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Effects of forest loss and fragmentation on bat-ectoparasite interactions

Alan Eriksson^{1,2} · Antoine Filion³ · Marcelo Bahia Labruna⁴ · Sebástian Muñoz-Leal⁵ · Robert Poulin³ · Erich Fischer¹ · Gustavo Graciolli¹

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Abstract

Human land use causes habitat loss and fragmentation, influencing host-parasite associations through changes in infestation rates, host mortality and possibly local extinction. Bat-ectoparasite interactions are an important host-parasite model possibly affected by such changes, as this system acts as both reservoirs and vectors of several pathogens that can infect different wild and domestic species. This study aimed to assess how the prevalence and abundance of bat ectoparasites respond to forest loss, fragmentation, and edge length. Bats and ectoparasites were sampled at twenty sites, forming a gradient of forest cover, in southwestern Brazil during two wet (2015 and 2016) and two dry (2016 and 2017) seasons. Effects of landscape metrics on host abundance as well as parasite prevalence and abundance were assessed through structural equation models. Nine host-parasite associations provided sufficient data for analyses, including one tick and eight flies on four bat species. Forest cover positively influenced the prevalence or abundance of four fly species, and negatively for the tick. In turn, number of fragments influenced the prevalence or abundance of four fly species, two positively and two negatively. Our results support species-specific responses of ectoparasites to landscape features, and a tendency of host-generalist ticks to benefit from deforestation while most host-specialist flies are disadvantaged. Differences in host traits and abundance, along with parasite life cycles and environmental conditions, are possible explanations to our findings.

Keywords Argasidae · Deforestation · Neotropical region · Phyllostomidae · Streblidae

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Alan Eriksson aferiksson@hotmail.com

- ¹ Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa E Silva S/N, CEP 79070-900 Campo Grande, Brasil
- ² Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Corrêa da Costa, nº 2367, CEP 78060-900 Cuiabá, Brasil
- ³ Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand
- ⁴ Department of Preventive Veterinary Medicine and Animal Health, Faculty of Veterinary Medicine, University of São Paulo, São Paulo, Brazil
- ⁵ Departamento de Ciencia Animal, Facultad de Ciencias Veterinarias, Universidad de Concepción, Av. Vicente Méndez 595, Casilla 537, 3780000 Chillán, Chile

Introduction

The intensification of human activities has threatened the global biodiversity by reducing biologically diverse areas into low diversity systems (Foley et al. 2005; Newbold et al. 2015). Land use for agriculture and livestock production, when not performed in a sustainable way, is a major cause of habitat loss and fragmentation, two combined processes that additionally create edge effects through abrupt transitions from natural to human-modified areas (Jose 2009; Meyer et al. 2016; Fletcher et al. 2018; Put et al. 2019). Such an increase of human land use has markedly caused declines in taxonomic and functional diversity of communities, contraction or disruption of species geographic distributions, and reductions of population size and genetic diversity of wild species, though providing an increased occupation by more generalist, invasive and/or synanthropic species (Brooks et al. 2002; Gonçalves et al. 2017; Lino et al. 2019). Therefore, the effects of landscape features on organisms

can greatly vary according to the group studied and their lifestyles. Parasites negatively affect their hosts directly and often indirectly as vectors of pathogens, establishing complex interactions that are poorly understood for many groups, and whose consequences after disturbances are still hard to predict, raising concerns to human health and wildlife (Morand and Lajaunie 2021; Speer et al. 2022).

Although some trends have been found, there are no consensus patterns regarding the effects of landscape changes on different host-parasite interactions, and the processes governing them are yet to be understood (Cottontail et al. 2009; Pilosof et al. 2012; Ramalho et al. 2018). The effects of landscape changes on parasitic organisms have been highly variable. On the one hand, habitat fragmentation can increase parasite prevalence in the host populations due to changes in habitat configuration and the decline of hosts diversity (Cottontail et al. 2009; Ogrzewalska et al. 2011). In addition, habitat fragmentation can negatively affect the hosts' immune system, the size and genetic diversity of their populations, which may result in their enhanced susceptibility to acquire parasites that can then more severely infest most local host individuals, further contributing to host population declines (Mbora and McPeek 2009; Lino et al. 2019; Belasen et al. 2019; Edworthy et al. 2019). On the other hand, as the number of host species decreases with habitat loss, the highly host-specific parasites can decline or suffer local extinction, whereas host-generalist ones may predominate or even increase in abundance through infestation of multiple host species (Dunn et al. 2009; Esser et al. 2019).

