 2009, Hornok et al. 2019). Esses carrapatos são comumente associados às famílias Phyllostomidae, Noctilionidae, Emballonuridae e Vespertilionidae (Dick et al. 2007, Presley and Willig 2008, Hornok et al. 2019) e, como ixodídeos, podem transferir patógenos entre morcegos, para os quais são importantes grupo de ectoparasitas para saúde humana e conservação de morcegos (Hornok et al. 2012, 2019, Buettner et al. 2013, Luz et al. 2019).

Quanto aos insetos ectoparasitas, possivelmente um dos grupos mais conspícuos do mundo são as pulgas (Siphonaptera), seguidas dos percevejos (Hemiptera) e das moscas (Diptera). Pulgas são conhecidas como ectoparasitas típicos de animais domésticos e parasitam principalmente roedores (Medvedev 2002, Medvedev and Krasnov 2006, Whiting et al. 2008). Em morcegos, as famílias Ischnopsyllidae e Tungidae (Ordem Siphonaptera) podem ser encontradas principalmente parasitando morcegos das famílias Phyllostomidae, Molossidae e Vespertilionidae (Tipton and

Machado-Allison 1972, Esbérard 2001, Whiting et al. 2008, Autino et al. 2011) e no Brasil há registro de Rhynchopsyllus pulex (Siphonaptera: Tungidae) em Molossus molossus no Rio de Janeiro (Esbérard 2001). Os hemípteros parasitas de morcegos podem pertencer a duas famílias, Cimicidae e Polictenidae. Percevejos da família Cimicidae são ectoparasitas de ampla variedade, que podem parasitar morcegos e outros grupos, como sapos, lagartos e pássaros (Marshall 1982, Whitaker et al. 2009). Esses insetos parasitam principalmente morcegos que vivem em cavernas e são conhecidos por transferir patógenos entre seus hospedeiros (Marshall 1982, Hornok et al. 2012). Polictenidae é uma família de hemípteros ectoparasitas obrigatórios de morcegos que parasitam exclusivamente morcegos da família Molossidae (Marshall 1982, Esbérard et al. 2005, Presley and Willig 2008, Whitaker et al. 2009). No Brasil existem registros desses ectoparasitas no Rio de Janeiro (Esbérard et al. 2005).

Finalmente, de todos os artrópodes hematófagos, as moscas são os ectoparasitas mais comuns em morcegos neotropicais. Moscas parasitas apresentam alto grau de especificidade em Chiroptera (Dick 2007, Aguiar and Antonini 2011, Eriksson et al. 2011). Além disso, já foi comprovado que as moscas podem ser reservatórios de bactérias zoonóticas (Morse et al. 2012a, 2012b), sendo possível a transmissão de parasitas sanguíneos entre seus hospedeiros direta ou indiretamente (Obame-Nkoghe et al. 2016, Ramanantsalama et al. 2018).

1.2 Moscas ectoparasitas

As moscas dos morcegos são agrupadas em duas famílias (Streblidae e Nycteriibidae) dentro da superfamília Hippoboscoidea (Diptera), juntamente com Hippoboscidae (moscas do piolho) e Glossinidae (moscas tsé-tsé) (Dittmar et al. 2006, 2015). Essas moscas diferem das demais por sua estratégia reprodutiva (viviparidade adenotrófica), na qual a mãe deposita larvas de terceiro estágio no refúgio, uma a uma, que pupa imediatamente, resultando em um adulto após alguns dias (Overal 1980, Lehane 2005, Dittmar et al. 2009). Streblidae e Nycteriibidae parasitam apenas hospedeiros da ordem Chiroptera e dentro desta ordem demonstram um alto grau de especificidade, principalmente no nível de subfamília e, em alguns casos, até no nível de gênero (Overal 1980, Dick and Patterson 2006, 2007, Dick 2007). Essas moscas apresentam uma grande diversidade morfológica e, dependendo de suas características, podem explorar melhor diferentes partes do hospedeiro (ter Hofstede et al. 2004, Hiller et al. 2018). Nesse sentido,

existem três guildas especializadas: corredores de pelos (hair runners), nadadores de pelos (hair nanizers) e rastreadores de asas (wing crawlers). Os corredores de pelos têm pernas traseiras alongadas (semelhantes às patas saltadoras dos ortópteros) e correm acima da superfície do pelo de seu hospedeiro. Os nadadores de pelos têm um corpo achatado e uma cabeça com ponta de pá, permitindo seu deslize no meio dos pelos do hospedeiro. Já os rastreadores de asas têm um corpo achatado, mas não têm uma cabeça especializada. Ao invés disso, os rastreadores de asas têm três pares de pernas curtos e fortes, o que lhes permite caminhar na superfície da asa (especificamente no patagium) dos morcegos (ter Hofstede et al. 2004, Dick and Gettinger 2005, Hiller et al. 2018). Nos últimos anos essas moscas foram mais estudadas e nelas foram encontrados fungos parasitas (hiperparasitas) (Haelewaters et al. 2018) e bactérias de interesse sanitário (Morse et al. 2012a, 2012b).

1.3 Ecologia das moscas ectoparasitas

Devido à especificidade desses ectoparasitas, a composição das espécies de mosca em muitas espécies de morcegos é bastante constante (Dick 2007, Tello et al. 2008), com pouca variação na presença/ausência ou abundância de cada espécie de mosca (Fritz 1983, Presley and Willig 2008, Tello et al. 2008). Essas variações se devem a características dos hospedeiros, como sexo, idade, uso de abrigos e época do ano (ter Hofstede and Fenton 2005, Patterson et al. 2007, Presley and Willig 2008, Esbérard et al. 2012, Freitas 2016, Fagundes et al. 2017). Variações devido ao sexo do hospedeiro são geralmente atribuídas aos hormônios esteróides e seu efeito imunossupressor em machos, o que facilita a invasão por parasitas (Zuk et al. 1996, Zuk and Stoehr 2002). Por esse motivo, a tendência nos vertebrados é de valores mais elevados nas taxas de parasitismo em machos (Morand et al. 2004, Krasnov et al. 2011), o que não é cumprido no caso de ectoparasitas de morcegos onde as fêmeas costumam apresentar uma maior carga parasitária e prevalência de moscas (Graciolli and Linardi 2002, Christe et al. 2007, Schaik and Kerth 2017). Esse fenômeno se deve ao fato de que as fêmeas tendem a formar grupos, o que representa uma maior abundância de recursos (hospedeiros) e oportunidades de transferência para as moscas ectoparasitas (Schaik and Kerth 2017). Em relação à idade, em geral os morcegos juvenis são mais parasitados por moscas ectoparasitas (Gannon and Willig 1995, Esbérard et al. 2012) e é possível que isso se deva ao fato de a epiderme dos juvenis ser muito mais fina (o que facilitaria a alimentação das moscas), seu sistema imunológico é fraco e eles ficam mais tempo com suas mães no

abrigo, com as moscas infestando-os com maior facilidade. Devido à estratégia reprodutiva dessas moscas (mencionada acima), o abrigo do hospedeiro é uma parte determinante para seu sucesso reprodutivo (Dittmar et al. 2009). Morcegos que habitam cavidades e cavernas tendem a ter cargas parasitárias maiores do que morcegos que usam vegetação como abrigo (ter Hofstede and Fenton 2005) e, em geral, o grau de proteção e duração dos abrigos influencia positivamente a prevalência e intensidade média de moscas nos Neotrópicos (Patterson et al. 2007). Por fim, em relação à estação do ano, não há um padrão definido em termos de taxas de parasitismo (Salinas-Ramos et al. 2018) e a influência desta variável pode estar relacionada ao comportamento sazonal de cada espécie hospedeira, embora a composição das moscas de uma assembleia local pode ser muito diferente entre a estação chuvosa e a estação seca (e.g. Zarazúa-Carbajal et al. 2016, Rivera-García et al. 2017). Além desses fatores, algumas características típicas dos morcegos podem influenciar a forma como são parasitados por moscas, como organização social e o asseio (Wilkinson 1986, ter Hofstede and Fenton 2005, Schaik and Kerth 2017).

1.4 Estudos com mosca parasitas de morcegos na Amazônia

O Brasil é um dos países com o maior número de estudos sobre moscas parasitas de morcegos (Lourenço et al. 2016, Barbier and Bernard 2017) e, graças a isso, 56 espécies de estreblídeos são conhecidas atualmente para a Amazônia, com 44 registros para o estado de Amapá (Lourenço et al. 2016, Graciolli 2021). Entre os estudos realizados na Amazônia, existem relativamente poucos inventários de moscas publicados (Graciolli and Bernard 2002, Graciolli and Linardi 2002, Dias et al. 2009, Santos et al. 2009, 2013, Hrycyna et al. 2019, Palheta et al. 2020, Silva et al. 2020), com alguns deles usando índices para descrever as relações com os hospedeiros (Santos et al. 2009, 2013) e dois descrevendo a ecologia desses ectoparasitas (Hrycyna et al. 2019, Palheta et al. 2020), um deles usando redes de interação (Palheta et al. 2020). Do total de trabalhos publicados, apenas um foi realizado no estado do Amapá (veja Hrycyna et al. 2019) e nenhum nas Savanas do Amapá, o quarto maior bloco de savana amazônica, que são um dos ecossistemas mais ameaçados da Amazônia devido à conversão da vegetação e do avanço de plantios comerciais, principalmente de eucalipto e soja (Carvalho and Mustin 2017, Mustin et al. 2017, Carvalho et al. 2019). Levando em consideração a grande lacuna que existe no conhecimento da fauna e flora das savanas amazônicas, que tem sido degradada

antes que tenhamos qualquer conhecimento sobre sua fauna (Carvalho and Mustin 2017), estudos devem ser feitos para melhorar nosso conhecimento sobre a fauna de artrópodes que parasitam morcegos nesse ecossistema.

