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Hosts and environment overshadow spatial distance as drivers of bat fly species composition in the Neotropics

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Abstract

Aim: Determine the relative influence of geographical distance, environmental differences, and host species composition on the similarity of bat fly species composition.

Location: Neotropics.

Taxon: Bats (Chiroptera: Phyllostomidae) and bat flies (Diptera: Streblidae).

Methods: Abundance data on bats and ectoparasites were obtained from published studies. The relative influences of environmental variation (annual precipitation, temperature seasonality, elevation, and NDVI), host species composition, and geographic distance on parasite community composition were analysed with Generalized Dissimilarity Modelling and variance partitioning. Additionally, we evaluated the influence of these environmental variables and geographic distance on host species composition.

Results: Our model explains 45.3% of the variance in the dissimilarity of bat fly species. Host species composition had the most significant influence on bat fly species composition across communities, followed by environmental effects. Variance partitioning showed that host species composition explained 14.9% and environmental characteristics explained 10.3% of the variance in bat fly species dissimilarity. Geographical distance alone had a negligible effect as it accounted for only 0.007% of the variance in bat fly species composition. Host species composition was mainly influenced by geographic distance (18.0%) and secondarily by environmental variables (9.8%). The most important environmental variables influencing parasite and host species composition were annual precipitation and temperature seasonality, respectively.

Main Conclusions: The lack of relationship between geographical distance and bat fly species composition may reflect either the high mobility or the high dispersal capacity of bat flies, or a combination of these. Alternatively, it could reflect a taxonomic artefact. Environmental differences seem to directly affect bat flies, as opposed to affecting them indirectly through their impact on the hosts. Our results support the fundamental role that host species composition plays in determining the species composition of highly host-specific parasites. However, we argue that host specificity is not the only trait impacting ectoparasite species composition.

KEYWORDS

biogeography, host-parasite interactions, Neotropical, Phyllostomidae, species composition, Streblidae

1 | INTRODUCTION

One of the main goals of community ecology is to determine which factors influence spatial community structure, i.e. the changes in species composition from one local community to the next. Several studies have demonstrated the importance of geographical distance and the biotic interactions between organisms as factors explaining similarity in species composition (Krasnov, Mouillot, Shenbrot, Khokhlova, & Poulin, 2010; Nekola & White, 1999; Varzinczak, Lima, Moura, & Passos, 2018). Notwithstanding, the importance of each of these variables and the strength of their relationships with species similarity vary depending on the region of the world and the groups of organisms studied (Chen, Jiang, Zhang, Li, & Qian, 2011; Poulin, 2003).

One strong pattern in community ecology is the effect of distance decay, i.e. the decrease in the similarity of species composition with increasing geographical distance between communities (Nekola & White, 1999; Poulin, 2003; Soininen, McDonald, & Hillebrand, 2007). Even though this relation looks simple and obvious, it raises important issues regarding the ecology and evolution of organisms. From an ecological point of view, the decrease in species similarity with increasing geographical distance reflects differences in the overall responses of species to different environmental conditions and resources (Fischer et al., 2018; Tuomisto, 2003). From an evolutionary perspective, increasing physical distances between communities could also increase the chance for new geographical barriers to occur, limiting the dispersal of organisms and causing the observed patterns (Nekola & White, 1999). These structuring phenomena form the basis of Hubbell's (2001) neutral theory of biodiversity.

As a rule, organisms usually thrive within their optimal range of suitable environmental conditions (Sunday, Bates, & Dulvy, 2011). Therefore, extreme environmental conditions can limit the distribution of some species (McCain, 2007). For instance, Neotropical bats are known to be poor thermoregulators, which can restrict some species to low elevations (Graham, 1983; Studier & Wilson, 1970). In a large-scale study on gamasid mites parasitic on rodents in the Palaearctic region, Vinarski, Korallo, Krasnov, Shenbrot, and Poulin (2007) found that environmental conditions were the most important factor impacting their community structures. Gamasids appear more sensitive to climatic conditions, such as temperature and humidity, than to the host species they exploit, which could explain the observed distribution patterns (Vinarski et al., 2007).

Resource availability is another major force driving the survival of organisms (Arlettaz, Christe, & Schaub, 2017), with hosts representing food sources in the case of parasites. For example, *Megistopoda aranea* (Diptera: Streblidae) is a highly host-specific ectoparasite on the bat *Artibeus jamaicensis* in Panama (Wenzel, Tipton, & Kiewlicz, 1966). This parasitic fly can only survive a few hours when attached to another bat species or without a host (Overal, 1980). In this light, one could expect that spatial community structures of highly host-specific parasites are driven by the similarities in host species composition. However, the only study exploring this relationship found that the species composition of fleas parasitic on small mammals from the Palaearctic was influenced mainly by environmental variables (Krasnov, Mouillot, Shenbrot, Khokhlova, & Poulin, 2010). In this flea-mammal system, a large part of the parasite's life cycle is spent off the host, which may explain the strong influence of the environment on flea community composition (Krasnov, Khokhlova, Fielden, & Burdelova, 2001; Krasnov, Mouillot, Shenbrot, Khokhlova, & Poulin, 2010). It is also surprising that the effects of host species composition on ectoparasite species composition have been stronger in systems where parasites are not host-specific (Krasnov et al., 2010; Maestri, Shenbrot, & Krasnov, 2017; Vinarski et al., 2007). Actually, the lack of studies on compound communities (i.e., the assemblage of parasites in a host community) of ectoparasites does not allow us to conclude to any general pattern of parasite species composition across larger geographical scales.

