

Habitat Patch Size and Landscape Structure Influence, Although Weakly, the Parasite Richness of an Arboreal Folivorous-frugivorous Primate in Anthropogenic Landscapes

Vinícius Freitas Klain

PUCRS: Pontifícia Universidade Católica do Rio Grande do Sul

Márcia Bohrer Mentz

Universidade Federal do Rio Grande do Sul

Sebastián Bustamante-Manrique

PUCRS: Pontifícia Universidade Católica do Rio Grande do Sul

Júlio César Bicca-Marques (✉ jcbicca@pucrs.br)

PUCRS: Pontifícia Universidade Católica do Rio Grande do Sul <https://orcid.org/0000-0002-5400-845X>

Research Article

Keywords: parasitic infection, landscape ecology, habitat fragmentation, habitat loss, parasite life cycle, brown howler monkey, Alouatta

Posted Date: May 18th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-509824/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Context

Anthropogenic habitat disturbances that affect the ecology and behavior of parasites and hosts can either facilitate or compromise their interactions and modulate the parasite richness.

Objectives

We assessed if the size of the habitat patch, the composition and configuration of the landscape (forest cover, patch density and mean distance to the nearest patch) and host group size influence the parasite richness of brown howler monkeys (*Alouatta guariba clamitans*) inhabiting forest fragments immersed in an anthropogenic matrix.

Methods

We collected fecal samples from 60 howler monkey groups inhabiting distinct forest fragments (one group/fragment) from January to July 2019. We used generalized linear models to assess the power of the independent variables in predicting parasite richness at the patch- and patch-landscape scales.

Results

We found 10 parasite taxa (five basal eukaryotes, four nematodes and one platyhelminth), nine of which also infect humans or domestic animals. Overall parasite richness showed an inverse relationship with habitat patch size and forest cover, and a direct relationship with the mean distance to the nearest patch and group size. Patch-landscape metrics and host group size also influenced the infection with parasites with direct cycle and transmission via ingestion of the infective stage in the arboreal environment or with parasites with indirect cycle and transmission via ingestion of intermediate hosts. However, all significant models presented low weight.

Conclusions

We suggest that characteristics of parasite and host populations among other factors are more critical modulators of the relationship between howler monkeys and their parasites in anthropogenic landscapes.

Introduction

Parasites are critical components of biodiversity and their interactions with hosts influence community structuring (Windsor 1997; Hudson et al. 2006; Lafferty et al. 2006). The outcome of their interactions depends on the characteristics of the interacting taxa and the modulating environmental factors (Combes 2001; Altizer et al. 2006). The life cycle of a parasite, for instance, influences the dynamics of parasitic infections. On one hand, the infection of a host with parasites with direct cycles (i.e. those requiring a single host species; Nunn and Altizer 2006) occurs via active skin or mucosa penetration by the infective

stage or via ingestion of contaminated water, food or soil (Nunn 2012). On the other hand, the infection with parasites with indirect cycles (i.e. those requiring at least two host species) occurs via the bite of a vector or the ingestion of larvae in infected intermediate or paratenic hosts (Thomas et al. 2005; Wobeser 2007; Chaisiri et al. 2019). Consequently, the patterns of parasite richness and prevalence in wild host populations reflect the hosts' density, diet, and home range size and pattern of use (Nunn et al. 2003; Gillespie and Chapman 2008; Calegaro-Marques and Amato 2010; Bicca-Marques and Calegaro-Marques 2016; Silveira and Calegaro-Marques 2016).

Parasites are often in equilibrium with their hosts; that is, they survive and reproduce without killing or making them sick (Dobson and May 1986). However, anthropogenic environmental disturbances that change the ecology and behavior of hosts and parasites, such as pollution, changes in habitat structure and reduction in food availability, can disrupt this equilibrium (Roberts et al. 2002; Sures 2006; Gillespie and Chapman 2008; Wright et al. 2009). For instance, sifakas (*Propithecus edwardsi*) living in disturbed habitats host a richer guild of endo- and ectoparasites than their conspecifics that range in more conserved habitats (Wright et al. 2009).

The reduction of habitat patch size via habitat loss and fragmentation is an environmental disturbance that can modify host-parasite relationships. While hosts that live in continuous forests and range over long distances are more likely to be exposed to parasites with direct and indirect cycles (Nunn et al. 2003), habitat fragmentation reduces habitat patch size, thereby promoting the reuse of potentially contaminated spaces and increasing the risk of infection with parasites with direct cycle (Trejo-Macías et al. 2007; Nunn 2012; Bicca-Marques and Calegaro-Marques 2016). The isolation of hosts in small habitat patches also increases population density, favoring the transmission of parasites with direct cycle among social individuals (Freeland 1979; Nunn et al. 2003; Altizer et al. 2006; Arroyo-Rodríguez and Dias 2010). The richness of gastrointestinal parasites of mantled howler monkeys (*Alouatta palliata aequatorialis*), for example, shows a direct relationship with group size (Helenbrook et al. 2015).

Arboreal species inhabiting small forest fragments may also need to cope with longer periods of scarcity of preferred foods, the frequent presence of humans and the contact with domestic animals (Arroyo-Rodríguez and Dias 2010; Chaves and Bicca-Marques 2016; Estrada et al. 2017). These factors can cause physiological and nutritional stress and increase the hosts' susceptibility to parasitic infections (Coop and Holmes 1996; Chapman et al. 2006a, 2006b, 2015; Gillespie and Chapman 2006; Nunn and Altizer 2006; Martínez-Mota et al. 2015; but see Chaves and Bicca-Marques 2016 and Chaves et al. 2018, 2019, for similar diet and physiological stress among brown howler monkey, *Alouatta guariba clamitans*, groups inhabiting <10-ha and >90-ha forest fragments).

The composition of the diet also influences the richness of parasites with indirect cycles whose infection occurs via ingestion of intermediate hosts (Anderson and May 1978; Mbora and McPeek 2009; Nunn 2012). Therefore, insectivorous species are more exposed to these parasites than folivorous and frugivorous ones (Vitone et al. 2004). However, the later foragers can also be infected with these parasites by inadvertently or intentionally ingesting prey to fulfill their energy demands when plant

resources are scarce or to benefit from an increase in invertebrate availability (Queiroz 1995; Nunn et al. 2003; Urquiza-Haas et al. 2008; Bicca-Marques et al. 2009; Kowalzik et al. 2010).

Habitats fragmented by urban development, farming and ranching also increase the contact of wildlife with humans and domestic animals. This contact increases parasite cross transmission, which increases the hosts' parasite richness compared with conspecifics that live in continuous habitats (Gillespie and Chapman 2006; Nunn and Altizer 2006; Gillespie et al. 2008; Kaur and Singh 2009; Kowalewski and Gillespie 2009). For instance, howler monkeys (*Alouatta* spp.) share 86% of their gastrointestinal parasites with humans (Kowalewski and Gillespie 2009).

Howler monkeys are good models to evaluate the influence of habitat patch size and landscape composition and configuration on the parasitic infections in wild species (e.g., Kowalewski and Gillespie 2009). These folivorous-frugivorous neotropical primates inhabit a wide range of forested habitats, from pristine forests to small forest fragments and orchards immersed in anthropogenic landscapes (Bicca-Marques 2003; Arroyo-Rodríguez and Dias 2010; Bicca-Marques et al. 2020).