1.5 Uso de métricas de redes para avaliar interações entre moscas parasitas e morcegos

Métricas de redes de interações são utilizadas para descrever as relações entre dois grupos tróficos, quantificando o número de conexões entre as espécies de ambos os grupos (Dormann et al. 2008, 2009, Blüthgen 2010). Essa abordagem permite que a rede de interações seja representada graficamente e descreva as interações entre grupos usando uma variedade de índices descritivos. Essa abordagem é usada para descrever principalmente as interações entre polinizadores e plantas (Dormann 2011), mas nos últimos anos é possível encontrar estudos que retratam redes antagônicas como aquelas formadas entre ectoparasitas e hospedeiros (Vázquez et al. 2005). A principal característica desses estudos é a representação gráfica das redes e os índices (Dormann et al. 2009), que permitem a comparação entre redes levando-se em consideração diferentes épocas do ano, diferentes tipos de vegetação ou diferentes graus de perturbação (Zarazúa-Carbajal et al. 2016, Fagundes et al. 2017, Durán et al. 2018, Hernández-Martínez et al. 2019, Saldaña-Vázquez et al. 2019, Palheta et al. 2020, Hiller et al. 2021, Urbieta et al. 2021).

Nos últimos anos, o uso de métricas de redes de interação tem permitido aos pesquisadores descrever melhor as características da ecologia das interações entre os organismos, favorecendo sobremaneira os estudos de parasitismo em morcegos (e.g. Zarazúa-Carbajal et al. 2016, Rivera-García et al. 2017, Saldaña-Vázquez et al. 2019, Urbieta et al. 2021). Em comparação com os índices clássicos, as redes permitem descrever muito mais padrões entre os diferentes grupos que interagem (por exemplo: abundância e exclusividade de interações entre organismos - Dormann et al. 2009, Blüthgen and Klein 2011) e revelar a contribuição de cada interação para o rede, enquanto os índices clássicos (sensu Bush et al. 1997) podem mostrar padrões em larga escala, mas mascarando muitas informações em nível de espécie, interações e abundância (tanto indivíduos quanto interações), uma vez que os índices são ponderados (prevalência) ou média (intensidade média).

Por isso, com o intuito de compreender melhor as relações entre as interações dos morcegos nas savanas do nordeste do Amazonas, no estado do Amapá, o objetivo deste trabalho é avaliar a influência do tempo, sexo e idade do hospedeiro na estrutura das redes antagonistas entre moscas ectoparasitas e morcegos.

2.   HIPÓTESE

Esperamos que a sazonalidade afete a estrutura das redes, promovendo menores valores de especialização e modularidade na estação chuvosa, enquanto sexo e idade influenciam, gerando maior especialização e modularidade por parte dos hospedeiros machos e adultos.

3.   OBJETIVOS
3.1 GERAL

- Verificar a influência da sazonalidade, do sexo e idade do hospedeiro na assembleia e estrutura de redes de interação antagônicas entre morcegos e moscas ectoparasitas nas Savanas do Amapá.

3.2 ESPECÍFICOS

- Determinar o efeito da sazonalidade na estrutura das redes de interação e assembleias de moscas.

- Determinar a influência do sexo e da idade do hospedeiro na estrutura das redes de interação e assembleias de moscas.

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5.   CAPÍTULO 1

Artigo científico

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

Artigo submetido ao periódico "Integrative Zoology"

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

Short running title: Bat–fly networks in Amazonian savannahs

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

PAMZ, LAVD and WDC originally formulated the idea; BSX, IJC and WDC conducted fieldwork; PAMZ, GLU and WDC performed statistical analyses and wrote the drafts of the main manuscript and the online resources. All authors contributed critically to the manuscript and gave final approval for publication.

COMPLIANCE WITH ETHICAL STANDARDS

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

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

5.1 Abstract

Bats are the second most diverse group of mammals in the world, and one of its main parasites are the flies of the Streblidae and Nycteribiidae families. In the Neotropics, the interaction between bats and bat flies has been studied mainly in Brazil. However, there are still different gaps in knowledge about this antagonistic interaction, as well as different factors (e.g. seasonality and sex of the host) can interfere in this type of interaction. Here, we compare the richness and composition of ectoparasitic flies, specialization, and modularity of the fly-bat relationship between the seasons of the year (wet *versus* dry), host sex, and age (adult females *versus* adult males, young females *versus* young males). For this, we captured bats and collected flies at 10 different sampling sites in the fourth largest block of Amazonian savannas located in the northeast of the Brazilian Amazon. Our results showed that rainy season drives the richness and composition of species of flies, as well as the bat–fly metrics of the network. Also, adult females had higher specialization and modularity than adult males, and juvenile females had higher specialization and modularity than juvenile males. Therefore, seasonality, host sex and age contribute in different ways to the species richness and composition, and network structure, and studies should take these different factors in their analyzes for the comparison and evaluation of the bat-bat fly interactions.

Key words: amazon biome, Cerrado do Amapá, Chiroptera, phyllostomid bats, Streblidae

5.2 INTRODUCTION

Bats are the second most diverse group of mammals in the world, and these mammals use environmental resources in a very diverse way, exploring a great variety of shelters (Lewis, 1995) and feeding on fruit, nectar, insects, other vertebrates, and even blood (Kalko and Handley, 2001; Schnitzler and Kalko, 2001; Kunz *et al.*, 2011). In addition to participating in different ecological processes and environmental services (Boyles *et al.*, 2011; Kunz *et al.*, 2011), bats are known as reservoirs for pathogens and zoonotic agents, some of them, a big concern for human health (Calisher *et al.*, 2006; Añez, Crisante and Soriano, 2009; Han *et al.*, 2015; Irving *et al.*, 2021). These mammals harbor different types of arthropods, such as mites, bugs, fleas, and flies (Whitaker, Ritzi and Dick, 2009). Specifically, bat flies of the families Streblidae and Nycteribiidae form a group of parasitic flies, along with Hippoboscidae and Glossinidae (Diptera: Hippoboscoidea – Dittmar et al. 2006, Petersen et al. 2007). This group of flies reproduces by adenotrophic viviparity (Lehane, 2005), which implies develop the larvae inside the mother, giving birth to third-stage larvae within the host's roost, that immediately pupate and hatches some days after (Lehane, 2005; Dick and Patterson, 2006). This mechanism is probably the reason for this flies high host specificity and dependency (Overal, 1980; Dick and Gettinger, 2005; Dick and Patterson, 2006, 2007).

The study of bat ectoparasites has been growing in recent decades and most of Neotropical data published comes from research carried out in different regions and biomes of Brazil. The literature available in Brazil is varied, with studies addressing inventories, ecology, evolution, biogeography, and even specificity experiments (Graciolli and Linardi, 2002; Moura, Bordignon and Graciolli, 2003; Esbérard *et al.*, 2005; Graciolli and Bianconi, 2007; Eriksson, Graciolli and Fischer, 2011; Graciolli and Carvalho, 2012; Barbier, Graciolli and Bernard, 2019; Eriksson *et al.*, 2019; Hrycyna, Martins and Graciolli, 2019). Among its different regions, the north of Brazil, being one of the regions with the greatest diversity of bats in the world, remains poorly studied (Lourenço, Almeida and Famadas, 2016; Barbier and Bernard, 2017). Specifically for this region, we found some specific studies from the states of Amazonas, Roraima, Pará, and Amapá (Graciolli and Bernard, 2002; Graciolli and Linardi, 2002; Hrycyna, Martins and Graciolli, 2019; Palheta *et al.*, 2020; Silva *et al.*, 2020). Therefore, this part of the Brazil,

specifically in the Amazon, still represents an important information gap, either for bat fauna (Delgado-Jaramillo *et al.*, 2020) or for some of its main parasites, such as Streblidae (Lourenço, Almeida and Famadas, 2016).

Parasitism rates and ecological patterns of bat flies are sensitive to environmental variables (e.g. season, and roosting behavior), and host characteristics like sex, age or reproductive status (ter Hofstede and Fenton, 2005; Patterson, Dick and Dittmar, 2007; Presley and Willig, 2008; Esbérard *et al.*, 2012; Fagundes, Antonini and Aguiar, 2017; Salinas-Ramos *et al.*, 2018; Mckee *et al.*, 2019; Saldaña-Vázquez *et al.*, 2019; Júnior, Araujo and Falcão, 2020; Urbieta, Graciolli and Vizentin-Bugoni, 2021). Despite some exceptions pointing that they may vary in each host species (Moura, Bordignon and Graciolli, 2003). That is the reason to study host-parasite relationships in different environments and conditions. A commonly use methods to study interactions between two trophic groups nowadays are bipartite networks. Lately, bipartite networks are being used to depict bat-bat fly interactions too; which allow us to represent the assemblages and make comparative studies using different network metrics (Zarazúa-Carbajal *et al.*, 2016; Durán *et al.*, 2018; Estrada-Villegas *et al.*, 2018; Saldaña-Vázquez *et al.*, 2019; Palheta *et al.*, 2020; Urbieta, Graciolli and Vizentin-Bugoni, 2021). This method, then, is a suitable tool for determining ecological trends and provides useful indices to explain these patterns. Furthermore, it allows the graphical visualization of interactions at different scales within a larger network, and thus, through this analysis, it is possible to evaluate different aspects in a set of ecological interactions (Dormann *et al.*, 2009).

