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## **Bats ectoparasites infracommunities structure patterns and interactions**

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## General Abstract

Parasite community structures result from a complex chain of interactions. These organisms interact with their hosts, conspecifics, and other parasites species, in addition to environmental requirements. Some of these structuring processes can be accessed using Metacommunity Theory. This theory mainly focuses into evaluate patterns and mechanisms contributing to species diversity across space, usually in local and regional scales. The local scale approach can be used to explore infracommunity structural processes. Infracommunity is the term used to identify all parasites of a particular individual host, and it shares some of characteristics and are under similar processes as those of free-living species. This dissertation is mainly about infracommunity structure and its population interactions. It is divided in three chapters, all using bats and their ectoparasites as model of study. In the first chapter, I used the metacommunity framework, more specifically the metacommunity pattern-based approach, to identify infracommunity patterns of ectoparasites on three bat species in the Pantanal. These species are *Artibeus planirostris* (Phyllostomidae), *Myotis nigricans* (Vespertilionidae) and *Noctilio albiventris* (Noctilionidae). Contrasting to most studies that use only one taxonomic group of ectoparasites, I identified the structure of infracommunity of all taxa assembled, as well as for each class (Insecta and Acarina) separately. For all three bat species, the infracommunity structure for all taxa assembled were the same, Clamped species loss, which one presented the 'quasi' version. The insect and acari infracommunities structure pattern were different of the pattern found for the total species for *N. albiventris* and *M. nigricans*, *Artibeus planirostris*'s Acari structure pattern was the only one equal to total's structure. These results showed that the exclusion of taxa while performing the Elements of Metacommunity Structure (EMS) analyzes can lead to misinterpretations and so I recommend that always use all species

present. The second chapter is about the effect of forest cover, the host characteristics, and the interaction between ectoparasites in the structure, abundance, and agglomeration of these ectoparasites in the infracommunities. For this I used a 2-year dataset from the Serra da Bodoquena. I found that the nested Random species loss structure was the most frequent for bat ectoparasites in this region. The number of quasi structures was less frequent in areas with higher forest cover, indicating a stronger effect of structuring processes. Also, the agglomeration (ICr) was higher on bats from areas with lower forest cover, maybe because of less availability of suitable roosts. Regarding the interaction between ectoparasite species, I found no evidence of competition but found an increase in the mean intensity of infestation of two species as the number of species increases in the infracommunity. So, there may be a facilitation process, or these species benefit from the same host conditions that led them to accumulate greater richness and abundance of ectoparasites. Finally, in the third chapter I tested the ectoparasites density-dependent sex ratio hypothesis, in which female ectoparasites would be more aggregated in some host individuals from the same host species, presumably due nutritional demands, whereas males would be more dispersed across host individuals. For this I used a large sample of *Anoura geoffroyi* captured in two caves of Minas Gerais with dip nets during daytime. I found results that did not corroborate with the density-dependent hypothesis but found that female hosts were more infested by *Exastinion clovisi* than males. I suppose that this happens due to lack of mobility as this was the only species found without the ability to fly, although there's no study evaluating the mobility capacity of these flies.



## Resumo Geral

As estruturas das comunidades de parasitas resultam de cadeias complexas de interações. Esses organismos interagem com os hospedeiros, outras espécies de parasitas, outros indivíduos da mesma espécie e sofrem pressão das variáveis ambientais. Alguns desses processos de estruturação podem ser acessados por meio da Teoria da Metacomunidade. Esta teoria se concentra em avaliar padrões e mecanismos que contribuem para a variação da diversidade de espécies no espaço, geralmente em escalas locais e regionais. A abordagem na escala local pode ser usada para explorar processos estruturais de infracomunidades. Infracomunidade é o termo usado para identificar todos os parasitas de um determinado indivíduo hospedeiro, compartilhando algumas das características e processos das populações de espécies de vida livre. Esta tese trata principalmente de estruturas de infracomunidades e das interações de suas populações. Está dividida em três capítulos, todos usando morcegos e seus ectoparasitas como modelo de estudo. No primeiro capítulo dessa tese usei a abordagem baseada em padrões da metacomunidade para identificar o padrão adequado às infracomunidades de ectoparasitos de três espécies de morcegos capturados no Pantanal. Essas espécies são *Artibeus planirostris*, *Myotis nigricans* e *Noctilio albiventris*. Como a maioria dos trabalhos usa apenas um grupo morfológico de ectoparasitas, identifiquei a estrutura de infracomunidades de todos os táxons e então para cada classe (Insecta e Acarina). Em todas as três espécies de morcegos, a estrutura de infracomunidade para todos os táxons foi o mesmo subconjunto de aninhada, *Clamped species loss*, dentre os quais um apresentava a versão "quasi". As infracomunidades de insetos e ácaros eram todos de padrões diferentes, com exceção de Acari em *Artibeus planirostris* que também era da estrutura *Clamped species loss*. Esses resultados mostraram que a exclusão de táxons durante a realização das análises dos Elementos da Estrutura da Metacomunidade

(EMS) pode levar a interpretações errôneas e, portanto, recomendamos que sempre se use todas as espécies presentes. O segundo capítulo trata do efeito da cobertura florestal, das características do hospedeiro e da interação entre ectoparasitas na estrutura, abundância e aglomeração desses ectoparasitas nas infracomunidades. Para isso usei um conjunto de dados de dois anos de coleta de ectoparasitas na Serra da Bodoquena. Encontrei que a estrutura aninhada *Random species loss* foi a mais frequente para ectoparasitas de morcegos neste conjunto de dados. O número de estruturas “quasi” foi menos frequente nas áreas com maior cobertura florestal, indicando que o efeito dos processos de estruturação nestas foi mais forte. Além disso, a aglomeração (ICr) foi maior em morcegos capturados em áreas com menor cobertura florestal, talvez devido à menor disponibilidade de abrigos adequados. Relacionado à interação entre as espécies de ectoparasitas, não encontrei evidência de competição entre elas, mas encontrei um aumento na intensidade média de infestação de duas espécies junto ao aumento da riqueza na infracomunidade. Então, pode haver um processo de facilitação ou essas espécies se beneficiaram das mesmas condições que levaram seus hospedeiros a acumularem maior riqueza de ectoparasitas. No terceiro capítulo testei a hipótese da razão sexual densidade-dependente dos ectoparasitas, em que os ectoparasitas fêmeas estariam mais agregados em hospedeiros específicos, presumivelmente devido às demandas nutricionais, e os machos estariam mais dispersos pela população hospedeira. Para isso utilizei uma amostra de *Anoura geoffroyi* capturados em cavernas de Minas Gerais. Encontrei resultados que não corroboravam com a hipótese proporção sexual densidade-dependente, mas encontrei que as fêmeas hospedeiras estavam mais infestadas por *Exastinion clovisi* do que os machos. Suponho que isso aconteça devido à falta de mobilidade, pois esta foi a única espécie encontrada sem capacidade de voar, embora não haja nenhum estudo avaliando a capacidade de mobilidade dessas moscas.

## General Introduction

Metacommunity theory can integrate local and regional dynamics to explore patterns of composition of parasitic communities (Mihaljevic 2012). Metacommunity is defined as the set of local communities that are linked by the dispersal of potentially interactive species (Leibold et al. 2004). This theory can generally be divided into pattern-based and mechanism-based approach. The mechanism-based uses four conceptual paradigms to describe metacommunities (Species-sorting, Mass-effects, Patch-dynamic and Neutral-model) (Leibold et al. 2004), while pattern-based uses a checkerboard structure, a random and six idealized patterns plus a quasi-variation of each one (Evenly spaced, Gleasonian, Clementsian and three types of Nested subsets) that results from specific processes (Presley et al. 2010). Bringing this to the symbionts, direct and indirect interactions between parasites can be observed in those two scales framed by the metacommunities theory: intra-host, local, and inter-host, regional (Mihaljevic 2012). The local scale meets the term infracommunity, which is defined as all parasites found in an individual host (Bush et al. 1997).

The parasite communities can also be seen as interactives or isolationists (Holmes & Price 1986). The isolationists follow the assumptions and predictions of population concentration and individualistic response hypotheses, those includes nonequilibrium communities that are unsaturated because low transmission rates, species are individualistically dispersed and insensitive to the presence of other guild members at infracommunity level (Bush et al. 1997). Interactives fit the assumptions of the competition hypothesis, which includes parasites that have high transmission rates, interspecific competition is important, weak individualistic responses and balanced communities (Bush et al. 1997).

Parasites commonly presents an aggregated distribution, few hosts highly infested and most hosts with low parasite load. Mechanisms proposed to generate this pattern usually originates from environmental heterogeneity and heterogeneity in host susceptibility (Poulin 2007, Morrill et al. 2017). Related to environmental heterogeneity, land use and habitat conversion studies are receiving more attention as fragmentation grows in several biomes. The stress caused by habitat loss in the host communities can affect their parasites loads. For example, higher avian malaria prevalence has been found in deforested areas and with diminishing host functional diversity (Fecchio et al. 2021). Heterogeneity in host susceptibility includes potential to attract, provide resources, and defend against parasites. In some cases, older hosts have more time to accumulate and carry heavier loads of parasites (Poulin, 2013). In others, there's significantly different behaviors between males and females of a host species that increases the chance of one sex being colonized by new parasites individuals, like having different home range (Hillegass et al. 2008). Host specific ecology will play a very important role to understand these factors, as every species have their own particularities.

In bats, the mammal order with the highest diversity of ectoparasites (Dick & Dittmar 2014), environmental heterogeneity has been related to roost type and use. Species using permanent roosts like caves and constructions are more prone to be infested and with heavier loads (Patterson et al. 2007). Also, Vieira et al. (2017) found that aggregation of an ectoparasite species differs between the Cerrado and Pantanal, suspecting that it was caused by differences in roosting behavior. The most common bat ectoparasites are acarines from several families and flies from Streblidae and Nycteribiidae families (Whitaker et al. 2009). These ectoparasites are highly specific, so

that their community composition is more dependent on the presence of their main hosts species at a specific site than distance from other communities (Ericksson et al. 2020).

Heterogeneity on bats susceptibility to acquire more ectoparasites is yet to be clarified. Some studies show that reproductive females tend to carry more ectoparasites than non-reproductive females and males, probably because during the reproductive period females aggregate in maternities which create an idealistic environment for ectoparasites proliferation, there is also the hypothesis that hormones may play an important role in this aspect (Christe et al. 2000, Patterson et al. 2008). Szentivanyi et al. (2017) found that females of an ectoparasite species was more abundant on female hosts, showing that there may be a preference for the host's sex, also registering a density-dependent sex bias in infracommunities. Female flies were more aggregated in hosts while males were more dispersed (Szentivanyi et al. 2017).

Another aspect to be considered in composition of parasitic communities is the interactions between concurrent species. If there is any, these can be positives, like facilitation process, or negatives, like competition resulting in exclusions. In bats ectoparasites until the present date no evidence of competition has been documented (Tello et al. 2008, Presley 2011).

Regarding infracommunities of bats ectoparasites and their patterns, in this dissertation I elaborated three chapters. In the first one, I tested the consequences of using only part of the species present on infracommunities while describing their structure with pattern-based approach of metacommunity framework, as most studies, in Brazil, about these ectoparasites do not include all community species. In the second, I verify whether (a) the forest cover affects the structure pattern of infracommunities; (b) certain morphological characteristics of hosts increase or decrease the abundance and agglomeration of infracommunities; (c) there is evidence of interspecific competition

between ectoparasites on infracommunities. Finally, in the third chapter, I tested the hypothesis that there is a density-dependent sex bias on infracommunities.

## **Chapter 1. Infracommunity structure pattern of bat ectoparasites in the Pantanal wetland**

### **Abstract**

Bats harbor a great diversity of ectoparasites species, commonly insects (Diptera) and arachnids such as mites and ticks. Most studies investigated only flies, disregarding other insects and arachnids. In this work I aimed to describe the entire infracommunity of bat ectoparasites, and to investigate the effect of group exclusion on the infracommunity structure. I used a dataset from six months of collections in the Pantanal from which I filtered the bats whose infested individuals was higher than 30 captures: *Artibeus planirostris* (Phyllostomidae); *Myotis nigricans* (Vespertilionidae); *Noctilio albiventris* (Noctilionidae). The structures of ectoparasite infracommunities were identified for each bat species in three categories, containing: only the insects; only the mites; all species. The infracommunity structures with all ectoparasite species did not differ among the three host species: Clumped species loss, subtype of nested. Except for infracommunities of mites from *A. planirostris* which was also identified with this structure, all the other five structures were different. Considering that different infracommunity structures emerged depending on clade exclusion, it should be considered the use of all species for understanding patterns of bat ectoparasite infracommunities.

**Keywords:** Bat flies, Acari, Pantanal, metacommunity.

## Resumo

Os morcegos abrigam uma grande diversidade de espécies de ectoparasitas, comumente insetos (Diptera) e aracnídeos como ácaros e carrapatos. A maioria dos estudos investigou apenas moscas, desconsiderando outros insetos e aracnídeos. Neste trabalho, tive como objetivo descrever toda a infracomunidade de ectoparasitas de morcegos e investigar o efeito da exclusão de grupos na estrutura da infracomunidade. Usei um conjunto de dados de seis meses de coletas no Pantanal a partir do qual filtrei os morcegos cujos indivíduos infestados eram superiores a 30 capturas: *Artibeus planirostris* (Phyllostomidae); *Myotis nigricans* (Vespertilionidae); *Noctilio albiventris* (Noctilionidae). As estruturas das infracomunidades de ectoparasitas foram identificadas para cada espécie de morcego em três categorias, contendo: apenas os insetos; apenas os ácaros; todas as espécies. As estruturas de infracomunidade com todas as espécies de ectoparasitas não diferiram entre as três espécies hospedeiras: *Clumped species loss*, subtipo de aninhado. Com exceção das infracomunidades de ácaros de *A. planirostris* que também foram identificadas com esta estrutura, todas as outras cinco estruturas foram diferentes. Considerando que diferentes estruturas de infracomunidades surgiram dependendo da exclusão do clado, deve-se considerar o uso de todas as espécies para a compreensão dos padrões de infracomunidades de ectoparasitas de morcegos.

**Palavras-chave:** moscas de morcegos, Acari, Pantanal, metacomunidade



## Introduction

Bats are cosmopolitan flying mammals with diverse ecosystem functions. These animals have a great diversity of ectoparasites from different taxa such as flies, mites, fleas, and bugs (Whitaker et al. 2009). Among them, flies and mites stand out for their richness and abundance (Krantz & Walter 2009).

The bat flies belong to two families, Streblidae and Nycteribiidae. In America, Streblidae species are found mainly on Phyllostomidae bats, while Nycteribiidae are found almost exclusively on Vespertilionidae bats (Dick & Miller 2010, Gracioli 2010). Both bat fly families are composed of species that spend their entire lives on their hosts and are dependent on their host daytime shelters for reproduction (Marshall 1970). Bat ectoparasitic mites are from several families and can complete their entire life cycle on hosts (Marshall 1981, Whitaker et al. 2009). The bugs belong to the Cimicidae and Polyctenidae families. Cimicidae is cosmopolitan and has species that parasitize humans as well (*Cimex lectularius*). They live on the roost and only come to the host to feed, while Polyctenidae spend all life on the hosts (Whitaker et al. 2009). Bat flea's species belong to the Ischnopsyllidae family. They are wingless, laterally compressed, jumping insects with ctenidia, and mostly only adults are parasitic while the larvae may be found in guano below the roost (Whitaker et al. 2009).

