

Specialization and modularity of a bat fly antagonistic ecological network in a dry tropical forest in northern Colombia

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Ecological networks represent the energy flow and interactions among the species of an ecological community. Streblidae is a family of bloodsucking flies specialized in parasitizing bats, thus forming an ecological network. The purpose of this study was to investigate the specialization and modularity of a bat fly antagonist ecological network in a tropical dry forest in northern Colombia. Bat hosts were sampled by using mist nets, while bat flies were collected directly from the hosts by using entomological forceps. The network was built with the Bipartite package from R software. The sampling effort resulted in 270 bat flies recorded on 45 host individuals. The network showed a high specialization ($H_2^* = 0.67$) and a low connectance ($C = 0.30$). *Paradyschiria parvuloides* was the most specialized fly ($d = 0.95$). The interactions exhibited a high modularity ($Q = 0.57$), with five modules. This study confirms the high specialization between bats and Streblidae flies, which is influenced by factors such as fidelity to the refuge and habitat, and host abundance.

Key words: flies, parasitism, Phyllostomidae, Streblidae

INTRODUCTION

Ecological networks represent the energy flow and interactions among different trophic levels of biological communities, meaning how each species is related to another (Lindeman, 1942; Piloosof *et al.*, 2017). These concepts have become a very important tool in ecology and conservation models, since they aid researchers in understanding the variables that influence biological community structures and their interactions (Lewis *et al.*, 2002). In the same way, the use of ecological networks allows the identification of key species by their position in the structure of ecological networks. Therefore, ecological network theory could help to understand the key species in the networks, in order to avoid the collapse of a community, and subsequently, the imbalance of the ecosystem (Tylianakis *et al.*, 2010).

Studies on ecological networks have been focused on describing the structure of mutualistic trophic networks, principally of the plant-animal interactions (Dunne *et al.*, 2002; Jordano *et al.*, 2009; Carstensen *et al.*, 2016). However, there are still few studies that address the structure of antagonist networks, such as in the host-ectoparasite system (Lewis *et al.*, 2002; Van Veen *et al.*, 2006; Zarazúa-Carbajal *et al.*, 2016). Antagonistic networks are considered bipartite because they are formed by two groups of organisms. It is formed by the beneficiaries' (such as parasites, parasitoids and predators) and the harmed individuals (hosts and prey) (Poulin, 2010). Particularly, the host-ectoparasite interaction is known to show a high degree of specialization (Blüthgen *et al.*, 2006), since a great percentage of ectoparasitic species do not share the same hosts (Wenzel *et al.*, 1966; Dick

and Patterson, 2007; Dick *et al.*, 2009). For this reason, interaction groups (modules) are generated where an ectoparasitic species is found on other host species, showing a specific modularity degree without losing the specialization (Carstensen *et al.*, 2016). In fact, Dormann and Strauss (2014) found a positive correlation among modularity and specialization.

Streblidae Kolenati, 1863 is a family of hematophagous flies which specialize on parasitizing bats. Its distribution includes all biogeographic regions, with great diversity in the American continent (Guerrero, 1993). Currently, Streblidae is divided into five subfamilies: Nycteriboscinae, Ascopterinae, Trichobiinae, Streblinae, and Nycterophilinae, the last three of which are endemic to the New World, with 26 genera and 158 species (Dick *et al.*, 2016).

This group of ectoparasites is an interesting model for studying antagonistic networks, since its specificity as bat parasites creates highly specialized relationships, due to historic associations of the evolutionary lineages between these two groups of organisms (Dick and Patterson, 2007). Therefore, understanding the structuring of the networks between streblid flies and bats would increase the comprehension of the evolutionary dynamics and ecology of these organisms. Studies on bats and flies have shown that their interactions are highly specialized. In addition, environmental variables, such as temperature, seasonality and anthropic variables, including human population density, may have very strong influences on the variation of this specialization (Pilosof *et al.*, 2012; Rivera-García *et al.*, 2016). In order to increase the knowledge about the interaction networks among bats and parasitic flies, we describe the structural parameters of the bat fly interaction network in a tropical dry forest of northern Colombia.