In the search for infectious diseases, bats have gained prominence in recent years (Calisher *et al.*, 2006; Han *et al.*, 2015; Irving *et al.*, 2021) and for this reason, all aspects of their biology must be studied in-depth, especially the arthropods that parasitize them, feed on their blood, and possibly transmit pathogens between individuals (Obame-Nkoghe *et al.*, 2016; Ramanantsalama *et al.*, 2018). Therefore, we aim to evaluate the bat-bat fly antagonistic networks and the structure of fly assemblages, creating sub-networks (interaction networks obtained by dividing a local network into smaller networks based on a variable or characteristic) according to the season of the year, sex, and age, in bats from the Savannahs of Amapá, in northeastern Brazilian Amazon. Specifically, we compared the richness and composition of ectoparasitic flies, specialization and modularity of bat-bat fly relationship between the seasons of the year

(wet *versus* dry), host sex, and age (adult females *versus* adult males, young females *versus* young males). We know that there is a greater abundance of bats in the wet season for our study area (Castro, 2009; Carvalho *et al.*, 2018), and this greater abundance is due to the increase in resources available for the hosts during the wet season (e.g. fruits and insects - Ramos et al. 2010). This will boost bat flies abundance due to the bigger number of bats in colonies (more resources for the bat flies), intensifying contact between bat fly infracommunities (*sensu* Bush et al. 1997), and promoting host-shift. Thus we expect lower values of specialization (<0.60) and modularity (<0.60) for interactions in the wet season, and due to the scarcity of resources, and lower abundance and bat species richness (Ramos, Marques and Palmeirim, 2010; Carvalho *et al.*, 2018) this values will be higher in the dry season. Furthermore, we assume that host sex will affect network topology in adult hosts sub-networks as females tend to harbor more parasites due to long exposure to flies in their roosts and during parental care (Wilkinson, 1985; Kerth, 2008; Rifkin, Nunn and Garamszegi, 2012).

5.3 MATERIALS AND METHODS
5.3.1 Study area

We captured all bats at 10 sites within forest patches in the Savannahs of Amapá, northeastern Brazilian Amazon (Fig. 1). The Savannahs of Amapá are the fourth largest block of Amazonian savannah, characterized by a wide array of savannah encrusted by forest patches, flooded fields and *buritizais* (gallery forests with the dominance of *Mauritia flexuosa* – Carvalho and Mustin 2017, Mustin et al. 2017). We chose forest patches based on accessibility by roads and trails, and all of them embedded in a matrix dominated by a type of savannah locally called parkland Cerrado (Mustin *et al.*, 2017). Open canopy cover and trees that do not exceed two meters in height characterize this type of savannah (Costa-Neto, 2017). All 10 sampling sites were equidistant by at least 2.5 km from each other, as individuals of some bat species (e.g. *Artibeus* spp.) tend to travel up to 5 km in the Amazonian savannahs (Bernard and Fenton, 2003). The average height of vegetation in the sampled forest patches was seven meters with some trees exceeding 25 meters (Carvalho *et al.*, 2020). Currently, the savannahs of Amapá have suffered from the advance of grain plantations (mainly soybeans), as they are considered the last agricultural frontier in Brazil (Carvalho and Mustin, 2017; Mustin *et al.*, 2017;

Carvalho, Mustin, *et al.*, 2019). The southeastern region of the Amazonian savannahs is characterized by a tropical monsoon climate (According to Köppen's classification), with a rainy season from December to July, and a dry season from August to November with local temperatures that do not vary greatly throughout the year, with an average of 27°C (Tavares, 2014).
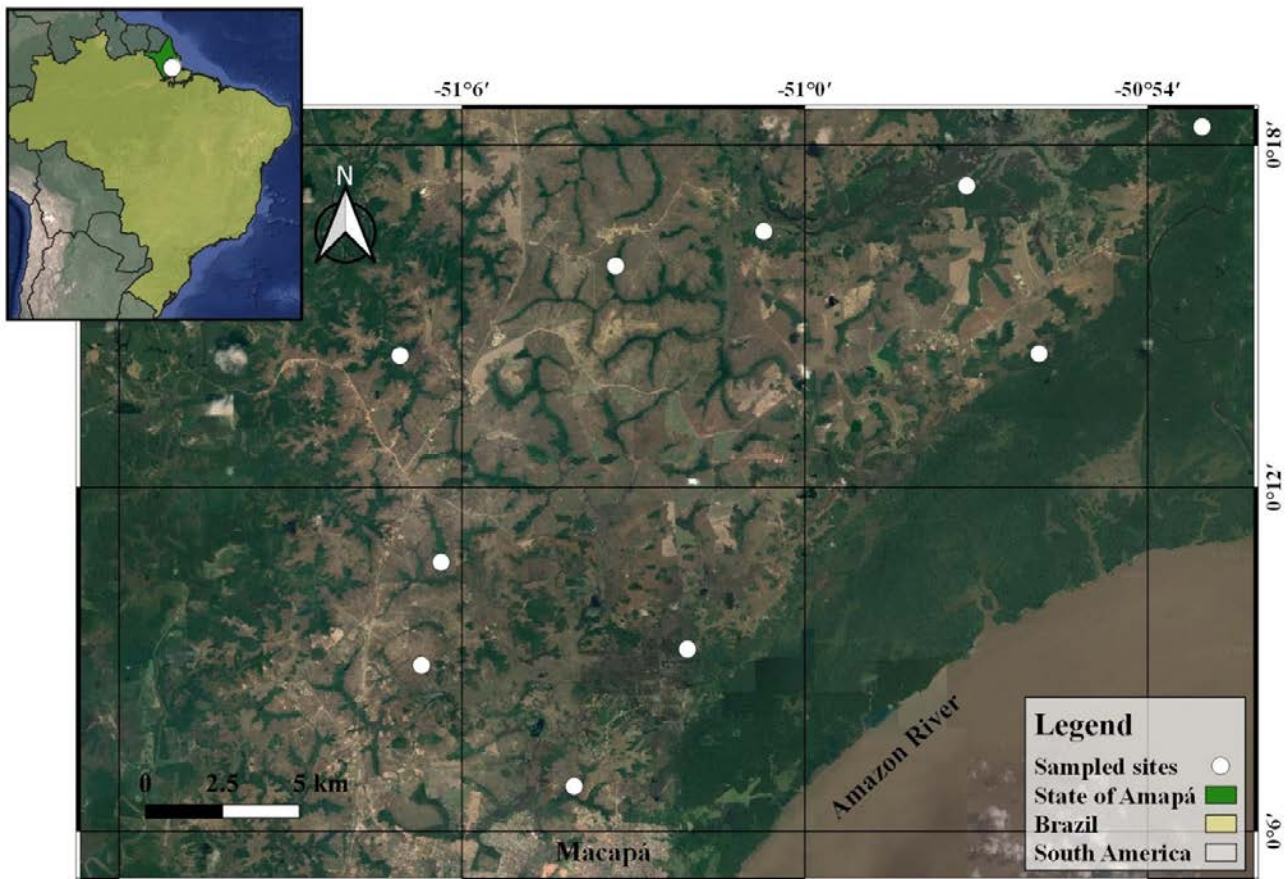
Figure 1 Brazil, state of Amapá and the 10 sites where bats were captured, and bat flies were collected. We carried out bat sampling between 2016 and 2018 along the Savannahs of Amapá, northeast of the Brazilian Amazon.

5.3.2 Bats and bat flies capture and identification

We captured the bats between august 2016 and august 2018 in approximately 110m transects at each site, with transects at least 30m from the edge of the patch to

minimize the edge's effect on bat capture (Meyer *et al.*, 2015). We used nine mist nets (12 x 3m) for four nights, two nights in the rainy season and two nights in the dry season at each site, totaling 40 nights of sampling. We carried out captures in the same site with a minimum interval of 30 days to reduce the effect of sampling for consecutive nights (Marques *et al.*, 2013; Esbérard, 2016). Our sampling effort was 12,960 m^2*h for each station (*sensu* Straube and Bianconi 2002).

We extracted the bats from mist nets and packed them in individual cotton bags to prevent sample contamination (i.e., accidental parasitism *sensu* Dick 2007). Then we identified them, recording sex and age, classifying them in adults or juveniles through differences in the degree of ossification of the epiphyses (Anthony, 1988). We identified bats following Lim & Engstrom (2001), Gardner (2008), Reis et al. (2017) and Lòpez-Baucells et al. (2018) . We followed bat species nomenclature according to Garbino (2020), and manipulated the specimens as stipulated by the American Society of Mammalogists (Sikes and Animal Care and Use Commitee of the American Society of Mammalogists, 2016). Finally, we collected all bat flies with fine-tipped forceps, storing them in microtubes containing 70% ethanol. Afterwards, we took the flies to the Laboratory of Morphophysiological and Parasitological Studies at the Federal University of Amapá (LEMP-UNIFAP) and identified them following Graciolli (2010), Guerrero (1993, 1994a, 1994b, 1995a, 1995b, 1996), and Theodor & Peterson (1964).