Most authors that evaluated the relationship between metrics of the quality of habitat patches (e.g. size, form and spatial isolation, continuous forest vs. forest fragment, forest edge vs. forest interior) and howler monkey parasite richness did not find significant relationships (Valdespino et al. 2010; Helenbrook et al. 2017; Martínez-Mota et al. 2018), whereas others found a lower richness in populations of small and more disturbed forest fragments than in those inhabiting better conserved habitats (Cristobál-Azkarate et al. 2010). Most of these studies have compared parasite richness at higher level taxonomic groups (e.g. Nematoda, Cestoda and Protozoa) based on small samples distributed in habitat patches that were classified binarily into continuous forest or forest fragment.

These analyses at the patch-scale level did not take into account that the edge of the habitat patch does not represent an actual barrier for many species (Fahrig 2003; Arroyo-Rodríguez et al. 2013). Primates, parasites and intermediate hosts can move between forest fragments and interact with matrix elements, such as plantations of exotic trees, roofs and open fields. Therefore, the matrix surrounding the habitat patch can directly or indirectly change the parasitic dynamics. A matrix composed of human settlements and pastures, for example, may increase the bidirectional exchange of parasites between howler monkeys and humans and domestic animals. Howlers may get infected with these shared generalist gastrointestinal parasites when they use matrix elements or when people, cattle, dogs, cats and other domestic animals defecate inside the forest fragment. Consequently, an approach at the patch-landscape-scale (Arroyo-Rodríguez and Fahrig 2014; Galán-Acedo et al. 2019a) that allows to assess the relationship between parasite richness and the characteristics of the composition and configuration of the patch-landscape can help identifying the factors that modulate parasite-host relationships in populations isolated in habitat patches immersed in anthropogenic matrices.

In this study, we identified the gastrointestinal parasites of brown howler monkey (*Alouatta guariba clamitans*) groups inhabiting forest fragments immersed in an anthropogenic matrix. We assessed the relationship between parasite richness (overall and by life cycle) and characteristics of the fragments and

the landscapes. We classified parasites according to their life cycles and modes of transmission into those with (a) direct life cycle and transmission via ingestion of the infective stage in the forest canopy (e.g. *Trypanoxyuris*), (b) direct cycle and transmission via ingestion of the infective stage on the ground (e.g. *Ascaris*, *Eimeria*, *Endolimax*, *Entamoeba*, *Giardia*, *Iodamoeba*, *Isospora* and *Trichuris*) and (c) indirect cycle and transmission via ingestion of intermediate hosts (e.g. *Bertiella*, *Moniezia* and *Paragonimus*; Stuart et al. 1998; Kowalewski and Gillespie 2009; Solórzano-García and Pérez-Ponce de Léon 2018). On one hand, we assumed in our approach at the patch level that the interaction of howlers with matrix elements is not sufficiently strong to increase their parasite richness. Therefore, howler-parasite interactions would be limited by the size of the habitat patch. On the other hand, we assumed in our approach at the patch-landscape level that howlers' use of the matrix surrounding forest fragments exposes them to a greater parasite richness. Alternatively, in the absence of matrix use, a greater presence of domestic animals and humans inside forest fragments can also increase the parasite richness of howlers if they share parasites.

Methods

Study region and groups

We run this study from January to July 2019 in the rural region of Viamão, Rio Grande do Sul state, Brazil, near the southern limit of the distribution of brown howler monkeys (Culot et al. 2019). The landscape of the region is composed of a mosaic of forest fragments with varying levels of disturbance, crops, pastures and rural and suburban human settlements. At the patch-scale, we analyzed fecal samples of 60 groups of howlers (2-9 individuals, mean=5, SD=2) that inhabited 60 isolated forest fragments (1.2-257 ha, mean=25.8, SD=50.5, median=6.7, Fig. 1a). We analyzed independent landscapes surrounding 32 of these forest fragments for the analysis at the patch-landscape-scale (Fig. 1b). Howler group size in this subsample ranged from two to seven individuals (mean=5, SD=2, N=32).

Fecal sample collection and parasitological analysis

We collected 295 fecal samples from all individuals of the 60 groups once for the analysis at the patch-scale. We used the subsample of 32 groups above for the analysis at the patch-landscape-scale. Our sampling was approved by the Brazilian System of Authorization and Information on Biodiversity (SISBIO license nr 66648-1), although the Brazilian legislation (Article 10 of IBAMA's Normative Instruction nr. 154, 1st March 2007) does not require a license for the collection of fecal samples outside of legally protected nature reserves.

We collected ca. 2 g of material from the center of each stool to avoid contamination with larvae, eggs and oocysts found on the forest floor (Gillespie 2006) using disposable wooden spatulas. We pooled all individual samples of each howler group for assessing their parasite richness and preserved them in 10% formalin. This pooling increases the likelihood of detecting the group's parasites because the release of eggs, oocysts and larvae is not continuous; that is, while a parasite of a given host may lay eggs in a

given day, a conspecific parasite in another host individual from the same species may not (Gillespie 2006). Therefore, the likelihood of sampling all parasite taxa may increase with an increase in the number of stools composing a group's fecal pool. We included the number of fecal samples (=howler group size) per patch or patch-landscape in the modelling to assess its potential effect on the patterns of parasite richness. We transported the fecal samples in ice within 8 h of collection and stored them in a refrigerator at ca. 2°C until analysis, which took place after one to eight months of collection.

We used the flotation and the centrifuge-sedimentation in formalin ethyl-acetate techniques (De Carli 2001) to separate eggs, oocysts, cysts, larvae and adult parasites from the fecal remains of 4 g of each group's fecal pool. We analyzed the slides under an Olympus CH30 stereoscopic microscope using 200x magnification lenses.

We classified the parasite richness (number of parasite species) of each fecal pool into four categories: (a) overall richness, and richness of species with (b) direct cycle and transmission via ingestion of the infective stage in the arboreal milieu (hereafter direct-arboreal), (c) direct cycle and transmission via ingestion of the infective stage on the ground (hereafter direct-soil) and (d) indirect cycle and transmission via ingestion of the intermediate host (hereafter indirect-IH). We took advantage of adult helminth specimens recovered in necropsies of howler monkeys that died in conflicts with the study region's anthropogenic environment (Jesus et al. submitted) to identify the helminths at the species or genus levels because the taxonomic identification of eggs is unreliable (Gillespie 2006; Solórzano-García and Pérez-Ponce de Léon 2017).

Sampling design

We treated each forest fragment as a sampling unit in the patch-scale approach. We estimated fragment area (size) using polygons created in Google Earth Pro version 7.1.8 (Google Inc. 2017). For the patch-landscape-scale approach, we estimated forest cover, matrix permeability, patch density and Euclidean mean distance to the nearest fragment (Table 1) in radii from the center of the focal fragment (Arroyo-Rodríguez and Fahrig 2014) of each of the 32 independent patch-landscape sampling units.