Ectoparasites usually have an aggregated distribution on their hosts, few hosts individuals contain the majority of parasites, for reasons that are yet to be clarified (Tello et al. 2008, Presley 2011). This is also a well-documented pattern for several parasite taxa (Poulin 2007). One way to explore the reasons for this aggregation would be to establish environmental gradients to be studied together with the analysis of elements of the metacommunity, followed by interpreting the structure found and the possible processes linked to it (Presley et al. 2010). The main objective of

metacommunity framework is to evaluate patterns of and mechanisms contributing to species diversity across space, generally in two scales: local and regional (Mihaljevic 2012). The local scale applied to parasites would be associated with the infracommunity concept, which means all parasite individuals of all species present on a single host (Bush et al. 1999), so that every host individual of this host harbors an infracommunity. Most of the works related to ectoparasitic arthropod bat communities commonly use one morphological group, usually bat flies, however other groups of ectoparasitic arthropods, mites, ticks, fleas, and bugs can be found co-occurring. It is noteworthy that there is some difficulty in identifying them, such as mite's stage of development and the lack of identification keys (Lourenço et al. 2020). The consequences of ignoring the interactions that these individuals provide to communities and infracommunities in general are unknown. This work aimed describe the infracommunity of bat ectoparasites and to verify how the infracommunities structure of these ectoparasitic arthropods, using the metacommunities framework (Mihaljevic 2012), are affected when removing one or more taxa.

## Methods

### *Data Collection*

The capture of bats and collection of ectoparasites took place in the Pantanal do Miranda (19°35'S and 57°01'W) where monthly expeditions were carried out for six months. Each expedition consisted of six nights of sampling, with eight mist nets (12 x 2.6 m) being opened for approximately six hours each night. To avoid uncontrolled recaptured data collection the hosts were earmarked with washable anti-toxic pen. Few individuals were killed for confirmation of identification and are available at Coleção Zoológica da Universidade Federal de Mato Grosso do Sul, Campo Grande. The sampling effort, calculating with Straube & Bianconi (2002)'s method would be the total area of the nets (8 x 12 x 2.6 m) multiplied by the time they were open (6 hours x 36 days), which will be equal to 53,916.6 m<sup>2</sup>.h. This region has mixed soils composed of sand and clay, where there is a predominance of floodplains interspersed with natural patches (0.5 to 5 ha) of seasonal semideciduous forests, circular or elliptical in shape (Pivari et al. 2008). The climate of the region is sub-humid tropical with an average annual rainfall of 1,100 mm, with rainfall concentrated between November and March, and an average annual temperature of 26 °C.

The captured bats were surveyed and their ectoparasites removed with fine-tipped tweezers and brushes moistened with alcohol and stored in 70% alcohol in individual containers for each host. Bats were identified using identification keys (Gardner 2008) and were released at the end of each capture section. The flies were identified with the aid of a stereomicroscope and identification keys (Guimarães & D'Andretta 1956, Wenzel et al. 1966, Wenzel 1976, Guerrero 1995, 1996). Spinturnicidae mites were mounted on slides for microscopy with Hoyer's solution and identification was performed using the key of Herrin and Tipton (1975). Mites and ticks

from other families were sent to Dr. Michel Paiva Valim, Museu de Zoologia da Universidade de São Paulo, for identification.

### *Data Analysis*

I used data from the most captured bats, three species from three distinct families:

Phyllostomidae, *Artibeus planirostris* (Leach) (327 total, 271 infested);

Vespertilionidae, *Myotis nigricans* (Schinz) (48, 32); Noctilionidae, *Noctilio albiventris*

(Linnaeus) (44, 44). In total I analyzed 347 infested individuals.

### *Infracommunity Description*

The structure of the infracommunities was identified with the interpretation of the elements of the metacommunity structure (EMS), coherence, turnover and boundary clumping, following Presley et al. (2010). These elements were calculated with the “metacom” package (Dallas 2020) in R (R Core Team 2020), with presence/absence matrices of ectoparasites in each host species for each category of infracommunity composition: insects, arachnids, and the total. The elements found were compared to elements of null matrices and then interpreted to a pattern and its associated processes.

There are six patterns and for each there's a ‘quasi’ version: Gleasonian, Clementsian, evenly spaced and nested distributions. The nested distributions are Random species loss, Clamped species loss and Hyperdispersed species loss, which are analogous to the others three.

## Results

At least 11 species of ectoparasites were identified on *Artibeus planirostris*, of which three are flies (Streblidae) and seven are acarines, eight on *Myotis nigricans*, two species of flies (Nycteribiidae), a species of flea (Ischnopsyllidae) and five species of acarines, and seven on *Noctilio albiventris*, three species of flies (Streblidae), a species of Cimicidae and three of acarines (Figure 1, Table 1).

Most of infracommunities, up to 91% of total, was composed by at maximum three species, 121 (34% of total) had a single species, 113 (32%) two species and 85 (25%) three species (Table 1). Clumped species loss structure, nested subset, were identified for the total infracommunities of the three bat species, in one of these the 'quasi' version (Table 2). Analyzing the infracommunities with only ectoparasitic insects, I had three different results: Random species loss, Random and Checkerboard. The infracommunities with only ectoparasitic species of the Acarina class also had different results: Clumped species loss, Random species loss and quasi-Random species loss.

Table 1 - All ectoparasites infracommunities compositions divided by Class taxa  
found on bats

| Host                         | Infracommunity/Infrapopulation                         | n   |
|------------------------------|--|-----|
| <i>Artibeus planirostris</i> |  |     |
| Insecta                      |  | 177 |
|                              | <i>Megistopoda aranea</i>                              | 68  |
|                              | <i>Aspidoptera phyllostomatis</i> + <i>M. aranea</i>   | 58  |
|                              | <i>A. phyllostomatis</i>                               | 50  |
|                              | <i>Trichobius angulatus</i>                            | 1   |
| Acarina                      |  | 236 |
|                              | <i>Perigliscrhus iheringi</i>                          | 137 |
|                              | Argasidae + <i>P. iheringi</i>                         | 33  |
|                              | <i>P. iheringi</i> + Trombiculidae                     | 26  |
|                              | Argasidae  | 9   |
|                              | Trombiculidae  | 7   |
|                              | Argasidae + Trombiculidae                              | 5   |
|                              | Argasidae + <i>P. iheringi</i> + Trombiculidae         | 4   |
|                              | <i>Chirnyssoides caparti</i> + <i>P. iheringi</i>      | 2   |
|                              | <i>C. caparti</i> + <i>P. iheringi</i> + Trombiculidae | 2   |
|                              | <i>Makronissoides kochi</i> + <i>P. iheringi</i>       | 2   |
|                              | <i>M. kochi</i> + Trombiculidae                        | 2   |
|                              | Argasidae + <i>M. kochi</i> + <i>P. iheringi</i>       | 2   |
|                              | <i>Makronissoides</i> sp.                              | 1   |
|                              | Argasidae + <i>Makronissoides</i> sp.                  | 1   |

|       |   |     |
|-------|---|-----|
|       | Argasidae + <i>Steatonyssus joaquimi</i>  | 1   |
|       | <i>Eudusbabekia</i> sp. + <i>P. iheringi</i>  | 1   |
|       | <i>C. caparti</i> + <i>M. kochi</i> + Trombiculidae + <i>P. iheringi</i>                        | 1   |
| <hr/> |   |     |
| Total |   | 271 |
| <hr/> |   |     |
|       | <i>P. iheringi</i>  | 54  |
|       | <i>M. aranea</i> + <i>P. iheringi</i>   | 33  |
|       | <i>A. phyllostomatis</i> + <i>M. aranea</i> + <i>P. iheringi</i>                                | 30  |
|       | <i>A. phyllostomatis</i> + <i>P. iheringi</i>   | 24  |
|       | <i>M. aranea</i>  | 13  |
|       | Argasidae + <i>M. aranea</i> + <i>P. iheringi</i>   | 12  |
|       | <i>A. phyllostomatis</i>  | 11  |
|       | Argasidae + <i>P. iheringi</i>  | 9   |
|       | <i>M. aranea</i> + <i>P. iheringi</i> + Trombiculidae   | 9   |
|       | Argasidae + <i>A. phyllostomatis</i> + <i>M. aranea</i> + <i>P. iheringi</i>                    | 9   |
|       | Trombiculidae   | 7   |
|       | <i>A. phyllostomatis</i> + <i>M. aranea</i>   | 6   |
|       | <i>A. phyllostomatis</i> + <i>P. iheringi</i> + Trombiculidae                                   | 6   |
|       | <i>A. phyllostomatis</i> + <i>M. aranea</i> + <i>P. iheringi</i> + Trombiculidae                | 6   |
|       | Argasidae   | 5   |
|       | Trombiculidae + <i>P. iheringi</i>  | 5   |
|       | <i>A. phyllostomatis</i> + Argasidae + <i>P. iheringi</i>                                       | 3   |
|       | <i>A. phyllostomatis</i> + Argasidae + <i>M. aranea</i> + <i>P. iheringi</i> +<br>Trombiculidae | 3   |
|       | Argasidae + Trombiculidae   | 2   |

|   |   |
|---|---|
| <i>A. phyllostomatis</i> + Argasidae                                      | 2 |
| <i>C. caparti</i> + <i>P. iheringi</i>                                    | 2 |
| <i>M. kochi</i> + <i>P. iheringi</i>                                      | 2 |
| <i>M. kochi</i> + Trombiculidae   | 2 |
| <i>C. caparti</i> + <i>P. iheringi</i> + Trombiculidae                    | 2 |
| <i>A. phyllostomatis</i> + Argasidae + <i>M. aranea</i>                   | 2 |
| <i>A. phyllostomatis</i> + <i>M. aranea</i> + Trombiculidae               | 2 |
| Argasidae + <i>M. aranea</i> + <i>M. kochi</i> + <i>P. iheringi</i>       | 2 |
| Argasidae + <i>S. joaquimi</i>  | 1 |
| Eudusbabekia sp. + <i>P. iheringi</i>                                     | 1 |
| <i>Makronissoides</i> sp.   | 1 |
| <i>T. angulatus</i>   | 1 |
| Argasidae + <i>Makronissoides</i> sp.                                     | 1 |
| Argasidae + <i>M. aranea</i> + Trombiculidae                              | 1 |
| <i>C. caparti</i> + <i>M. kochi</i> + Trombiculidae + <i>P. iheringi</i>  | 1 |
| <i>A. phyllostomatis</i> + Argasidae + <i>P. iheringi</i> + Trombiculidae | 1 |

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*Myotis nigricans*


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|   |    |
|---|----|
| Insecta   | 25 |
| <i>Basilia speiseri</i>                           | 18 |
| <i>Basilia carteri</i>                            | 4  |
| <i>M. wolffsohni</i>                              | 1  |
| <i>B. carteri</i> + <i>B. speiseri</i>            | 1  |
| <i>B. carteri</i> + <i>Myodopsylla wolffsohni</i> | 1  |

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|                             |  |    |
|-----------------------------|--|----|
| Acarina                     |  | 12 |
|                             | Argasidae  | 3  |
|                             | <i>Macronyssus sp.</i>   | 3  |
|                             | <i>Spinturnix americanus</i>   | 3  |
|                             | <i>Macronyssus meridionalis</i>  | 1  |
|                             | <i>Macronyssus sp.</i> + <i>S. americanus</i>  | 1  |
|                             | <i>Steatonyssus joaquimi</i> + <i>Macronyssus sp.</i>                                  | 1  |
| Total                       |  | 32 |
|                             | <i>B. speiseri</i>   | 16 |
|                             | <i>B. carteri</i>  | 3  |
|                             | Argasidae  | 2  |
|                             | <i>Macronyssus sp.</i>   | 2  |
|                             | <i>M. meridionalis</i>   | 1  |
|                             | <i>S. americanus</i>   | 1  |
|                             | Argasidae + <i>B. speiseri</i>   | 1  |
|                             | <i>B. carteri</i> + <i>B. speiseri</i>   | 1  |
|                             | <i>B. speiseri</i> + <i>S. americanus</i>  | 1  |
|                             | <i>B. carteri</i> + <i>S. americanus</i>   | 1  |
|                             | <i>Macronyssus sp.</i> + <i>M. wolffsohni</i>  | 1  |
|                             | <i>Macronyssus sp.</i> + <i>S. americanus</i>  | 1  |
|                             | <i>B. carteri</i> + <i>M. wolffsohni</i> + <i>Macronyssus sp.</i> + <i>S. joaquimi</i> | 1  |
| <i>Noctilio albiventris</i> |  |    |
| Insecta                     |  | 44 |

|   |    |
|---|----|
| <i>Paradischyria parvula</i> + <i>Noctiliostrebla morena</i>                                  | 37 |
| <i>P. parvula</i>   | 4  |
| <i>N. morena</i>  | 1  |
| <i>Latrocimex spectans</i> + <i>P. parvula</i> + <i>N. morena</i>                             | 1  |
| <i>L. spectans</i> + <i>N. morena</i> + <i>P. parvula</i> + <i>Xenotrichobius noctilionis</i> | 1  |
| Acarina   | 24 |
| Argasidae   | 20 |
| Argasidae + <i>Mitonyssus noctilio</i>  | 2  |
| <i>M. noctilio</i>  | 1  |
| Argasidae + <i>Chiroptonyssus robusticeps</i>   | 1  |
| Total   | 44 |
| Argasidae + <i>N. morena</i> + <i>P. parvula</i>  | 17 |
| <i>N. morena</i> + <i>P. parvula</i>  | 16 |
| <i>P. parvula</i>   | 3  |
| Argasidae + <i>M. noctilio</i> + <i>N. morena</i> + <i>P. parvula</i>                         | 2  |
| <i>N. maai</i>  | 1  |
| Argasidae + <i>P. parvula</i>   | 1  |
| <i>N. morena</i> + <i>M. noctilio</i> + <i>P. parvula</i>                                     | 1  |
| Argasidae + <i>C. robusticeps</i> + <i>N. morena</i> + <i>P. parvula</i>                      | 1  |
| <i>L. spectans</i> + <i>N. morena</i> + <i>P. parvula</i> + <i>X. noctilionis</i>             | 1  |
| Argasidae + <i>L. spectans</i> + <i>N. morena</i> + <i>P. parvula</i>                         | 1  |

Table 2 – Elements of metacommunity analysis and structure interpretation for bats ectoparasites infracommunities. \* Significant values, Abs number of embedded absences (coherence), Rep number of replacements (turnover), I Morisita's index (boundary clumping).

| Taxa                         | n   | Abs  | Rep    | I     | Structure (Presley et al. 2010) |
|------------------------------|-----|------|--------|-------|---------------------------------|
| <i>Artibeus planirostris</i> |     |      |        |       |                                 |
| Total                        | 271 | 763* | 79246* | 8,7*  | Clumped species loss            |
| Insecta                      | 177 | 0*   | 3634*  | 0     | Random species loss             |
| Acarina                      | 236 | 344* | 23403* | 10,6* | Clumped species loss            |
| <i>Myotis nigricans</i>      |     |      |        |       |                                 |
| Total                        | 32  | 23*  | 760    | 3*    | Quasi-Cumped species loss       |
| Insecta                      | 25  | 28*  | 133    | 7,6*  | Checkerboard                    |
| Acari                        | 12  | 0*   | 59     | 1,9   | Quasi-Random species loss       |
| <i>Noctilio albiventris</i>  |     |      |        |       |                                 |
| Total                        | 44  | 29*  | 138*   | 5,6*  | Clumped species loss            |
| Insecta                      | 44  | 6    | 0      | 14*   | Random                          |
| Acarina                      | 24  | 2*   | 52*    | 2,9   | Random species loss             |