5.3.3 Data analysis

First, we used Hill numbers to evaluate sample coverage, comparing values between sub-networks, aiming to determine whether the differences between networks are due to biological processes or just because of sampling success. Hill numbers are suitable for comparing various datasets, evaluating species richness and sampling success by measuring coverage (Chao *et al.*, 2014; Roswell and Dushoff, 2021). Here, sampling coverage means the proportion of fly species found on more than one single bat. Because the bat flies can occur in groups of several individuals (in some cases more than 20 on a single host), we used the number of infected hosts per fly species as a measure of sample size. Thus, we calculate coverage using the 'iNEXT' package (Hsieh, Ma and Chao, 2014), instructing the package to estimate species richness ($q = 0$), based on the number

of bats, with 100 knots (knots = 100), 95% confidence interval (se = TRUE, conf = 0.95), and 1000 iterations (nboot = 1000).

Subsequently, to compare bat flies species richness between sub-networks, we estimated the species richness for each sample site, considering separately the seasonality (rain *versus* dry), sex and age of bats (adult males *versus* adult females and young males *versus* young females). We constructed species richness curves considering a sample size up to twice the size of the smallest sample, as recommended by Chao et al. (2014). Thus, for seasons, we compared a sample of 390 bats (sample size of 195 on dry season), for adult bats up to 452 (sample size of 226 for adult males) and for young bats up to 52 (sample size of 26 for juvenile male bats). To compare the expected richness curves for the sub-networks, we used the overlapping confidence intervals between the curves (Chao and Chiu, 2016). Whenever the 95% confidence intervals did not overlap, we considered the difference significant at $\alpha = 0.05$ level (Chao and Chiu, 2016). However, when intervals overlap, we used diversity estimates and standard errors to judge significance, as proposed by Schenker & Gentleman (2001).

We evaluated the species composition of bat flies between sub-networks through a similarity analysis (ANOSIM), considering the Bray-Curtis distance (Clarke, 1993). Through this analysis, we constructed a dissimilarity matrix for seasonality (rain *versus* dry), host sex and host age (adult males *versus* adult females and young males *versus* young females). To estimate ANOSIM significance, we ran a permutation test with 9,999 iterations. Subsequently, we visualized the differences or similarities between species compositions through a Non-Metric Multidimensional Scaling (NMDS) ordination. To estimate the contribution of each parasitic bat fly species when verifying differences in species composition through ANOSIM, we used the similarity percentage decomposition procedure (SIMPER), also considering the Bray-Curtis index. We performed ANOSIM, SIMPER and the NMDS using the Past.

To assess network metrics between bats and parasitic flies, we constructed a meta-network adding all sampling sites (regional scale) and six sub-networks considering the season, host sex, and host age. The meta-network provides the entire pool of species and interactions found in the Savannah of Amapá and the sub-networks provide different perspectives of the interactions found in the pooled network. We constructed each network using a matrix where rows corresponded to bat species, and columns to bat fly

species, where intersections corresponded to the frequency of interactions between bats and bat flies. We calculated bat species richness, bat fly species richness, number of links (interations), number of compartments, specialization (H2' index), and modularity (Q). The specialization (H2') indicates the degree of exclusivity of the connections in the network and can be considered a measure of niche differentiation (Blüthgen and Klein, 2011); this index goes from 0 to 1, with 1 indicating perfect specialization. In our case, we consider values above 0.8 as high specialization (Zarazúa-Carbajal *et al.*, 2016) (Q) identifies subgroups of species strongly connected within the network and its value goes from 0 to 1, with suggesting 1 a highly modular network. To calculate the modularity, we used the *DIRTLPAwb+* algorithm (Beckett, 2016). These metrics adequately describe patterns of specificity in networks and quantify how fly species share or differ in resource use (Blüthgen *et al.*, 2007; Almeida-Neto and Ulrich, 2011; Beckett, 2016; Palheta *et al.*, 2020). Also we used null models to test the significance of specialization (H2') and modularity (Q) based on 1,000 matrices generated by the *vaznull* algorithm (Vázquez and Aizen, 2006) which keeps the number of connections constant and, therefore, it is suitable for analyzing antagonistic networks with a high degree of specificity (e.g., Urbieta et al. 2021). We compared the estimated index values with the 95% confidence interval of the null model to establish whether they show different values than expected by chance (Dormann *et al.*, 2019). All analyzes were performed using the 'bipartite' package in the R software (R Core Team, 2021).

5.4 RESULTS
5.4.1 Bats and bat flies assemblage structure, composition and richness

We captured 1,221 bats belonging to 27 species of the Vespertilionidae and Phyllostomidae families (Table S1). The most abundant bat species were *Artibeus planirostris* (n = 256), *Carollia perspicillata* (n = 221), and *Artibeus lituratus* (n = 152). More than one third (37.51%) of bats were parasitized by at least one fly (Table 1; Table S1, Supporting Information). Among adult bats, females were proportionally more parasitized than males (female = 41.75%; males = 32.12%). Young bats were less parasitized than adult bats (young = 36.91%; adults = 37.59%), with young males being more parasitized than young females (females = 39.39%; males =40.90%) (Table 1). Regarding seasonality, we captured 748 bats in the rainy season (41.04% parasitized) and

473 in the dry season (31.92% parasitized).

Table 1 – Network structure and bat-bat fly interaction networks from Savannah of Amapá, northeast of the Brazilian Amazon. Bold indicates statistically significant results, i.e., when the observed value is higher than the 95% confidence interval. FEADU = Female adult bats; FEJUV = Female juvenile bats; MADU = Male adult bats and MAJUV = Male juvenile bats.

Metrics	Rainy	Dry	FEADU	MADU	FEJUV	MAJUV	Meta-Network
Sample Coverage	0.986	0.974	0.965	0.948	0.916	0.586	0.987
Bat Species	24	16	22	20	8	12	27
Bat Abundance	307	151	228	169	41	20	458
Fly Species	35	25	33	32	13	15	39
Number of Links	50	28	44	41	16	18	56
Number of Flies	1,185	398	826	562	117	78	1,583
Number of Compartments	12	13	13	12	15	9	12
Specialization (H2′)	0.83 (0.22 – 0.70)*	0.98 (0.53 – 0.87)*	0.88 (0.36 – 0.81)*	0.87 (0.22 – 0.71)*	0.75 (0.14 – 0.78)	0.92 (0.41 – 0.81)*	0.88 (0.27 – 0.74)*
Modularity (QuanBiMo)	0.66 (0.19 – 0.61)*	0.80 (0.37 – 0.74)*	0.73 (0.25 – 0.69)*	0.67 (0.17 – 0.62)*	0.46 (0.14 – 0.59)	0.69 (0.37 – 0.70)	0.70 (0.19 – 0.66)*

We collected 1,583 flies belonging to 39 species. The most abundant species were *Trichobius joblingi* (n = 613), *Trichobius parasiticus* (n = 139), *Speiseria ambigua* (n = 94), *Strebla wiedemanni* (n = 88), and *Mastoptera minuta* (n = 78; Table S2, Supporting Information). The bat fly richness curve comparison between seasons shows the presence of more species in the rainy season (Fig. 2A). Regardless of the sex of the adult hosts, there is no difference in the richness of bat flies (Fig. 2B). However, on young male bats, we recorded greater richness of bat flies than on young females (Fig. 2C).
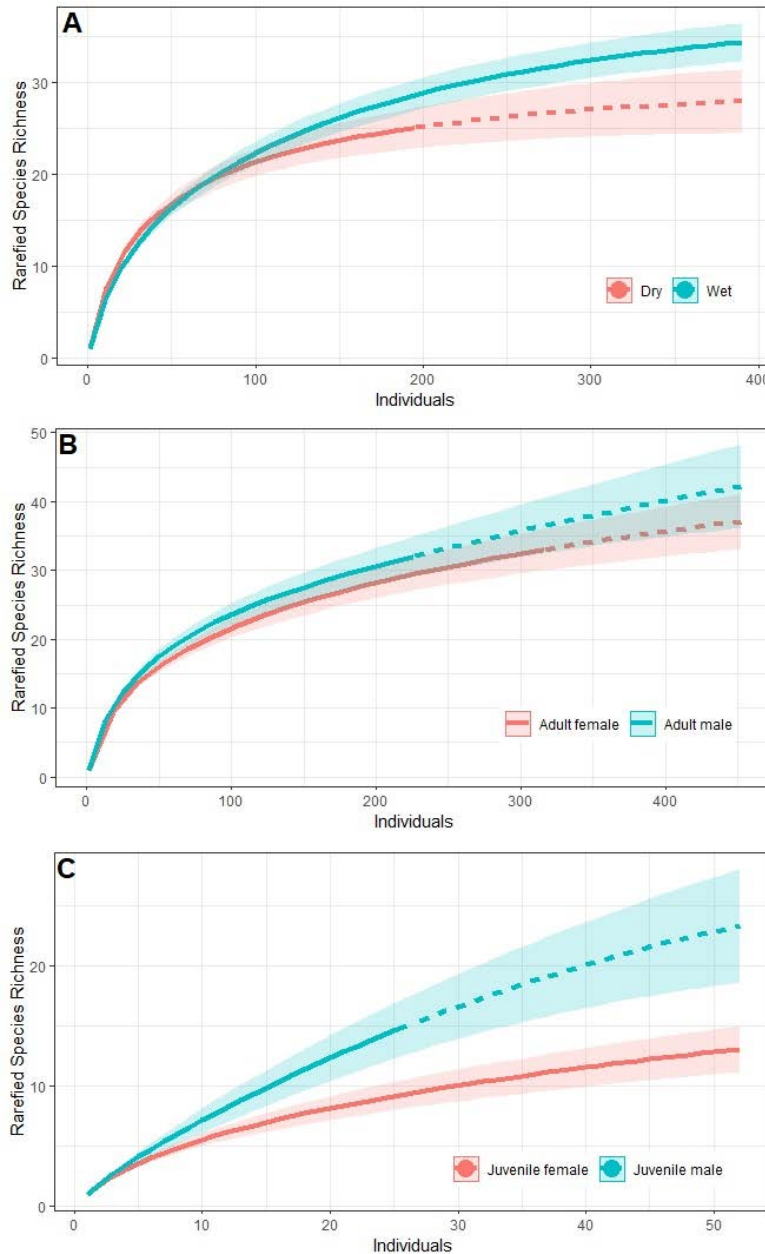
Figure 2 Species richness estimated with Hill numbers ($q = 0$) for bat flies parasitizing bats between seasons (A), between adult male and female bats (B), and between juvenile male and female bats (C). Bat flies collected from bats captured between 2016 and 2018 in forest patches in the Savannahs of Amapá, northeast of the Brazilian Amazon. The shaded area represents the 95% confidence interval.