We quantified the types of land cover in each landscape using satellite images with 30-m spatial resolution made available by the Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomass, collection 4). We classified the land cover types following MapBiomass: forest formation (including dense, open and mixed ombrophilous forests, semideciduous and deciduous seasonal forests, and secondary forest), planted forest of commercial tree species, grasslands, farming (including annual and perennial crops and pasture), wetlands, water (rivers and lakes) and urban infrastructure (urban areas with a predominance of non-vegetated surfaces, including buildings and roads and other transportation infrastructure). The mapping of the MapBiomass Project has an accuracy of 85.8% for the Atlantic Forest biome. We used ArcGis 10.3 (Esri 2014) for the GIS processing and Fragstats (McGarigal et al. 2012) to calculate the landscape metrics described below.

The proportion of the patch-landscape covered by forest is the main metric of habitat availability for arboreal primates such as howler monkeys. A larger forest cover may promote a lower richness of direct-soil parasites because howlers will be less likely to descend to the ground to cross non-forest matrix elements. It may also promote a lower richness of direct-arboreal parasites because howlers will be able to use larger home ranges, thereby reducing the risk of reinfection (see Bicca-Marques and Calegaro-Marques 2016).

The type of matrix influences the effectiveness of fragment isolation via its permeability to species dispersal (Metzger and Décamps 1997). A permeable matrix that allows howlers to move between forest fragments increases their risk of infection with direct-soil parasites. We classified the permeability of land cover types in a gradient from low (weight 1) to high (weight 10) by calculating the mean of their weights in the literature (Galán-Acedo et al. 2019b; Rabelo et al. 2019; Jardim et al. in prep.; see Supplementary Material Table A1).

Patch density is a measure of the fragmentation of the patch-landscape. A highly fragmented patch-landscape may reflect a greater presence of people and domestic animals in the landscape and inside the target forest fragment. This presence increases the howlers' risk of contact with generalist direct-soil parasites shared with these hosts.

The mean Euclidean distance to the nearest forest fragment is a measure of between-fragment isolation in the patch-landscape. The higher the isolation between fragments in a given patch-landscape, the longer the distance that howlers have to cross in the matrix to move between habitat patches. Consequently, the higher the risk of infection with direct-soil parasites.

We identified the spatial scale with the greatest explanatory power (scale of effect) of the categories of parasite richness in the analysis at the patch-landscape-scale (Jackson and Fahrig 2012). We built buffers with radii of 250, 500, 750 and 1,000 m from the center of the target forest fragment of each patch-landscape (Fig. 2). We used 250 m as the smallest radius because the likelihood of successful howler dispersal through a non-forest matrix between discrete habitat patches decreases significantly at distances longer than 200 m (Mandujano and Estrada 2005). We calculated the effect of each patch-landscape metric (Table 1) for each category of parasite richness inside each buffer. The 750-m buffer, for instance, showed the greatest effect of forest cover on overall parasite richness. Then, we generated an equation containing all patch-landscape metrics and their scales with greatest effects to model their potential as predictors of parasite richness. The equation for the modelling of overall parasite richness was:

where is the forest cover inside the 750-m buffer, is the patch density inside the 1,000-m buffer, is the mean Euclidean distance to the nearest forest fragment inside the 1,000-m and is the permeability of the matrix inside the 1,000-m buffer.

We used the variance inflation factor (VIF) to check for multicollinearity between variables at the patch-landscape-scale. We excluded matrix permeability from all equations because it was strongly collinear

with forest cover ($VIF > 4$; Supplementary Material Table A2) in all models. The remaining three metrics were not colinear (all $VIF < 4$; Supplementary Material Table A3). Therefore, we modelled the effect of forest cover, patch density and mean Euclidean distance to the nearest forest fragment on the four categories of parasite richness.

Data analyses

We used generalized linear mixed models (GLMMs) to assess the relationship between habitat patch (forest fragment) size or patch-landscape metrics and the four categories of parasite richness. We checked the normality, homoscedasticity and autocorrelation of residuals to validate the models. We built the models with the Gaussian family because these assumptions were met. Moreover, we used the logit family to build binomial models with binary variables. We used fragment size and howler group size as fixed factors and season of fecal sample collection as random factor in the global model of the analysis at the patch-scale. Similarly, we used group size and the three patch-landscape metrics as fixed factors and season of fecal sample collection as random factor in the global model of the analysis at the patch-landscape-scale. We included the season of fecal sample collection because it may influence the dynamics of parasitic infections due to seasonal fluctuations in climatic conditions (Altizer et al. 2006). We used the function *dredge* of the MuMIn package of R (Barton 2016) to assess the influence of all predictor combinations on the four categories of parasite richness.

We used the Akaike Information Criterion (AIC) to select the model(s) with the greatest explanatory power of the predictor effects on parasite richness. Specifically, we used the AICc as recommended for small samples (Burnham and Anderson 2003). Although the model with the lowest AICc has the best adjustment, all models with $\Delta AICc < 6$ are equally parsimonious (Richards 2015). We considered that a given patch-landscape metric explains the parasite richness of howler monkeys if it is included in the best model or in many parsimonious models (Richards 2011) and if its relationship with parasite richness is significant. We run all analyses in R 3.5.1 (R Core Team 2018) using the lme4, car and MuMIn packages (Bates et al. 2015; Barton 2016; Fox and Weisberg 2019). We set a level of significance of 0.05 in all analyses.

Data availability

All associated data will be available in a data repository when the paper is published.

Results

We found 10 taxa parasitizing howler monkeys at the patch-scale: the basal eukaryotes *Balantidium* sp., *Eimeria* sp., *Entamoeba* sp., *Giardia* sp. and *Isospora* sp., the nematodes *Strongyloides* sp., *Trichuris* sp., *Trypanoxyuris minutus* and an unidentified Ancylostomatidae, and the platyhelminth cestode *Bertiella studeri* (Supplementary Material Figure A1). Whereas the sampling reached sufficiency at the patch-scale, it accounted for 77% of the expected richness at the patch-landscape-scale (Supplementary Material

Figure A2). Most of the howlers' parasites ($n=8$ taxa or 80%) have direct-soil cycles (Table 2). A single species has direct-arboreal cycle (*T. minutus*) and another has indirect-IH cycle (*B. studeri*).

The parasites with higher prevalence in the patch-scale approach ($N=60$) were *Strongyloides* sp. (45%), *Isospora* sp. (41%), *B. studeri* (40%) and *T. minutus* (33%; Supplementary Material Figure A3). They were also the most prevalent in the patch-landscape-scale approach (*Strongyloides* sp. and *Isospora* sp., both 47%; *T. minutus*, 41%; *B. studeri*, 40%; Supplementary Material Figure A3). The overall parasite richness per group ranged from zero to seven taxa in the patch-scale approach and from zero to six taxa in the patch-landscape-scale approach (Supplementary Material Figure A4; both approaches: mean=3 taxa/group, median=3). Most samples contained at least one parasite taxon in both approaches (patch-scale: $n=53$ or 88%; patch-landscape-scale: $n=30$ or 93%).