Previous studies on the bat fly ecological networks in tropical dry forests found that the associations between ectoparasitic flies and their bat hosts are highly specialized ($H'_2 > 0.7$ — Zarazúa-Carbajal *et al.*, 2016). Therefore, we expect that the interaction network evaluated in this study will also be highly specialized. Additionally, we expect that the modularity of host-bat fly networks will be high ($Q > 0.50$), as the specialization has a positive relationship to the modularity of the ecological network. A higher specialization will show a high specificity of the flies to the host, generating specific groups of interaction between flies and bats (Dick, 2007; Dick and Patterson, 2007).

MATERIALS AND METHODS

Study Area

This research was developed in the Reserva Forestal Protectora Serranía de Coraza, Sucre region, Colombia (09°31'58.02"N, 75°20'59.85"E) (Fig. 1). The area corresponds to a tropical dry forest (Bs-T) (Holdridge, 1979) with a warm climate. Temperature averages 26.8°C and relative humidity averages 77%. The annual precipitation is between 1,000 and 1,200 mm (Aguilera, 2005). A detailed description of the vegetation can be found in Cuervo *et al.* (1986).

Fieldwork

Bat sampling was carried out for nine months from June 2013 to March 2014. Four mist nets (6 × 2.5 m) were opened at the understory level from 18:00 to 12:00 and checked at 15 min intervals. Captured bats were transported individually in cloth bags to the field camp, where we carefully carried out the ectoparasites collection. Cloth bags were previously disinfected and used only one time for each sampling. Bats were identified using the taxonomic keys by Linares (2000) and Muñoz (2001).

The ectoparasitic flies were extracted directly from the body of the bats with the aid of entomological forceps. Then, the bat flies were individually placed in glass vials with 70% ethanol. The Streblidae were identified by following Guerrero's taxonomic keys (1993, 1994a, 1994b, 1995a, 1995b, 1996). Diptera were deposited at the Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul (ZUFMS), Campo Grande (Brazil) and at the Entomology Laboratory of the Sucre University (LEUS), in Sincelejo (Colombia).

Data Analysis

An incomplete survey of the ecological interactions results in a bias of the indexes describing the structures of the ecological network (Chacoff *et al.*, 2011; Falcão *et al.*, 2016). Therefore, to evaluate the completeness of our ecological interactions sampling, we constructed an accumulation curve. We used a matrix (bats in columns and flies in rows), in which the abundances of the collected flies constituted the sampling effort, since these were used to represent the interactions. This matrix was randomized 100 times to obtain its confidence interval (Colwell and Coddington, 1994; Gotelli and Colwell, 2001). Moreover, we calculated the efficiency of the samplings by the formula: (Observed interactions/Expected interactions) × 100. The expected interactions were calculated using the Chao 1 index. This estimator is very sensitive to the occurrence of singletons and takes into account the abundances of the samples (Chao, 1984; Chao and Lee, 1992).

The interaction matrix was created excluding those bat fly associations that were considered accidental (Supplementary Table 1S). In our study, accidental bat fly associations were: 1) interactions that were not reported in the literature before, and 2) total of individuals of a fly species representing 5% or less in a certain host bat species (Dick, 2007). These criteria resulted in the exclusion of 30 batfly individuals from our sampling. We obtained the specialization index measures (H'_2 and d') for the community and batfly species throughout the construction of a host-parasite interaction matrix. These matrices