Bat flies species composition was different between seasons (Global R = 0.123; p = 0.046 – Fig. 3A). Five species of flies contributed 53% to the dissimilarity between the wet and dry season: *Trichobius joblingi* (25%), *Speiseria ambigua* (9%), *Trichobius*

parasiticus (7%), *Aspidoptera phyllostomatis* (6%), and *Strebla guajiro* (6 % - Fig. 4). However, when we considered sex in adult hosts, we did not find any difference (Global R = -0.05; p < 0.837 – Fig. 3B). The same is repeated when we consider sex in juvenile hosts (Global R = 0.028; p < 0.262 – Fig. 3C).
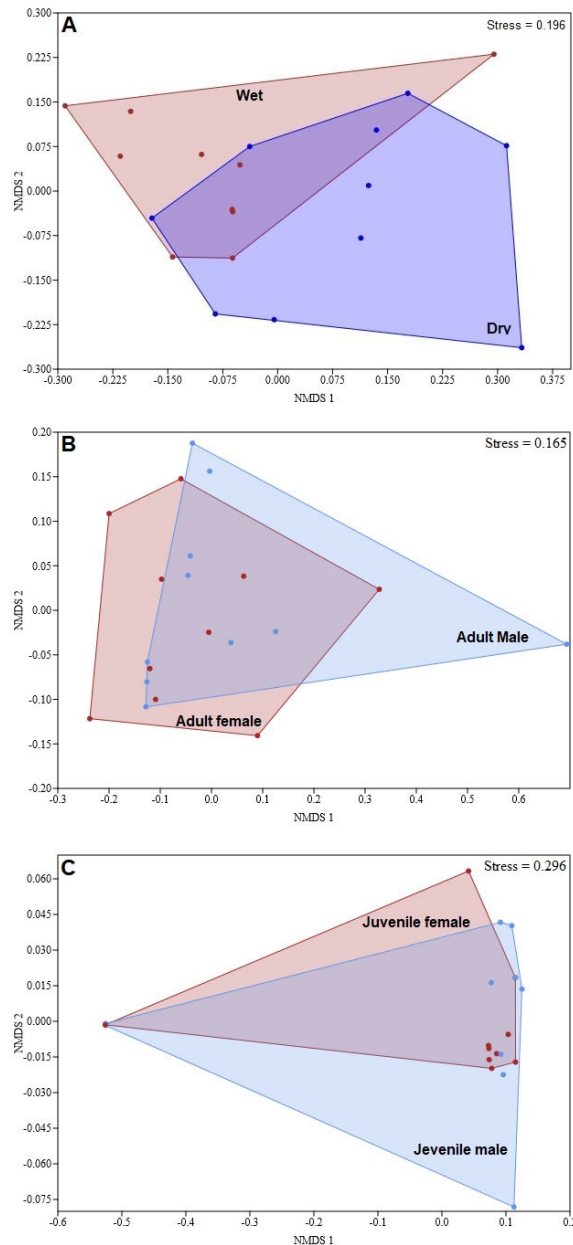
Figure 3 Non-metric multidimensional scaling (NMDS) ordination chart, showing differences in species composition of bat flies between (A) seasons, (B) adult male and female bats, and (C) juvenile male and female bats. Bat flies collected from bats captured between 2016 and 2018 in forest patches in the Savannahs of Amapá, northeast of the Brazilian Amazon.
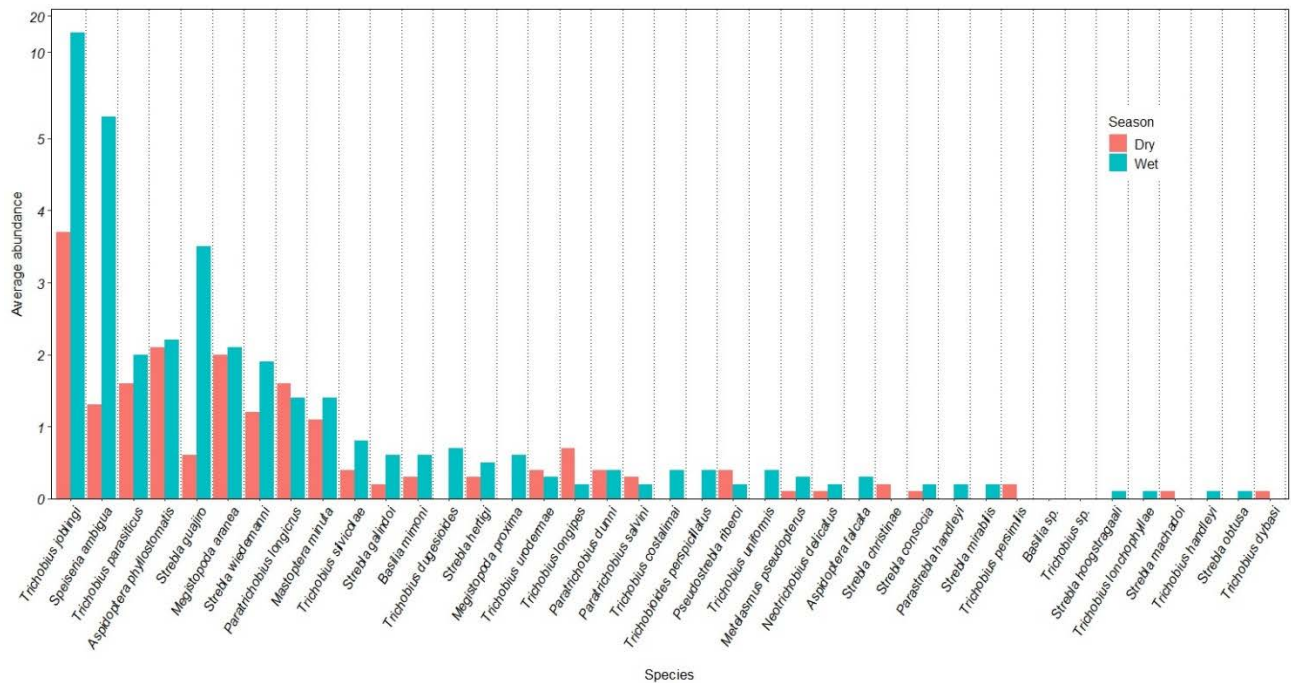
Figure 4 Estimated mean abundance (estimated by SIMPER) of bat flies collected from bats captured between 2016 and 2018 in forest patches in Savannahs of Amapá, northeastern Brazilian Amazon.