Flies in the family Streblidae are exclusively ectoparasitic on bats. They are distributed worldwide, but the tropical western hemisphere harbours the highest species diversity (Dick & Patterson, 2006). Most streblid species occur on bats from the family Phyllostomidae, the New World family of leaf-nosed bats (Dick & Patterson, 2006). One of the main characteristics of bat flies is their high host specificity. Controlled surveys in Paraguay showed 87% of the species associated with a single bat species, with most bat fly individuals on their primary host (Dick & Gettinger, 2005). The life cycle of bat flies occurs almost entirely on the host, except for pupae, which are deposited directly by females on the walls of bat roosts (Dick & Patterson, 2006). After pupation, the newly emerged adult fly needs to rapidly find a host to parasitise. Because of this characteristic, bat roosts can play a significant role in bat fly abundance (ter Hofstede & Fenton, 2005; Vieira et al., 2019). Bat species living in permanent roosts, such as caves, carry larger numbers of bat flies than bat species using ephemeral roosts, e.g. leaf tents (Patterson, Dick, & Dittmar, 2007). Despite the well-known effect of bat roost type on bat fly abundance, the potential environmental effects are still debated (Barbier, Graciolli, & Bernard, 2019). Temperature and precipitation were positively related with bat fly abundance in Venezuela (Pilosof, Dick, Korine, Patterson, & Krasnov, 2012), and seasonality affected bat fly species composition in Mexico (Zarazúa-Carbajal, Saldaña-Vázquez, Sandoval-Ruiz, Stoner, & Benitez-Malvido, 2016). In contrast, in northeast Brazil, Barbier et al. (2019) did not find any relationship between rainfall and bat fly abundance across bat species.

In this study, we ask whether dissimilarity in host species composition, differences in environmental factors, and geographical distance influence the dissimilarity of bat fly species composition across distinct localities in the Neotropics. Since bat flies are highly host-specific and spend most of their lives on the host, we expect that the dissimilarity of bat species composition will explain most of the variation in the dissimilarity of bat fly species composition. Even though the effect of geographical distance on community structure is well established (Soininen et al., 2007), we do not expect a large effect from this variable, since it does not seem to exert a great influence on the species composition of Phyllostomidae (López-González, Presley, Lozano, Stevens,

& Higgins, 2015; Varzinczak et al., 2018). Finally, the role of environmental variables in bat fly species composition is not easy to predict due to inconsistent findings in the current literature. Nonetheless, since part of the bat fly life cycle occurs off the host (i.e., the pupal stage), we expect to find some direct effect from environmental variables.

2 | MATERIALS AND METHODS

2.1 | Data collection

We obtained all data from papers published until April 2019. Literature searches were carried out in the SciELO and Web of Science databases using the following terms: (bat OR morcego OR murciélago OR chiroptera) AND (ectoparasites OR ectoparasitas OR ectoparasitos OR “bat fly” OR “bat flies” OR Streblidae). Furthermore, we searched articles in the regional journal *Chiroptera Neotropical*, which specialises in publishing studies on Neotropical bats (this journal is not indexed in either of the above databases). Only papers that provided information on the abundance of bat flies (number of individuals of each fly species recovered from all bats sampled), the abundance of bats (number of individuals from each bat species recorded during sampling), and the geographical location were retained for the analysis. Some of the studies collected data for more than one locality. For these, sampling units were merged into a single one if the localities were separated by less than 10 kilometres from each other; in such cases, the central geographical position was used as the reference point of the sampling unit. We only considered studies covering all seasons that used mist-netting to sample bat communities, followed by careful removal of bat flies from each individual host caught. In addition, we computed Chao1 indices to estimate bat and ectoparasite richness for each locality, and disregarded those with a number of observed species lower than 70% of that estimated by Chao1. In the end, 26 sampling units were selected for subsequent analyses (Table 1, Figure 1; Appendix 3.2 and 3.3 in Appendix S3).

We followed the American Society of Mammalogists’ Mammal Diversity Database (2019) and Dick and Graciolli (2018) for the accepted species names of bats and bat flies, respectively, with the following corrections or exceptions. *Sturnira lilium* and *Carollia brevicauda* from Belize (ter Hofstede et al., 2004) were changed to *Sturnira parvidens* and *Carollia sowelli*, respectively (Baker, Hoffmann, & Solari, 2002; Velazco & Patterson, 2013). In the case of bats assigned as *S. lilium* in Colombia (Durán de la Ossa, Álvarez García, & Graciolli, 2017; Tarquino-Carbonell et al., 2015) and northern Brazil (Santos et al., 2009; Santos et al., 2012), we did not change the identity since there are more than one possible species in these locales (Velazco & Patterson, 2013). *Platyrrhinus helleri* in the Brazilian Amazon and northern Colombia (Durán de la Ossa et al., 2017; Santos et al., 2012) were changed to *P. incarum* (Velazco & Patterson, 2008). *Artibeus phaeotis* and *A. toltecus* (Zarazúa-Carbajal et al., 2016) were changed to *Dermanura phaeotis* and *D. tolteca*, respectively (Hoofer, Solari, Larsen, Bradley, & Baker, 2008). Finally, *Lophostoma silvicola* was corrected to *L. silvicolum* (Barbier & Graciolli, 2016; Simmons, 2005). For bat flies, we considered *Strebla carolliae* as a synonym of *S. guajiro* (Wenzel, 1976; Zarazúa-Carbajal et al., 2016) and maintained *Strebla harderi* found on the bat *Anoura caudifer*, though it could be identified as *S. carvalhoi* (Graciolli, 2003).