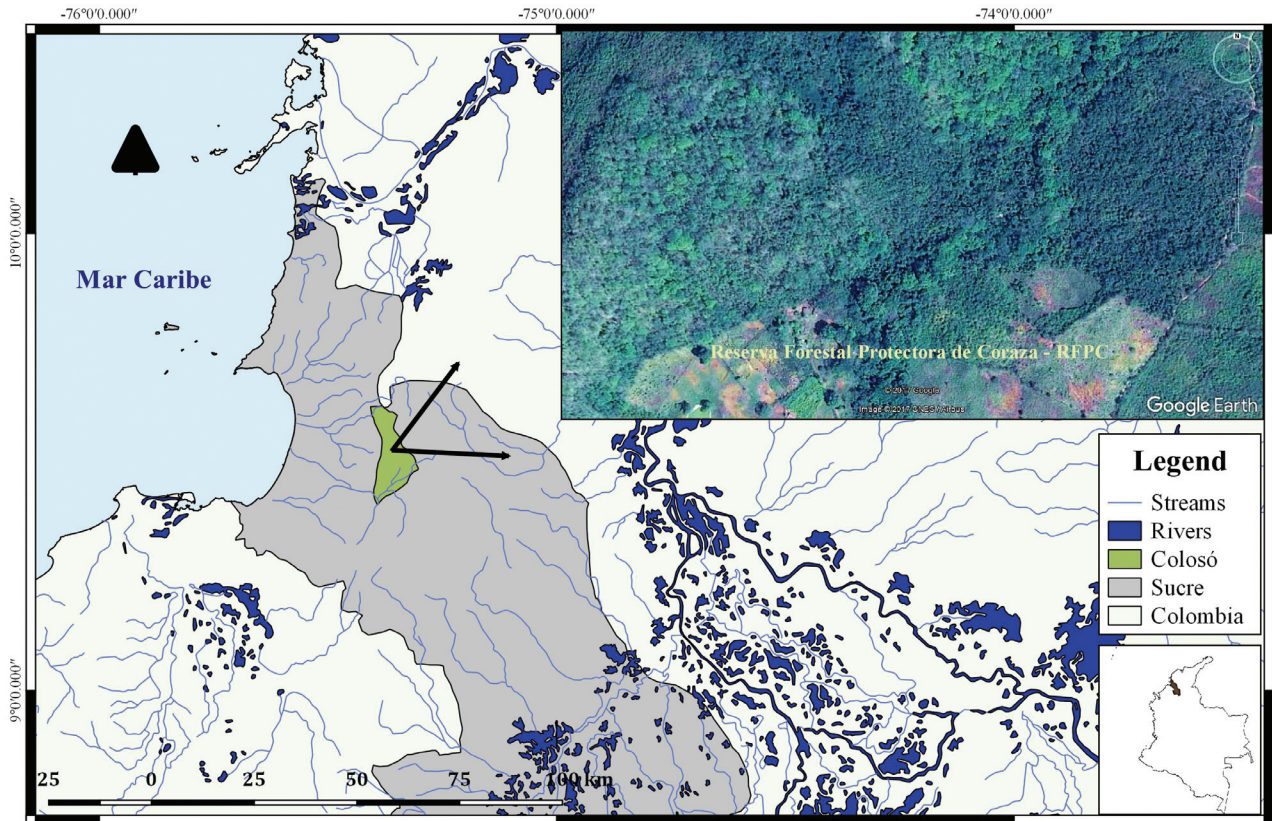


FIG. 1. Location of tropical dry forest in the Reserva Forestal Protectora de Coraza (RFPC), Sucre region, Colombia

contained the bat fly species observed in the rows and the hosts in the columns. Each cell contains the number of flies collected over each bat species observed. Values of H_2' and d' approaching 0 suggest low specialization or high redundancy of interactions in the network, while values approaching 1 suggest high specialization or low complementarity of interactions of the network (Blüthgen *et al.*, 2006). We calculated connectance with the C index, which represents the number of links observed between bats and their ectoparasitic flies considering all potential interactions (rows \times columns) (Blüthgen *et al.*, 2006). C index values closer to 1, imply more connectance in the network. We calculated network modularity using QuanBiMo (Q) algorithm (Dormann and Strauss, 2014). This algorithm creates 10^6 permutations of the network, obtaining a Q value for each permutation. Q indicates the modularity level of the network. Due to the heuristic nature of the algorithm, the result can vary in each run, therefore, the maximum value of 50 different runs was obtained (Q observed) (Carstensen *et al.*, 2016). The network graphics were made using the 'plotweb' and the 'plotModuleWeb' function of the Bipartite package, 2.02 version for R software 3.2 version (Dormann *et al.*, 2008; R Core Team, 2014).