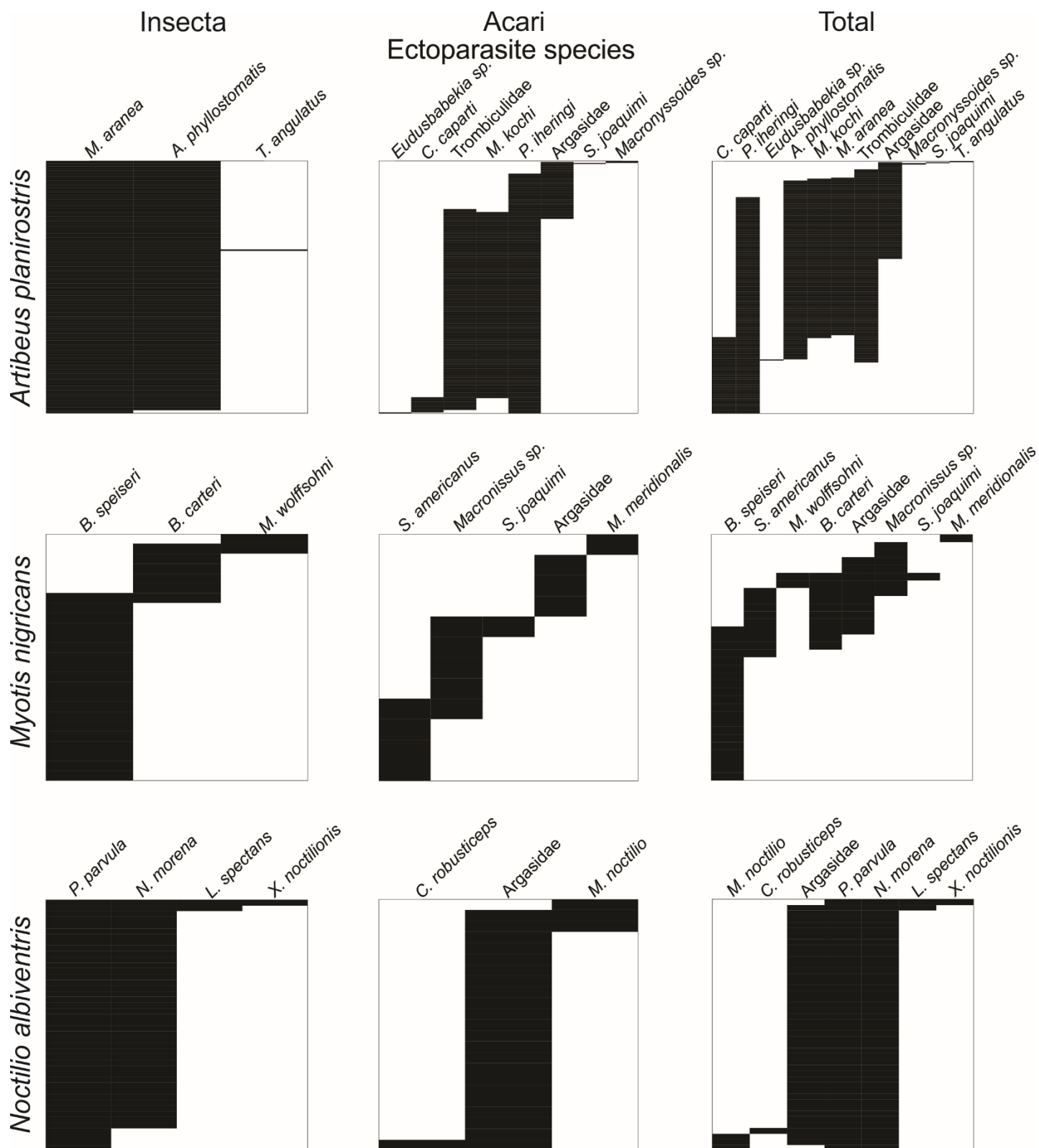


Figure 1 – Infracommunity structure of bats ectoparasites divided by classes which they belong and the structure of the full range of species.

## Discussion

The predominance of infracommunities with one to three species of ectoparasites has already been recorded (Barbier & Graciolli 2016, Dornelles & Graciolli 2017, Dornelles et al. 2017, Hrycyna et al. 2019). This majority of host with low abundance and richness of parasites and minority with high load agrees with the aggregation pattern already well-documented for parasites (Poulin 2007, Tello et al. 2008, Presley 2011). I found the nested structure Clumped species loss for the complete infracommunities of the three host species ectoparasites. Clumped species loss means that the distribution limits of ectoparasites in infracommunities are more clustered than expected for random matrices (Presley et al. 2010). The nested pattern for bat ectoparasites has already been found by Presley (2011) in five of 11 host species and in half of the 31 studied by Patterson et al. (2009). This pattern often occurs when there is variation in species dispersal or habitat specialization, along with colonization or sequenced extinction (Patterson & Atmar 1986).

The infrastructure of the infracommunities changed in all cases if I compare the complete infracommunities with the partial ones, except for the infracommunities of Acarina in *Artibeus planirostris* which presented the same structure. Thus, I showed that the analysis when incomplete can generate misinterpretations, such as the identification of infracommunities of ectoparasitic insects of *Myotis nigricans* as Checkerboard, and they can be part of a larger nested structure, subtype Clumped species loss. Due to the difference observed in the structure of infracommunities when only part of the species is used for the analysis, it should be considered the use of all species for studying these processes and structures.

## **Chapter 2. Structure patterns and interactions in bat ectoparasite infracommunities across a forest cover**

### **Abstract**

Parasite infracommunities share similar processes with those defined in Metacommunities theory. I applied this knowledge to identify the structure of bat ectoparasite infracommunities, in which I investigated whether they were influenced by environmental quality, host quality and competition between ectoparasites. In addition to the description of the general structure, the infracommunities were individually represented by the infracommunity crowding index (ICr). For environmental quality, I used the percentage of forest cover, which can be closely related to the availability of shelters and, in turn, to the successful dispersal of these ectoparasites. For host quality, I used characteristics that have already been found to influence the parasite load, such as sex, age, and body condition. I identified infracommunity structures by analyzing meta-community elements. I assessed the effect of environmental and host quality on abundance and ICr through generalized linear models. Competition between ectoparasites from the same infracommunity was investigated through the difference in mean infestation intensities. I found that bat infracommunities in general are of the nested pattern Random species loss, evidence that the distribution of ectoparasite species follows an environmental gradient. Furthermore, the structuring effect would be stronger as the vegetation cover increases. In the models, the variable with the greatest effect was forest cover, which had a negative effect on the abundance and ICr of infracommunities, while the variables explored as host qualities were not very informative. I did not find evidence of competition between ectoparasites. In general, in this work I found evidence that

vegetation cover affects bat ectoparasites infracommunities and that there are hosts on which ectoparasites aggregate, but the reasons for this aggregation would not be directly related to the morphological characters of bats.

**Keywords:** metacommunity, forest cover, infracommunity crowding index, competition

## Resumo

Infracomunidades de parasitos compartilham processos semelhantes com os definidos na teoria de Metacomunidades. Aplicamos esses conhecimentos para identificar a estrutura das infracomunidades de ectoparasitos de morcegos, nas quais investigamos se sofriam influência da qualidade do ambiente, da qualidade dos hospedeiros e de competição entre os ectoparasitos. As infracomunidades também foram representadas individualmente pelo índice de aglomeração de infracomunidades (ICr). Para qualidade do ambiente utilizamos o percentual de cobertura florestal, que pode estar relacionado à disponibilidade de abrigos e ao sucesso de dispersão desses ectoparasitos. Para a qualidade dos hospedeiros utilizamos características com evidências de influenciar na carga parasitária, como sexo, idade e condição corporal. Identificamos as estruturas das infracomunidades com a análise de elementos da metacomunidade. Acessamos o efeito da qualidade ambiental e do hospedeiro na abundância e ICr através de modelos lineares generalizados. A competição entre os ectoparasitas da mesma infracomunidade foi investigada através das intensidades médias de infestação. A maioria das infracomunidades que encontramos são do padrão aninhado *Random species loss*, evidência de que a distribuição desses ectoparasitos segue um gradiente ambiental. Além disso, o processo estruturante seria mais forte conforme a cobertura vegetal aumenta. Nos modelos a variável de maior efeito foi a cobertura florestal, efeito negativo na abundância e ICr das infracomunidades, enquanto as características do hospedeiro não foram informativas. Não encontramos competição entre os ectoparasitos. Neste trabalho encontramos evidências de que a cobertura vegetal afeta as infracomunidades de ectoparasitos de morcegos e de que existem hospedeiros nos quais os ectoparasitos se agregam, mas os motivos dessa agregação não estariam diretamente relacionados aos caracteres morfológicos dos morcegos.

**Palavras-chave:** metacomunidade, cobertura florestal, índice de aglomeração, competição.



## Introduction

The parasite community of a given host species can be isolationist or interactive (Holmes & Price 1986). An isolationist community has few species and low colonization rates. More specifically, in each individual host, infrapopulations of parasitic species (all parasites of the same species in the same individual host) tend to be small and co-occur with other species at levels low enough not to result in interactions. An interactive community would be composed of many species, with high rates of colonization on host individuals and often result in infracommunities (all parasites of different species found in the same host individual) with great species richness and high potential for interactions. Although Holmes and Price (1986) have proposed these two concepts, other authors argue that there is not a dichotomy, but a continuum between these extremes, observed through the degree of interactivity or isolationism within a parasitic community (Dove 1999, Poulin & Luque 2003, Ferrari et al. 2016).

The structure of ectoparasite infracommunities (eg. parasite abundance and richness) varies from a random distribution, purely stochastic sets of co-occurring species, to a highly structured set of species (Poulin 2007). One way to access the structure of these infracommunities is through the standards-based approach brought by the metacommunities theory (Mihaljevic 2012). This approach assesses the characteristics of species distribution along environmental gradients and thereby identifies the structure (Presley et al. 2010). These structures are random, checkerboard, nested, evenly spaced, Gleasonian and Clementsian, and these last four also have a “quasi” version resulting from weaker structuring forces (Presley et al. 2010). Random occurs when species distribution does not suffer structuring effects, checkerboard when competition between pairs of species is strong and mutually exclusive, nested when species from less rich sites are subsets of richer sites, evenly spaced when there is a tradeoff in competitive ability, Gleasonian when a continuous change in species

composition along environmental gradients is found, and Clementesian when species distribution is more clustered than expected by random and distribution limits are coincident (Presley et al. 2010). Nested structures can be Hyperdispersed, Clumped or Stochastic species loss, and are respectively analogous to evenly spaced, Clementsian and Gleasonian (Presley et al. 2010).

Interactions between parasites are one of the main forces that can shape infracommunities into non-random structures. These interactions can sometimes be positive, for example, when a species of parasite interferes with the host's defense mechanism to facilitate exploitation by a second species (Poulin 2007). More commonly these interactions will be negative, with the presence of a particular species of parasite decreasing the infestation rates of another species (Poulin 2007). In addition to positive and negative interspecific interactions within infracommunities, biological aspects of the host population such as body size, sex, diet, geographic distribution, and density were found to affect the occurrence of non-random patterns in various parasitic communities (Poulin & Valtonen 2001, Calvete et al. 2004, Krasnov et al. 2005, 2011a). These factors are related to the “recycling” of parasites in infracommunities, that is, probability and how new parasites are recruited in infracommunities and mortality, considering the particularities of each taxon. For example, larger hosts may be easier to colonize because they have larger surface area, ingest more food or greater mobility, and larger individuals tend to be older when compared to others in the same community and have had more time to accumulate parasites (Poulin 2007).

One of the main issues in community ecology has been the understanding of which factors determine the occurrence, pattern, and degree of non-randomness in assemblages. Bat arthropod ectoparasites infracommunities are convenient models for this type of study. Bats are cosmopolitan and have the greatest diversity of ectoparasites among mammals (Dick & Dittmar 2014). For Brazil, 181 species of bats have already

been recorded (Garbino et al. 2020). In its component community of ectoparasites can be found flies (Nycteribiidae and Streblidae), Siphonaptera (Ischnopsyllidae), Hemiptera (Cimicidae and Polyctenidae), Dermaptera (Arixeniidae) and several of families of Acarina (Whitaker et al. 2009). Bat flies and mites are found in greater frequency and abundance. In Brazil, 96 valid species of Streblidae (Graciolli 2021a), 26 of Nycteribiidae (Graciolli 2021b) and 50 of mites (Silva et al. 2017, Almeida et al. 2016) are known.

Although little studied in Brazil, most bat ectoparasites, in richness and abundance, are mites (Whitaker et al. 2009). About 1400 species have been recorded on bats (Krantz & Walter 2009). These parasites can spend their entire lives on hosts or remain in the shelter, where they also lay their eggs, and feed during the bat's inactive hours (Marshall 1981).

Streblidae and Nycteribiidae are hematophagous flies exclusive to bats, with Streblidae being the most specious and abundant in the New World and Nycteribiidae in the Old World (Dick & Miller 2010, Graciolli 2010). A specific feature of these families is that they have adenotrophic viviparity, the larva hatches from the egg in the maternal uterus and feeds through an accessory "milk" gland where it develops to the third instar, when it is expelled by the female in the vicinity of the host and pupates (Marshall 1970). Thus, we have that this group has a free-living phase in the form of pupae, fixed on the surface of the host's daytime shelter, and a parasitic, adult phase in bats.

As most of these flies spend all or most of their lives in their hosts and in the day shelter, characteristics of these shelters play a fundamental role in this parasite-host relationship (Dick and Dittmar 2014). A study involving 130 species of bats found a positive correlation between the time they used a particular type of shelter and the protection it offers with higher prevalence values, average infestation intensity and

number of parasite species in the component community (Patterson et al. 2007). That is, bat species that frequent more permanent shelters are more likely to be infested and carry larger amounts of parasites. Thus, disturbances regarding the use of daytime shelters for bats can affect their parasitic community. One of the expected effects of environmental fragmentation is the reduction of available shelters, reducing the possibility of periodic changes between shelter places in the same region and favoring infestation of arthropod ectoparasites.

Biological aspects of bats, as for other host species (Poulin & Valtonen 2001, Calvete et al. 2004, Krasnov et al. 2005, 2011b), potentially affect the occurrence and intensity of parasite infestation, although responses are not always consistent. Patterson et al. (2008a), in a study involving 24,978 bats from 130 species, found that females have higher rates of infestation than males, perhaps because they are more selective in terms of shelter quality and because most of them frequent maternity colonies. The density in these colonies helps to maintain the body temperatures necessary for the rapid development of young bats and facilitates the transmission of ectoparasites (Patterson et al. 2008). This factor can result in greater aggregation of ectoparasites and with higher infestation intensities (number of parasites per host), also increasing the opportunity for interaction of ectoparasite species in female bats. In addition to bat sex, body size, grooming behavior and immunological defenses are possible variables that affect parasitism by bat ectoparasites (ter Hofstede & Fenton 2005, Patterson et al. 2007, 2008b).

In this study assesses the structure of bat ectoparasites infracommunities as well as the possible factors shaping them. Our hypotheses are that infracommunities will respond mainly to environmental quality, the greater the forest cover, the greater the availability of adequate shelters and lower parasite load, to the quality of the host, the ectoparasites will be more aggregated on hosts with favorable characteristics, and that

these effects may be weak if evidence of strong competition between the ectoparasites is found.

## **Methods**

### *Study area*

The study was carried out in the Serra da Bodoquena (21°08' - 20°38' S & 56°49' - 56°44' W), Mato Grosso do Sul. This region is in the Miranda River basin, which makes up the upper basin Paraguay. The Miranda River watershed has a physical area of about 43,000 km<sup>2</sup> and its altitude varies between 80 m at the mouth of the Miranda River and 750 m at the Bodoquena mountain range (Pott et al. 2014).