2.2 | Environmental variables

Because the effect of environmental variables on bat fly species composition is not well known, we did a preliminary analysis with bioclimatic variables alone. We used a generalised dissimilarity model (GDM, see below) including all 19 bioclimatic variables provided by WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) as explanatory variables and bat fly species composition as the response variable. Then, we selected the bioclimatic variables with variable importance values ≥1 (Table S1 in Appendix S1). This value indicates the percentage change in deviance explained by the full model and the deviance explained by a model fit with the permutated variable in question. After this procedure, five bioclimatic variables were selected (isothermality, temperature seasonality, minimum temperature of the coldest month, annual precipitation, and precipitation of the wettest quarter). Additionally, we included elevation and the maximum and minimum values of the normalised difference vegetation index (NDVI), totalising eight environmental variables. Afterwards, all variables were correlated and those that showed a correlation greater than 0.7 were excluded from the analysis (Dormann et al., 2013; Figure S1 in Appendix S1). This gave us a subset of five environmental variables suspected to affect bat flies (Frank, Mendenhall, Judson, Daily, & Hadly, 2016; Rivera-García, Sandoval-Ruiz, Saldaña-Vázquez, & Schondube, 2017; Zarazúa-Carbajal et al., 2016)—temperature seasonality, annual precipitation, elevation, and maximum and minimum values of the NDVI (Appendix 3.1 in Appendix S3). All environmental variables were scaled to have a mean of 0 and a standard deviation of 1 before the analyses.

Data on elevation were obtained from the 250-m resolution shuttle radar topography mission (SRTM) map, downloaded from CGIAR's Consortium for Spatial Information (srtm.csi.cgiar.org, accessed on 28 September 2018). The maximum and minimum values of NDVI were specifically obtained for the sampling periods provided in each paper. The NDVI values were provided by the vegetation index and phenology (VIP) tool (version VIP15.004; Didan & Barreto, 2016) for studies published before 2015, and obtained from the MODIS/Terra Vegetation Indices 13C1 (version 006; Didan, 2015) for the remaining studies. Both collections were provided twice monthly at a 0.05-degree (5,600 metres) spatial resolution in a geographical (latitude and longitude) grid format. We downloaded these data from the Land Processes Distributed Active Archive Center on the United States Geological Survey website, from the National Aeronautics and Space Administration (https://lpdaac.usgs.gov/, accessed on 25 May 2019), and extracted variables from the maps using the packages 'raster' (Hijmans & van Etten, 2019) and 'rgdal' (Bivand, Keitt, & Rowlingson, 2019) in software R version 3.6.0 (R Core Team, 2019).

TABLE 1 Number of species and individuals (Ind) of Streblidae bat flies and Phyllostomidae bats from the selected studies in 30 localities. Asterisks indicate studies removed from the final analyses as their numbers of observed species were lower than 70% of those expected through Chao1 estimates

Sample	Reference	Streblidae species (Ind)	Phyllostomidae species (Ind)
1	Zarazúa-Carbajal et al. (2016)	20 (201)	9 (120)
2	ter Hofstede et al. (2004)	20 (548)	14 (385)
3*	Durán de la Ossa et al. (2017)	17 (260)	14 (78)
4	Tarquino-Carbonell et al. (2015)	11 (172)	8 (107)
5	Santos et al. (2009)	15 (192)	9 (158)
6	Soares et al. (2013)	15 (351)	10 (281)
7	Barbier et al. (2019)	14(325)	7(190)
8	Barbier et al. (2019)	23(1,995)	12(618)
9*	Santos et al. (2012)	8(79)	7(51)
10	Soares, Rocha, Mikalauskas, Graciolli, and Ferrari (2017)	14 (252)	10 (243)
11	Bezerra, Vasconcelos, and Bocchiglieri (2016)	7 (129)	5 (101)
12	Bezerra and Bocchiglieri (2018)	13 (260)	11 (486)
13	Rios, Sá-Neto, and Graciolli (2008)	2 (100)	3 (36)
14*	Komeno and Linhares (1999)	10 (156)	7 (172)
15	Azevedo and Linardi (2002)	8 (48)	8 (54)
16	Barbier and Graciolli (2016)	19 (830)	10 (683)
17	Eriksson et al. (2011)	16 (266)	8 (297)
18	Moras, Bernardi, Graciolli, and Gregorin (2013)	11 (70)	7 (33)
19	Dornelles, Graciolli, Odon, and Bordignon (2017)	13 (506)	8 (389)
20	Graciolli, Passos, Pedro, and Lim (2006)	9 (92)	5 (327)
21	França et al. (2013)	9 (126)	7 (301)
22	Lourenço, Patrício, Pinheiro, Dias, and Famadas (2014)	22 (1,105)	18 (738)
23*	Almeida, Silva, Serra-Freire, and Valim (2011)	9 (171)	9 (164)
24	Bertola et al. (2005)	15 (391)	12 (498)
25	Anderson and Ortêncio-Filho (2006)	6 (169)	4 (625)
26	da Silva and Ortêncio-Filho (2011)	5 (39)	5 (140)
27	Dornelles and Graciolli (2017)	22 (421)	15 (375)
28	Graciolli and Bianconi (2007)	6 (119)	2 (78)
29	Rui and Graciolli (2005)	7 (104)	4 (324)
30	Camilotti et al. (2010)	3 (40)	3 (81)