To evaluate the significance of the Q observed value of our network we compared it with the averages of Q values obtained of 100 permutations (from null models) which we called (Qnull). Next, to evaluate if there was a significantly difference between the Q observed and Qnull values, we obtained the ZQ value [$ZQ = (Q_{\text{observed}} - \text{mean of } Q_{\text{null}}) / \text{SD}Q_{\text{null}}$]. Z-values greater than 1.96 indicate that there are differences with the null model (Carstensen *et al.*, 2016). In addition, we compared H_2' to the null model r2 table (Patefield, 1981). This creates new

interaction matrices without modifying the size of the matrix and the number of links, only changing the distribution of the interactions, which is more appropriate to evaluate the differences between the said matrices, using the P -value. A $P \leq 0.05$ indicates statistically significant differences (Carstensen *et al.*, 2016).

RESULTS

The field work resulted in the capture of 105 bats, with only 45 individuals infected by ectoparasitic flies. These individuals represented 11 species, belonging to two bat families (Phyllostomidae, 10 species, and Noctilionidae, one species). In total we collected 270 flies belonging to nine species and six genera, from the family Streblidae. Twenty-nine fly bat associations were observed and 31.49 estimated by the Chao 1 index (Fig. 2). The completeness of the interactions was 92.08%, reaching the asymptote of the accumulation curve (Fig. 3).

The bat fly antagonist network had a low connectance ($C = 0.30$) and high specialization ($H_2' = 0.67$). In addition, we registered a high modularity ($Q = 0.7$), presenting five modules. The third and fifth modules were the tightest, *Strebla wiedemanni* Kolenati, 1856 — *Glyphonycteris daviesi* (Hill,