Fragment size showed an inverse relationship with overall parasite richness in the patch-scale approach (Table 3, Fig. 3a). However, the significance of this relationship disappears with the exclusion of the two largest fragments (>250 ha) and their negative samples (parameter=-0.008, SE=0.008, $p=0.275$). The richness of direct-soil parasites showed a weak inverse relationship with fragment size (Table 3, Fig. 3b). This relationship also weakens substantially with the exclusion of the two largest fragments and their samples (parameter=-0.001, SE=0.003, $p=0.592$). Group size showed a direct relationship only with the occurrence of indirect-IH parasites (Fig. 3c).

All models of overall parasite richness in the patch-landscape-scale approach showed $\Delta\text{AICc}<6$ and low weight (maximum=0.293, minimum=0.036; Supplementary Material Table A4). The model with the lowest ΔAICc included forest cover (inverse relationship with richness) and group size (weak direct relationship with richness; Table 4, Figs. 4a and 4b). The mean Euclidean distance to the nearest forest fragment also showed a direct relationship with overall parasite richness in the third model (Table 4, Fig. 4c).

No patch-landscape metric showed a significant relationship with the richness of direct-soil parasites in the 14 models with $\Delta\text{AICc}<6$. The model with the lowest ΔAICc only included the mean Euclidean distance to the nearest forest fragment (Table 4, Supplementary Material Table A5). The relationship between this metric and richness category is stronger when group size is entered as a random factor in the modelling (parameter=0.014, SE=0.007, $p=0.048$; Fig. 4d).

Forest cover was the only metric with a significant (inverse) relationship with the occurrence of direct-arboreal parasites (Fig. 4e). It was also the unique variable included in the model with lowest ΔAICc from the 13 models with $\Delta\text{AICc}<6$, whose weights ranged from 0.287 to 0.017 (Table 4, Supplementary Material Table A6).

Finally, patch density showed a direct relationship with the occurrence of indirect-IH parasites (Table 4). The model with lowest ΔAICc only included patch density (Fig. 4f). Group size also showed a direct relationship with the occurrence of *B. studeri* (Fig. 4g). However, all models had low weight (maximum=0.171, minimum=0.012; Table 4, Supplementary Material Table A7).

Discussion

The 10 gastrointestinal parasite taxa that we found in the fecal samples, most with direct-soil cycles, were shared with humans and domestic animals at least at the genus level (Kowalewski and Gillespie 2009) and included the first record of *Balantidium* sp. for the brown howler monkey. This basal eukaryote had been reported for *Alouattacaraya*, *A. pigra* and *A. seniculus* (Solórzano-García and Pérez-Ponce de Léon 2018). The overall parasite richness of our sample was similar to that recorded in studies that sampled 15+ groups of *Alouatta* spp. (Trejo-Macías and Estrada 2012: 11, Helenbrook et al. 2015, 2017: 19 and 23, respectively) and is compatible with the arboreal lifestyle and folivorous-frugivorous diet of howlers. However, this richness is low compared with the parasite fauna of neotropical primates that ingest animal matter (Solórzano-García and Pérez-Ponce de Léon 2018), even if we add those blood parasites with filaria transmission via invertebrate vectors, such as *Dipetalonema gracile* found in necropsies (Jesus et al. submitted), that are not detected in coprological examinations. The similar group prevalence of parasites in the analyses at the patch- and patch-landscape-scales shows that the subsample of independent patch-landscapes did not bias the pattern found in the full patch sample.

Despite the likely relationship between patch size and the proximity to humans and domestic animals, this patch-scale metric played a minor role in modulating the groups' parasite richness. The inverse relationship between patch size and overall parasite richness was weak and biased by the two largest fragments. However, the inverse relationship between forest cover and overall richness and the direct relationship between the mean Euclidean distance to the nearest fragment and overall richness in the analysis at the patch-landscape-scale are compatible with a greater proximity between howler monkeys and humans and domestic animals in more fragmented landscapes, either in the matrix or inside the fragment itself. This hypothesis is supported by the sharing of most parasites by howlers and humans or domestic animals at least at the genus level. If people and domestic animals enter the forest fragment and defecate on the floor, howlers may contact the infective stages of direct-soil parasites when descending to the ground to cross canopy gaps (Bicca-Marques and Calegaro-Marques 1995; Prates and Bicca-Marques 2008). The infective stages may be transferred to the hands and ingested accidentally (Vitazkova 2009; Gallagher et al. 2019). An alternative non-mutually exclusive explanation for these relationships is that small fragment size and low forest cover are associated with low food availability. This condition could increase the probability of howlers of using the matrix to move between habitat patches in their search for food, thereby exposing them to direct-soil parasites. This outcome is compatible with the fact that the mean Euclidean distance to the nearest fragment was a good predictor of parasite richness.

The analyses of the relationships of the occurrence of *T. minutus* (the only howler parasite with a direct-arboreal cycle in this study) at the patch- and patch-landscape-scales produced contrasting results. While fragment size did not predict the occurrence of this pinworm at the patch-scale, forest cover showed a negative relationship with its occurrence at the patch-landscape-scale. The latter could be explained by the howlers' habit of rubbing the perianal region on tree trunks after defecation (Hirano et al. 2008). This habit increases the release of pregnant female pinworms in the substrate, thereby increasing the risk of

infection and reinfection of group members via ingestion of eggs, particularly in smaller home ranges. If reinfection increases parasitic load, it shall increase the likelihood of finding eggs in howlers' feces. However, given that the model's weight was low, that patch size did not predict this pinworm's occurrence at the patch-scale and that necropsies of 36 howlers from the same region showed a prevalence of 100% with this nematode (Jesus et al. submitted), it is more likely that this relationship with forest cover is spurious.

The interpretation of the positive relationship between the occurrence of the only parasite with indirect-IH cycle, *B. studeri*, and patch density and group size focuses on the ecology of howlers and the oribatid mite intermediate hosts (Denegri 1993). These mites can either live in the forest dossel (Schäffer et al. 2020) or be important phytophagous, predators or coprophagous components of the soil fauna (Behan e Hill 1983; Denegri 1993; Denegri et al. 1998).

On one hand, the aforementioned rubbing behavior after defecation can release *B. studeri*'s eggs on the trunks and create opportunities for infection if the mites live in the canopy. Under this scenario, larger howler groups impose higher risks of canopy contamination via rubbing than smaller groups. This contamination might be particularly critical as the reuse of small home ranges is higher in more fragmented landscapes characterized by higher densities of forest fragments. The higher infection of folivorous New World monkeys (*Alouatta*, *Ateles* and *Brachyteles*) compared with those that do not eat leaves (*Callimico*, *Cebuella* and *Mico*; Dunn 1962) is compatible with the ingestion of mites during leaf eating (Souza Jr et al. 2008; Oliveira et al. 2011). Whether these mites are herbivorous, predators, coprophagous or omnivorous is another open question.