The Neotropics harbour an amazing diversity of bat species (Burgin et al. 2018), which reflects their importance to the ecosystems, acting as pollinators, seed dispersers, predators that control prey populations, and hosts, reservoirs, or vectors of parasites and diseases that affect both wildlife and human populations (Kuzmin et al. 2011; Moratelli and Calisher 2015; Hayman 2016; Wang and Anderson 2019). Ectoparasites of bats are potential vectors of diseases among bat populations, an aspect still poorly studied (Dick and Dittmar 2014; Tahir et al. 2016). It is expected that highly hostspecific parasites maintain pathogens among conspecific bats in different populations, whereas generalist parasites could act as vectors of pathogens to different host species (Loftis et al. 2005; Socolovschi et al. 2012; Dick and Dittmar 2014; Muñoz-Leal et al. 2018).

Neotropical bats host a myriad of ectoparasites, with bat flies and ticks being the most conspicuous and widespread groups (Dick and Patterson 2006; Nava et al. 2017). Most bat flies are highly host-specific, whereas ticks often are generalists that can parasitize different mammal taxa (Dick 2007; Nava et al. 2017). Recent studies focused on land use changes have shown that the response of bat ectoparasites to habitat loss, fragmentation, and human density tend to be species-specific (Pilosof et al. 2012; Bolívar-Cimé et al. 2018; Hiller et al. 2020). For instance, in Costa Rica, human disturbances have led to a decrease of bat fly abundance on Artibeus planirostris and Pteronotus parnellii bats, but to an increase on *Carollia perspicillata*. These findings are possibly related to roosting habits, as the former species use less exposed roosts and the last roosts in exposed places, which are prone to be affected by environmental conditions (Pilosof et al. 2012). The presence of riparian forests was associated with an increase of bat fly prevalence on Artibeus jamaicensis bats in Mexico (Hernández-Martínez et al. 2018), while Ramalho et al. (2018) found a higher prevalence of the bat fly Trichobius joblingi on C. perspicillata in preserved compared to degraded habitats. However, to the best of our knowledge, the effects of landscape changes on the abundance of ticks on bats have not yet been addressed, though fragmentation has been found to increase the prevalence of ticks on birds (Ogrzewalska et al. 2011). Overall, the available studies on the effects of landscape features on bat ectoparasites abundance suggest that the direction of the responses is host species and parasite species-specific (Mello et al. 2023). Here, we evaluate changes in the prevalence and abundance of bat ectoparasites across landscapes forming a gradient of forest loss and fragmentation, in the Serra da Bodoquena region, Brazilian Cerrado. We ask whether and how forest cover area, number of forest fragments, length of forest edge, and host abundance can influence the prevalence and abundance of ectoparasites on bats.

Methods

Study region

The study was carried out in the karstic region of Serra da Bodoquena (18,000 km²; 150–800 m altitude), southwestern Brazil (Fig. 1). The climate is type Aw of Köppen-Geiger (Kottek et al. 2006), with the wet season from November to April and the dry season from May to September. The mean annual rainfall ranges from 1300 to 1700 mm, and the mean annual temperature, from 22 to 26 °C (Hijmans et al. 2005). The vegetation is mainly composed of deciduous and semi-deciduous forests, woody savannas, and grasslands (Baptista-Maria et al. 2018; Scremin-Dias et al. 2018). The Serra da Bodoquena National Park comprises the two largest continuous areas of pristine habitats (the northern area with 28,000 ha, and the southern area with 49,000 ha), being surrounded by small natural fragments of lands modified for agricultural and livestock production (Fig. 1). After dividing the entire region (18,000 km²) in 360 hexagons of 5000 ha using satellite images and measuring the forest area in each one, we selected 20 sample sites in the centre of 20 hexagons forming a gradient from 3 to 100% of forest cover. Additional criteria for selection of sites were accessibility,

Fig. 1 Distribution of the 20 sampling sites (black dots) in the region of Serra da Bodoquena (red mark in South America). Green represents forest areas. At right, examples of the buffer areas (0.5, 1, 2.5 and 5 km radius) corresponding to three sites (A, B, and C)



presence of watercourses, authorization from landowners, and avoidance of nearby sites with similar values of forest cover.

