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IMMUNOLOGY AND HOST-PARASITE INTERACTIONS - ORIGINAL PAPER

Host ecology moderates the specialization of Neotropical bat-fly interaction networks

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Abstract

The transmission of diseases through parasites is a key mechanism in the regulation of plant and animal populations in ecosystems. Therefore, it is necessary to investigate the relative effect of the variables that can shape the specificity of host-parasite interactions. Previous studies have found that specialization of antagonistic interactions between fly ectoparasites and bats changes according to forest type, host richness, and roosting ecology of bats. In this study, we tested these hypotheses using data from 48 bat communities. In general, our results support previous findings that bat-fly interactions are specialized, resulting in lower niche overlap among bat flies species. In addition, we found that the specificity of bat-fly interactions is lower in tropical mountain forests and is positively related with the richness of bat host species of each study site. Finally, there was a higher bat flies niche overlap in smaller bat-fly interaction networks recorded in bat roosts in caves. We conclude that the roosting ecology of bats could be a key factor to understand the mechanisms related to the horizontal transmission of ectoparasitic flies among bats.

Keywords Chiroptera · Ecological networks · Ecoregions · Neotropics · Streblidae

Introduction

The study of the specificity of parasite-host interactions is fundamental to understand the mechanisms behind parasitism and, therefore, the biodiversity-functioning relationship (Frainer et al. 2018), since parasites play an important role in the regulation of populations and species-host assemblages (Krasnov et al. 2006). It has been largely documented that parasitic species are not randomly distributed among their hosts (Fontaine et al. 2011; Poulin 1996; Poulin 2007) but show a positive relationship between the richness of host species and the richness of parasitic species in a studied community (Krasnov et al. 2006; Poulin 2007). This suggests a higher specialization and diversification of parasites related to host richness, and that there are limiting factors in the structure of parasite-host associations.

The limiting factors in parasite-host interactions are host ecology and parasite ecology. From the perspective of host ecology, it has been shown that the turnover of host species, promoted by climatic and vegetation variation, affects the richness and the specificity of parasite-host interactions (Barbier and Bernard 2017; Rivera-García et al. 2017; Zarazúa-Carbajal et al. 2016). In the case of parasite ecology, the "encounter filter" hypothesis explains the specificity of parasite-host interactions (Marshall 1976; Combes 1991). The encounter filter hypothesis proposes that parasites cannot encounter and colonize potential hosts due to behavioral or ecological factors related with the host (Dick and Patterson 2006). Therefore, we could expect that when host behavior

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increases encounters with host species, the specialization of parasite-host interactions could decrease.

Bats and their parasitic flies (Diptera: Streblidae) in Neotropical forests are a good biological model to evaluate the limiting factors that shape the specificity of parasite-host interactions. Bat flies are obligate blood sucking ectoparasites that occupy the fur and flight membranes of bats (Dick and Patterson 2006). Like other dipterans, they are holometabolous and must metamorphose to complete their development. Pupation takes place off the host in the bat roosts and lasts a few weeks. Emergent flies generally need to find a particular bat species within a few hours after pupation in order to survive (Patterson et al. 2007). Therefore, bat flies are highly host-specific, with most species parasitizing from one to four bat species (Krasnov et al. 2006).

The objective of this study was to evaluate the effect of host ecology on the specialization of bat-fly interactions. We predicted that bat-fly interactions in temperate vegetation types would have a lower degree of specialization, since previous studies have documented that bat species richness is reduced in temperate forests, thus promoting a higher niche overlap of bat flies species (de Carvalho et al. 2019; Patterson et al. 1996). In addition, we expected bat community richness to be related to the specificity of bat-fly interactions because one bat species is infected at least by one specific fly species (Fonseca de Vasconcelos et al. 2015). Finally, we expected that bat flies niche overlap in bat roosts in caves would be higher, since bat flies increase their probability of encountering and colonizing new hosts compared with bat-fly interactions observed in forests (Rivera-García et al. 2017).

Materials and methods

Literature review

From November 2018 to February 2019, we conducted an extensive review of available literature related to Neotropical bat-fly interactions through Google Scholar and Web of Science™. The list of sources was supplemented with studies cited in reference lists of the surveyed articles. The keywords used were "bats", "streblidae", "ectoparasites", "bat flies", "bat-fly", "murciélagos", "ectoparásitos", "moscas de murciélagos", "morcegos", "moscas de morcegos", and "parasitas de morcegos". We restricted these terms to appear only in the title of the article when we used Google Scholar. In Web of Science™, "bats" was restricted to appear only in the title, and "streblidae", "ectoparasites", "bat flies", and "bat-fly" in the topic of the paper. We did not limit the search by year of publication. We only selected studies that contained detailed data about: (1) bat flies species or morphospecies, (2) bat host species, (3) the number of bat flies collected on each bat host species, (4) geographical coordinates of the study site(s), and (5) reports of total bat species richness independent of bat species infected with ectoparasites.