5.4.2 Topology, specialization and modularity

The meta-network was highly specialized (0.88), and modular (0.70) with a total number of 27 bat species, and 39 bat fly species (Fig. 5). We recorded sub-networks with wide variation of bat species (8-24), bat fly species (15-35), links (18-50), interactions (78-1,185), and number of compartments (9-15) (Table 1; Fig. 6). Except for the sub-network representing young females and the modularity in the young males sub-network, all the networks presented significant indexes values, high specialization (>0.75) and high modularity (>0.66) (Table 1). When comparing between seasons, the dry season sub-network was more specialized (0.98) and modular (0.80). On the other hand, the rainy season sub-network has a greater number of bat and fly species, and interactions. Regarding host sex, the adult females sub-network was more specialized (0.88), more modular (0.73), and larger in all other parameters (Table 1). As for young hosts, we recorded small subnets with few species richness of bats and bat flies. Specialization in the young male's sub-network was the only showing significant metrics in this comparison (Table 1; Fig. 6).
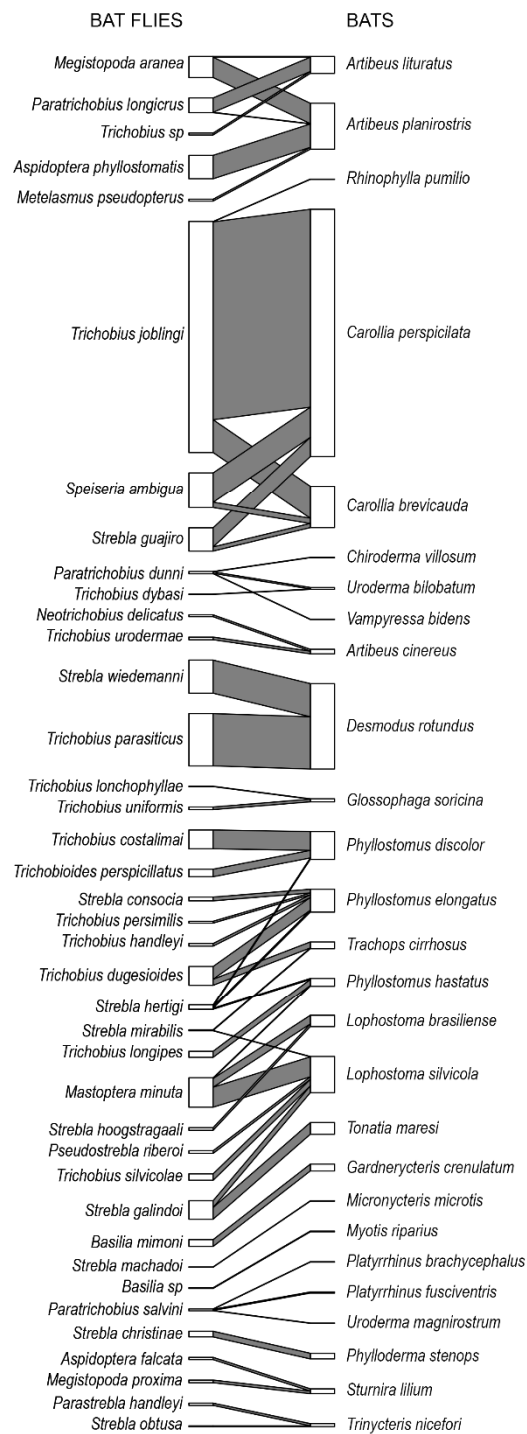
Figure 5 Local interaction network between bats and bat flies. Bat flies collected from bats in forest patches in the Savannahs of Amapá, northeastern Brazilian Amazon between 2016 and 2018.
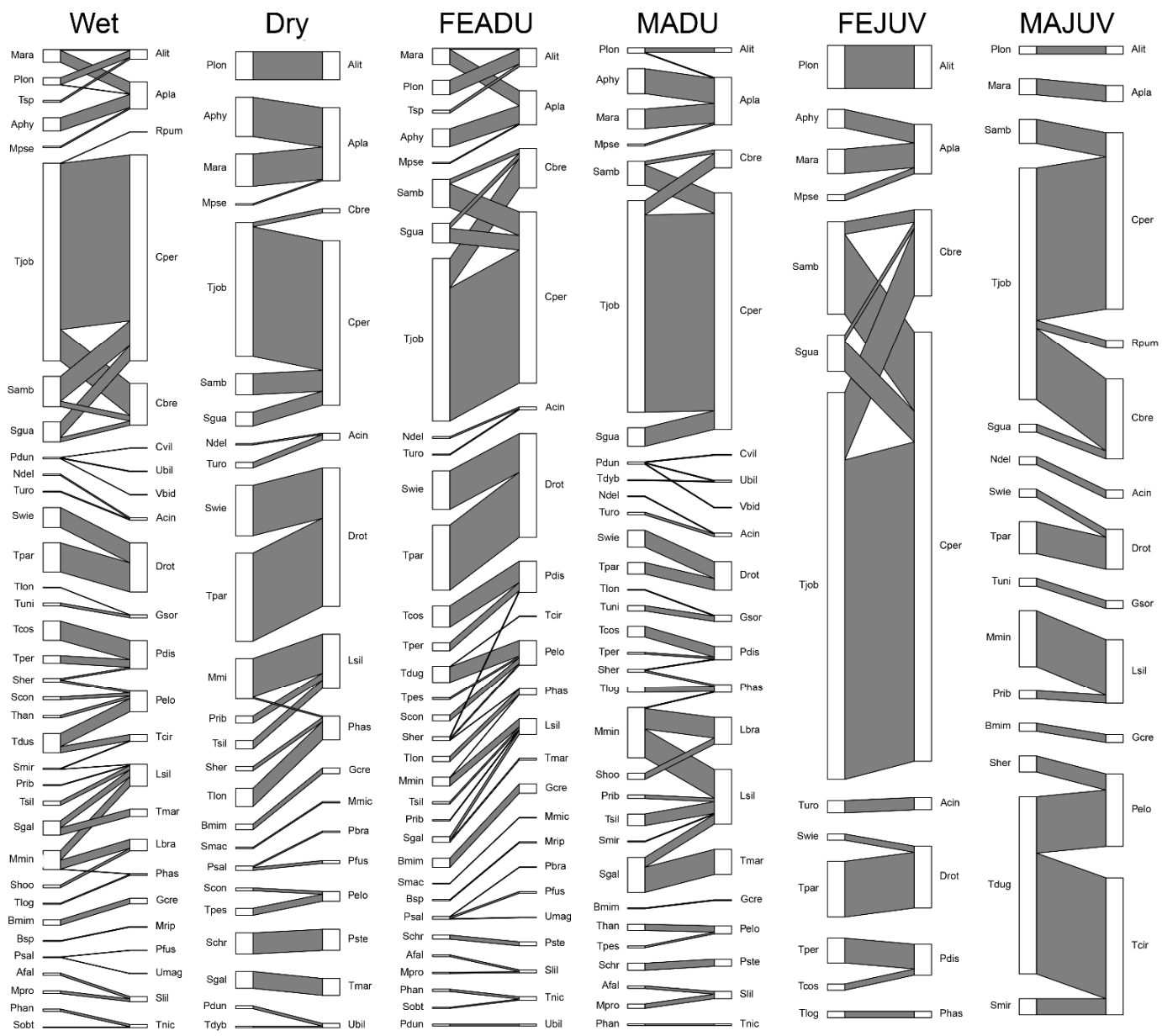
Figure 6 Sub-networks between bats (in the left column) and bat flies (in the right column), divided by season, host sex, and host age. FEADU= female adult bats; MADU= male adults bats; FEJUV= female juveniles bats; MAJUV= juvenile male bats. Bat flies collected from bats that captured in forest patches in the Savannahs of Amapá, northeastern Brazilian Amazon between 2016 and 2018. Bats: Alit= *Artibeus planirostris;* Apla= *A. planirostris;* Rpum= *Rhinophylla pumilio;* Cper= *Carollia perspicillata;* Cbre= *C. brevicauda;* Cvil= *Chyroderma villosum;* Ubil= *Uroderma bilobatum;* Vbid= *Vampyressa bidens;* Acin= *A. cinereus;* Drot= *Desmodus rotundus;* Gsor= *Glossophaga soricina;* Pdis= *Phyllostomus discolor;* Pelo= *P. elongatus;* Tcir= *Trachops cirrhosus;* Phas= *P. hastatus;* Lbra= *Lophostoma brasiliense;* Lsil= *L. silvicola;* Tsau= *Tonatia maresi;* Mcre= *Gardnerycteris crenulatum;* Mmic= *Micronycteris microtis;* Mrip= *Myotis riparius;* Pbra= *Platyrrhinus brachycephalus;* Pfus= *P. fusciventris;* Umag= *U. magnirostrum;* Pste= *Phylloderma stenops;* Slil= *Sturnira lilium;* and Tnyc= *Trinycteris nicefory.* Bat flies: Mara= *Megistopoda aranea;* Plon= *Paratrichobius longicrus;* Tsp= *Trichobius sp;* Aphy= *Aspidoptera phyllostomatis;* Mpse= *Metelasmus pseudopterus;* Tjob= *T. joblingi;* Samb= *Speiseria ambigua;* Pdun= *Paratrichobius dunni;* Tdyb= *T. dybasi;* Ndel= *Neotrichobius delicatus;* Turo= *T. urodermae;* Swie= *S. wiedemanni;* Tpar= *T. parasiticus;* Tlon= *T.lonchophyllae;* Tuni= *T. uniformis;* Tcos= *T. costalimai;* Tper= *Trichobioides perespicillatus;* Scon= *S. consocia;* Tpes= *T. persimilis;* Than= *T. handleyi;* Tdug= *T. dugesioides;* Sher= *S. hertigi;* Smir= *S. mirabilis;* Tlog= *T. longipes;* Mmin= *Mastoptera minuta;* Shoo= *S. hoogstragali;* Prib= *Pseudostrebla riberoi;* Tsil= *T. sylvicolae;* Sgal= *S. galondoi;* Bmim= *Basilia mimoni;* Smac= *S. machadoi;* Bsp= *Basilia sp.;* Psal= *P. salvini;* Schr= *S. christinae;* Afal= *A. falcate;* Mpro= *M. proxima;* Phan= *Parastrebla handleyi;* and Sobt= *S. obtusa.*

5.5 DISCUSSION

According to our predictions, bats and bat flies were more abundant in the rainy season. On the other hand, specialization and modularity were high regardless of the season. The high values of these metrics in the dry season indicate little resource and contact between host species on perches. Confirming our prediction, female hosts harbor more parasites than males, directly affecting network specialization, modularity, and topology. Finally, although female hosts bear more parasites, host age does not clearly affect interactions. This study is only the ninth inventory of ectoparasitic bat flies carried out throughout the Amazon biome, complementing previous studies in other ecosystems in the state of Amapá (Hrycyna, Martins and Graciolli, 2019), and joining the scarce literature describing bat–bat flies interactions in northern Brazil, including other Amazonian savannahs (Graciolli and Bernard, 2002; Graciolli and Linardi, 2002; Dias *et al.*, 2009; Santos *et al.*, 2009, 2013, 2020; Hrycyna, Martins and Graciolli, 2019; Palheta *et al.*, 2020). Therefore, our data address seasonal differences in an unprecedented way, along with the influence of host sex, in bat-bat fly relationships in Amazonian savannah environments.