On the other hand, given that the heterogeneity of the landscape for forest living species, such as howlers, increases with increasing density of forest fragments, the relationship between patch density and *B. studeri* occurrence is compatible with the hypothesis that the intermediate host mites are terrestrial and coprophagous. This hypothesis assumes that howler group size and relative density are inversely related to habitat patch size (Peres 1997) and that larger groups produce larger fecal clusters on the forest floor as a consequence of their behavior of defecating synchronously in "latrines" after resting periods (Gilbert 1997; Kowalewski and Zunino 2005; Pouvelle et al. 2009). Larger fecal clusters are likely to be more attractive to coprophagous mites. Given that howlers descend more often to the forest floor to cross canopy gaps or to move between habitat patches in smaller and more disturbed forest fragments (Prates and Bicca-Marques 2008; Bicca-Marques et al. 2020), the contact with mites might occur on the ground. However, the ingestion of mites is likely to occur intentionally during self- or allogrooming or unintentionally during feeding, both in the canopy, as howlers do not groom on the ground and rarely feed in this environment.

The low predictive power of forest cover, patch density and mean Euclidean distance to the nearest fragment suggest that these patch-landscape metrics are weak modulators of the interactions between howler monkeys and their parasites. Two non-mutually exclusive hypotheses may explain these findings. First, these metrics are inadequate to represent the influence of humans and domestic animals as

potential sources of parasites shared with howlers. Second, howlers use the matrix only rarely. It is likely that the density of humans and domestic animals, their parasite richness and prevalence and their use of forest fragments are stronger modulators of the contamination of the environment with the infective stages of parasites with direct-soil cycles and of howlers' infection. The identification of humans and domestic animals as the likely sources of the infection of howlers (*A. pigra*, Vitazkova and Wade 2006, 2007; Vitazkova 2009) and gorillas (*Gorilla beringei*, Graczyk et al. 2002) with *Giardia* spp. supports the importance of evaluating the influence of these refined metrics on parasite-wildlife interaction in anthropic landscapes. It is also necessary to identify and study the biology of intermediate hosts, such as orbatid mites, to uncover the relationship between the landscape and the interaction of parasites like *Bertiella* spp. with arboreal primate hosts.

In sum, we did not find strong evidence that the potential use of the anthropogenic matrix and of other elements of the patch-landscape by the howler monkeys has increased their interaction with parasites. It is more likely that howler groups limit their activities to the fragment interior and to a narrow strip of the surrounding matrix. The low power of all models at the patch- and patch-landscape-scales in identifying the predictors of howler-parasite relationships in anthropogenic landscapes highlights the importance of uncovering the relevant habitat and matrix characteristics that interact with parasite and host populations to promote the dynamics of infection and cross-species exchange. Future studies should also include direct measures of the presence of humans and domestic animals in the matrix (e.g., population density) and the interior of forest fragments together with metagenomic analyses of the fecal samples of these hosts and howler monkeys to assess whether their parasites are shared at the species level. This sharing would support a critical role of the characteristics of host populations in modulating the relationship between howler monkeys and their parasites in anthropogenic landscapes.

Declarations

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Acknowledgments

We thank the land owners for the permission to access the forest fragments and the Gomes family for hosting VFK during the study. We thank Víctor Arroyo-Rodríguez for his advice on the analysis at the patch-landscape-scale and Ana Cristina Aramburu da Silva, Carlos Graeff-Teixeira, Cláudia Calegaro-Marques, Márcia Maria de Assis Jardim and Víctor Arroyo-Rodríguez for their constructive comments on an earlier draft of the manuscript. We also thank the personnel from the Laboratório de Helmintologia/UFRGS for the collaboration and the Brazilian National Council of Scientific and Technological Development/CNPq for MSc fellowships to VFK and SBM and a Research Productivity fellowship to JCBM (PQ 1C #304475/2018-1).

References

1. Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P (2006) Seasonality and the dynamics of infectious diseases. *Ecol Lett* 9:467–484
2. Anderson RM, May R (1978) Regulation and stability of host-parasite population interactions. *J Anim Ecol* 47:219–247
3. Arroyo-Rodríguez V, Dias PA (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. *Am J Primatol* 72:1–16
4. Arroyo-Rodríguez V, Fahrig L (2014) Why is a landscape perspective important in studies of primates? *Am J Primatol* 76:901–909
5. Arroyo-Rodríguez V, Moral EC, Mandujano S, Chapman CA, Reyna-Hurtado R, Fahrig L (2013) Assessing habitat fragmentation effects for primates: the importance of evaluating questions at the correct scale. In: Marsh LK, Chapman CA (eds) *Primates in fragments, developments in primatology: progress and prospects*. Springer, New York, pp 230–257
6. Barton K (2016) Package ‘MuMIn’: multi-model inference. R Package Version 1.15.6
7. Bates G, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
8. Behan V, Hill S (1983) Feeding habits of sixteen species of Oribatei (*Acaris*) from an acid peat bog, glenamoy-ireland. *Rev Ecol Biol Soil* 20:221–267
9. Bicca-Marques JC, Calegaro-Marques C (1995) Locomotion of black howlers in a habitat with discontinuous canopy. *Folia Primatol* 64:55–61
10. Bicca-Marques JC, Calegaro-Marques C (2016) Ranging behavior drives parasite richness: a more parsimonious hypothesis. *Am J Primatol* 78:923–927
11. Bicca-Marques JC, Chaves OM, Hass G (2020) Howler monkey tolerance to habitat shrinking: lifetime warranty or death sentence? *Am J of Primatol* e23089
12. Bicca-Marques JC, Muhle CB, Prates HM, Oliveira SG, Calegaro-Marques C (2009) Habitat impoverishment and egg predation by *Alouatta caraya*. *Int J Primatol* 30:743–748
13. Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York
14. Calegaro-Marques C, Amato SB (2010) Helminths of introduced house sparrows (*Passer domesticus*) in Brazil: does population age affect parasite richness? *Ilheringia Série Zoologia* 100:73–78
15. Chaisiri K, Dusitsittipon S, Panitvong N, Ketboonlue T, Nuamtanong S, Thaenkham U, Morand S, Dekumyoy P (2019) Distribution of the newly invasive new guinea flatworm *Platydemus manokwari* (Platyhelminthes: Geoplanidae) in Thailand and its potential role as a paratenic host carrying *Angiostrongylus malayensis* larvae. *J Helminthol* 93:711–719
16. Chapman CA, Schoof VA, Bonnell TR, Gogarten JF, Calmé S (2015) Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. *Philos T B R Soc* 370:20140112