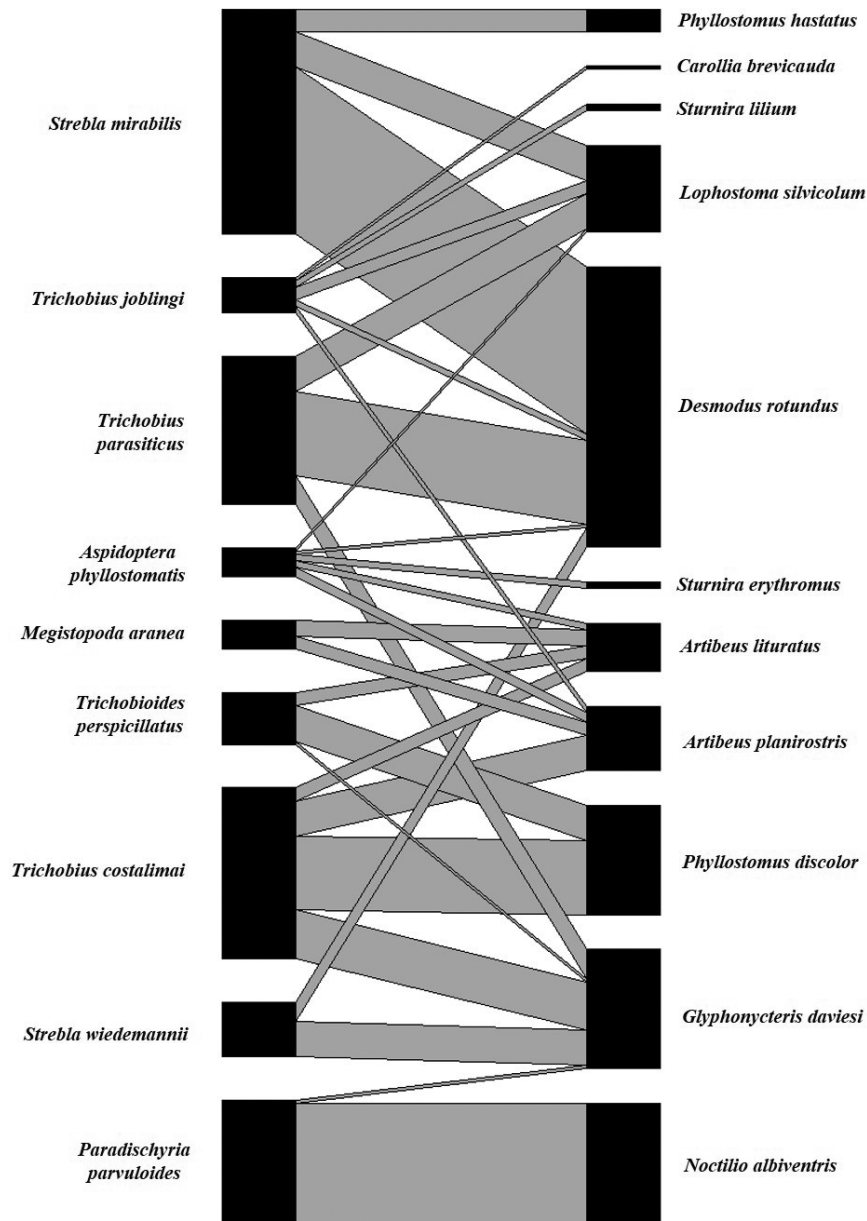


FIG. 2. Bat fly antagonistic network in a tropical dry forest in Colombia. Grey bars indicate the interaction between the two types of organisms (black bars); thickness indicates the strength of such interaction

1964) and *Paradyschiria parvuloides* Wenzel, 1966 — *Noctilio albiventris* Desmarest, 1818, respectively (Fig. 4).

Ectoparasite specialization to their hosts varied between ectoparasite species. *Paradyschiria parvuloides* obtained the highest value ($d = 0.95$), whereas *Trichobius parasiticus* Gervais, 1844 ($d = 0.32$) and *S. wiedemannii* ($d = 0.36$) had the lowest values (Table 1). Comparisons with null models showed differences ($Z = 25.7$; $Q_{\text{observed}} = 0.57$, $Q_{\text{null}} = 0.14$). Finally, the comparison between H_2 observed values and null model values, showed significant differences ($P < 0.01$ — Supplementary Fig. 1S).

DISCUSSION

Our results confirmed the hypothesis that specialization would be high in the bat fly antagonist network due to the low connectance of the host-parasite interactions. In this sense, Blüthgen *et al.* (2006) explain that the lower the connectance of a network, the greater its specialization. In this study, we found an important modularity (Q), driving the specificity of the flies to their host. In other words, the nodes (species) of the bat fly network have reduced connections among them, because they form specific modules (Fig. 4). *Paradyschiria*

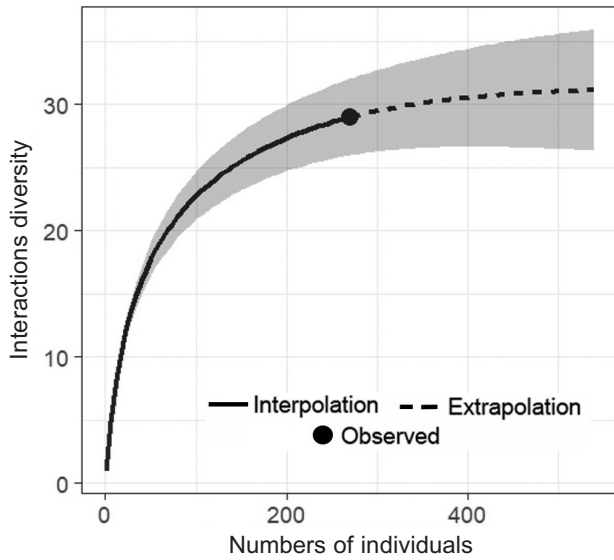


FIG. 3. Accumulation curve of the interactions in the network generated in the study area

parvuloides is a host-specific parasite of the Noctilionidae family (Wenzel, 1976; Guerrero, 1997; Dick and Gettinger, 2005), which would explain the high specialization value found to this species ($d = 0.95$ — see Table 1). The preference of bat flies for certain hosts generates a high modularity ($Q = 0.57$), resulting in groups of interaction more connected within modules (Fig. 4 — Poulin, 2010; Carstensen *et al.*, 2016).