The Serra da Bodoquena comprises the sources of the Miranda River basin, being an area composed mostly of limestone rocks (Filho et al. 2004). It is in contact regions between the Cerrado, Chaco, Pantanal, and Atlantic Forest formations, increasing the expected biodiversity for this area and its biological relevance (Françoso et al. 2011). The average annual rainfall in this region is between 1300 and 1700 mm, with greater frequency of precipitation between the months of October and April and a dry period between May and September. The average annual temperature ranges between 20 and 22 °C. The Phytophysiognomies presents in this area are deciduous seasonal forests, submontane seasonal semideciduous forests and alluvial semideciduous seasonal forests predominate, in addition to fields and flooded areas (Scremin-Dias et al. 1999).

### *Data collection*

A total of 2,113 bats, 1,731 infested by ectoparasite arthropods were captured. For the capture of these bats and collection of ectoparasites were established in 20 hexagons of 6.25 km<sup>2</sup> with vegetation cover ranging from 10% to 100%. Bernard & Fenton (2003)

found distances less than 2.5 km between the collection point and the bat's shelter, and less than 600 m between different shelters that the same bat used, thus 6.25 km<sup>2</sup> should cover the area where the shelter of the captured individuals is located. 132 m of mist net with a height of 2.6 m were set up. The mist nets were opened for 6 hours from sunset and were inspected every 30 minutes. Over two years of sampling, each site was visited four times, so that the sampling effort was 132 x 2.6 (mist net area) multiplied by 4 visits x 20 sites x 6 hours (time), totaling 164,736 m<sup>2</sup>.h. (Straube & Bianconi 2002).

The bats captured were placed in cloth bags and subsequently screened for ectoparasites. During visual inspection of the host's bodies, the ectoparasitic arthropods were manually removed with fine-tipped tweezers and, in some cases, with brushes moistened with alcohol, and fixed in 70% ethyl alcohol in individual containers for each host. To identify the bats, available identification keys were used (Gardner 2008). The bats were later released at the same location as the capture. To identify recaptures, the bats examined were marked with a collar with a ring. Few individuals from each sampling site were collected for identification confirmation and deposited as vouchers in the Zoological Collection of the Federal University of Mato Grosso do Sul. The flies were identified with the aid of a stereomicroscope using generic and specific keys (Guimarães & D' Andretta 1956, Wenzel et al. 1966, Wenzel 1976, Guerrero 2019). Spinturnicidae mites were mounted on slides for microscopy with Hoyer's solution and for their identification the key of Herrin and Tipton (1975) was used. Mites from other families, ticks, and bugs were sent to specialists for identification.

#### *Data analysis*

I used data from bats with at least 100 captures, they are: *Artibeus planirostris* (936 individuals, 190 non infested); *Carollia perspicillata* (273, 78); *Glossophaga soricina* (100, 34); *Platyrrhinus lineatus* (225, 72); *Sturnira lilium* (373, 97).

To identify the structure of infracommunities I used the analysis of elements of the structure of the metacommunity (EMS), whose interpretation is based on three metrics: coherence, turnover, and boundary clumping. Coherence is the degree to which the distribution of species is related to the same environmental gradient; turnover is the tendency of species to substitute each other at each site; and boundary clumping is the extent to which species distribution boundaries are grouped together (Leibold & Mikkelsen 2002, Presley et al. 2010). I performed this analysis in R (R Core Team 2020), package “metacom” (Dallas 2020), with the “Metacommunity” function.

To assess the effect of forest cover in the EMS analysis I used the frequency of infracommunities structures and the z-score of coherence and turnover. Data on bats and their ectoparasites were compiled according to the proportion of forest cover existing in the site where they were captured, being grouped into four forest cover intervals: 0-25% (n = 4); 25-50% (9); 50-75% (3); 75-100% (4). For each bat species, the infracommunity structures in these intervals were identified. Furthermore, only for *Artibeus planirostris* that had sufficient capture across the entire forest cover gradient, I identified the structure of infracommunities 1000 times with a subset of 30 random individuals in each vegetation cover interval to reduce the effect of other local variables non-controlled. To verify if there was a difference in the frequency of occurrence of the structures found in the four intervals, I used the chi-square test.

To identify the degree of interaction/isolationism of ectoparasitic arthropod infracommunities on bats, the infracommunity agglomeration index was used (ICr; Ferrari et al. 2016). This index measures the opportunity that each species of parasite has to interact with other species of parasites in that infracommunity. The ICr is calculated for each host individually, which allows the analysis of the effects of extrinsic and intrinsic factors to the hosts on parasite infracommunities (Ferrari et al.

2016). In this index, by defining  $x_a$ ,  $x_b$  and  $x_c$  as the number of individuals of species A, B and C, respectively, each individual of species A can interact with  $x_b + x_c$ , and the entire cluster of A can be expressed as  $x_a * (x_b + x_c)$ . The calculation of the mean agglomeration of all species by the total number of parasites of an individual host is given by the equation:

$$ICr = 2 * \sum_{j=1}^{S-1} x_j$$

Where  $x_j$  represents the abundance of parasite species  $j$ ,  $S$  the total number of parasite species within the infracommunity and  $N$  the total parasite abundance. In a hypothetical community with richness ( $S$ ) 3 of parasites and abundance ( $x_j$ ) 2, 4, and 3 individuals of the species, respectively, A, B and C, gives a total of 9 parasites. Each parasite of species A would suffer from agglomeration with 4 parasites B and 3 parasites C, that is,  $2*(4+3) = 14$ . Similarly, this calculation would result in  $4*(2+3) = 20$  for B and  $3*(4+2) = 18$  for C. The agglomeration of the total infracommunity can be obtained by adding this value for the three species and divided by the total number of individuals,  $(14+20+18)/9=5.77$ . In other words, in this infracommunity, a parasite can interact on average with 5.77 other parasites.

To verify how the abundance and degree of isolationism/interactivity of ectoparasitic arthropod infracommunities varies between bat species, I made pairwise comparisons using the Wilcoxon test with continuity correction, once that the distribution of abundances and ICr within each host species was not normal. I also calculated which bat species had the highest proportion of ICrs equal to zero, which would be bats without or infested with only one species of ectoparasite.

To investigate the effect of forest cover and morphological aspects of hosts, sex, age and body condition, on the abundance and agglomeration (ICr) of their respective



ectoparasites, generalized linear models in R were assembled using the “MuMIn” package (Barton 2020). The bat body condition index (BCI) was calculated by dividing the mass (g) by the forearm length (mm) (Pearce et al. 2008). Age was verified by ossification of the phalanges and bats considered young or adult. The best models were selected using the corrected Akaike Information Criterion (Akaike 1973; Hurvich & Tsai 1993).

The infracommunities of each host species were compiled into groups according to the composition of the parasitic species. After that, the frequencies in which they occurred were counted and I used those that appeared more than 10 times. I used the One-Way Anova test with 1000 permutations with the Quantitative Parasitology 3.0 web application (Reiczigel et al. 2019) to compare the mean intensity of each ectoparasite species across the groups in which it was found. I consider that there is competition between two species when the average intensity of one of them in the presence of the other is significantly lower.

## Results

### *Structure of infracommunities*

The EMS analysis showed that the structure of the found infracommunities are from nested subsets, Random/Clumped species loss. The most frequent was Random species loss ( $n = 16$ ) in all bat species (Table 1, Figure 1). Only on *Artibeus planirostris* there was the structure Clumped species loss, in the second and fourth intervals of vegetation cover (25-50 and 75-100%). For *Carollia perspicillata*, *Glossophaga soricina* and *Platyrrhinus lineatus*, the number of captures in the areas with the first vegetation cover interval (0-25%) was not enough for the analysis to calculate the coherence and turnover.

In the infracommunity structures of *A. planirostris* subsets, I noticed that there is a higher frequency of the Quasi-Random species loss structure in bats in areas ranging from 0 to 25% of forest cover and a lower frequency of it in the larger intervals (Figure 2 and 3, Table 2). There was also a higher frequency of Clumped and Quasi-Clumped species loss structures in the 50-75% and 75-100% intervals, respectively (Table 2, Figure 3). Regarding the turnover z-score, there is an overlap between all areas, while in terms of consistency, areas with less than 25% of vegetation cover are further away from the others (Figure 4). Moreover, the only median that is below 2 (threshold of significance of z values) in the z of turnover is the smallest range of forest cover.

Table 1 - Infracommunity structure of bat ectoparasites in categories of capture site forest cover proportion

| <i>Artibeus planirostris</i>  | n   | Abs   | Rep    | I     | Structure (Presley et al. 2010) |
|-------------------------------|-----|-------|--------|-------|---------------------------------|
| Total                         | 746 | 1010* | 115088 | 0     | Quasi-Random species loss       |
| 0-25                          | 89  | 167*  | 8116*  | 4,1   | Random species loss             |
| 25-50                         | 400 | 501*  | 41020* | 13,8* | Clumped species loss            |
| 50-75                         | 165 | 85*   | 2391*  | 0     | Random species loss             |
| 75-100                        | 92  | 117*  | 3736*  | 7,5*  | Clumped species loss            |
| <i>Carollia perspicillata</i> |     |       |        |       |                                 |
| Total                         | 194 | 124*  | 2579*  | 0     | Random species loss             |
| 0-25                          | 5   | x     | x      | x     | x                               |
| 25-50                         | 63  | 2*    | 204*   | 0     | Random species loss             |
| 50-75                         | 87  | 53*   | 562*   | 0     | Random species loss             |
| 75-100                        | 39  | 0*    | 97*    | 0     | Random species loss             |
| <i>Glossophaga soricina</i>   |     |       |        |       |                                 |
| Total                         | 66  | 20*   | 862    | 0     | Quasi-Random species loss       |
| 0-25                          | 3   | x     | x      | X     | x                               |
| 25-50                         | 33  | 7*    | 151    | 2,1   | Quasi-Random species loss       |
| 50-75                         | 19  | 0*    | 83*    | 0     | Random species loss             |
| 75-100                        | 11  | 5*    | 35*    | 3     | Random species loss             |
| <i>Platyrrhinus lineatus</i>  |     |       |        |       |                                 |
| Total                         | 153 | 57*   | 4881*  | 0     | Random species loss             |
| 0-25                          | 8   | x     | x      | x     | x                               |
| 25-50                         | 69  | 25*   | 1032*  | 0     | Random species loss             |
| 50-75                         | 44  | 8*    | 440    | 0     | Quasi-Random species loss       |
| 75-100                        | 32  | 15*   | 188*   | 5     | Random species loss             |
| <i>Sturnira lilium</i>        |     |       |        |       |                                 |
| Total                         | 276 | 78*   | 17193* | 0     | Random species loss             |
| 0-25                          | 25  | 3*    | 204*   | 0     | Random species loss             |
| 25-50                         | 62  | 16*   | 576*   | 0     | Random species loss             |
| 50-75                         | 30  | 7*    | 197*   | 0     | Random species loss             |
| 75-100                        | 159 | 39*   | 6443*  | 0     | Random species loss             |

Fields that the analysis couldn't calculate were filled with an 'x'. \* Significant value, Abs number of embedded absences, Rep number of replacements, I Morisita's index



Figure 1. Infracommunities of bats arthropods ectoparasites found in each category of forest cover. Colors: purple = Diptera; desert blue = Acari.

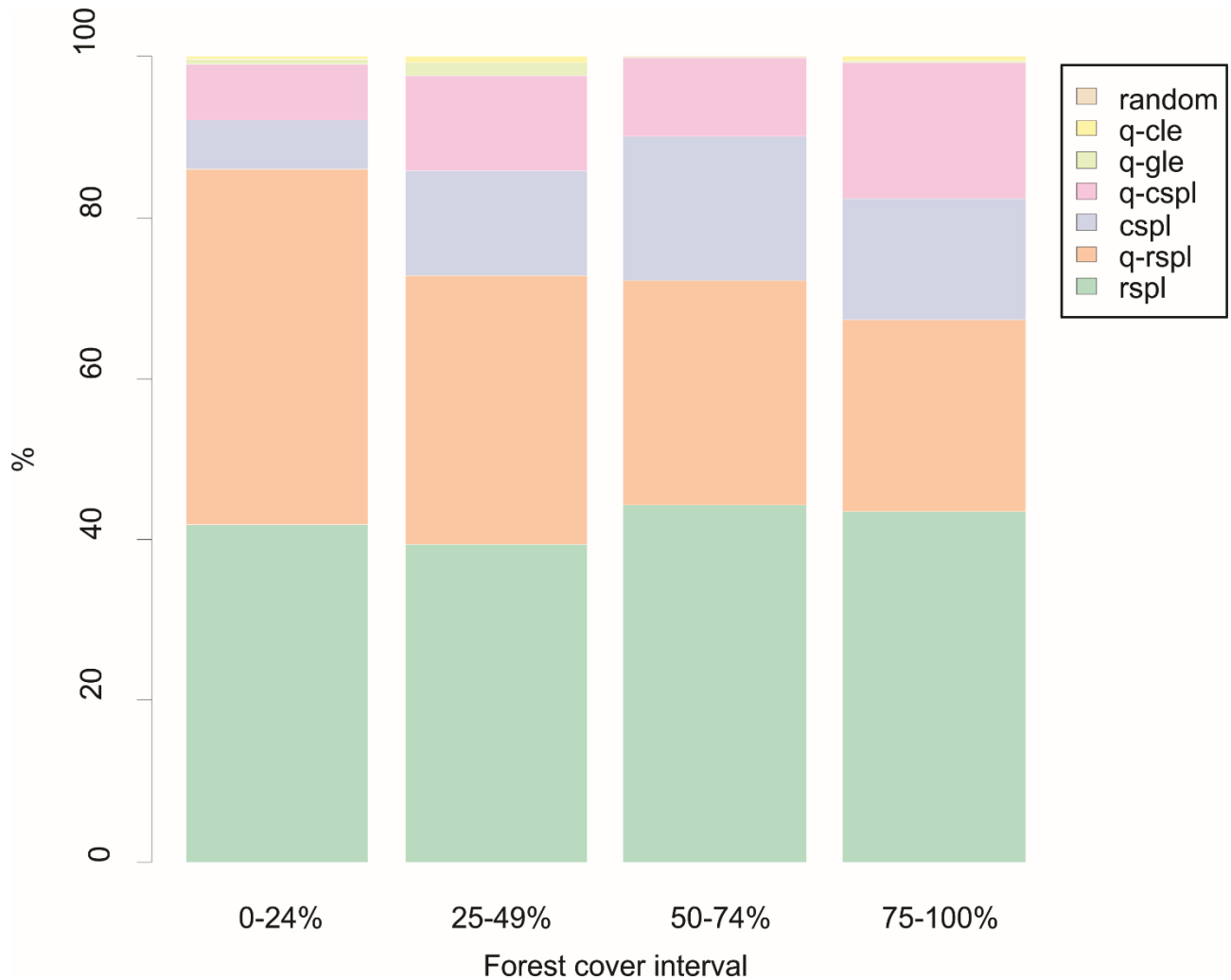


Figure 2. Proportion of infracommunity structure of ectoparasites identified 1000 times with 30 random sampled *Artibeus planirostris* individuals in each category of forest cover. Labels: q-cle = Quasi-Clementsian; q-gle = Quasi-Gleasonian; q-cspl = Quasi-Clumped species loss; cspl = Clumped species loss; q-rspl = Quasi-Random species loss; rspl = Random species loss.