Bat-fly interaction matrices and calculation of their degree of specialization

As a result of the literature search, a total of 48 studies that presented useful data were obtained (see Supplementary Material 1). We added a bat-fly interaction matrix that was not published previously. The data used were taken from a study by Saldaña-Vázquez et al. (2013). Matrices of quantitative bat-fly interactions were constructed for each bat community. In these matrices, bat species were placed in rows and bat flies species or morphospecies in columns (see Supplementary Material 2). In each cell, the frequency of the observed interactions was noted. "Frequency" refers to the total number of bat flies collected on each bat host species.

In order to determine the degree of specialization for each interaction matrix, the complementary specialization (H_2') and the niche overlap (NO) indexes were used (Dormann et al. 2009; Blüthgen 2010). Both indexes are ideal for evaluating niche overlap or redundancy of interactions within a community. H_2' describes the deviation of a species' realized number of interactions from a completely neutral configuration of interactions (Dormann et al. 2009; Blüthgen 2010). The NO index calculates the mean similarity of interaction patterns between species of the same trophic level (Dormann et al. 2009). Values for both indexes range from 0 to 1. In H_2', values close to 0 indicate a lower degree of specialization in an interaction, and 1 indicates a higher degree of specialization (Blüthgen 2010). In NO, values close to 0 indicate that there is no niche overlap, and 1 indicates complete niche overlap in the same trophic level (Dormann et al. 2009). The calculation of the H_2' and NO indexes was performed using the "network level" and the "group level" functions of the bipartite package in R (Dormann et al. 2009). There are two factors that can affect the values of both indexes. The first one is the reliability of the observed interaction, and the second one is the sensitivity of H_2' and NO to network size and interaction sampling intensity, respectively. Network size is defined as the number of species in both levels of the interaction matrix, while sampling intensity is defined as the number of interactions observed in the whole interaction matrix (Dormann et al. 2009; Henriksen et al. 2019).

To deal with both possible effects, we first evaluated the statistical significance of H_2' and NO calculated in each interaction matrix by testing whether it could be explained solely by chance. The shuffle of the interaction matrix was done using a null model designed to change cell values while keeping row and column sums constant. This null model is named "r2dtable" (Dormann et al. 2009). After each shuffle, H_2' and NO were measured, and this procedure was repeated 1000 times using the bipartite package for R (Dormann et al. 2009). To then evaluate if there was a significant difference between the observed index values and the calculated null values, we obtained the Z value in the following way: Z = observed index matrix value − mean null index value / standard deviation of null values. Z values greater than 1.96 indicate that there are differences with the null model (Durán et al.2018). We found that all H_2' and NO values observed in each interaction matrix were different by chance (Supplemental Material 3). In order to test the possible effect of network size and sampling intensity on both calculated indexes, we performed a Spearman correlation (rS) analysis between both indexes and network size and sampling interaction intensity, and found that only network size was negatively correlated with bat flies NO ($r\text{S} = -0.62$, $P < 0.001$, Fig. 1, Supplemental Material 3). Therefore, network size was used as another predictor variable in the bat flies NO index variation analysis.

Obtaining specialization predictor variables

From each study, we recorded the vegetation type, the host richness, and the site (cave or forest) where bat-fly interactions were observed. In order to evaluate the hypothesis that these variables explain the variation in the specialization of bat-fly interactions, the vegetation of each studied community was assessed using the geographical coordinates of each study and matching them with the global ecological zones of FAO (2012). When studies did not report geographical coordinates, study locations were used to search coordinates in Google Earth version 7.3.0.3830. If a location presented more than one point of collection for bats and flies, a unique coordinate was obtained from a geographical centroid of the sampling sites. These coordinates were calculated on QGis Desktop version 2.10.1-Pisa, using the vector geoprocessing tools-convex Hull to generate the polygon and then calculating the centroid using the vector Geometry tools-polygon centroids. Host richness and the site where bat-fly interactions were observed (cave or forest) in each study were obtained from the "Results and Methods" sections of each paper.