2.3 | Data analyses

We evaluated the factors determining the structure of community composition of both parasites and hosts through generalized dissimilarity modelling (GDM), which accounts for non-linearity of community dissimilarity across environmental gradients (Ferrier, Manion, Elith, & Richardson, 2007; Maestri et al., 2017). Briefly, the GDM analysis calculates three I-spline coefficients for each explanatory variable when all other variables are constant. Higher coefficients indicate higher rates of change of the response variable along the gradient of the explanatory variable (Ferrier et al., 2007; Maestri et al., 2017). The significance of each model was calculated by matrix permutation (1,000 permutations) by comparing the deviance explained by the original model with the distributions of the deviance calculate to all permutations.

We performed three analyses. One focused on host communities to test whether dissimilarity in bat species composition is itself explained by geographical distance and/or environmental similarity. Then, to address our main issue on parasite communities, we tested whether dissimilarity in bat fly species composition is explained by dissimilarity in bat species composition, geographical distance, and environmental similarity. Finally, because available studies are spatially concentrated in the Brazilian Cerrado and Atlantic Forest, we conducted a third analysis including only these two regions to evaluate how much the uneven geographical distribution of samples can drive our results. All analyses were performed in R 3.6.0, using the packages 'gdm', 'vegan', and 'iNEXT'; models were created using function *gdm* and the significance