The high specialization of flies in Neotropical bats (Wenzel, 1976; Dick, 2007; Vasconcelos *et al.*, 2016) has been commonly attributed to characteristics of both the host and ectoparasite flies. Bats influence the parasitic parameters of flies by the type of roost used and the time over which it is used, as well as the size and reproductive condition of the infected bat, among other factors (Patterson *et al.*, 2007). Meanwhile, the morphology of the flies (i.e. the size of legs, wings and body size) influences the body parts where they could be found on the bat, (Hofstede *et al.*, 2004; Dick and Patterson, 2007; Presley and Willig, 2008; Dick *et al.*, 2009; Hiller *et al.*, 2018). These factors influence the specificity of the fly to the host and affect the specialization observed in a parasite-host ecological network (Dick and Patterson, 2007; Dick *et al.*, 2009). Studies on antagonistic bat fly interaction networks have shown very specialized associations (Zarazúa-Carvajal *et al.*, 2016; Durán *et al.*, 2017; Fagundes *et al.*, 2017), where certain species of flies have preferences for particular bat species. The monoxenous associations result in high values of the d' index (Table 1 and Fig. 2), therefore, many

monoxenous associations result in a very specialized network (Blüthgen *et al.*, 2006).

Some authors, including Marshall (1976, 1982) and Wenzel *et al.* (1966), suggest that the mobility of the flies can be an important factor in specificity. Those parasites with less mobility are less able to find a different host species to colonize, unlike those that have greater mobility. Nevertheless, ter Hofstede *et al.* (2004) did not find evidence that support these explanations, whereas Komeno and Linhares (1999) affirmed that the inter-specific competition can be a factor that influences the parasite-host specificity in bats and flies. In this study, six species of flies have developed wings (used for flight) and they had lower d' values (0.3–0.6) compared with the single apterous species (*P. parvuloides*, $d' = 0.95$). These observations match the hypothesis that bat flies mobility contribute to the specialization of bat flies, suggested by Marshall (1976, 1982) and Wenzel *et al.* (1966). However, species with undeveloped wings, but with long legs, such as *Megistopoda aranea*, present high values of specialization ($d' = 0.60$), therefore, we suggest that mobility is not the main factor that explains the specialization of flies over their bat hosts.

Even so, ecological determinants of specificity to the host are difficult to isolate and it can include local climate conditions and geographic climate range experienced by the host or body mass (Krasnov *et al.*, 2004, 2005; Patterson *et al.*, 2008; Zarazúa-Carvajal *et al.*, 2016). Although the influence of the host body mass over the parasitism of batflies was not evaluated (due to the low number of individuals per species), a tendency can be observed, where larger bats (> 50 g, i.e. *Artibeus planirostris*, *A. lituratus*, *Desmodus rotundus*) have more associations with flies, compared with smaller species such as *Carollia* and *Sturnira* spp. This pattern was found by Patterson *et al.* (2008), where

TABLE 1. Specialization index of species (d) registered on the ectoparasite bat flies in the study area

Ectoparasite	Specialization index (d)
<i>Aspidoptera phyllostomatis</i>	0.41
<i>Megistopoda aranea</i>	0.60
<i>Paradyschiria parvuloides</i>	0.95
<i>Strebla mirabilis</i>	0.60
<i>S. wiedemannii</i>	0.36
<i>Trichobius perspicillata</i>	0.52
<i>T. costalimai</i>	0.59
<i>T. joblingi</i>	0.42
<i>T. parasiticus</i>	0.32