17. Chapman CA, Speirs ML, Gillespie TR, Holland T, Austad KM (2006a) Life on the edge: gastrointestinal parasites from the forest edge and interior primate groups. *Am J Primatol* 68:397–409
18. Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006b) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *Am J Phys Anthropol* 131:525–534
19. Chaves ÓM, Bicca-Marques JC (2016) Feeding strategies of brown howler monkeys in response to variations in food availability. *Plos One* 11:e0145819
20. Chaves ÓM, Bicca-Marques JC, Chapman CA (2018) Quantity and quality of seed dispersal by a large arboreal frugivore in small and large Atlantic forest fragments. *Plos One* 13:e0193660
21. Chaves ÓM, Fernandes FA, Oliveira GT, Bicca-Marques JC (2019) Assessing the influence of biotic, abiotic, and social factors on the physiological stress of a large Neotropical primate in Atlantic forest fragments. *Sci Total Environ* 690:705–716
22. Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. University of Chicago Press, Chicago
23. Coop RL, Holmes PH (1996) Nutrition and parasite interaction. *Inter J Parasitol* 26:951–962
24. Cristóbal-Azkarate J, Hervier B, Vegas-Carrillo S, Rodríguez-Luna E, Veà JJ (2010) Parasitic infections of three Mexican howler monkey groups (*Alouatta palliata mexicana*) living in forest fragments in Mexico. *Primates* 51:231–239
25. Culot L, Pereira LA, Agostini I, Almeida MAB, Alves RSC, Aximoff I, Bager A, Baldovino MC et al (2019) Atlantic-primates: a dataset of communities and occurrences of primates in the Atlantic forests of South America. *Ecology* 100:e02525
26. De Carli GA (2001) Parasitologia clínica: seleção de métodos e técnicas de laboratório. Atheneu, São Paulo
27. Denegri GM (1993) Review of oribatid mites as intermediate hosts of tapeworms of the Anoplocephalidae. *Exp Appl Acarol* 17:567–580
28. Denegri GM, Bernadina W, Perez-Serrano J, Rodriguez-Caabeiro F (1998) Anoplocephalid cestodes of veterinary and medical significance: a review. *Folia Parasit* 45:1–8
29. Dobson AP, May RM (1986) Disease and conservation. In: Soule M (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, pp 345–365
30. Dunn FL (1962) Acanthocephalans and cestodes of South American monkeys and marmosets. *J Parasitol* 49:717–722
31. Eckert KA, Hahn NE, Genz A, Kitchen DM, Stuart MD, Averbeck GA, Stromberg BE, Markowitz H (2006) Coprological surveys of *Alouatta pigra* at two sites in Belize. *Int J Primatol* 27:227–238
32. Esri (2014) Environmental systems research institute. ArcGIS 10.3 Geostatistical Analyst. Available at: <https://desktop.arcgis.com/en/arcmap/>

33. Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A et al (2017) Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 3:e1600946
34. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S* 34:487–515
35. Freeland WJ (1979) Primate social groups as biological islands. *Ecology* 60:719–728
36. Fox J, Weisberg S (2019) An R companion to applied regression. Sage publications, Thousand Oaks
37. Galán-Acedo C, Arroyo-Rodríguez V, Cudney-Valenzuela SJ, Fahrig L (2019a) A global assessment of primate responses to landscape structure. *Biol Rev* 94:1605–1618
38. Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G (2019b) Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecol* 34:147–158
39. Gallagher C, Beierschmitt A, Cruz K, Choo J, Ketzis J (2019) Should monkeys wash their hands and feet: A pilot-study on sources of zoonotic parasite exposure. *One Health* 7 doi:10.1016/j.onehlt.2019.100088
40. Gilbert KA (1997) Red howling monkey use of specific defecation sites as parasite avoidance strategy. *Anim Behav* 54:451–455
41. Gillespie TR (2006) Noninvasive assessment of gastrointestinal parasite infections in free-ranging primates. *Int J Primatol* 27:1129–1143
42. Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. *Conserv Biol* 20:333–336
43. Gillespie TR, Chapman CA (2008) Forest fragmentation, the decline of an endangered primate, and changes in host–parasite interactions relative to an unfragmented forest. *Am J Primatol* 70:222–230
44. Gillespie TR, Nunn CL, Leendertz FH (2008) Integrative approaches to the study of primate infectious disease: implications for biodiversity conservation and global health. *Am J Phys Anthropol* 51:51–69
45. Google incorporation (2017) Google Earth pro version 7.1.8. California, USA. Available at: <https://www.google.com.br/earth/download/gep/agree.html>
46. González-Hernández M, Dias PA, Romero-Salas D, Canales-Espinosa D (2011) Does home range use explain the relationship between group size and parasitism? a test with two sympatric species of howler monkeys. *Primates* 52:211–216
47. Graczyk TK, Bosco-Nizeyi J, Ssebide B, Thompson RC, Read C, Cranfield MR (2002) Anthroponozoonotic *Giardia duodenalis* genotype (assemblage A) infections in habitats of free-ranging human-habituated gorillas, Uganda. *J Parasitol* 88:905–909
48. Helenbrook WD, Stehman SV, Shields WM, Whipps CM (2017) Association of anthropogenic disturbances and intestinal parasitism in ecuadorian mantled howler monkeys, *Alouatta palliata aequatorialis*. *Folia Primatol* 88:307–322
49. Helenbrook WD, Wade SE, Shields WM, Stehman SV, Whipps CM (2015) Gastrointestinal parasites of ecuadorian mantled howler monkeys (*Alouatta palliata aequatorialis*) based on fecal analysis. *J*

50. Hirano ZB, Correa IC, Oliveira DAG (2008) Contexts of rubbing behavior in *Alouatta guariba clamitans*: a scent-marking role? Am J Primatol 70:575–583
51. Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21:381–385
52. Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecol 27:929–941
53. Jesus SL, Calegaro-Marques C, Klain VF, Chaves ÓM, Bicca-Marques JC (Submitted) Necropsies disclose a low helminth parasite diversity in arboreal folivorous-frugivorous primates in a periurban landscape. Biodiv Conserv.
54. Kaur T, Singh J (2009) Primate-parasitic zoonoses and anthropozoonoses: a literature review. In: Huffman MA, Chapman CA (eds) Primate parasite ecology: the dynamics and study of host-parasite relationships. Cambridge University Press, Cambridge, pp 190–230
55. Kowalewski MM, Gillespie TR (2009) Ecological and anthropogenic influences on patterns of parasitism in free-ranging primates: a meta-analysis of genus *Alouatta*. In: Garber PA (ed) Developments in primatology: progress and prospects. Springer, Illinois, pp 433–461
56. Kowalewski MM, Salzer JS, Deutsch JC, Raño M, Kuhlenschmidt MS, Gillespie TR (2011) Black and gold howler monkeys (*Alouatta caraya*) as sentinels of ecosystem health: patterns of zoonotic protozoa infection relative to degree of human-primate contact. Am J Primatol 73:75–83
57. Kowalewski M, Zunino GE (2005) The parasite behavior hypothesis and the use of sleeping sites by black howler monkeys (*Alouatta caraya*) in a discontinuous forest. Neotropical Primates 13:22–26
58. Kowalzik BK, Pavelka MS, Kutz SJ, Behie A (2010) Parasites, primates and ant-plants: clue to the life cycle of *Controrchis* spp. in black howler monkeys (*Alouatta pigra*) in southern Belize. J Wildlife Dis 46:1330–1334
59. Lafferty KD, Dobson AP, Kuris AM (2006) Parasites dominate food web links. P Natl A Sci 103:11211–11216
60. Mandujano S, Estrada A (2005) Detección de umbrales de área y distancia de aislamiento para la ocupación de fragmentos de selva por monos aulladores, *Alouatta palliata*, en Los Tuxtlas, México. Universidad y Ciencia 2:11–21
61. Martínez-Mota R, Kowalewski MM, Gillespie TR (2015) Ecological determinants of parasitism in howler monkeys. In: Kowalewski M, Garber P, Cortés-Ortiz L, Urbani, Youlatos D (eds) Developments in primatology: progress and prospects. Springer, New York, pp 259–285
62. Martínez-Mota R, Pozo-Montuy G, Sánchez YM, Gillespie TR (2018) Effects of anthropogenic stress on the presence of parasites in a threatened population of black howler monkeys (*Alouatta pigra*). Therya 9:161–169
63. Mbora DN, McPeek MA (2009) Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. J Anim Ecol 78:210–218