Table 2 - Pearson's Chi-squared test for infracommunity structures occurrence in each forest cover %

|        | Observed |        |        |         | Expected |        |        |         |
|--------|----------|--------|--------|---------|----------|--------|--------|---------|
|        | 0-24%    | 25-49% | 50-74% | 75-100% | 0-24%    | 25-49% | 50-74% | 75-100% |
| rspl   | 418      | 395    | 442    | 435     | 423.03   | 417.06 | 426.02 | 423.89  |
| q-rspl | 443      | 333    | 279    | 238     | 323.66   | 319.09 | 325.94 | 324.31  |
| cspl   | 61       | 129    | 179    | 150     | 129.91   | 128.08 | 130.83 | 130.18  |
| q-cspl | 69       | 120    | 98     | 170     | 114.39   | 112.78 | 115.20 | 114.63  |

X-squared = 181.57, df = 9, p-value < 2.2e-16. q-cspl = Quasi-Clumped species loss; cspl = Clumped species loss; q-rspl = Quasi-Random species loss; rspl = Random species loss

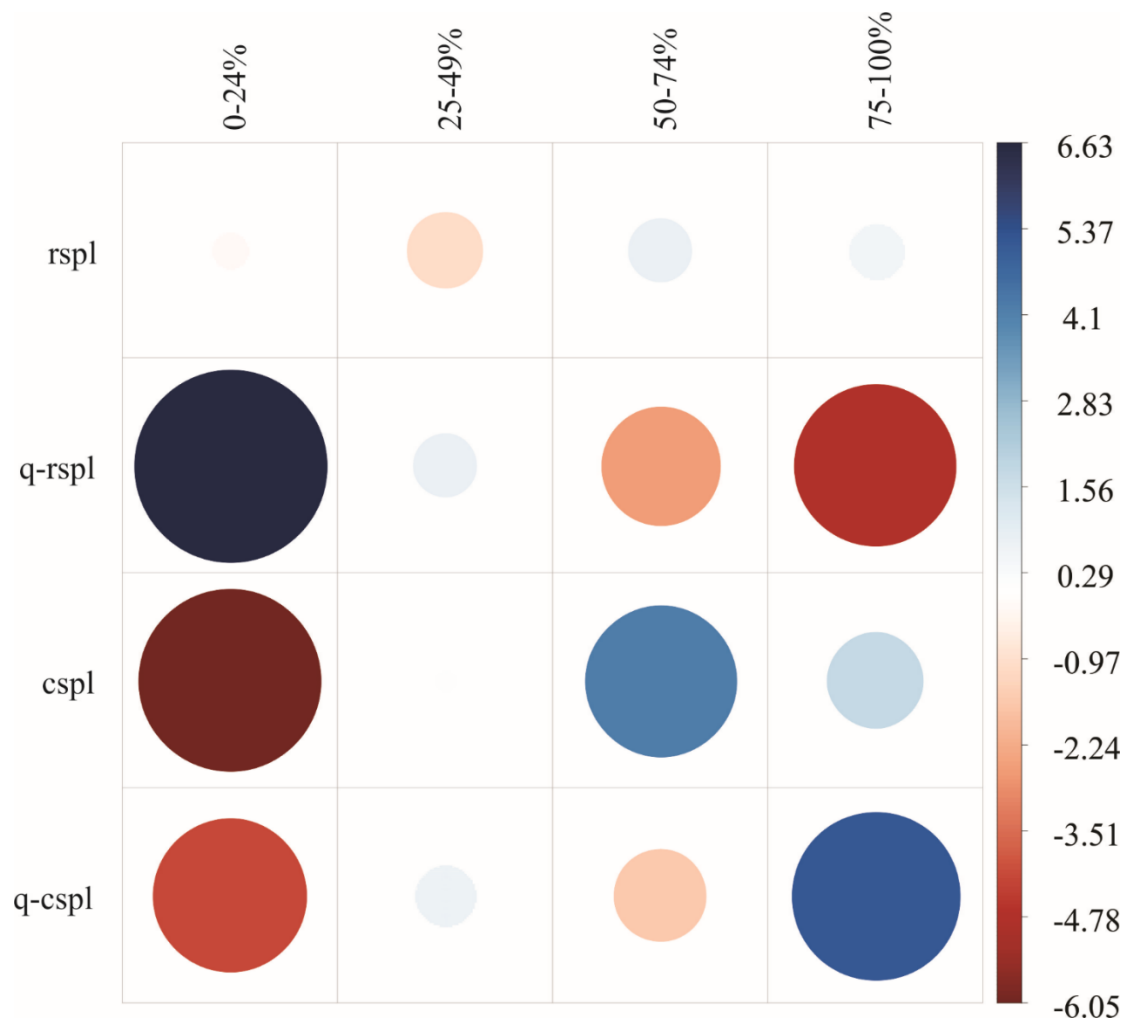


Figure 3. Residuals of chi-square test for infracommunity structures occurrence in each forest cover %. Size of circle is proportional to the cell contribution.

Color gradient for positive (darkest blue) to negative (darkest red) correlation as indicate by scale.

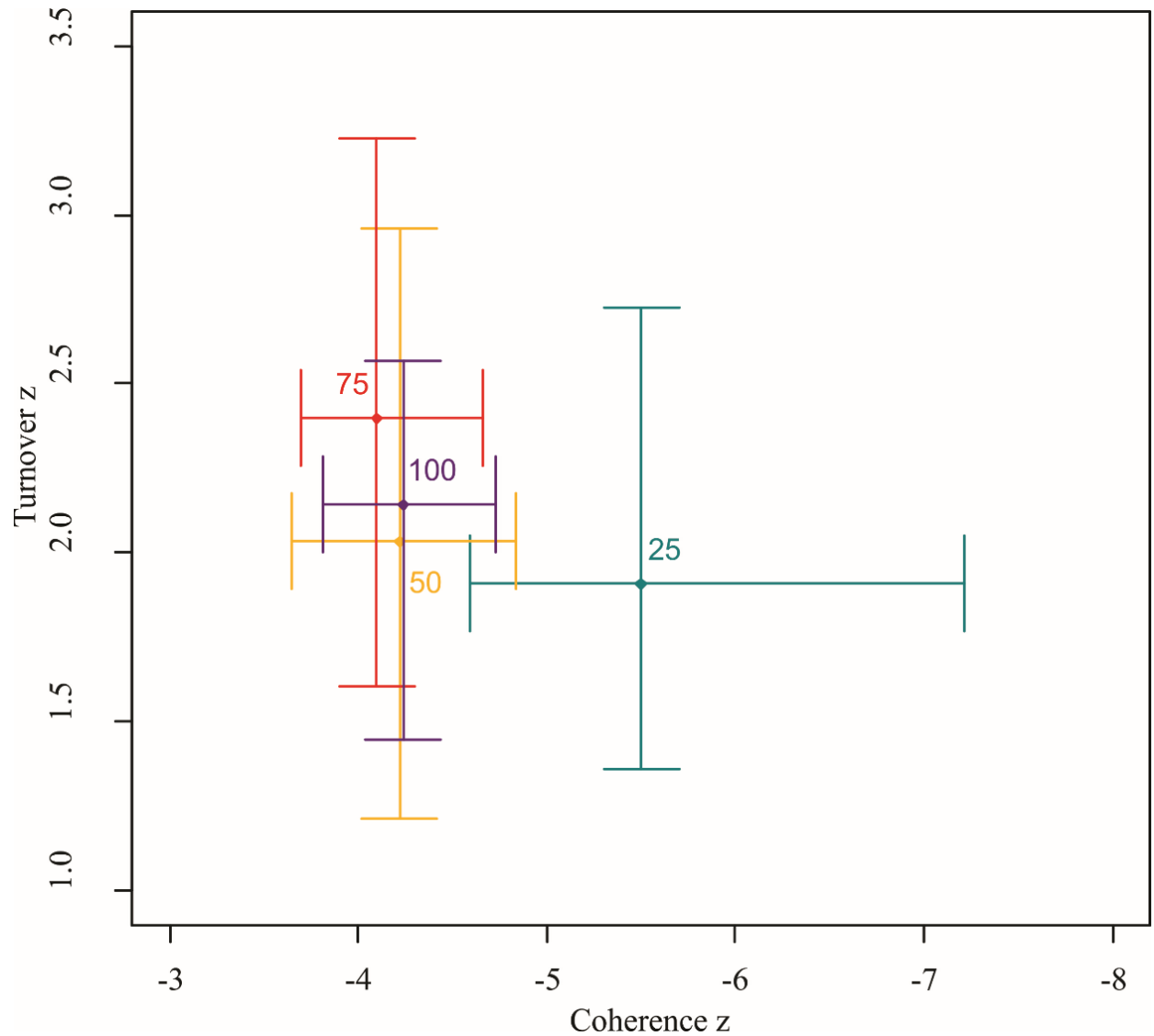


Figure 4. Z scores of coherence and turnover of ectoparasites infracommunity structure identified 1000 times with 30 random samples of *Artibeus planirostris* host individuals in each category of forest cover. Points represent the median and bars represents 50% quantiles. Labels: 25 = 0-24%; 50 = 25-49%; 75 = 50-74%; 100 = 75-100%.



### *Infracommunity crowding index and abundance*

I expected to find a gradient in which bats that contained greater richness and abundance of ectoparasites in the component community would have a greater degree of opportunity for interaction (ICr) in their infracommunities. Against this, with the Wilcoxon test I identified that *Artibeus planirostris* (component community richness = 6 spp.) was the bat species that presented infracommunities with the highest ICr and abundance (Table 3 and 4, Figure 5 and 6). However, *Glossophaga soricina* (4 spp.), which had the second highest richness and lowest abundance, had ICr lower than *Sturnira lilium* (3 spp.), did not differ from *Platyrrhinus lineatus* (3 spp.) and *Carollia perspicillata* (3 spp.). I also identified that the bat species that presented the highest proportion of infracommunities with ICr = 0, that is, individuals that were without or with only one species of ectoparasite, was *C. perspicillata* (Figure 7).

Table 3. Pairwise comparisons between bat species infracommunities ICr using Wilcoxon rank sum test with continuity correction

|  | <i>A. planirostris</i> | <i>C. perspicillata</i> | <i>G. soricina</i> | <i>P. lineatus</i> |
|--|------------------------|-------------------------|--------------------|--------------------|
| <i>C. perspicillata</i>  | 2.5e-06                | x                       | x                  | x                  |
| <i>G. soricina</i>   | 4.4e-05                | 0.4809                  | x                  | x                  |
| <i>P. lineatus</i>   | 0.0016                 | 0.1423                  | 0.0637             | x                  |
| <i>S. liliium</i>  | 0.0167                 | 0.0021                  | 0.0021             | 0.1021             |
| Kruskal-Wallis chi-squared = 51.811, df = 4, p-value = 1.511e-10 |                        |                         |                    |                    |

Table 4. Pairwise comparisons between bat species infracommunities abundance using Wilcoxon rank sum test with continuity correction

|   | <i>A. planirostris</i> | <i>C. perspicillata</i> | <i>G. soricina</i> | <i>P. lineatus</i> |
|---|------------------------|-------------------------|--------------------|--------------------|
| <i>C. perspicillata</i>   | 3.6e-08                | -                       | -                  | -                  |
| <i>G. soricina</i>  | 3.6e-08                | 0.01377                 | -                  | -                  |
| <i>P. lineatus</i>  | 0.00023                | 0.33641                 | 0.00446            | -                  |
| <i>S. liliium</i>   | 2.1e-05                | 0.10944                 | 0.00056            | 0.66802            |
| Kruskal-Wallis chi-squared = 72.708, df = 4, p-value = 6.08e-15 |                        |                         |                    |                    |

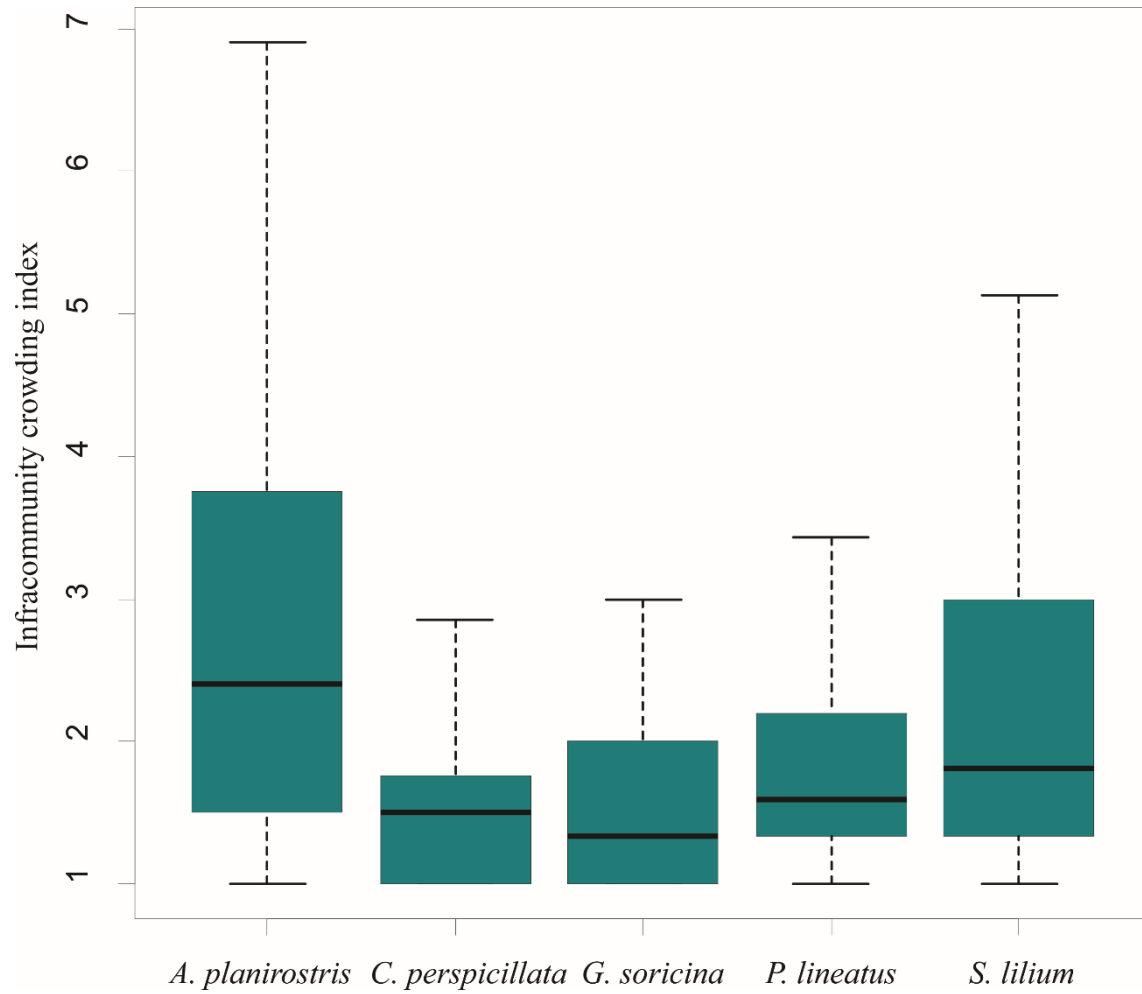


Figure 5. Infracommunity crowding index distribution among bat hosts. The 0 values representing infracommunities with zero or only one species of ectoparasites were excluded.