Bat and ectoparasite sampling

To sample the bat species and their ectoparasites across the 20 sites, we mistnetted bat individuals in four field expeditions, including two rainy seasons (2015, 2016) and two dry seasons (2016, 2017). Each site was sampled one night per field expedition, thus totalizing four nights per site; except three sites that were sampled for three nights in total because they were inaccessible during one expedition. Each night we set ten 12×2.6 m mistnets per site during six hours after dusk; all nets were placed in deciduous or semideciduous forest understories. All captured bats were kept in individual cloth bags before being inspected for ectoparasites. Bat identifications and classification followed Gardner (2007). All ectoparasite individuals found on the bats' bodies and inside the bags were removed manually or with tweezers and placed in vials containing 99% ethanol; each vial corresponding to one host bat. In the laboratory, we counted and identified the ectoparasites based on Wenzel (1976), Guerrero (1995), and Muñoz-Leal et al. (2016). Only bat species that occurred in all 20 sampling sites were included in the final analyses. Samplings were carried out under authorization of the Brazilian environmental ministry (ICMBio – authorization number 41652–1).

Parasitological indices

We used two parasitological indices, prevalence and abundance (Bush et al. 1997), to describe the ectoparasite populations on their hosts. Prevalence represents the proportion of individuals of a particular host species infested by one parasite species in a sample. Abundance is the number of individuals of a parasite species on an individual host, either infested or non-infested (abundance = zero).

Landscape metrics

We recorded landscape metrics at four spatial scales through concentric buffers with 0.5, 1, 2.5, and 5 km of radius around each sample site (Fig. 1). We used landscape variables at different scales because home range is expected to differ among bat species and may vary between regions. For each site and buffer size, we calculated the proportion of forest cover area, number of forest fragments, and the total length of forest edges in kilometres. Landscape variables were calculated using a map created with 2012 Landsat images (30 m resolution), after checking for no significant landscape changes from 2012 to the period of field data collection using maps and reports provided by the Non-Governmental Organization "SOS Pantanal" (SOS Pantanal 2017). The images were rasterized and processed with FRAGSTATS (McGarigal et al. 2012). Forest patches ≥ 0.1 ha were classified as 'fragment'. Buffers were created and landscape variables were calculated with the R packages rgeos (Bivand et al. 2019) and spatialEco (Evans 2018), respectively. Because the spatialEco package mistakenly counts the buffer's perimeter segments over forested areas as edges, we manually measured these perimeter segments in the images of each buffer and subtracted them from the values calculated by the package.

Data analyses

Landscape variable correlations and scale selection

To choose the buffer size in which each landscape metric should be incorporated into final models (see below), i.e., the scale representing the strongest response for each parasite (Put et al. 2019; Amiot et al. 2021), we used Akaike information criteria (AIC) to rank models with ectoparasite prevalence or abundance as response and each landscape metric of different buffer sizes as predictor. For each ectoparasite species on a given host bat species, we then selected the buffer scale for each landscape metric whose model presented $\Delta AIC = 0$ (Table S1 – Supplementary material 1). Afterward, to account for collinearity in the final models, we correlated the selected variables to check and avoid cases when r > 0.7 (Dormann et al. 2013). Edge length in the 5 km radius buffer and number of fragments in this same buffer size were the only highly correlated variables (Figure S1 – Supplementary material 1). Therefore, when these two variables were initially selected for inclusion in the same final model (corresponding to each parasite-host species association; see below), we switched the choice of buffer size based on the one that presented the second lowest Δ AIC value (Table S1 – Supplementary material 1).