64. McGarigal K, Cushman SA, Ene E (2012) Fragstats v4: spatial pattern analysis program for categorical and continuous maps. Available at: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
65. Metzger JP, Décamps H (1997) The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Ecol* 18:1–12
66. Nunn CL (2012) Primate disease ecology in comparative and theoretical perspective. *Am J Primatol* 74:497–509
67. Nunn CL, Altizer S (2006) Infectious diseases in primates: behaviour, ecology and evolution. Oxford University Press, Oxford
68. Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasite species richness in primates. *Am Nat* 162:597–614
69. Oliveira SG, Prates HM, Bicca-Marques JC (2011) Prevalência de *Bertiella* sp. em um grupo de bugios-pretos, *Alouatta caraya* (Humbolt, 1812). In: Melo FR, Mourthé I (eds) A Primatologia no Brasil. Sociedade Brasileira de Primatologia, Belo Horizonte, pp 273–279
70. Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). *Folia Primatol* 68:199–222
71. Pouvelle S, Jouard S, Feer F, Tully T (2009) The latrine effect: impact of howler monkeys on the distribution of small seeds in a tropical rain-forest soil. *J Trop Ecol* 25:239–248
72. Prates HM, Bicca-Marques JC (2008) Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an orchard forest. *Int J Primatol* 29:703–715
73. Projeto MapBiomas (2019) MapBiomas Project, Collection [4] of the Annual Land Use Land Cover Maps of Brazil. <http://mapbiomas.org>
74. Queiroz HL (1995) Preguiças e guaribas: os mamíferos folívoros arborícolas do Mamirauá. Conselho Nacional de Desenvolvimento Científico e Tecnológico, Diretoria de Unidades de Pesquisa
75. R Core Team (2018) R: A language and environment for statistical computing. Vienna, AUT. Available at: <http://www.R-project.org/>
76. Rabelo RM, Aragón S, Bicca-Marques JC, Nelson BW (2019) Habitat amount hypothesis and passive sampling explain mammal species composition in Amazonian river islands. *Biotropica* 51:84–92
77. Richards SA (2015) Likelihood and model selection. In: Fox GA, Yankelevich SN, Sosa VJ, (eds) Ecological statistics: contemporary theory and application. Oxford University Press, Oxford, pp 58–80
78. Richards SA, Whittingham MJ, Stephens PA (2011) Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behav Ecol Soc* 65:77–89
79. Roberts MG, Dobson AP, Arneberg P, Leo GA, Krecek RC, Manfredi MT, Lanfranchi P, Zaffaroni E (2002) Parasite community ecology and biodiversity. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) The ecology of wildlife diseases. Oxford University Press, Oxford, pp 63–82

80. Schäffer S, Koblmüller S, Krisper G (2020) Revisiting of arboreal life in oribatid mites. *Diversity* 12:255
81. Silveira TS, Calegaro-Marques C (2016) Helminth parasite diversity discloses age and sex differences in the foraging behaviour of southern lapwings (*Vanellus chilensis*). *Austral Ecol* 41:549–558
82. Solórzano-García B, Pérez-Ponce de León G (2017) Helminth parasites of howler and spider monkeys in Mexico: insights into molecular diagnostic methods and their importance for zoonotic diseases and host conservation. *Int J Parasitol Parasite Wildl* 6:76–84
83. Solórzano-García B, Pérez-Ponce de León G (2018) Parasites of neotropical primates: a review. *Int J Primatol* 39:155–182
84. Souza Jr JC, Goulart JA, Varnier S, Denegri G, Filho HH, Hirano ZMB, Avila-Pires FD (2008) Bertielloisis in Brazilian non-human primates: natural infection in *Alouatta guariba clamitans* (Cabrera, 1940) (Primates: Atelidae) in Santa Catarina state, Brazil. *Revista de Patologia Tropical* 37:48–56
85. Stoner KE (1996) Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implications for conservation biology. *Conserv Biol* 10:539–546
86. Stuart M, Pendergast V, Rumfelt S, Pierberg S, Greenspan L, Glander K, Clarke M (1998) Parasites of wild howlers (*Alouatta* spp.). *Int J Primatol* 19:493–512
87. Stuart MD, Greenspan LL, Glander KE, Clarke MR (1990) A coprological survey of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. *J Wildlife Dis* 26:547–549
88. Sures B (2006) How parasitism and pollution affect the physiological homeostasis of aquatic hosts. *J Helminthol* 80:151–157
89. Thomas F, Renaud F, Guégan GF (2005) Parasitism and ecology. Oxford University Press, Oxford
90. Trejo-Macías G, Estrada A (2012) Risk factors connected to gastrointestinal parasites in mantled *Alouatta palliata mexicana* and black howler monkeys *Alouatta pigra* living in continuous and in fragmented rainforests in Mexico. *Curr Zool* 58:375–383
91. Trejo-Macías G, Estrada A, Cabrera MM (2007) Survey of helminth parasites in populations of *Alouatta palliata mexicana* and *A. pigra* in continuous and fragmented habitat in southern Mexico. *Int J Primatol* 28:931–945
92. Urquiza-Hass T, Serio-Silva JC, Hernández-Salazar LT (2008) Traditional nutritional analyses of figs overestimates intake of most nutrient fractions: a study of *Ficus perforata* consumed by howler monkeys (*Alouatta palliata mexicana*). *Am J Primatol* 70:432–438
93. Valdespino C, Rico-Hernández G, Mandujano S (2010) Gastrointestinal parasites of howler monkeys (*Alouatta palliata*) inhabiting the fragmented landscape of the Santa Marta mountain range, Veracruz, Mexico. *Am J Primatol* 72:539–548
94. Vitazkova SK (2009) Overview of parasites infecting howler monkeys, *Alouatta* sp., and potential consequences of human-howler interactions. In: Huffman MA, Chapman CA (eds) Primate parasite

- ecology: the dynamics and study of host-parasite relationships. Cambridge University Press, Cambridge, pp 371–385
95. Vitazkova SK, Wade SE (2006) Parasites of free-ranging black howler monkeys (*Alouatta pigra*) from Belize and Mexico. Am J Primatol 68:1089–1097
96. Vitazkova SK, Wade SE (2007) Effects of ecology on the gastrointestinal parasites of *Alouatta pigra*. Am J Primatol 28:1327–1343
97. Vitone ND, Altizer S, Nunn CL (2004) Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. Evol Ecol Res 6:183–199
98. Windsor DA (1997) Equal rights for parasites. Perspec Biol and Med 40:222–229
99. Wobeser GA (2007) Disease in wild animals: investigation and management. Springer, New York
100. Wright PC, Arrigo-Nelson SJ, Hogg KL, Bannon B, Morelli TL, Wyatt J, Ratelolahy F (2009) Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. In: Huffman MA, Chapman CA (eds) Primate parasite ecology: the dynamics and study of host-parasite relationships. Cambridge University Press, Cambridge, pp 311–330