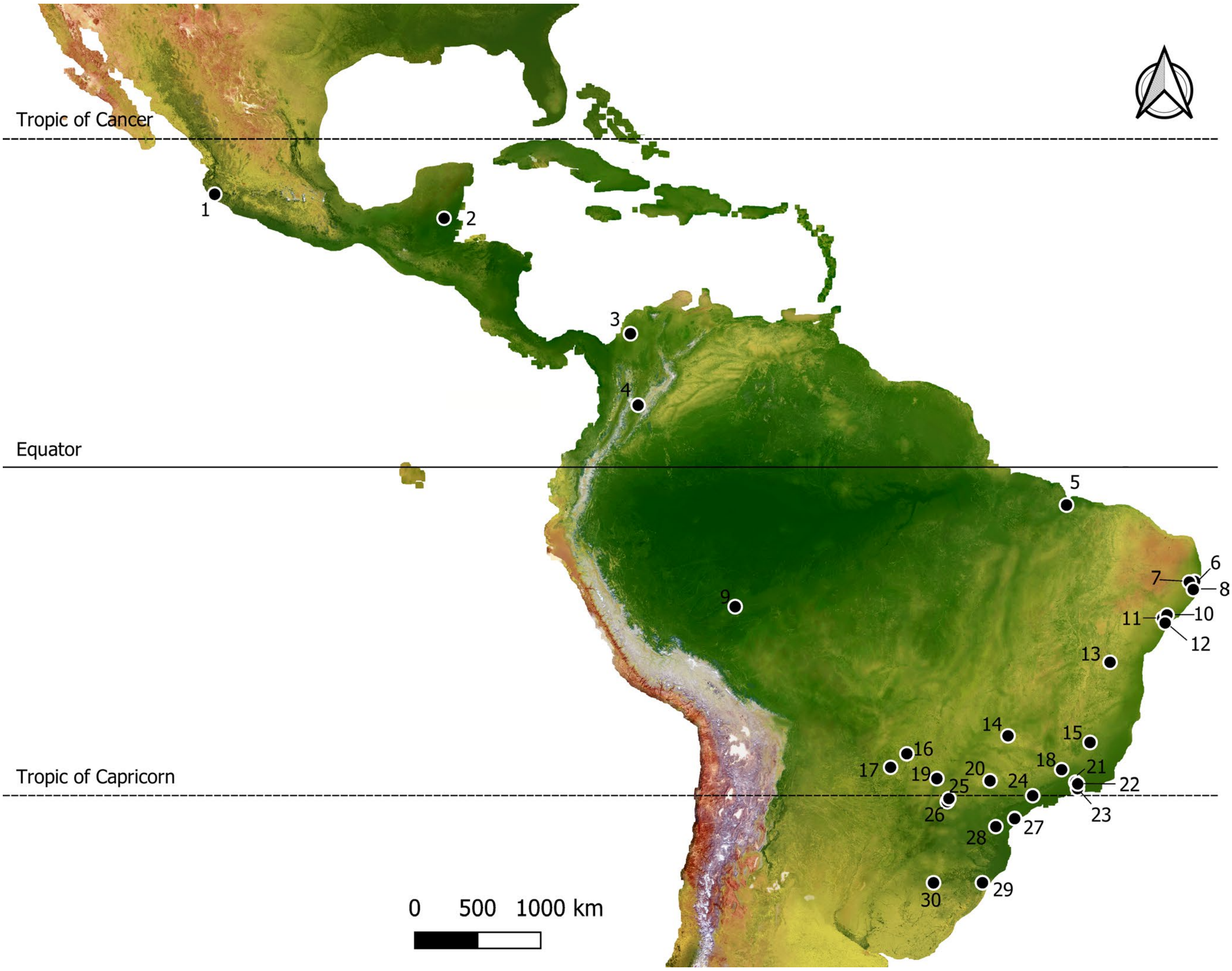

FIGURE 1 Distribution of the sampling units selected for the study. Samples number 3, 9, 14, and 23 were removed from the final analysis since the number of observed species were lower than 70% of the Chao1 estimate. Made with Natural Earth. 1 Zarazúa-Carbajal et al. (2016); 2 ter Hofstede et al. (2004); 3 Durán de la Ossa et al. (2017); 4 Tarquino-Carbonell et al. (2015); 5 Santos et al. (2009); 6 Soares et al. (2013); 7 Barbier et al. (2019); 8 Barbier et al. (2019); 9 Santos et al. (2012); 10 Soares et al. (2017); 11 Bezerra et al. (2016); 12 Bezerra and Bocchiglieri (2018); 13 Rios et al. (2008); 14 Komeno and Linhares (1999); 15 Azevedo and Linardi (2002); 16 Barbier and Graciolli (2016); 17 Eriksson et al. (2011); 18 Moras et al. (2013); 19 Dornelles et al. (2017); 20 Graciolli et al. (2006); 21 França et al. (2013); 22 Lourenço et al. (2014); 23 Almeida et al. (2011); 24 Bertola et al. (2005); 25 Anderson and Ortêncio-Filho (2006); 26 da Silva and Ortêncio Filho (2011), 27 Dornelles and Graciolli (2017), 28 Graciolli and Bianconi (2007), 29 Rui and Graciolli (2005), 30 Camilotti et al. (2010) [Colour figure can be viewed at wileyonlinelibrary.com]

was calculated with the function *modTest.gdm* (Manion et al., 2018, Hsieh, 2019, Oksanen et al. 2019, see Appendix S2 for details).

To assess variance partitioning of effects by the explanatory variables, we initially created GDM models separated for each explanatory variable (host species composition, environmental similarity, and geographical distance), then models with all possible pairs of explanatory variables, and finally a model with all three explanatory variables. The single and combined effects of the explanatory variables on the dissimilarity in host or parasite species composition were calculated by subtracting the percentage of deviance explained for each separate and paired model from the model with all variables, using the method proposed by Borcard, Legendre, and Drapeau (1992) (Appendix S2).

To create the distance matrices of parasite and host species, we used the Bray-Curtis dissimilarity index, which is most reliable when using species abundance data, and which facilitates comparison with data from different studies (Magurran, 2004; Vinarski et al., 2007). All data were transformed into relative abundances prior to creating the distance matrices in order to reduce the impact of raw abundance resulting from different sample sizes among the published studies (see Appendix S2 for R codes, and Appendix S3 for matrices).

3 | RESULTS

Most of the 26 localities covered by the analysis are situated in the Atlantic Forest and Cerrado of Brazil and are only separated by a few hundred kilometres. However, a few sites are thousands of kilometres apart, all the way up to Mexico (Figure 1). Bat species richness ranged from 2 to 18 species and bat abundance ranged from 33 to 683 individuals per sampling unit. Bat fly species richness ranged from 2 to 23 species and their abundance ranged from 39 to 1,995 individuals per sampling unit (Table 1). In total, 48 species of phyllostomid bats and 67 species of streblid bat flies were represented (Appendix 3.2 and 3.3 in Appendix S3). Host and parasite species richness were strongly positively correlated across communities ($r^2 = .76$, $p < .001$).

Geographic distance and environmental similarity accounted for 40.6% of the variation in the dissimilarity in host (bat) species composition (Table 2). Both explanatory variables influenced the dissimilarity in host species composition. Geographical distance alone explained 18.0% of the variance in host species composition and pure environmental similarity explained only 9.8%; the pooled effect of geographical distance and environmental similarity accounted for 12.8% of the variance (Figure 2a). The environmental variable with the highest relative importance was temperature seasonality and, to a lesser extent, annual precipitation (Table 3).

In our main analysis, the model including the three explanatory variables—dissimilarity in host species composition, dissimilarity in environmental variables, and geographical distance—explained 45.3% of the variation in the dissimilarity in bat fly species composition (Table 2). The influence of hosts on the structure of bat fly communities was most prominent (Figure 3). When the variance of the explanatory variables was partitioned, pure host effects were responsible for 14.9% of the variance in parasite community structure (Figure 2b). Environmental similarity and geographical distance explained 10.3% and 0.007%, respectively, of the variance in the species composition of bat flies (Figure 2b). Among the environmental variables, annual precipitation was the most important, followed by temperature seasonality (Table 3, Figure 3).

In the final analysis, which was restricted to 21 sampling units located in the Cerrado and Atlantic Forest, the model with all three variables explained 57.3% of the variance in bat fly species composition. Although the explained variance increased when compared to that of the model comprising all sampling units, the importance of each explanatory variable remained roughly the same. Host species composition was responsible for 21.7% of the variation in bat fly species composition, whereas environmental similarity accounted for 12.0% and geographical distance for less than 0.005% (Figure S2 Appendix S1).

4 | DISCUSSION

Our main results support the proposition that host species composition and environmental conditions play major roles in predicting bat fly species composition across the Neotropics, whereas geographical distance is less important for this host-specific group of ectoparasites. The uneven spatial distribution of our sampling units throughout the Neotropics did not influence the general pattern, as the relative importance of the predictor variables remained nearly the same when we analysed only the subset of close sites in the Cerrado and Atlantic Forest. Moreover, this model explained an increased proportion of the variance in bat fly species composition. Thus, we focus on our main model, which included all 26 sampling units, successfully recovering factors structuring bat fly communities at a continental scale. This model explained 45.3% of the dissimilarity in species composition for bat flies among localities spanning thousands of kilometres. The few comparable studies on compound communities of ectoparasites have shown lower explanatory power in their models using linear approaches.