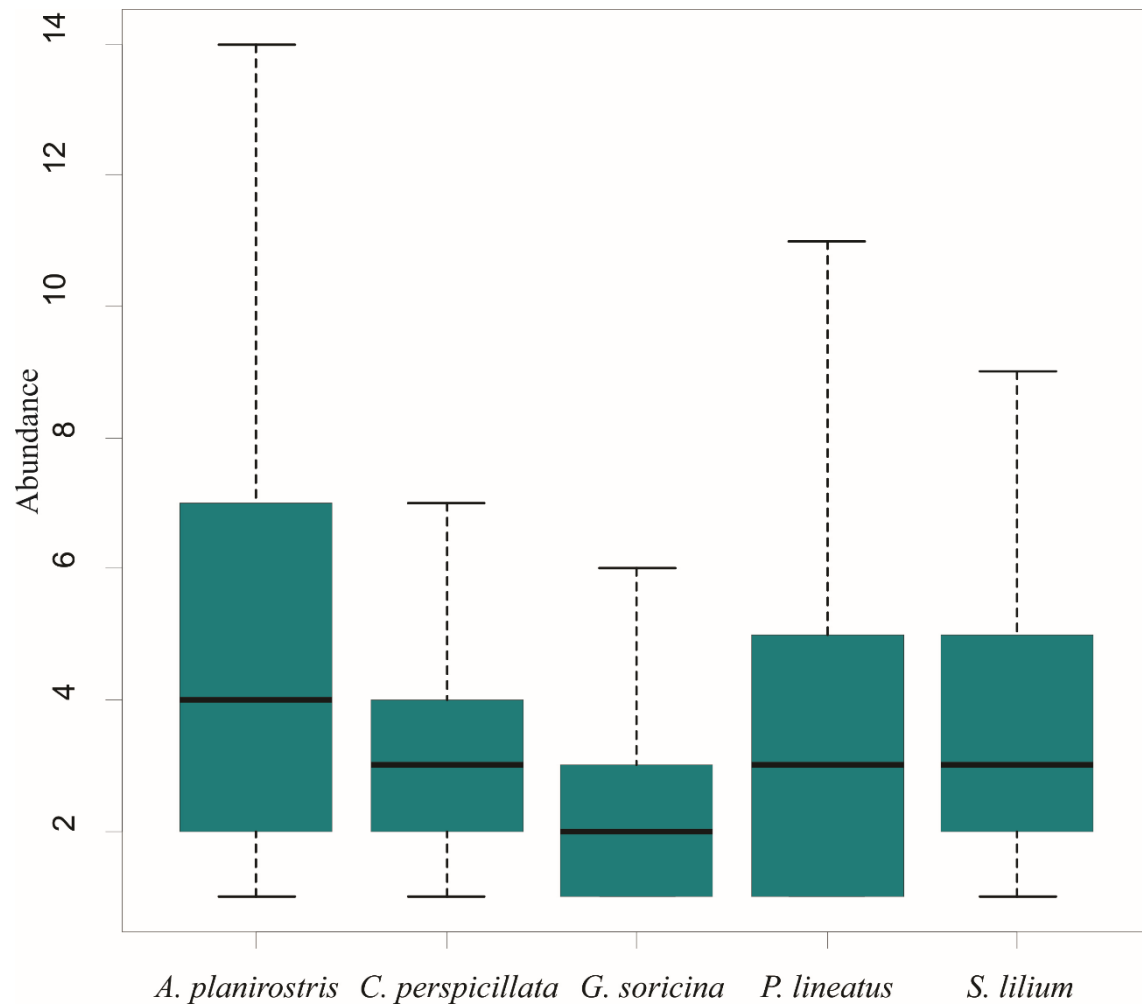


Figure 6. Abundance of ectoparasites in infracommunities distribution among bat hosts. The 0 values were excluded.

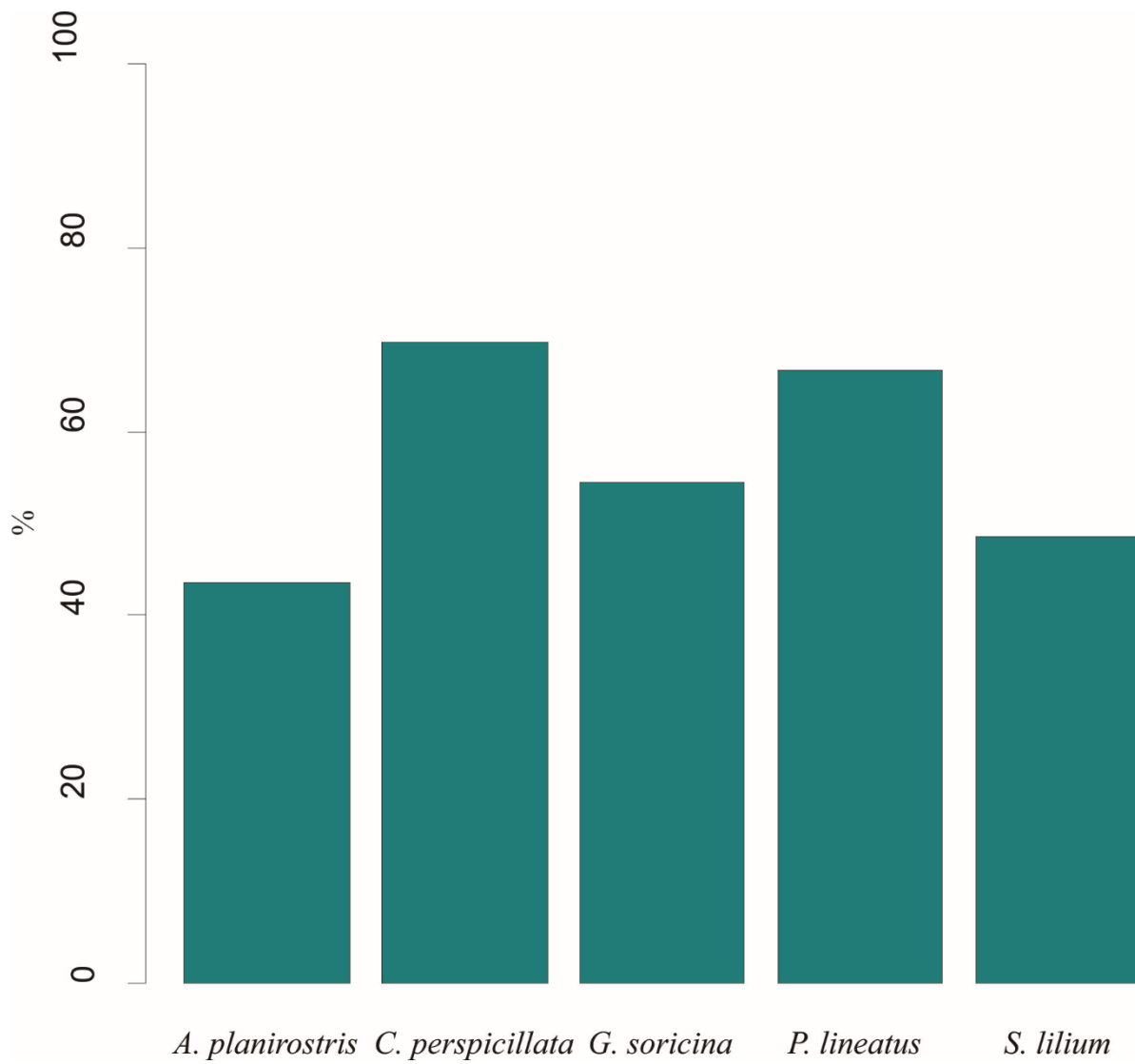


Figure 7. Proportion of infracommunities with ICr value 0 in each host species.

### *Models*

The best supported models,  $\Delta > 2$  in relation to the null model, were found for *Artibeus planirostris* and *Sturnira lilium* (Table 5 and 6). For *Carollia perspicillata* and *Glossophaga soricina* among the best models was null for both abundance and ICr and *Platyrrhinus lineatus* had better models than null only for abundance of ectoparasites. I also identified in the coefficients (Table 7 and 8) that the abundance and interspecific agglomeration of ectoparasites on these hosts decreased as vegetation cover increase. Males had more ectoparasites than females of *A. planirostris* and the opposite in *S. lilium*. *Platyrrhinus lineatus* with the highest body condition had fewer ectoparasites than the other host species.

### *Competition*

I did not identify competition between any species of ectoparasite, going against our hypothesis that the model effects would be weak because of this. However, I found evidence of facilitation among ectoparasite species on *Glossophaga soricina* (*Trichobius dugesii*) and *Artibeus planirostris* (*Periglischrus iheringi*) (Figure 8), which had an increase in their average intensity in the groups with greater richness of ectoparasites.

Table 5. Model selection table for ICr in infracommunities of bats ectoparasites.

| Bat species             | Forest   |             |                |     |     |       | df       | AICc          | delta        | weight       |
|-------------------------|----------|-------------|----------------|-----|-----|-------|----------|---------------|--------------|--------------|
|                         | Model    | Int         | Body condition | Age | Sex | cover |          |               |              |              |
| <i>A. planirostris</i>  | 9        | 2.50        |                |     |     | -1.68 | 3        | 3369.1        | 0            | 0.317        |
|                         | 13       | 2.43        |                |     | x   | -1.67 | 4        | 3370          | 0.94         | 0.199        |
|                         | 10       | 2.52        | -0.01          |     |     | -1.69 | 4        | 3371          | 1.89         | 0.123        |
|                         | <b>1</b> | <b>1.72</b> |                |     |     |       | <b>2</b> | <b>3380.2</b> | <b>11.15</b> | <b>0.001</b> |
| <i>C. perspicillata</i> | 3        | 0.57        |                | x   |     |       | 3        | 535.6         | 0            | 0.187        |
|                         | <b>1</b> | <b>0.53</b> |                |     |     |       | <b>2</b> | <b>536.1</b>  | <b>0.52</b>  | <b>0.145</b> |
| <i>G. soricina</i>      | <b>1</b> | <b>0.74</b> |                |     |     |       | <b>2</b> | <b>184.9</b>  | <b>0</b>     | <b>0.27</b>  |
|                         | 3        | 0.79        |                | x   |     |       | 3        | 186.4         | 1.5          | 0.127        |
| <i>P. lineatus</i>      | <b>1</b> | <b>0.64</b> |                |     |     |       | <b>2</b> | <b>446.7</b>  | <b>0</b>     | <b>0.191</b> |
|                         | 2        | 1.38        | -1.49          |     |     |       | 3        | 447           | 0.32         | 0.163        |
| <i>S. lilium</i>        | 13       | 1.99        |                |     | x   | -0.94 | 4        | 1049.1        | 0            | 0.202        |
|                         | 14       | 2.07        | -0.07          |     | x   | -0.97 | 5        | 1049.6        | 0.52         | 0.156        |
|                         | 9        | 1.85        |                |     |     | -0.91 | 3        | 1049.9        | 0.79         | 0.136        |
|                         | <b>1</b> | <b>1.24</b> |                |     |     |       | <b>2</b> | <b>1053.3</b> | <b>4.22</b>  | <b>0.025</b> |

Null models in bold.

Table 6. Model selection table for abundance in infracommunities of bats ectoparasites.

| Bat species             | Body     |             |           | Forest |     |       | df       | AICc          | delta       | weight       |
|-------------------------|----------|-------------|-----------|--------|-----|-------|----------|---------------|-------------|--------------|
|                         | Model    | Int         | condition | Age    | Sex | cover |          |               |             |              |
| <i>A. planirostris</i>  | 13       | 6.15        |           |        | x   | -2.62 | 4        | 4712.8        | 0           | 0.315        |
|                         | 14       | 6.20        |           | x      | x   | -2.57 | 5        | 4713.9        | 1.01        | 0.189        |
|                         | <b>1</b> | <b>5.32</b> |           |        |     |       | <b>2</b> | <b>4719.3</b> | <b>6.4</b>  | <b>0.013</b> |
| <i>C. perspicillata</i> | <b>1</b> | <b>3.21</b> |           |        |     |       | <b>2</b> | <b>894.9</b>  | <b>0</b>    | <b>0.271</b> |
|                         | 9        | 3.52        |           |        |     | -0.56 | 3        | 896.6         | 1.69        | 0.116        |
| <i>G. soricina</i>      | <b>1</b> | <b>2.43</b> |           |        |     |       | <b>2</b> | <b>266.1</b>  | <b>0</b>    | <b>0.245</b> |
|                         | 3        | 2.57        |           | x      |     |       | 3        | 267.2         | 1.12        | 0.14         |
| <i>P. lineatus</i>      | 10       | 9.83        | -9.51     |        |     | -2.66 | 4        | 762.4         | 0           | 0.363        |
|                         | 12       | 9.57        | -9.07     | x      |     | -2.71 | 5        | 764.3         | 1.85        | 0.144        |
|                         | <b>1</b> | <b>3.67</b> |           |        |     |       | <b>2</b> | <b>768.6</b>  | <b>6.3</b>  | <b>0.016</b> |
| <i>S. liliium</i>       | 13       | 5.13        |           |        | x   | -1.74 | 4        | 1366.2        | 0           | -0.295       |
|                         | 15       | 5.07        |           | x      | x   | -1.77 | 5        | 1367.6        | 1.37        | 0.149        |
|                         | 14       | 5.2         | -0.07     |        | x   | -1.77 | 5        | 1367.9        | 1.63        | 0.13         |
|                         | 9        | 4.83        |           |        |     | -1.67 | 3        | 1368          | 1.7         | 0.126        |
|                         | <b>1</b> | <b>3.72</b> |           |        |     |       | <b>2</b> | <b>1371.7</b> | <b>5.46</b> | <b>0.019</b> |

Null models in bold.



Table 7. ICr model-averaged coefficients.

| Bat species             |                     | estimate     | Std. Error  | z value     | Pr(> z )        |
|-------------------------|---------------------|--------------|-------------|-------------|-----------------|
| <i>A. planirostris</i>  | <b>Intercept</b>    | <b>2.5</b>   | <b>0.57</b> | <b>4.37</b> | <b>2e-16***</b> |
|                         | <b>Forest cover</b> | <b>-1.65</b> | <b>0.46</b> | <b>3.55</b> | <b>2e-04***</b> |
|                         | SexM                | 0.19         | 0.17        | 1.1         | 0.29            |
|                         | AgeYoung            | -0.09        | 0.23        | 0.38        | 0.73            |
|                         | Body condition      | -0.01        | 0.014       | 0.94        | 0.69            |
| <i>C. perspicillata</i> | Intercept           | 0.72         | 0.4         | 1.75        | 0.07            |
|                         | Forest cover        | 0.14         | 0.36        | 0.38        | 0.7             |
|                         | SexM                | -0.02        | 0.13        | 0.18        | 0.85            |
|                         | AgeYoung            | -0.31        | 0.18        | 1.65        | 0.09            |
|                         | Body condition      | -1.18        | 1.17        | 1           | 0.31            |
| <i>G. soricina</i>      | Intercept           | 0.82         | 0.35        | 2.26        | 0.02            |
|                         | Forest cover        | -0.39        | 0.56        | 0.57        | 0.48            |
|                         | SexM                | -0.05        | 0.23        | 0.24        | 0.82            |
|                         | AgeYoung            | -0.22        | 0.27        | 0.27        | 0.41            |
|                         | Body condition      | 0.03         | 1.98        | 0.01        | 0.98            |
| <i>P. lineatus</i>      | Intercept           | 1.07         | 0.62        | 1.69        | 0.08            |
|                         | Forest cover        | -0.38        | 0.47        | 0.8         | 0.42            |
|                         | SexM                | 0.07         | 0.17        | 0.42        | 0.66            |
|                         | AgeYoung            | -0.01        | 0.21        | 0.04        | 0.96            |
|                         | Body condition      | -1.59        | 1.17        | 1.35        | 0.17            |
| <i>S. liliium</i>       | <b>Intercept</b>    | <b>1.87</b>  | <b>0.35</b> | <b>5.2</b>  | <b>1e-07***</b> |
|                         | <b>Forest cover</b> | <b>-0.95</b> | <b>0.39</b> | <b>2.41</b> | <b>0.01*</b>    |
|                         | SexM                | -0.34        | 0.2         | 1.71        | 0.08            |
|                         | AgeYoung            | 0.16         | 0.21        | 0.75        | 0.44            |
|                         | Body condition      | -0.07        | 0.06        | 1.17        | 0.23            |

Significant coefficients in bold.