Data analysis

To evaluate the effect of vegetation type, host species richness, and site where bat-fly interactions were observed (cave or forest) on H_2' and bat flies NO, two generalized linear models (GLM) were adjusted, respectively (Crawley 2007). The first model had the following syntax: $H_2' \sim$ vegetation + host species richness, family = quasibinomial. The second model had the syntax: bat flies NO ~ site + network size, family = quasibinomial. Finally, to test the significance of the variables adjusted to each model, a post hoc X^2 analysis for standardized coefficients was performed. All analyses were carried out using the "glm" and "anova" functions in R (R Core Team 2018).

Results

In general, the H_2' index of the 48 matrices was greater than 0.8 (Fig. 1a), indicating that specialization in the bat-fly interaction networks is high. On the other hand, the NO index of bat flies in all studies was lower than 0.3 (Fig. 1b), indicating a low niche overlap among bat flies.

Both host richness ($X^2 = 1.24$, d.f. = 1, $P < 0.001$) and vegetation type ($X^2 = 1.14$, d.f. = 7, $P = 0.037$) had a significant effect on H_2' specialization index. Host richness was positively related with the H_2' specialization (Fig. 2), while the

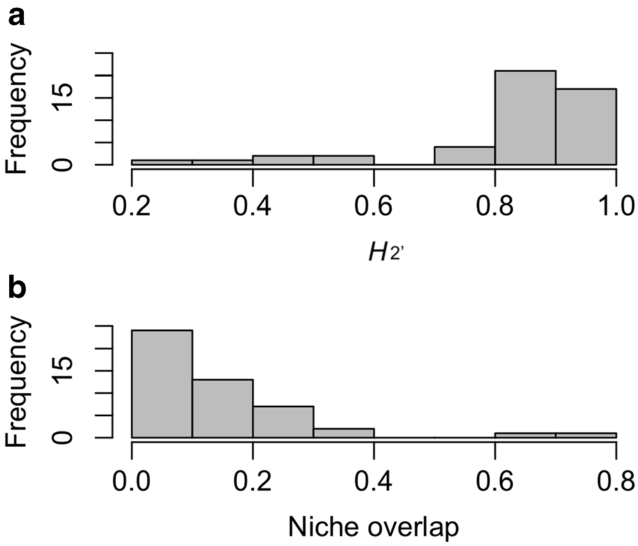

Fig. 1 Histograms of the frequency of values of the H_2' (**a**) and NO (**b**) indexes observed in 48 Neotropical bat-fly interaction networks

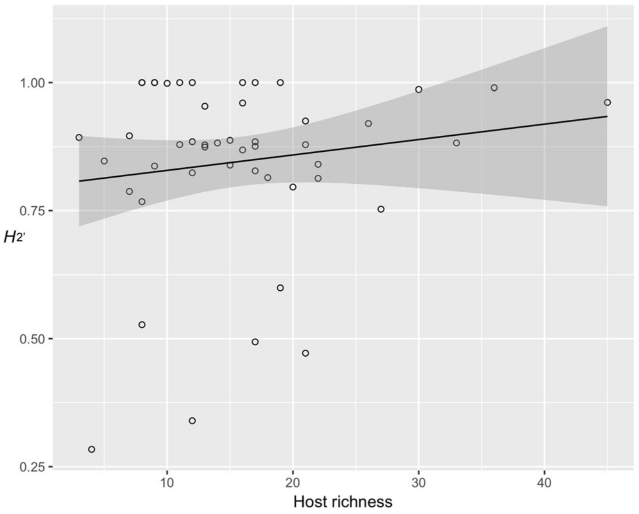

Fig. 2 Relationship between host richness observed in each bat community and the H_2' specialization index of bat-fly interactions. The black line represents the predicted values according to the adjusted GLM and the gray shadow is the standard error of the predicted values

vegetation type with the lowest H_2' specialization index value was the tropical mountain system (Table 1).

Finally, the variation of bat flies NO was significantly associated with sites where bat-fly interactions were observed ($X^2 = 1.79$, d.f. = 1, $P < 0.001$, Fig. 3a) and with network size ($X^2 = 1.29$, d.f. = 1, $P < 0.001$, Fig. 3b). The mean value of bat flies NO for bat-fly interactions in caves was 0.32, while for interactions recorded in forests, it was 0.11. The mean network size of bat-fly interactions in caves was 21 in caves and 26 in forests.

Discussion

Our research confirms the hypothesis that vegetation type and bat ecology predict the variation in the specialization of bat-fly interaction networks (Barbier and Bernard 2017; Patterson et al. 2007). Because bat-fly interactions in temperate forest had a reduced specialization and bat flies observed in bat roosts in caves had a higher niche overlap than those observed in forests. This suggests that ecology of bats is an important driver of horizontal transmission of bat flies.