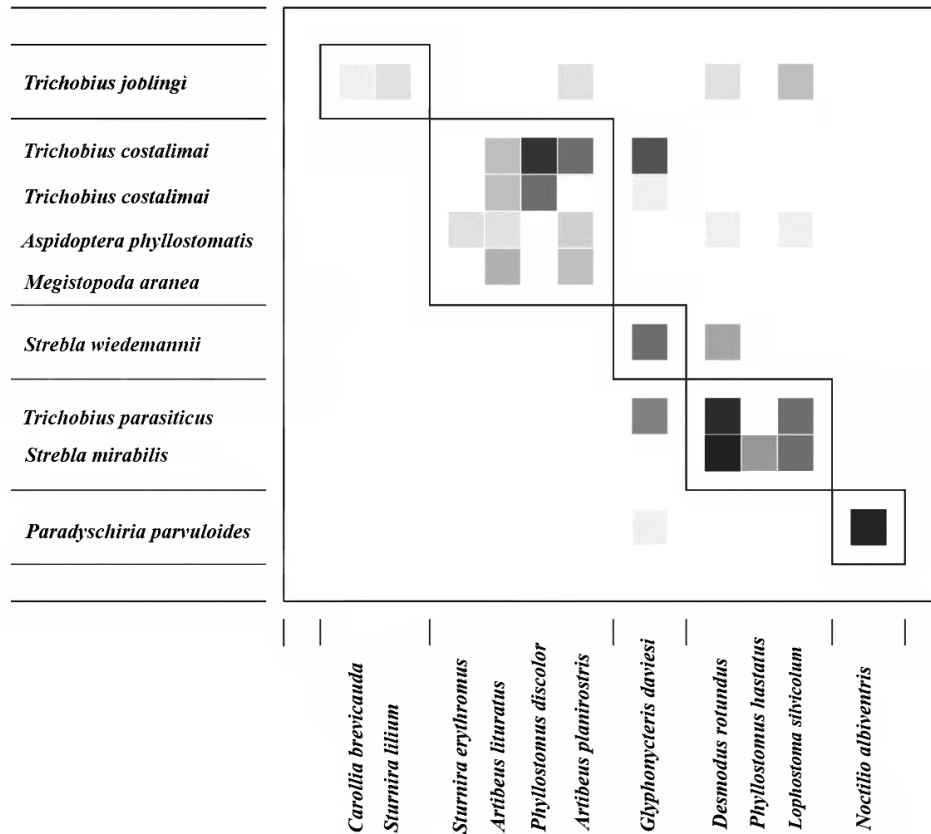


FIG. 4. Representation of the modules generated for the bat fly antagonist network in the study area. The intensity in the colors indicates the strength of the interaction, due to the number of individuals associated in said interaction

larger bats such as *A. lituratus*, *Lophostoma silvicolum* and *A. planirostris* had more than four associations with flies, in contrast to smaller bats (< 25 g), such as *Sturnira lilium*, *Carollia brevicauda*, *Sturnira erythromus* and *N. albiventris*, which did not present on more than one association.

Modularity is intrinsically related to the batfly-bat specificity (Dormann and Strauss, 2014; Fagundes *et al.*, 2017). As can be seen in Fig. 4, five modules were found, three of which show great strength in the interaction and therefore high specificity, which most likely influences the high Q value reported in this study ($Q = 0.70$). Fagundes *et al.* (2017) suggests that modularity in bat fly interactions is explained by the similarity of the type of refuge used by the bat species that make up each module. Although the type of refuge was not considered in the present study, according to the literature, it can be established that, in the larger module (*A. planirostris*, *A. lituratus*, *S. erythromus*, and *Phyllostomus discolor* — Fig. 4), bats use the same type of refuge, tree holes (Muñoz, 2001; Oprea *et al.*, 2006; Gardner, 2007), while in the second module in size (*D. rotundus*, *Phyllostomus hastatus*, *L. silvicolum*), bats use caves as their main type of

shelter (Greenhall *et al.*, 1983; Santos *et al.*, 2003; Kalko *et al.*, 2006).

The null models, on the other hand, are important tools to determine if there is randomness in the process that generates some ecological patterns (Vilchis, 2000; Dormann and Strauss, 2014). To be precise, they serve to evaluate if the observed data, compared to hypothetical data, is caused or not, by ecological and evolutionary events. According to this, we compared modularity Q and specialization H_2^2 values of the network and found that observed values are different to those reported by the null models. This corroborates our explanations that the network metrics generated are non-random, but rather explained by ecological process between the parts involved (Dick, 2007; Poulin, 2010; Presley *et al.*, 2015) and probably influenced by external factors, such as biogeographical and environmental aspects. In conclusion, this study confirmed the hypothesis regarding higher specialization in the bat fly antagonist network, given the low connectance of their interactions. Furthermore it contributes new observations that suggest that bat fly mobility and host roost associations promote the specialization of bat fly antagonist networks.

SUPPLEMENTARY INFORMATION

Contents: Table S1. Interaction matrix of fly-bat associations in a tropical dry forest in northern Colombia. Fig. S1. Plot of randomized H_2' values (null models) with H_2' observed. Supplementary Information is available exclusively on BioOne.

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