Main models

We used structural equation models (Piecewise SEM) to assess the direct effects of the landscape variables on the prevalence of ectoparasites and the abundance of ectoparasites and hosts, as well as the indirect effects of landscape on parasites through the host abundance. Bat individuals were the sampling units in all analyses. Host abundance per site was measured as Nm⁻² h⁻¹, expressing the number of captured bats (N) divided by the netting effort in terms of net area (m^2) and netting time (h). We used generalized linear mixed models (GLMM) with binomial distribution to assess the effects of landscape metrics and host abundance on ectoparasite prevalence, and with negative binomial distribution for effects on ectoparasite abundance (Zuur et al. 2009). The site ID was included as random effect in all the models of prevalence and abundance of ectoparasites, in order to account for spatial stochasticity among sites (Dormann et al. 2007). Finally, we normalized host abundance through squared root transformation and analysed it as a response of landscape metrics with generalized linear models (GLM) and gaussian link-function. It was not possible to use mixed models in the analyses of host abundance since the correlation of the response variable and the random effects was identical. Before performing the analyses, we checked for spatial autocorrelation of the response variables using the Moran's I index (Table S2 – Supplementary material 1). The predictor variables were scaled to have a mean of 0 and a standard deviation of 1, allowing comparisons (Zuur et al. 2009). We considered that a variable had an effect if the 95% confidence intervals of the estimated regression coefficients did not overlap zero in the regression estimates plot. Analyses were conducted with the package piecewiseSEM (Lefcheck 2019) in the R environment (R Core Team 2020). The raw data is provided in the supplementary material 2.

Results

We captured 2,091 bats of 23 species in four families – Molossidae, Noctilionidae, Phyllostomidae, and Vespertilionidae. Phyllostomidae was the most abundant and speciose, with 2,050 individuals and 20 species sampled. Four phyllostomids that accounted for 85% of all captures matched our criteria (i.e., recorded at all sites) to be included in the analyses – *Artibeus planirostris, Sturnira lilium, Carollia perspicillata*, and *Platyrrhinus lineatus*. The number of captured individuals varied from 224 to 930 among the four host species. The mean (\pm SD) abundance relative to the capture effort per site was 0.58 \pm 0.35 Nm⁻² h⁻¹ for *A. planirostris*, 0.17 \pm 0.20 Nm⁻² h⁻¹ for *C. perspicillata*, and 0.23 \pm 0.35 Nm⁻² h⁻¹ for *S. lilium*. Eight bat flies and one tick species

parasitized these four bat species (Table 1); their prevalence varied from 9.8 to 66.9, with *Ornithodoros hasei* on *A. planirostris* being the least prevalent, and *Trichobius joblingi* on *C. perspicillata* the most prevalent (Table 1). Mean abundance of ectoparasites varied from 0.27 to 0.98, which corresponded to the occurrence of *Paratrichobius longicrus* on *P. lineatus* and *Aspidoptera falcata* on *S. lilium*, respectively (Table 1). The percentage of forest cover area ranged from 3.2 to 100 among sites and buffer sizes, while the number of fragments and edge length varied from 1 to 326 and from zero to 361 km, respectively (Table S3 – Supplementary material 1).

The effects of the landscape variables on the abundance of *A. planirostris* were in the opposite direction to those on the abundance of the other three host bats. Forest cover and number of forest patches negatively affected *A. planirostris* abundance, while edge length positively influenced it (Fig. 2). On the contrary, the abundances of *C. perspicillata* and *P. lineatus* responded positively to forest cover and number of patches, but negatively to edge length; and *Sturnira lilium* followed these same trends except that number of patches slightly negatively affected it (Fig. 3).

At least one landscape variable affected, directly or indirectly through host abundance, the prevalence or abundance of six fly and one tick species (Fig. 4), but two fly species (*T. joblingi* and *P. longicrus*) were not directly nor indirectly affected. The effect direction of forest cover on the prevalence and abundance of the ectoparasites were host and parasite-specific. On the one hand, forest cover negatively influenced, directly and indirectly, the prevalence of the tick *O. hasei* (path coefficient = -0.44) as well as the abundance of *M. aranea* flies on *A. planirostris* bats; though it indirectly

 Table 1
 Prevalence and mean abundance (95% confidence interval)
 of ectoparasite species on four species of phyllostomid bats in the
 Serra da Bodoquena, southwestern Brazil