TABLE 2 Percentage of deviance explained in generalised dissimilarity modelling (GDM), model and null deviance, intercept, and the I-spline predictor variables of the GDM models for bat fly and host species dissimilarity

	Bat fly					Host				
		I-spline					I-spline			
		1	2	3	All		1	2	3	All
% of deviance explained	45.34					40.62				
GDM model deviance	31.06					33.82				
Null deviance	56.83					56.95				
Intercept	0.31					0.49				
p	<.001					<.001				
Predictor variables										
Geographical distance		0.024	0.000	0.000	0.024		0.194	0.000	1.441	1.635
Annual precipitation		0.734	0.000	0.106	0.840		0.313	0.000	0.051	0.364
Temperature seasonality		0.212	0.058	0.574	0.844		0.000	0.712	0.187	0.899
Elevation		0.000	0.008	0.407	0.415		0.009	0.023	0.116	0.148
NDVI maximum		0.000	0.014	0.003	0.017		0.022	0.000	0.000	0.022
NDVI minimum		0.179	0.000	0.000	0.179		0.008	0.077	0.000	0.085
Host composition		0.000	0.000	1.239	1.239		—	—	—	—

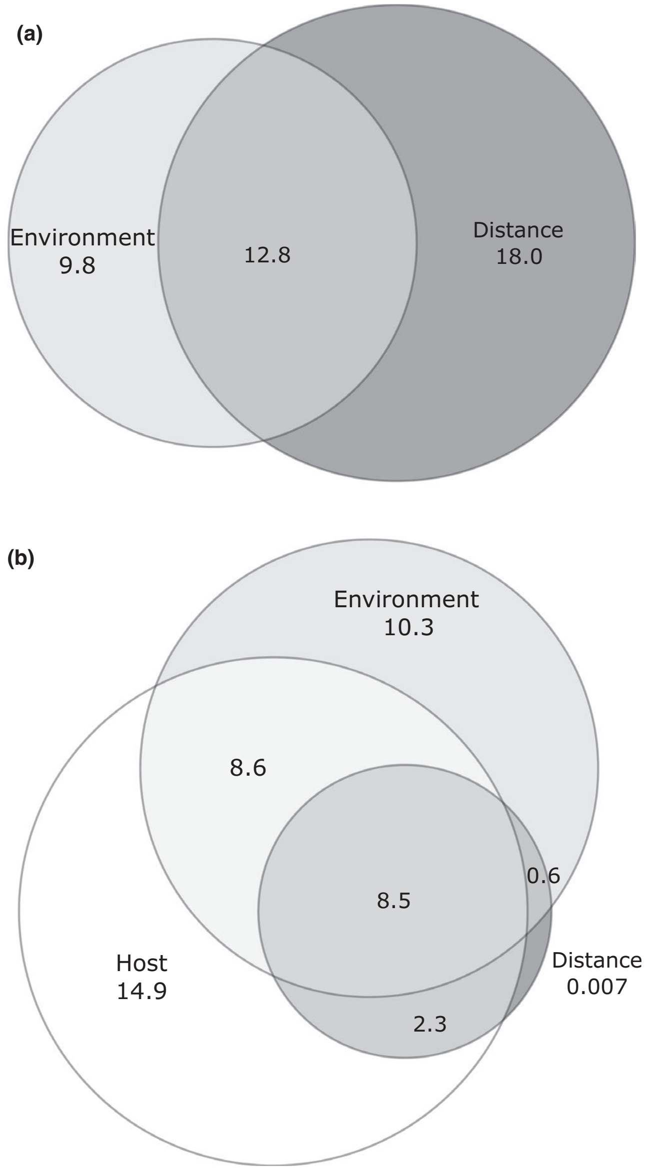

FIGURE 2 Venn diagram with the sole and mixed effects of environmental similarity, geographical distance, and host species composition on a) bat species composition and b) bat fly (Streblidae) species composition. Values are in percentage of the variance explained, the area of each circle corresponds to the relative amount of the variance explained

In a subset of highly host-specific fleas, the model of Krasnov et al., (2010) explained only 8% of the variation in species composition using the same variables we used here. When including all flea species, the model explained 32% of the species composition (Krasnov et al. 2010). Using a different dataset, with host phylogenetic distance, environmental distinctness, and geographical distance as explanatory variables, the same authors' best models for similarity in species composition of fleas and mites parasitic on small mammals accounted for 18% and 24% of the variation, respectively (Krasnov, Mouillot, Shenbrot, Khokhlova, Vinarski, et al., 2010). Remarkably, Maestri et al. (2017) found that 24% and 68% of the variation in flea species turnover in Mongolia was explained by linear and non-linear analyses, respectively.