5.5.1 Seasonality, bats and bat flies composition

The rainy season favored a greater number of interactions between bats and bat flies. The reproductive strategy of these flies, result in a complete dependence on host availability, since adult bat flies emerge in the roost, and need a host to feed immediately or they die in a few hours (Overal, 1980; Dick and Patterson, 2007; Dittmar *et al.*, 2009). This dependence determined that the seasonal differences in the composition of bat assemblages (the composition of hosts in the network), influenced the topology of the sub-networks and the range of interactions between bats and bat flies. In this case, previous studies have found significant differences in the composition of bat species assemblages between wet and dry seasons in the Savannahs of Amapá, with greater abundance of bats in rainy season, especially for *Carollia perspicillata* and *Artibeus* spp. (Castro, 2009; Carvalho *et al.*, 2018). In addition, *C. perspicillata*, *A. planirostris* and *A. lituratus* have the highest reproductive rates in the rainy season in tropical forests (Carvalho, Martins, *et al.*, 2019), representing the most captured species in our study. These factors modify bats' social and roosting behavior (McCracken and Wilkinson,

2000; Garbino and Tavares, 2018), promoting the formation of seasonal groups, colonies, and aggregations (McCracken and Wilkinson, 2000; Kerth, 2008), and increasing the probability of bats to be parasitized by bat flies. Moreover, in rainy season, it is possible to find aggregation behavior, even in solitary species where solitary males actively seek for females. According to Klingbeil and Willig (2010), bat foraging patterns are different in the wet season too, due to their reproductive cycles, reducing their home range and their time of activity, but resorting to greater distances seeking greater resources.

McCracken and Wilkinson (2000) and Wilkinson (1986) also indicate that during bat's mating dynamics, groups of bats constantly exchange members, with males seeking for harems and competing for their control, while females constantly change from one harem to another in some species. Therefore, it is possible that males in this period are likely to share roosts with males from other species that have similar mating and roosting behaviors (Garbino and Tavares, 2018), increasing the probability of contact with ectoparasites coming from another bat species, transferring them to the females during mating. Hence, similar roosting behavior and the mobility of individuals would explain the seasonality of some interactions, as in the case of *Megistopoda aranea* interacting with *Artibeus lituratus,* and *Paratrichobius longicrus* with *Artibeus planirostris* (Fig. 6). Host's social and ecological dynamics can have an impact in the way they interact with their ectoparasites, offering more hosts for the newly emerged flies in the roost, giving them a larger and more diverse pool of hosts (Fagundes, Antonini and Aguiar, 2017; Saldaña-Vázquez *et al.*, 2019). Furthermore, low roost availability in the Amazonian savannahs (Aguirre, Lens and Matthysen, 2003), could be a limiting factor for bats, forcing them to share the best roosts for shelter and as maternity colonies after mating season (Wilkinson, 1985; Kunz and Hood, 2000; Kerth, 2008). Therefore, bat flies emerged in a roost with a greater number of bats of different species tend to be more likely to be associated with a greater number of hosts and with bat species different than their main host (Saldaña-Vázquez *et al.*, 2019), resulting in a greater number of interactions in the bat-bat fly networks.

The rainy season also favors the capture of bats (see Carvalho et al. 2018) and flies, and our data points that this consequently increases the number of interactions and links. The higher capture rate and host species richness could even increase the risk of contamination, resulting in a higher number of reports of atypical interactions (Dick, 2007; Hiller *et al.*, 2021). On the other hand, the dry season induced changes in specialization and modularity. During dry season, some bats lower their reproductive rates

(Mello *et al.*, 2004; Klingbeil and Willig, 2010; Carvalho, Martins, *et al.*, 2019), juveniles (both males and females), disperse, abandoning their parental groups (Dobson, 1982; Morrison and Handley, 1991), and adults return to solitary behavior. This reduce the size of the groups, with bats possibly abandoning large and stable roosts and maternity colonies, switching to less stable roosts, closer to food resources (Racey, 1982; Lewis, 1995; McCracken and Wilkinson, 2000; Klingbeil and Willig, 2010), which at this time tend to be scarce (Pinheiro *et al.*, 2002; Mello *et al.*, 2004; Janzen and Schoener, 2013). In addition, in this season, solitary bats have little contact with other bats, while species that maintain groups of females, become more stable, with constant composition (McCracken and Wilkinson, 2000). Contact between bats of different species reduced along with the probability of sharing ectoparasites, as bat flies that manage to survive outside their main host most likely die by grooming throughout this period, and disappear without being able to reproduce (Overal, 1980; Wilkinson, 1986; Combes, 1991; Dick and Patterson, 2007). Finally, the reduction in environmental humidity could play an important role. This because it could affect in the viability of the larvae for some bat fly species (Patterson, Dick and Dittmar, 2007; Pilosof *et al.*, 2012), considering that the bats in neotropical savannahs roost mainly in vegetation, more susceptible to variations in temperature and humidity (Aguirre, Lens and Matthysen, 2003; Patterson, Dick and Dittmar, 2007; Pilosof *et al.*, 2012). Consequently, the presence of some bat flies could be limited to groups of hosts (within their host range) that permanently share more stable shelters during the dry season. The difference in composition and richness of bat flies in the wet season could also influence the structure of this sub-network, differentiating itself more from the dry-season's sub-network and would explain at the same time the broad differences we found in specialization and modularity. Then we could assume that the ecology and behavior of the bats, together with the composition and richness of species of bat flies, contribute to the structure of the networks in a combined way.

5.5.2 Interactions, metrics and hosts

The local bat-bat fly interaction network in the Savannahs of Amapá was highly specialized and modular. Specialization (H2') value is lower to others reported in Mexico (H2'=0.92-0.98 - Zarazúa-Carbajal et al. 2016) and Panama (H2'=0.97 - Hiller et al. 2021), and higher than other networks reported in Jalisco state (Mexico - Hernández-Martínez et al. 2019) and Colombia (Durán *et al.*, 2018). This is mainly because

specialization is sensitive to variables such as the vegetation type, host ecology (Saldaña-Vázquez *et al.*, 2019), and possibly to broader ones such as latitude and altitude. Our local network's high specialization and modularity, represents a structural difference with networks reported in other Brazilian ecoregions (Barbier and Bernard, 2017; Fagundes, Antonini and Aguiar, 2017; Palheta *et al.*, 2020; Urbieta, Graciolli and Vizentin-Bugoni, 2021). Palheta et al., (2020) report in the north of the state of Pará a network with greater number of links and with numerous atypical interactions, which could be due to contamination effect while collecting the samples. This network's structure differs widely from our data in the state of Amapá, mainly taking *C. perspicillata* in their network as an example, with more than 20 different interactions, although this species commonly carries just three bat fly species: *Trichobius joblingi*, *Speiseria* sp., and *Strebla guajiro* (Fritz, 1983; Tello, Stevens and Dick, 2008). The network described by Fagundes et al. (2017), presents atypical interactions as well, although the network has better defined compartments. In comparison with our network, we noted Fagundes et al, (2017) shows many more interactions, including conspicuous atypical interactions, once again taking as an example *C. perspicillata* with *T. tiptoni*, *T. dugesii*, and *P. longicrus*, which could be a product of contamination. It was also possible to see the same in *D. rotundus*, associated with *S. mirabilis*, *T. furmani*, *S. wiedemanni*, and *T. parasiticus*, although, this bat species usually interacts only with *S. wiedemanni* and *T. parasiticus*, as reported by other authors (Rojas *et al.*, 2008; Abundes-Gallegos *et al.*, 2018). Additionally, this network reports a low specialization value (H2'=0.65) compared to our network (H2'=0.88) and it is expected for a network of interactions between bat flies and bats in the Neotropics (H2'>0.80) (Zarazúa-Carbajal *et al.*, 2016). The network reported by Urbieta et al. (2021) in urban environments has a lower species richness than the rest of the mentioned networks (n = 7), especially in relation to our network (n = 39). This network is highly modular (Q=0.61) and is highly specialized (H2'=0.86) (Zarazúa-Carbajal *et al.*, 2016), as well as our network (Q=0.70, H2'=0.88). The authors report six unusual interactions, which indicate possible accidental connections since the host species in their network have the similar roosting behavior (Urbieta, Graciolli and Vizentin-Bugoni, 2021). We believe that this pattern of atypical bat fly occurrences is because of their hosts are sharing roosts, and that these seasonal host switches occur during rainy season. This because the interactions (*M. aranea* and *A. phyllostomatis* in *A. lituratus*), reported by Urbieta et al. (2021), were recorded in the period of greatest rainfall in the region (Soriano, 1997) and such pattern is repeated in our rainy season sub-network

in the savannahs of Amapá (Fig. 6a).