Host (N)	Prevalence	Mean abundance
Ectoparasite (N)		
Artibeus planirostris (930)		
Megistopoda aranea (903)	49.1 (45.9–52.4)	0.97 (0.88–1.06)
Aspidoptera phyllostomatis (446)	26.5 (23.6–29.4)	0.48 (0.42–0.55)
Ornithodoros hasei (589)	9.8 (8.0–11.9)	0.63 (0.44–1.03)
Sturnira lilium (346)		
Megistopoda proxima (310)	48.6 (43.2–54.0)	0.90 (0.77-1.04)
Aspidoptera falcata (446)	44.8 (39.5–50.2)	0.98 (0.83-1.18)
Carollia perspicillata (269)		
Trichobius joblingi (515)	66.9 (60.9–72.5)	1.91 (1.67–2.20)
Strebla guajiro (78)	22.0 (17.1–27.4)	0.29 (0.22-0.37)
Platyrrhinus lineatus (224)		
Trichobius angulatus (149)	33.9 (27.8–40.5)	0.67 (0.51-0.87)
Paratrichobius longicrus (61)	18.8 (13.9–24.5)	0.27 (0.19-0.38)

affected positively (path coefficient = 0.07) the prevalence of *A. phyllostomatis* on this host bat (Fig. 2). On the other hand, the prevalence and abundance of the flies *A. falcata*, *S. guajiro*, and *T. angulatus*, occurring on *S. lilium*, *C. perspicillata*, and *P. lineatus*, respectively, were positively affected by forest cover (Fig. 3).

The effect of edge length on ectoparasite abundance and prevalence presented opposite direction between ticks and flies (Fig. 4). The abundance of O. hasei decreased, and that of the flies M. proxima, A. falcata, and S. guajiro increased, as edge length increased. The net effect of edge length on the prevalence of O. hasei was positive (path coefficient = 0.16) because the negative direct effect was lower than the positive indirect effect through host abundance, whereas the prevalence of A. phyllostomatis was negatively affected (path coefficient = -0.16) indirectly only (Fig. 2). Effects of number of fragments also differed depending on the parasite-host species identity. The number of fragments negatively influenced the abundance of A. phyllostomatis on A. planirostris, as well as the abundance and prevalence of M. proxima on S. lilium. On the other hand, the prevalence of S. guajiro on C. perspicillata and the prevalence and abundance of T. angulatus on P. lineatus were positively affected by the number of fragments (Fig. 3).

Discussion

Our results support that responses of bat ectoparasites to forest loss and fragmentation are host and parasite specific. The effect direction of forest amount on the ectoparasite prevalence or abundance seems to be greatly dependent on the host identity. The prevalence or abundance of the tick O. hasei and the fly M. aranea on the large-sized bat A. planirostris are negatively affected by forest area, contrasting with the positive effect of forest cover on the prevalence or abundance of flies parasitizing the comparatively small bats S. lilium, C. perspicillata, and P. lineatus. Edge length and number of patches, which reflect forest fragmentation, also affect prevalence and abundance in different directions depending on the parasite-host species association. The effect of edge length supports opposite responses between the host-generalist tick (O. hasei) and the host-specialist flies, with the former negatively, and the flies positively, influenced by increasing edge length. This contrasting response between ticks and flies is reinforced by the absence of effect of edge length on the flies parasitizing the same host (A. planirostris) as the O. hasei ticks in the Serra da Bodoquena region. Likewise, different responses between ticks and flies occur regarding the influence of the number of fragments, which had no effect on ticks but positively or negatively affected fly species. Some similar studies also reveal different patterns among different ectoparasite-host Fig. 2 Path analyses of the interactions between Artibeus planirostris bats and three ectoparasite species in the Serra da Bodoquena region. Arrows represent the direction of the effect, and thickness represents the values of the standardized regression estimates. Solid and dashed lines indicate positive and negative correlations, respectively. Only significant relationships are showed. Aphy=Aspidoptera phyllostomatis, Mara = Megistopoda aranea, Ohas = Ornithodoros hasei, and Apla=Artibeus planirostris





Fig. 3 Path analyses of the six host-parasite relationships in the Serra da Bodoquena region. Arrows represent the direction of the effect, and thickness represents the values of the standardized regression estimates. Solid and dashed lines indicate positive and negative correlations, respectively. Only significant relationships are showed.

species associations. For instance, the prevalence of *M. aranea* on *Artibeus jamaicensis* bats (same size as, and closely related to *A. planirostris*) increases with forest cover in Mexico (Bolívar-Cimé et al. 2018), though prevalence of this same fly species on *A. planirostris* was unaffected by, and its abundance negatively responded to forest cover in the Serra