Table 8. Abundance model-averaged coefficients

| Bat species             |                       | estimate     | Std. Error  | z value     | Pr(> z )          |
|-------------------------|-----------------------|--------------|-------------|-------------|-------------------|
| <i>A. planirostris</i>  | <b>Intercept</b>      | <b>6,77</b>  | <b>1,67</b> | <b>4,03</b> | <b>2e-16***</b>   |
|                         | <b>Forest cover</b>   | <b>-2,61</b> | <b>1,14</b> | <b>2,3</b>  | <b>0,02*</b>      |
|                         | <b>SexM</b>           | <b>0,96</b>  | <b>0,42</b> | <b>2,25</b> | <b>0,02*</b>      |
|                         | AgeYoung              | -0,57        | 0,58        | 0,98        | 0,32              |
|                         | Body condition        | 0,01         | 0,1         | 0,1         | 0,9               |
| <i>C. perspicillata</i> | <b>Intercept</b>      | <b>3,37</b>  | <b>0,74</b> | <b>4,5</b>  | <b>6,2e-06***</b> |
|                         | Forest cover          | -0,55        | 0,92        | 0,59        | 0,55              |
|                         | SexM                  | 0,12         | 0,34        | 0,36        | 0,71              |
|                         | AgeYoung              | -0,13        | 0,47        | 0,3         | 0,75              |
|                         | Body condition        | -0,76        | 2,89        | 0,26        | 0,79              |
| <i>G. soricina</i>      | <b>Intercept</b>      | <b>2,7</b>   | <b>0,78</b> | <b>3,39</b> | <b>6e-04***</b>   |
|                         | Forest cover          | 0,24         | 1,04        | 0,23        | 0,81              |
|                         | SexM                  | 0,08         | 0,44        | 0,19        | 0,84              |
|                         | AgeYoung              | -0,5         | 0,5         | 0,8         | 0,42              |
|                         | Body condition        | -2,98        | 3,64        | 0,8         | 0,42              |
| <i>P. lineatus</i>      | <b>Intercept</b>      | <b>8,79</b>  | <b>2,44</b> | <b>3,57</b> | <b>3e-04***</b>   |
|                         | <b>Forest cover</b>   | <b>-2,63</b> | <b>1,33</b> | <b>1,96</b> | <b>0,04*</b>      |
|                         | SexM                  | 0,07         | 0,49        | 0,147       | 0,88              |
|                         | AgeYoung              | 0,33         | 0,62        | 0,53        | 0,59              |
|                         | <b>Body condition</b> | <b>-8,98</b> | <b>3,36</b> | <b>2,65</b> | <b>7e-03**</b>    |
| <i>S. liliium</i>       | <b>Intercept</b>      | <b>4,92</b>  | <b>0,62</b> | <b>7,82</b> | <b>2e-16***</b>   |
|                         | <b>Forest cover</b>   | <b>-1,74</b> | <b>0,69</b> | <b>2,49</b> | <b>0,01*</b>      |
|                         | <b>SexM</b>           | <b>-0,7</b>  | <b>0,35</b> | <b>1,94</b> | <b>0,05*</b>      |
|                         | AgeYoung              | 0,29         | 0,39        | 0,74        | 0,45              |
|                         | Body condition        | -0,06        | 0,1         | 0,6         | 0,54              |

Significant coefficients in bold.

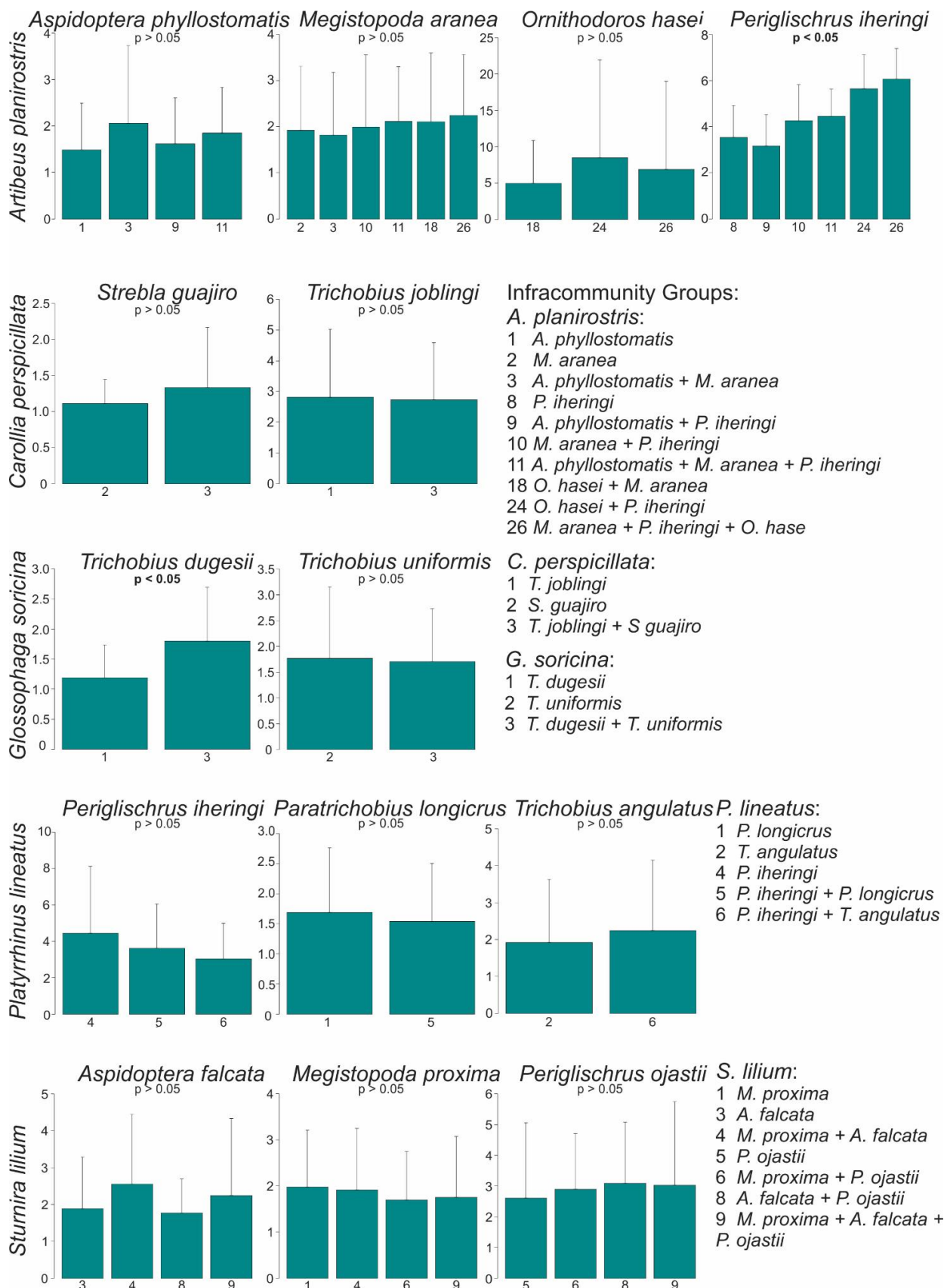


Figure 8. Mean intensity of infestation plus confidence interval of each ectoparasite alone vs with additional species for each bat host species.

## Discussion

### *Infracommunity structures*

In general, I find that the bat-ectoparasitic arthropod infracommunity belongs to the Random species loss, subset of the nested structure. This structure pattern is analogous to the Gleasonian, it occurs when the species distribution is undergoing structuring processes of certain environmental gradients. In this case, the environmental gradient in evidence would be that of forest cover. When I separate this gradient into intervals and place the host individuals as the environmental variable in evidence, I also mostly find the Random species loss structures and its quasi shape, showing that the infracommunities in these individuals would be under structuring processes of a qualitative gradient of hosts.

With random sampling in *A. planirostris* infracommunities, I identified that this gradient tends to be stronger in areas with greater forest cover, since there is a decrease in the frequency of quasi structures. In addition, I found in environments with greater forest cover an increase in the frequency of Clumped species loss structures and its quasi version, a nested subset analogous to Clementsian, for the infracommunities of *Artibeus planirostris*, indicating that the distribution of species of its ectoparasites along the hosts is more clustered than expected and the distribution limits are coincident (Presley et al. 2010).

### *Degree of isolationism/interactivity and abundance*

The ICr found shows that even bat species with equal richness of ectoparasites may have infracommunities with a different average interactivity, which reinforces Presley's (2011) statement that the set of factors responsible for shaping the assemblages of these ectoparasites is specific for each host taxon. Using as an example the species *Sturnira lilium* and *Carollia perspicillata*, this shows that the distribution of co-occurrence of

ectoparasites in these species follows different patterns, since the average abundance of their infracommunities was not different. I also observed that the host species with the lowest ICr averages are the same ones that present the highest proportions of infracommunities with none or only one species of ectoparasite.

### *Models*

Removing the models with uninformative parameters (Arnold, 2010) from those with delta AICc less than 2, I observed that forest cover was part of all the best models and always in a negative way, that is, the greater the forest cover, the lower the abundance and the ICr. I believe that this is caused by what was hypothesized, a decrease in the availability of shelters. However, the same effect should have been observed for *Carollia perspicillata* and *Glossophaga soricina*, which usually use hollows, buildings, and caves as daytime shelter (Almeida et al. 2002, Bonaccorso et al. 2006, Peñuela-Salgado & Peres-Torres 2015). It may be that the number of captures of individuals infested with these two species along the gradient was insufficient to identify the effect or even that the areas where the species were more abundant had specific elements with a stronger impact on their parasite load than the availability of shelters.

The body condition, sex and age of the hosts were not very informative. For *Sturnira lilium* the effect of sex was negative for males, and positive for *Artibeus planirostris*. On one hand we have evidence that female bats may contain higher parasite loads (Patterson et al. 2008a), on the other hand we have the general pattern for males providing better resources for the parasites due to the immunosuppressive effect caused by androgens (Krasnov et al. 2011b). In this work I considered that there was no dominance of any of these patterns. As for body condition, although other studies have found this effect in a more comprehensive way (Patterson et al. 2008b) and even if inconsistent (Presley & Willig 2008), here I found it for only one of the five species,

*Platyrrhinus lineatus*, showing that de In general, other factors, possibly non-morphometric, behavioral, and ecological, are becoming more important for the abundance and ICr of infracommunities. Finally, age does not appear in any of the best models, showing that there was no difference between young and adult bats in terms of their parasite load.

### *Aggregation*

No approach so far has identified competition between bat ectoparasites. Tello et al. (2008) used null species co-occurrence model analysis and found no evidence that competition affects the distribution of bat fly's species among hosts but found evidence for interspecific aggregation. Presley (2011) analyzed the co-occurrence and correlation of abundances of ectoparasite species of bats and found only results that corroborated for the aggregation of ectoparasites in the hosts instead of segregation. In this work, I tried once again to find evidence of competition using the average infestation intensity as a metric. I analyzed whether the mean intensity of species due to the presence of others would decrease, especially when in the presence of species that use the same microhabitat in the bat. I found only two species of ectoparasites, from different host species, that had their mean infestation intensities increasing according to the richness of the infracommunity. This evidences that these infracommunities are more likely to be aggregative than segregative and that these species benefited more from the conditions that led their hosts to accumulate greater richness of ectoparasites.

### **Chapter 3. Female host of *Anoura geoffroyi* (Chiroptera) preference by *Exastinion clovisi* (Streblidae) and density-independent sex ratio in ectoparasite infracommunities**

#### **Abstract**

Sex bias is common to be found in host-parasite interactions. In bat ectoparasites, female hosts with higher parasite loads and infracommunities with density-dependent sex ratio have been recorded. In this study I used a considerable sample of ectoparasites found on *Anoura geoffroyi* bats captured in two caves in the state of Minas Gerais, Brazil, to test two hypotheses: I – female hosts will have more ectoparasites; II – the sex ratio of the ectoparasites will be density-dependent, males will predominate bats with low abundance of ectoparasites, and the situation will be reversed in the more abundant hosts. For this I built generalized linear models with data from 4773 ectoparasites from 1144 hosts. I did not find results that corroborated the first hypothesis, and our results partially corroborated the second. In four out of 16 models, I found significant results showing that females were slightly more infested by *Exastinion clovisi* flies, demonstrating the existence of a preference for these ectoparasites.

**Keywords:** Bat flies, sex bias, cave.

## Resumo

Viés de gênero são comuns de serem encontrados em relações parasitárias. Em ectoparasitos de morcegos já foi registrado hospedeiras fêmeas contendo maiores cargas parasitárias além de infracomunidades com proporção sexual densidade-dependente. Neste estudo utilizamos uma amostra considerável de ectoparasitos encontrados em morcegos *Anoura geoffroyi* capturados em duas cavernas no estado de Minas Gerais, Brasil, para testarmos duas hipóteses: I – as hospedeiras fêmeas terão mais ectoparasitos; II – a proporção dos sexos dos ectoparasitos será densidade-dependente, os machos predominarão nas infracomunidades menos abundantes e a situação se inverterá nas infracomunidades mais abundantes. Para isso construímos modelos lineares generalizados com os dados de 4773 ectoparasitos de 1144 hospedeiros. Não encontramos resultados que corroborasse com a primeira hipótese e nossos resultados corroboraram parcialmente com a segunda. Em quatro de 16 modelos encontramos resultados significativos evidenciando que as fêmeas estavam levemente mais infestadas por moscas da espécie *Exastinion clovisi*, demonstrando a existência de uma preferência desses ectoparasitos.

Palavras-chave: moscas de morcego, viés de sexo, caverna.



## Introduction

Parasites are commonly found asymmetrically in their hosts and one of the causes for this is the diversity of qualities that each individual, understood as the habitats, can present (Poulin 2007). Host characteristics such as sex, size, mass, and age tend to affect their parasite loads to some degree (eg. Junker et al. 2021). More specifically about sex, these differences are often attributed to sexual dysmorphia, specific behaviors, hormone levels, and immunity (Hillegass et al. 2008, Patterson et al. 2008, Krasnov et al. 2011b, Kiffner et al. 2014).

In this context of parasitic relationships, bats stand out for having the greatest diversity of ectoparasites among mammals (Dick & Dittmar 2014). Among the groups associated with these animals, the most common and abundant are the Diptera, Streblidae (Dick & Miller 2010) and Nycteribiidae (Graciolli 2010) families, and the mites (Whitaker et al. 2009). It has been found that female bats have higher parasite loads than males, because females of many species shelter in dense maternity colonies during the reproductive period, so facilitating the transmission of ectoparasites (Patterson et al. 2008). Furthermore, it was observed that pregnant females were more infested than non-reproductive ones, possibly due to hormonal influences (Christe et al. 2000).

Sex bias has also been found in ectoparasite infracommunities. Larvae develop into bat flies in the uterus of females. To complete their development, females temporarily abandon their hosts to deposit larvae on the walls of the day shelter (Dick & Patterson 2007). Thus, it is possible that when bats go out to forage, there is a population of females in the shelter, so that when these individuals are captured, more males are found. The sex determination system of these ectoparasites is still unknown, however, Dittmar et al. (2011) found a greater number of females emerging from the puparia, a bias that was not maintained in the adult population of hosts captured at the

shelter. Another issue regarding sex bias in bat ectoparasites infracommunities is the preference for specific hosts. It is possible that males are more dispersed in intrapopulations, while females are more agglomerated in individuals with specific qualities, presumably reflecting nutritional demands, generating a density-dependent sex ratio (Szentivanyi et al. 2017).