The dissimilarity in species composition of the hosts themselves across our localities was influenced by geographical distance and environmental variables similarity (18.1% and 9.8%, respectively). This result differs from that reported at a narrower spatial scale for bat species composition in Mexico, where host species composition was mostly explained by local environmental factors (López-González et al., 2015). However, our result is coherent with that found in a large-scale study on phyllostomid bats in the Neotropics, where spatial processes accounted for 12.5% of the variance in beta diversity, and environmental variables had no effect on species composition (Varzinczak et al., 2018). Therefore, the environment is apparently more important in structuring Neotropical bat species composition at smaller spatial scales while geographical distance becomes more relevant at larger scales (López-González et al., 2015; Stevens, López-González, & Presley, 2007; Varzinczak et al., 2018). Rather than a general pattern, however, this conclusion could arise from the fact that the small-scale studies were performed in areas with high environmental variation (López-González et al., 2015).

TABLE 3 Importance of the environmental variables to bat fly species and host bat species composition calculated by generalised dissimilarity modelling

Variables	Bat fly	Host
Annual precipitation	14.212	4.381
Temperature seasonality	9.350	18.765
Elevation	5.377	0.824
NDVI maximum	0.009	0.022
NDVI minimum	1.334	0.298

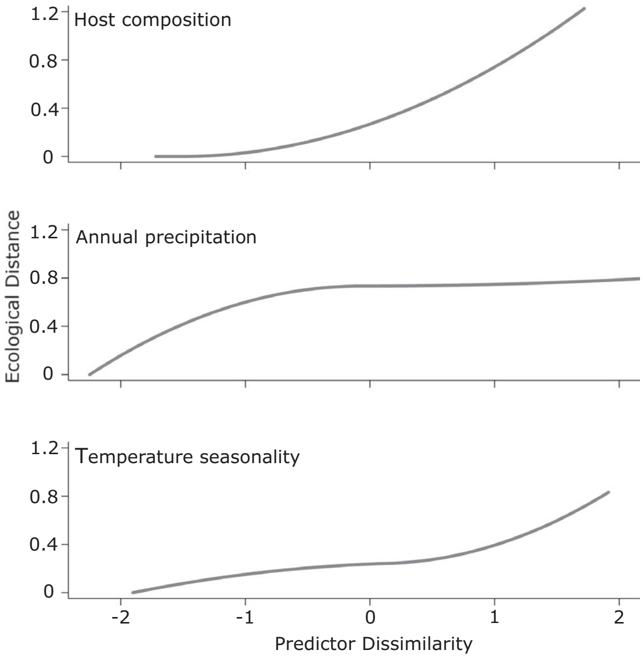

FIGURE 3 Relationship between the observed predictors dissimilarities and the fitted values of the I-splines (ecological distance) calculated by generalised dissimilarity modelling

As expected for host-specific parasites, host species composition emerged as a major factor structuring bat fly species composition when the three explanatory variables were included in our main model. Host effect is also reflected in the strong correlation that we found between bat and bat fly species richness among localities, which is a common pattern across multiple host-parasite associations (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014). Host species composition has also been reported as the most important variable explaining bat fly diversity at small spatial scales (Barbier et al., 2019; Hernández-Martínez et al., 2018). However, our results differ from those of Krasnov et al., (2010), who found that the environment was the main factor influencing the dissimilarity in host-specific flea species composition. They attributed the lack of influence of host species assemblages on flea species composition to two factors: (a) the broad geographical distribution of the hosts, and (b) the fact that parasites such as fleas are locally specialised but globally opportunistic (Krasnov et al., 2010). However, these characteristics also apply to some extent to bat flies. For instance, the bat *Artibeus lituratus* has broad geographical distribution, ranging from central Mexico to southern Brazil (Barquez, Perez, Miller, & Diaz, 2015) where it is parasitised by *Paratrichobius longicrus* (Camilotti, Graciolli, Weber, Arruda, & Cáceres, 2010; Zarazúa-Carbajal et al., 2016). Bat flies also include species that are local specialists but global generalists. This is the case for *M. aranea*, found on *A. jamaicensis*, *Artibeus planirostris*, and *Artibeus fimbriatus*, in Central America, central Brazil, and southern Brazil, respectively (Eriksson, Graciolli, & Fischer, 2011; Rui & Graciolli, 2005; ter Hofstede, Fenton, & Whitaker, 2004). Here, it is important to note two key features. Firstly, all bat species parasitised by *M. aranea* have similar sizes, feeding habits, and roost usage (Gardner, 2007; Zortéa, 2007). These features reinforce the idea that particular adaptations of bat flies, like leg length, are essentially associated to host species with similar traits (Hiller, Honner, Page, & Tschapka, 2018). Secondly, *M. aranea* has been accepted as one evolutionary unit, but it might eventually be split into different species after a deep taxonomic review and use of molecular markers (G. Graciolli, personal observation); the same may also be true for some flea species currently considered generalists (van der Mescht, Matthee, & Matthee, 2015). Although both systems are host specific (bat/bat flies and small mammals/fleas), they differ in how much time the parasite spends on the host. While bat flies are highly dependent of their hosts to live, fleas spend most of the time off their host (Krasnov et al., 2001; Overal, 1980). In this sense, it would seem that the factors affecting parasite species composition are mostly related to the amount of time spent by individual ectoparasites on their host than host specificity per se.