Parasites: Mpro=*Megistopoda proxima*, Afal=*Aspidoptera falcata*, Tjob=*Trichobius joblingi*, Sgua=*Strebla guajiro*, Plon=*Paratrichobius longicrus*, and Tang=*Trichobius angulatus*. Hosts: Slil=*Sturnira lilium*, Cper=*Carollia perspicillata*, and Plin=*Platyrrhinus lineatus*

da Bodoquena. Furthermore, Frank et al. (2016) found no evidence of forest cover effects on bat fly abundance across Costa Rican phyllostomids, but Mello et al. (2023) reported negative effects of forest cover on the prevalence of bat fly species across a human-dominated tropical landscape in Brazil. Therefore, the response of bat ectoparasites to changes Fig. 4 Regression estimates, standard error (bold bars), and 95% confidence intervals (tick lines) of the GLMM models. Colours indicate the predictors (green = forest cover, blue = edge length, and orange = number of fragments) and shapes indicate response variables (square = ectoparasiteprevalence, and circle = ectoparasite abundance). Ectoparasites: Afal=Aspidoptera falcata, Aphy=Aspidoptera phyllostomatis, Mara=Megistopoda aranea, Mpro=Megistopoda proxima, Ohas = Ornithodoros hasei, Sgua=Strebla guajiro, and Tang = Trichobius angulatus



in land use appears to be intricate, highlighting the need for further data on their biology and ecology. Next, we discuss some particularities of hosts and parasites that may explain the contrasting effects of landscape features on different batectoparasite associations.

The abundance of A. planirostris bats increased as forest area declined and edge length increased, an opposite response compared to that of S. lilium, C. perspicillata, and P. lineatus bats across our study sites. This indicates that A. planirostris differs from the other three frugivorous bats by taking advantage of forest reduction and fragmentation, as indeed supported by previous studies in our region (Silveira et al. 2018; Lino et al. 2021). Ticks Ornithodoros hasei are generalist parasites on bats and other mammals. Immature forms have been recorded on more than 30 bat species, mostly on phyllostomids, and adult ticks are found in bat roosts only (Muñoz-Leal et al. 2016; Nava et al. 2017). In our records, only O. hasei larvae occurred on A. planirostris and the prevalence of this species declined as forest cover increased. The free-living stages of some tick species respond positively to temperature and negatively to humidity (Randolph 2004), thus less covered areas could promote the occurrence of O. hasei because they become warmer and drier with evapotranspiration reduction (Davin and de Noblet-Ducoudré 2010). Such climatic changes in less covered and more fragmented landscapes can possibly reduce the proportion of forest areas safe from ticks, and consequently contribute to increase tick prevalence on A. planirostris. Furthermore, O. hasei might prevail on treeroosting bats rather than on cave-dwelling ones (Jones et al. 1972; Muñoz-Leal et al. 2016), and A. planirostris commonly roosts in tree holes or foliage (Garbino and da Tavares 2018). Therefore, the positive response of *A. planirostris* abundance to fragmentation may render it susceptible to *O. hasei* ticks, comparatively to the other three hosts with an opposite response to fragmentation.

Bats may use different roosting places intermittently as a strategy to escape ectoparasite infestation (Evelyn and Stiles 2003; Gorresen and Willig 2004; Saldaña-Vázquez et al. 2013). The low overall availability of roosting trees expected in landscapes with less forest cover may lead more bats to use the same roosts for longer, and to a greater aggregation of individuals roosting together (Hernández-Martínez et al. 2018). In our region, A. planirostris can roost in small-hollow thinner trees, and even in isolated ones in more altered forests, and records of radio-tracked individuals showed that adult males (N=5) forage only near their roosts, likely defending them against others (Martins 2016). This situation leads to a continuous use of the same roosts by several bats, thus contributing to ectoparasite transmission and to a higher prevalence of O. hasei ticks and abundance of M. aranea flies on A. planirostris in more deforested areas.