Previous studies found that bat species that roost in caves had higher bat-fly specificity compared with bat species that roost in tree foliage, under and on rolled leaves (Patterson et al. 2007). It is important to note that the study by Patterson et al. (2007) was done using available literature on roost fidelity. In contrast, our data came from direct observations of cave roosts and using network ecology indexes. This explains the opposite pattern in our results compared with those of Patterson et al. (2007). Bat flies have been found to be able to change primary hosts in the absence of dispersal barriers (Dick et al. 2009). Therefore, the higher niche overlap observed in bat flies species from bats roosting in caves could be explained by bat flies in this site having a less limited dispersal to other hosts. Previous studies on bat-fly interaction specificity carried out in bat roosts in caves support this hypothesis (Rivera-García et al. 2017). When migrant bat species arrive at cave roosts, there is a reduction in the degree of specialization that results in a higher niche overlap of bat flies.

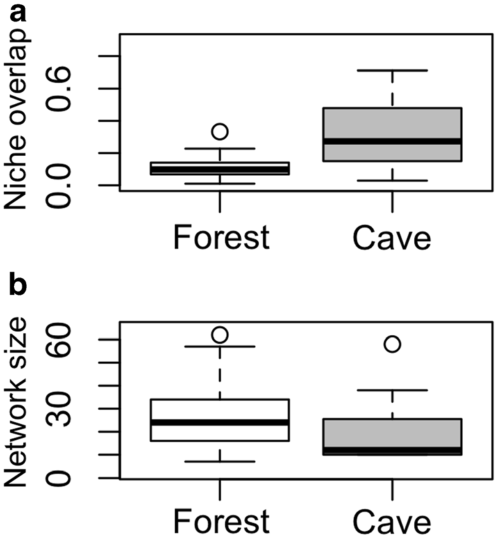

Fig. 3 Boxplots of the effect of the sites where bat-fly interactions were observed, cave (gray color) or forest (white color), on the bat flies NO index (**a**) and bat-fly interactions network size (**b**)

Another factor that promotes a higher niche overlap of bat flies species observed in bat roosts in caves is network size. It has been proposed, using null models of pollination interactions, that the niche overlap index is not sensitive to network size (Dormann et al. 2009). Our results do not support this hypothesis and emphasize the importance of being cautious when making generalizations about the behavior of ecological network indexes when using null models that do not take into account the ecology and natural history of the biological system (see Luna et al. 2017).

Finally, our study highlights the importance of two factors that have been poorly evaluated in the discussion of the specificity of bat-fly interactions: the environment and host community richness (but see Zarazúa-Carbajal et al.2016; Barbier and Bernard 2017). Tylianakis and Morris (2017) proposed that environmental conditions could promote species turnovers that had an effect on the structure of ecological networks. Our results support this hypothesis, since we observed a significant variation in the H_2' specialization network index related with the vegetation type and bat host richness of each studied

Table 1 Parameters obtained from the GLM adjusted for ecoregions; *t* and *P* correspond to values of the *t* test probe to compare the coefficients adjusted to the null model

Vegetation type	Coefficient estimate	Mean H_2' value	*t*	*P*
Subtropical mountain system	0.41	0.82	0.60	0.54
Subtropical steppe	0.07	0.85	0.09	0.92
Tropical dry forest	0.62	0.81	1.24	0.22
Tropical moist forest	0.27	0.84	0.62	0.53
Tropical moist forest—tropical rainforest	0.31	0.98	0.23	0.81
Tropical mountain system	1.67	0.61	2.94	0.005
Tropical rainforest	0.01	0.86	0.02	0.98

community. The vegetation type with less specialization was the tropical mountain system (H_2' mean = 0.61). This vegetation type was represented by two studies, one from Mexico and another from Brazil. Interestingly, the study from Mexico had the lowest H_2' value (0.33) and was obtained from bat-fly interactions observed in a bat roost in a cave. Therefore, the effect of vegetation type on the specialization of bat-fly networks should be treated with caution.

On the other hand, the observed bat host richness in each study was positively related with the H_2' specialization network index. This variable supports previous studies that found a relationship between bat host richness and bat fly richness (Barbier and Bernard 2017). Additionally, it agrees with the hypothesis that species richness has an effect on the structure of ecological networks (Tylianakis and Morris 2017). In conclusion, our study shows that bat-fly specificity is affected by the environment and host ecology, and emphasizes the importance of bat roost ecology as a key mechanism of ecological responses in bat-fly interactions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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