5.5.3 Adult hosts

Female hosts seem to generate greater specialization and modularity. Possibly this is since the seasonal behavior of female bats is more stable than male's, as in general, in the majority of bat species females tend to form stable groups throughout the year, which at the same time are more faithful to their roosts (Lewis, 1995; McCracken and Wilkinson, 2000). In addition, females exhibit mobility between groups during the mating season, but all of this mobility may be restricted to groups within a single colony (McCracken and Wilkinson, 2000; Kerth, 2008), while males move further, since they change location while competing to control harems (Morrison, 1979; Morrison and Handley, 1991; Kunz and McCracken, 1996). Besides, social grooming in grouped females (Wilkinson, 1986), could be efficient in eliminating foreign bat flies acquired from other species in the roost. Furthermore, we found no significant differences in bat flies species richness and composition between sexes, so we consider that host sex itself do not contribute to the differences found between sub-networks and we noted the importance of bat species social dynamics in network structure.

5.5.4 Juvenile hosts

Our study represents a unique case, as juvenile bats were less parasitized, regardless of gender, and habitat could be the main cause. Juvenile bats usually held more parasites than adult bats (Bertola *et al.*, 2005; Esbérard *et al.*, 2012), possibly because during their first weeks of life they remain alt the roost longer and are more susceptible to be parasitized by larvipositing females and newly emerged adult bat flies (Overal, 1980; Patterson, Dick and Dittmar, 2007; Pilosof *et al.*, 2012). Neotropical savannahs in general offer a lower number of roosts, mainly consisting of vegetation (Kunz, 1982; Aguirre, Lens and Matthysen, 2003), which would limit colony size and thus, parasitism rates (Chruszcz and Barclay, 2002; Solick and Barclay, 2006; Rifkin, Nunn and Garamszegi, 2012). In addition, Wilkinson (1986) established that female *Desmodus rotundus* constantly groom newborns and juveniles. This species is particularly social and known to groom each other, probably the rest of the Phyllostomidae species in our network show the same behavior. Wilkinson (1986) also mentions that social grooming

does not significantly influence parasite load, but the combination of this behavior with reduced colony sizes could explain the patterns found in our data. On the other hand, other variables could contribute too, such as the active search for females by bat flies, reported in European bat mites by Christe et al. (2007). Our data shows that host sex and age contribute in different ways to the network structure. Is essential to evaluate and take care of sample sizes to complement the results, and to understand better their parasitism patterns. This because more than a third of the bat flies we found in juvenile male host were present in a single bat (sample coverage = 59% - Table 1). This indicates that these records could be due to accidental horizontal transfer (ectoparasites that move between individuals in the colony) and not because they prefer juveniles, thus affecting the structure of this sub-network.

The sub-network of juvenile males was much more specialized than that of other types of hosts, while the sub-network of adult females was the more modular. Structure was different between these two sub-networks. This indicates that bat flies behave in a more specialist way with the juvenile bats (Table 1). Once again, this could be because bat flies actively search for female hosts and they accidentally end up over juveniles (Christe *et al.*, 2007). Hence, bat flies may consider juvenile male bats as a low quality resource and only take one as a host by accident, or in case they were not able to parasitize an adult female. The role of sex in the structure of interaction networks of juvenile hosts is still not clear and it is necessary to invest more effort in study this age group in the future, together with specific behavioral information and use techniques that allow to estimate the age of the hosts with greater precision.

Here, we bring new data for the bat-bat fly interactions for the fourth largest block of Amazonian savannahs (Carvalho and Mustin, 2017). Based on these data, we highlight that there is a strong seasonal influence, with the rainy season driving the richness and composition of species of bat flies, as well as the bat–fly metrics in the network. Furthermore, there is also an influence of host sex, with adult females having higher specialization and modularity than adult males, and juvenile females having higher specialization and modularity than juvenile males. Therefore, seasonality, host sex and age contribute in different ways to the species richness and composition, and network structure, and studies should take these different factors in their analyzes for the comparison and evaluation of the bat-bat fly interactions.

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6.   CONCLUSÕES

Com base nesses dados, destacamos que existe uma forte influência sazonal, com a estação das chuvas impulsionando a riqueza e composição das espécies de moscas-morcego, bem como as métricas de mosca-morcego na rede.

Além disso, há também uma influência do sexo do hospedeiro, com as fêmeas adultas tendo maior especialização e modularidade do que os machos adultos, e as fêmeas juvenis tendo maior especialização e modularidade do que os machos juvenis.

Supporting Information

Table S1 List of species and abundance of bats that carried flies. Bats captured in forest patches in the Savannahs of Amapá, northeast of the Brazilian Amazon between 2016 and 2018. FEADU = Female adult; FEJUV = Female juvenile; MADU = Male adult and MAJUV = Male juvenile.

Bat Species	Wet	Dry	FEADU	MADU	FEJUV	MAJUV	Meta
Artibeus lituratus	15	16	21	4	5	1	31
Artibeus planirostris	38	37	36	34	4	1	75
Carollia brevicauda	36	1	21	9	4	3	37
Carollia perspicillata	125	42	82	63	17	5	167
Chiroderma villosum	1	0	0	1	0	0	1
Artibeus cinereus	5	5	3	4	2	1	10
Desmodus rotundus	23	16	25	11	2	1	39
Glossophaga soricina	4	0	0	3	0	1	4
Lophostoma brasiliense	1	0	0	1	0	0	1
Lophostoma silvicola	20	11	11	18	0	2	31
Gardnerycteris crenulatum	6	3	7	1	0	1	9
Micronycteris microtis	0	1	1	0	0	0	1
Myotis riparius	1	0	1	0	0	0	1
Platyrrhinus brachycephalus	0	1	1	0	0	0	1
Phyllostomus discolor	4	0	2	1	1	0	4
Phyllostomus elongatus	6	2	5	2	0	1	8
Platyrrhinus fusciventris	1	2	3	0	0	0	3
Phyllostomus hastatus	2	7	4	4	1	0	9
Phylloderma stenops	0	2	1	1	0	0	2
Rhinophylla pumilio	1	0	0	0	0	1	1
Sturnira lilium	6	0	1	5	0	0	6
Trachops cirrhosus	2	0	1	0	0	1	2
Trinycteris nicefori	3	0	2	1	0	0	3
Tonatia maresi	3	2	1	4	0	0	5
Uroderma bilobatum	2	3	3	2	0	0	5
Uroderma magnirostrum	1	0	1	0	0	0	1
Vampyriscus bidens	1	0	0	1	0	0	1
Total	307	151	233	170	36	19	458

Table S2 List of species and abundance of bat flies collected from bats captured in forest patches in the Savannahs of Amapá, northeastern Brazilian Amazon between 2016 and 2018. FEADU = Female adult; FEJUV = Female juvenile; MADU = Male adult and MAJUV = Male juvenile.

Batfly Species	Wet	Dry	FEADU	MADU	FEJUV	MAJUV	Meta
Aspidoptera falcata	6	0	3	3	0	0	6
Aspidoptera phyllostomatis	34	28	31	28	3	0	62
Basilia mimoni	14	4	16	1	0	1	18
Basilia sp.	2	0	2	0	0	0	2
Mastoptera minuta	49	29	15	56	0	7	78
Megistopoda aranea	33	23	28	22	4	2	56
Megistopoda proxima	7	0	2	5	0	0	7
Metelasmus pseudopterus	4	1	2	2	1	0	5
Neotrichobius delicatus	4	1	3	1	0	1	5
Parastrebla handleyi	6	0	4	2	0	0	6
Paratrichobius dunni	4	2	3	3	0	0	6
Paratrichobius longicrus	19	20	25	6	7	1	39
Paratrichobius salvini	2	3	5	0	0	0	5
Pseudostrebla riberoi	2	5	2	4	0	1	7
Speiseria ambigua	79	15	49	27	15	3	94
Strebla christinae	0	15	7	8	0	0	15
Strebla consocia	8	2	10	0	0	0	10
Strebla galindoi	37	12	10	39	0	0	49
Strebla guajiro	52	10	34	21	6	1	62
Strebla hertigi	9	3	7	3	0	2	12
Strebla hoogstragaali	7	0	0	7	0	0	7
Strebla machadoi	0	1	1	0	0	0	1
Strebla mirabilis	3	0	0	1	0	2	3
Strebla obtusa	2	0	2	0	0	0	2
Strebla wiedemanni	52	36	67	19	1	1	88
Trichobioides perspicillatus	20	0	14	2	4	0	20
Trichobius costalimai	50	0	37	12	1	0	50
Trichobius dugesioides	50	0	28	0	0	22	50
Trichobius dybasi	0	1	0	1	0	0	1
Trichobius handleyi	7	0	0	7	0	0	7
Trichobius joblingi	517	96	283	238	63	29	613
Trichobius lonchophyllae	1	0	0	1	0	0	1
Trichobius longipes	3	13	9	6	1	0	16
Trichobius parasiticus	76	63	113	13	9	4	139
Trichobius persimilis	0	5	3	2	0	0	5
Trichobius silvicolae	11	6	4	13	0	0	17
Trichobius (persimilis) sp.	5	0	5	0	0	0	5
Trichobius uniformis	7	0	0	6	0	1	7
Trichobius urodermae	3	4	2	3	2	0	7

| **Total** | 1185 | 398 | 826 | 562 | 117 | 78 | 1583 |