Edge length directly and positively affected the prevalence and abundance of *M. proxima* and *A. falcata* flies, both on *S. lilium*. This bat also roosts in tree hollows, though it apparently depends on large cavities of large-diameter trees of old-growth forests (Evelyn and Stiles 2003). Increased edge length can lead to low availability of large cavity-bearing trees as forest borders mainly comprise pioneer trees and lianas, and it additionally enables an easy access for logging in forest interiors (Harper et al. 2005). This could partially explain the decline of *S. lilium* abundance as fragmentation progresses, and also the positive relationships between edge length and parasitic infestation because few suitable roosts could increases host aggregation facilitating horizontal transmission (Morand and Poulin 1998).

We recorded two fly species on each of the three small bat species - S. lilium, C. perspicillata, and P. lineatus. On each of these hosts, forest cover positively influenced one fly species and had no effect on the other fly species. Such different responses between fly species on the same host may emerge due to difference of traits between them and/ or through interspecific interactions with asymmetrical outcomes (Linhares and Komeno 2000; Hiller et al. 2018). The prevalence and abundance of A. falcata, S. guajiro, and T. angulatus (on S. lilium, C. perspicillata, and P. lineatus, respectively) were higher in sites with higher forest cover, thus on bats roosting in less altered environmental conditions. Bat fly life cycles depend on the host roost conditions since their pupae are deposited in its internal walls until the emergence of the adults, which promptly need to find a bat to parasitize (ter Hofstede and Fenton 2005; Patterson et al. 2007). The greater fluctuations of temperature and humidity inside roosts at sites with low forest cover could be harmful for A. falcata, S. guajiro, and T. angulatus pupae development (Davies-Colley et al. 2000; Pilosof et al. 2012), which may explain the lower abundance of these ectoparasites in less forested landscapes. However, the absence of effect of forest cover on *M. proxima*, and no effect of any landscape variables on T. joblingi and P. longicrus (on S. lilium, C. perspicillata, and P. lineatus, respectively), show that they could tolerate more variable conditions or deposit their pupae deeper inside roosts, thus less exposed to external environmental conditions (Dittmar et al. 2009). Nonetheless, it is intriguing that Mello et al. (2023) found no effect of forest cover on the prevalence of A. falcata in an anthropogenic landscape, while the prevalence of *M. proxima*, *S.* guajiro, and T. joblingi increases in deforested areas. These contradictory results support that the biology of bat fly and host bat species per se do not influence alone the ectoparasite responses to landscape changes, and that local extrinsic factors may additionally account for them.

Overall results and previous studies indicate that responses of bat-ectoparasite interactions to forest loss and fragmentation are species-specific and dependent on the local context. Our results further highlight that responses of bat flies can vary due to their different life history traits, to the type and usage of roosts by their hosts, and to variable host abundance in different ways. Further data on the biology of multiple bat fly species are critical to shed light on the mechanisms behind different patterns of bat fly and bat species interactions in the Serra da Bodoquena. Since changes in land use can potentially lead to widespread disease outbreaks and epidemiological emergencies (Kitron 1998; Satjanadumrong et al. 2019), the higher prevalence of ticks on bats in deforested areas is of special concern. *Ornithodoros hasei* is a potential vector of pathogenic microorganisms, such as *Rickettsia* and *Bartonella* (Davoust et al. 2016; Tahir et al. 2016). Ticks carrying *Rickettsia* species can transmit spotted fever agents (Satjanadumrong et al. 2019), and bats are potential reservoirs of human pathogenic *Bartonella* spp. in the northern hemisphere (Veikkolainen et al. 2014). As a host-generalist ectoparasite, *O. hasei* is likely able to infest, and thus spread pathogens, to several mammal species and, ultimately, to domestic animals and humans (Mühldorfer 2013; Nava et al. 2017; Kingsley and Taylor 2017). Based on this concern and on our findings for *O. hasei* prevalence and abundance, we stress the importance of forest maintenance in order to prevent zoonotic diseases.

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Authors' contributions Alan Eriksson, Erich Fischer, and Gustavo Graciolli conceived the study design; Alan Eriksson collected the field data and the landscape metrics; Alan Eriksson, Antoine Filion, and Robert Poulin performed the statistical analyses; Alan Eriksson, Gustavo Graciolli, Marcelo Bahia Labruna, and Sebástian Muñoz-Leal carried out the laboratory analyses and taxonomic identifications; Alan Eriksson led the writing and all authors contributed to the discussion of the results.

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Data availability The raw data are available as supplementary material.

Declarations

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