In this work I had the objective to verify if the proportion of sex of ectoparasites varies according to the abundance in the infracommunities and if the abundance of the infracommunity varies according to the sex of the host, separating even for each sex of the ectoparasites. Our hypotheses are that: I – smaller intrapopulations will have male predominance and this will reverse as abundance increases; II – female hosts will have a greater number of ectoparasites.

To test our hypotheses, I used the phyllostomid species *Anoura geoffroyi*. This bat is mainly polynivorous, but it also consumes fruits, nectar, and insects (Ortega & Alarcon-D 2008). *A. geoffroyi* shelters in a variety of refuges including caves and tunnels (Reid 1997). Individuals of *A. geoffroyi* have been found infested by five species of streblid bat flies (Graciolli & Cunha Coelho 2001; Komeno and Linhares 1999). These bat flies belong to two subfamilies, Streblinae and Trichobiinae. *Anastrebla mattadeni*, *A. modestini* and *Strebla harderi* are the Streblinae species, they have genal ctenidium and developed wings. The Trichobiinae species, *Trichobius propinquus*, have developed wings, while *Exastinion clovisi* have reduced wings not functional for flight (Guerrero 2019).

## **Methods**

### *Study area*

*Anoura geoffroyi* individuals were captured in two caves, one in the municipality of Caeté (Loca dos Morcegos) and the other in Brumadinho (MJ-05). Loca dos Morcegos

(19°48'51"S and 43°41'12"W – 1,220 alt.) is in Serra da Piedade, in an area owned by the Nossa Senhora da Piedade Sanctuary. Its phytophysiology is typical of the Atlantic Forest at the foot, of rupestrian fields at the top and with patches of cerrado in the surroundings (Bueno 1992). The climate is classified as semi-humid tropical and high altitude tropical. The average temperature ranges from 18°C in the coldest month to 22°C in the hottest month, and at the top the annual average is 16°C (Vianello & Maia, 1986). Regarding precipitation, there is a rainy season between November and March and a dry season between May and August (Marques & Lemos-Filho, 2008).

Cave MJ-05 (20° 5'40"S and 44° 4'36"W – 1,072 alt.), has a climate of the Cwb type, classified as subtropical in altitude, with dry winter and rainy summer (Ribas 2010). Regarding vegetation, the cave is in a region of Atlantic Forest domain, with the presence of seasonal semideciduous forests, in addition to highland and rocky fields (Markus 2003).

#### *Data collect*

Over the course of a year, from March 2017 to May 2018, 12 daytime visits were carried out in each of the two caves. Bats were captured with a dip net and individuals collected were individually packed in cloth bags. Each bag was used only once during each capture session. Then, the bats were inspected outside the cave to collect the ectoparasites. The collected ectoparasites were fixed in 92% alcohol in individual eppendorf tubes for each host, properly labeled with the registration number. A total of 498 bats infested in Brumadinho cave and 647 in Caeté cave were collected. The identification of ectoparasites was performed under a stereomicroscopic magnifying glass according to the keys of Graciolli & Carvalho (2001) and Guerrero (2019). Collected material was deposited in the collection of the Federal University of Mato Grosso do Sul (UFMS).

All procedures performed for data collection used in this work have authorization (#019/2016) from the Ethics Committee on Animal Use (CEUA) of the Pontifical Catholic University of Minas Gerais (PUC Minas) and authorization (#55700/2) for activities with scientific purpose issued by the Biodiversity Authorization and Information System of the Chico Mendes Biodiversity Institute (SISBio/ICMBio). After collecting the data, the bats were released into the caves, except for the specimens collected and deposited as vouchers in the Coleção de referência de Biologia de Vertebrados at PUC Minas.

### *Data analysis*

To verify if the abundance of each sex of each bat fly species in the infracommunities was affected by the host sex, I used generalized linear models in R (R Core Team 2020). I performed the analyzes for each species of ectoparasite separately and for all together. For each of them, I tested four models: sexual proportion of ectoparasites as a function of the abundance of infracommunities; abundance of ectoparasites in infracommunities depending on the sex of the hosts; abundance of female ectoparasites as a function of host sex; abundance of male ectoparasites as a function of host sex. The sex ratio was calculated so that its value ranges from 0 to 1, with 0 being an infracommunity composed of only females, 0.5 an infracommunity with the same proportion of males and females, and 1 composed of only males.

## **Results**

A total of 4773 ectoparasites of three Streblidae species were collected from 1144 hosts, namely: *Anastrebla modestini* (766 males and 531 females), *Exastinion clovisi* (1414 and 1430) and *Trichobius propinquus* (328 and 304). In total I found a sex ratio of 0.53,

indicating that there are more male ectoparasites than females. Regarding host sex, more males ( $n = 673$ ) than females ( $n = 471$ ) were captured.

I found significant results in only four of the 16 models (Figure 1, Table 1). The hypothesis that there would be a density-dependent sex ratio was not supported. None of the four models involving this aspect was significant. Female hosts were more infested by female flies of all species, and also more infested by *Exastinion clovisi* than male bats, with larger infrapopulations, larger number of female and male flies, corroborating the hypothesis that females would present larger parasitic loads, although these differences are imperceptible observing only the distributions represented by the boxplots (Figure 1).

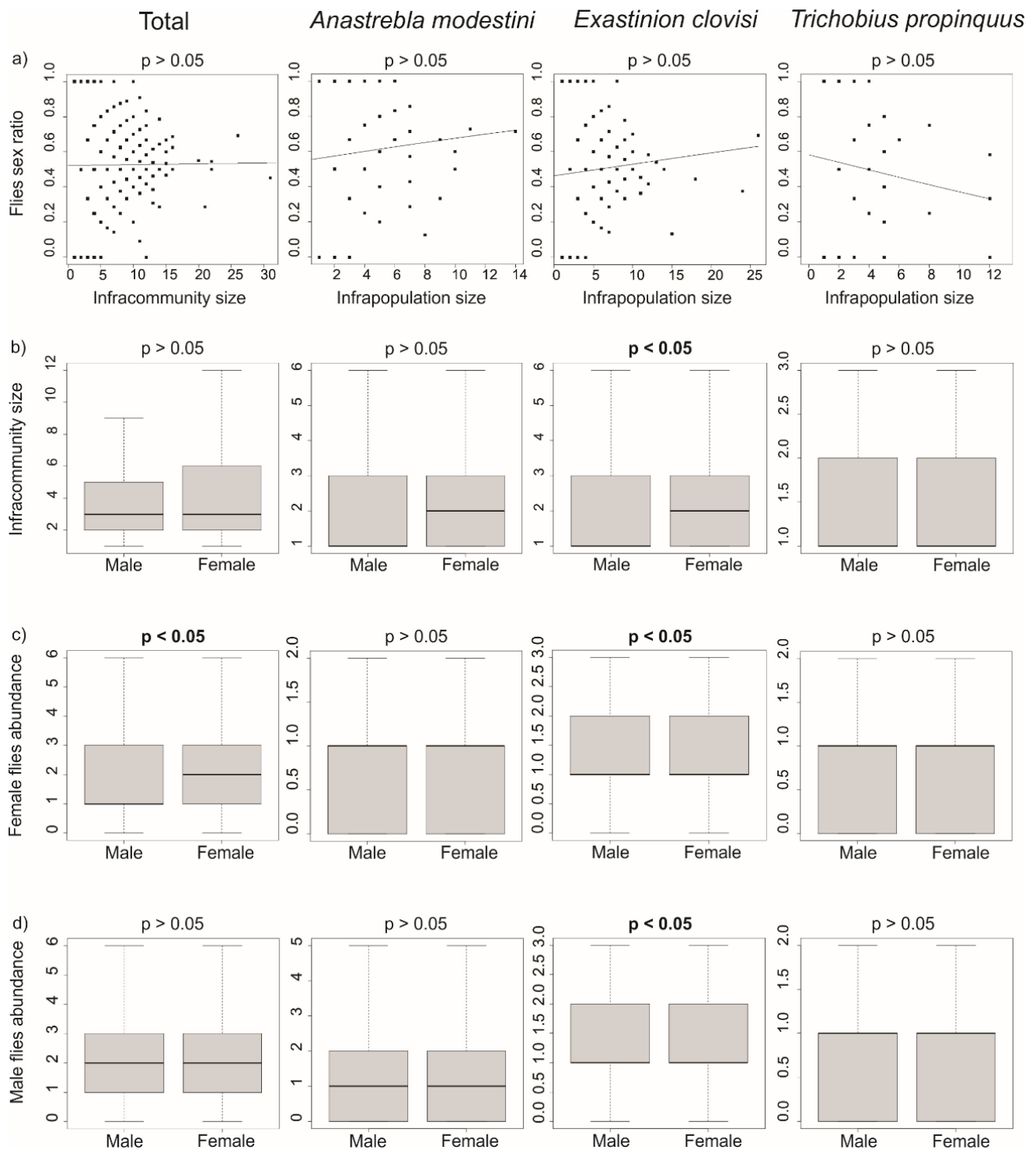


Figure 1 - Models and distributions of ectoparasites of *Anoura geoffroyi*. a) models for the influence of abundance in sex ratio. Line is the model predict. Models for effect of host sex in b) infracommunity size, c) female ectoparasites abundance, d) male ectoparasites abundance.

Table 1. Models for each ectoparasite species of *Anoura geoffroyi* captured in caves of Brumadinho and Caeté municipalities. $\beta$  = beta coefficient, SE = standard error.

| Model                           | Total        |              |              |              | <i>Anastrebla modestini</i> |       |             | <i>Exastinion clovisi</i> |              |              | <i>Trichobius propinquus</i> |       |   |
|---------------------------------|--------------|--------------|--------------|--------------|-----------------------------|-------|-------------|---------------------------|--------------|--------------|------------------------------|-------|---|
|                                 | Coefficient  | $\beta$ (SE) | t            | p            | $\beta$ (SE)                | t     | p           | $\beta$ (SE)              | t            | p            | $\beta$ (SE)                 | t     | p |
| Sex ratio ~ infracommunity size |              |              |              |              |                             |       |             |                           |              |              |                              |       |   |
| Intercept                       | 0.08 (0.09)  | 0.9          | 0.3          | 0.19 (0.13)  | 1.399                       | 0.162 | -0.14 (0.1) | -1.39                     | 0.165        | 0.3 (0.1)    | 1.91                         | 0.056 |   |
| Infracommunity size             | 0.01 (0.01)  | 0.1          | 0.9          | 0.05 (0.05)  | 1.023                       | 0.307 | 0.02 (0.02) | 0.995                     | 0.32         | -0.08 (0.07) | -1.1                         | 0.256 |   |
| Abundance ~ host sex            |              |              |              |              |                             |       |             |                           |              |              |                              |       |   |
| Intercept                       | 4.4 (0.16)   | 27.4         | 2E-16        | 2.1 (0.1)    | 22.4                        | 2E-16 | 3.4 (0.12)  | 27                        | 2E-16        | 1.7 (0.16)   | 10.6                         | 2E-16 |   |
| Host sex M                      | -0.4 (0.20)  | -1.9         | 0.05         | -0.02 (0.12) | -0.2                        | 0.8   | -0.5 (0.17) | -3.4                      | <b>0.001</b> | 0.06 (0.18)  | 0.3                          | 0.7   |   |
| Female abundance ~ host sex     |              |              |              |              |                             |       |             |                           |              |              |                              |       |   |
| Intercept                       | 2.1 (0.08)   | 25.2         | 2.E-16       | 0.8 (0.06)   | 15.6                        | 2E-16 | 1.8 (0.07)  | 24.9                      | 2E-16        | 0.9 (0.12)   | 7.6                          | 2E-13 |   |
| Host sex M                      | -0.3 (0.11)  | -3.1         | <b>0.001</b> | -0.05 (0.08) | -0.6                        | 0.5   | -0.4 (0.09) | -4.3                      | <b>1E-05</b> | -0.16 (0.14) | -1.1                         | 0.2   |   |
| Male abundance ~ host sex       |              |              |              |              |                             |       |             |                           |              |              |                              |       |   |
| Intercept                       | 2.2 (0.1)    | 23.2         | 2E-16        | 1.2 (0.07)   | 16.6                        | 2E-16 | 1.6 (0.07)  | 21.9                      | 2E-16        | 0.7 (0.1)    | 7.4                          | 8E-13 |   |
| Host sex M                      | -0.04 (0.12) | -0.4         | 0.7          | 0.02 (0.1)   | 0.2                         | 0.8   | -0.1 (0.09) | -1.7                      | <b>8E-02</b> | 0.2 (0.1)    | 1.9                          | 0.056 |   |

## Discussion

In this work I tested the hypothesis that the sex ratio of bat flies tends to a greater number of females in larger infrapopulations, based on the results found by Szentivanyi et al. (2017), which was not corroborated. Szentivanyi et al. (2017) found that the proportion of females increased according to the abundance in the infrapopulations, I did not identify the sex ratio being density-dependent for any of the three species analyzed. Even the model closest to a significant probability ( $p = 0.056$ ) would increase the proportion of males as the abundance of the infrapopulation increases, being a result contrary to what was previously found.

I also tested the hypothesis that there would be a difference in the parasite load according to the sex of the host. Our results were inconclusive in this regard. In four models I found significant values, but not in 12. The difference observed in the female fly abundance model by host sex for complete infracommunities may be a consequence of the same significant result found for the *Exastinion clovisi* species, since this was the most abundant (approximately 63% of the total), having greater weight in the analysis. Only part of the results found for *E. clovisi* follow that found by Szentivanyi et al. (2017), the ratio of the highest number of female flies on female hosts. However, the same was found for male flies. Vidal et al. (2021) also found higher abundance of *E. clovisi* on *Anoura geoffroyi* in caves of the same state, showing that the species in general may have preference for female hosts or are under some structural process that difficulties the dispersion of this organism through the host population. *E. clovisi* is a streblid species with short legs and nonfunctional wings, contrary to the other two species found that possesses longer legs and developed wings, it's mobility can be worse, and the time took to disperse can be longer. This would be more plausible if there's events of high ectoparasite infestation, reproduction, and transmission during female bats reproduction period on maternities and *E. clovisi*'s lack of mobility to



disperse through males cause this sex bias. But there is no evidence recorded of different mobility for these species of ectoparasites.

## General conclusions

In this dissertation I covered some aspects that may affect the communities of bat ectoparasites, at infracommunity level. In the first chapter I highlighted the importance of consideration of all species present on the host since they can interact with each other. The results showed that the infracommunity structure found when taxa are excluded, mostly, is a different pattern than the structure found of all ectoparasites, leading to misinterpretation of the processes that can be occurring.

For the second chapter, our results showed that bat ectoparasite infracommunities are usually nested, of the Random species loss subset, possibly varying to quasi structure as vegetation cover decreases. *Artibeus planirostris* was the bat species with infracommunities with greater abundance and ICr. The abundance of infracommunities decreased in three of the five host species as the forest cover increased, in two the abundance was influenced by the host sex, one positive and one negative, and the third by the host body condition. In addition, the ICr of infracommunities decreased in two of the five host species according to the increase in forest cover, in one of them the ICr was also influenced by sex. Finally, I found no competition in infracommunities. I consider that with these results there's evidence that vegetation cover has some influence on the abundance and ICr of bat ectoparasite infracommunities and that the hosts in which the ectoparasites aggregate, but the reasons for this aggregation would not be directly related to the morphological characters of the bats.

In chapter three I tested two hypotheses about the sex ratio and distribution patterns of bat flies, which I did not find substantial results to corroborate with. No density-dependence model significant was found and for the other hypothesis four of 16 models were, all these models involved the ectoparasite species *Exastinion clovisi* and in all cases the species was subtly more abundant in female hosts. I suspect that it was

caused by the presumably lack of mobility this ectoparasite presents, making it difficult to disperse after specific events of high population growth.

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