Environmental similarity also influenced bat fly species composition across Neotropical localities, with annual precipitation and temperature seasonality being the most important environmental variables. Earlier studies have shown the effects of seasonality and precipitation on bat fly abundance (Barbier et al., 2019; Pilosof et al., 2012; Salinas-Ramos, Zaldívar-Riverón, Rebollo-Hernández, & Herrera-M, 2018). However, these environmental variables do not always have similar effects on bat flies associated with different hosts. For instance, during the wet season, bat fly prevalence seems to increase on *Pteronotus parnellii* and to decrease on *Leptonycteris yerbabuenae* (Salinas-Ramos et al., 2018). In addition, bat fly abundance on *A. jamaicensis* and *Carollia perspicillata* responded negatively to precipitation, but positively when found on *Desmodus rotundus* (Pilosof et al., 2012). Moreover, we found that the most important environmental variable influencing species composition differs between hosts and bat flies. While bat fly species composition is influenced mainly by annual precipitation, their host communities are influenced primarily by temperature seasonality. These results indicate that, even if the responses of bat flies to seasonality and precipitation are host-specific, there is an environmental component that directly affects bat flies (i.e., annual precipitation), regardless of their host. We suggest that this environmental effect could, therefore, be associated with the stage of the bat fly life cycle decoupled from the host (i.e., the pupal stage). In this case, the negative effects of annual precipitation would be higher for bat flies on hosts inhabiting more exposed roosts. Indeed, Pilosof et al. (2012) and Salinas-Ramos et al. (2018) found that environmental conditions negatively affect bat fly abundance on bats that use more exposed roosts. On the other hand, female bat flies on cave-roosting bats can actively search for protected places to deposit their pupae (Dittmar, Dick, Patterson, Whiting, & Gruwell, 2009). External climatic variables used here do not properly reflect the microclimate conditions inside bat roosts. Therefore, part of the unexplained variance (54.7%) in bat fly species composition could be recovered if microclimatic data for different roost types were available.

Geographical distance alone had no influence on the dissimilarity in bat fly species composition. Even though the pattern of distance decay in the similarity of species composition is quite common (Nekola & White, 1999; Soininen et al., 2007), we did not expect it to strongly affect bat flies. Compared to other mammal taxa, Neotropical bat species have a low degree of genetic differentiation across their geographical ranges, likely because flight improves dispersal ability (Ditchfield, 2000). For this reason, geographical distance has little to no effect on the structure of bat species composition (López-González et al., 2015; Stevens et al., 2007; Varzinczak et al., 2018). Bat flies are incapable of surviving long periods when decoupled from their hosts and, even though some species have functional wings, they still depend on their hosts for dispersal (Dick & Patterson, 2006; Komeno & Linhares, 1999; Overal, 1980). In this sense, the high mobility of bats and the dependence of bat flies on host dispersal could contribute to homogenise the composition of parasite communities, potentially reducing the effects of geographical distance on the similarity in bat fly species composition.

Nevertheless, it is challenging to reconcile the fact that bat fly community structure is not influenced by geographical distance when host species composition does show a distance-decay pattern. On one hand, the dispersal capacity of bat flies may be higher than the area covered by the flight range of individual hosts, contributing to the homogenisation of bat fly species across host communities. In some bat species, juveniles are more heavily parasitised by bat flies than adults

(Esbérard, Astúa, Geise, Costa, & Pereira, 2012; Rui & Graciolli, 2005). Komeno and Linhares (1999) suggested the higher infestation on juvenile bats as a potential strategy for dispersal, since juveniles commonly leave their original colonies when approaching maturity (Moussy et al., 2013). On the other hand, bat fly species homogenisation across geographical areas may be a taxonomic artefact. As mentioned above for *M. aranea*, some presumably generalist bat fly species may actually comprise multiple cryptic species, which may be revealed after taxonomic revision. Indeed, a recent review of the genus *Noctiliostrebla* raised the number of known species from four to eleven (Alcântara, Graciolli, & Nihei, 2019). On the other hand, bat taxonomic descriptions have increased significantly in the last years; more than 300 new bat species have been described since 2003 (Burgin, Colella, Kahn, & Upham, 2018). When a more detailed phylogeny of bat flies becomes available, we might expect a higher, but still weak, relationship between bat fly species composition and geographical distance. Interestingly, the decay in dissimilarity of parasite species composition with increasing distance is not a universal law in parasite ecology, even though it is a very common pattern for free-living organisms (Nekola & White, 1999; Poulin, 2007; Soininen et al., 2007; Vinarski et al., 2007). Studies testing for this relationship in different parasite communities have found inconsistent patterns, which could result from the specific responses of the parasite group studied (Krasnov et al., 2010; Vinarski et al., 2007).

5 | CONCLUSIONS

Our model successfully identified factors influencing bat fly species composition at a continental scale. Host species composition proved the most important factor structuring bat fly communities, which reinforces the high dependence of bat flies on particular hosts. Although the influence of environmental variables on bat fly species abundance is not well known, we found a clear effect of the environment on species assemblage composition (Barbier et al., 2019; Luna et al., 2017; Salinas-Ramos et al., 2018). In its turn, geographical distance is less important to determine bat fly species composition across the Neotropical region, a pattern that may be related to the high mobility of bat hosts and/or the dispersal capacity of bat flies, or simply a taxonomic artefact. Overall, our study reveals substantial differences between the key factors shaping bat fly communities and those shaping communities of flea and mite ectoparasites on small mammals, highlighting an apparent idiosyncratic nature of host-parasite associations. Nonetheless, different lengths of time spent by the ectoparasites off their hosts could generate the different patterns among ectoparasite groups; thus, it seems an important factor to be addressed in further studies.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The main R scripts and all data used in the analyses are available as supplementary material.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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