Tables

Table 1. Predictor metrics used in the analysis at the patch-landscape-scale (based on McGarigal et al. 2002; Gálán-Acedo et al. 2019a)

Metrics	Definition
<i>Landscape composition</i>	
Forest cover	Percentage of forest cover in the patch-landscape
Matrix permeability	Suitability of the matrix for the displacement of howler monkeys as the sum of the percentage of each land cover type in the patch-landscape multiplied by its suitability to howler dispersal
<i>Landscape configuration</i>	
Patch density	Number of forest fragments divided by 100 ha of the patch-landscape
Mean Euclidian distance to the nearest forest fragment	Mean of the shortest distances (m) between the edges of the forest fragments in the patch-landscape

Table 2. Parasites found in fecal samples of howler monkeys (*Alouatta guariba clamitans*) living in forest fragments immersed in the anthropogenic landscape of Viamão, Rio Grande do Sul, Brazil, according to their mode of transmission. The sharing of these parasites at the genus level with humans and domestic animals is also shown

		Shared with	
Mode of transmission (cycle)	Taxon	Humans	Domestic animals
<u>Direct via ingestion of the infective stage on the ground</u>			
	<i>Ancylostomidae</i>	Yes	Dog and cattle
	<i>Balantidium</i> sp.	Yes	Pig
	<i>Eimeria</i> sp.	No	Chicken
	<i>Entamoeba</i> sp.	Yes	Dog and cattle
	<i>Giardia</i> sp.	Yes	Dog and cattle
	<i>Isospora</i> sp.	Yes	Dog and cattle
	<i>Strongyloides</i> sp.	Yes	Dog and cattle
	<i>Trichuris</i> sp.	Yes	Dog and cattle
-			
<u>Direct via ingestion of the infective stage in the arboreal milieu</u>			
	<i>Trypanoxyuris minutus</i>	No	No
-			
<u>Indirect via ingestion of the intermediate host</u>			
	<i>Bertiella studeri</i>	Yes	Dog

Table 3. Best generalized linear models of the relationship between forest fragment size and the parasite fauna (overall richness and richness of parasites with direct cycle with infection via ingestion of the infective stage on the ground, and the occurrence of parasites with direct cycle with infection via ingestion of the infective stage in the arboreal milieu and the occurrence of parasites with indirect cycle with infection via ingestion of intermediate hosts) of howler monkeys inhabiting forest fragments in southern Brazil in comparison with the null model (Intercept). The Akaike Information Criterion (AICc), the relative difference between the best model and the null model (ΔAICc), the p value and the Akaike weight (w) are shown. The sign of β indicates the direction (positive or negative) of the relationship between the factor and the response variable. Significant results in bold

Parasite richness	Predictor	β	<i>p</i>	AICc	ΔAICc	<i>w</i>
Overall	Fragment size	-0.010	0.010	235	0	0.48
	Intercept	2.650	0.235	239	4.1	0.06
Direct-soil	Fragment size	-0.006	0.054	217	0	0.50
	Intercept	1.900	0.356	219	1.47	0.24
Direct-arboreal	Fragment size	-0.007	0.315	82	0.83	0.29
	Intercept	-0.069	0.404	81	0	0.44
Indirect-intermediate host	Fragment size	-0.015	0.200	79	0	0.51
	Group size	0.415	0.016	79	0	0.51
	Intercept	-0.268	0.205	86	6.0	0.17

Table 4. Best generalized linear models between the patch-landscape metrics and the parasite fauna (overall richness and richness of parasites with direct cycle with infection via ingestion of the infective stage on the ground, and the occurrence of parasites with direct cycle with infection via ingestion of the infective stage in the arboreal milieu and the occurrence of parasites with indirect cycle with infection via ingestion of intermediate hosts) of howler monkeys inhabiting forest fragments in southern Brazil in comparison with the null model (Intercept). The Akaike Information Criterion (AICc), the relative difference between the best model and the null model (ΔAICc), the *p* value and the Akaike weight (*w*) are shown. The sign of β indicates the direction (positive or negative) of the relationship between the factor and the response variable. Significant results in bold

Parasite richness	Predictor	β	<i>p</i>	AICc	ΔAICc	<i>w</i>
Overall	Forest cover 750 m	-0.030	0.028	128	0	0.19
	Group size	0.334	0.058	128	0	0.19
	Intercept	27.500	0.000	131	3.0	0.04
Direct-soil	Mean Euclidian distance to the nearest forest fragment 250 m	0.014	0.048	116	0	0.31
	Intercept	1.548	0.000	117	0.2	0.28
	Forest cover 500 m	-0.039	0.023	44	0	0.28
Direct-arboreal	Intercept	0.251	0.023	48	3.8	0.04
Indirect-intermediate host	Patch density 500 m	0.433	0.026	43	0	0.17
	Group size	0.548	0.048	44	1	0.10
	Intercept	0.379	0.063	47	3.9	0.02

Figures

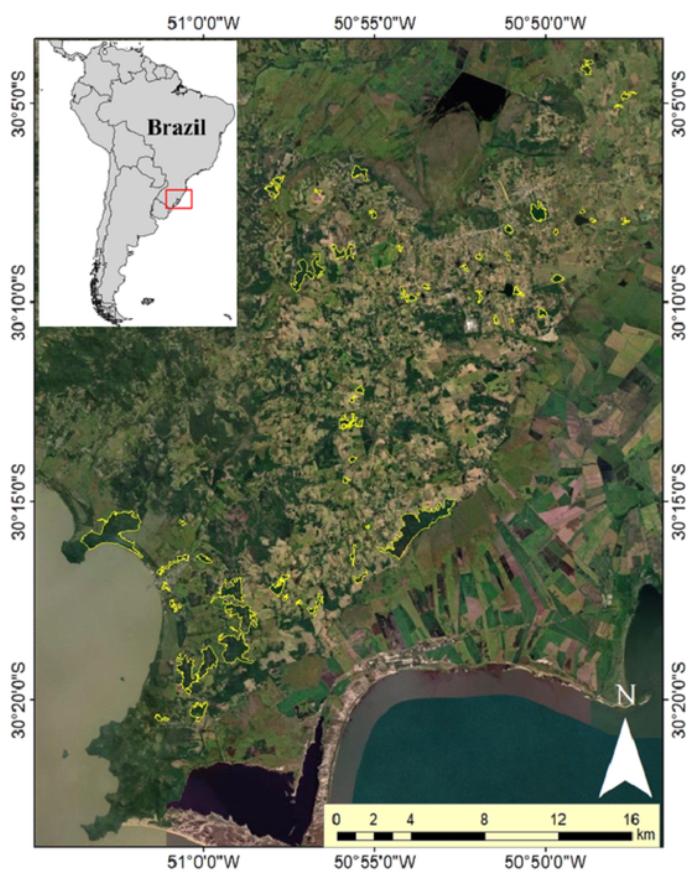
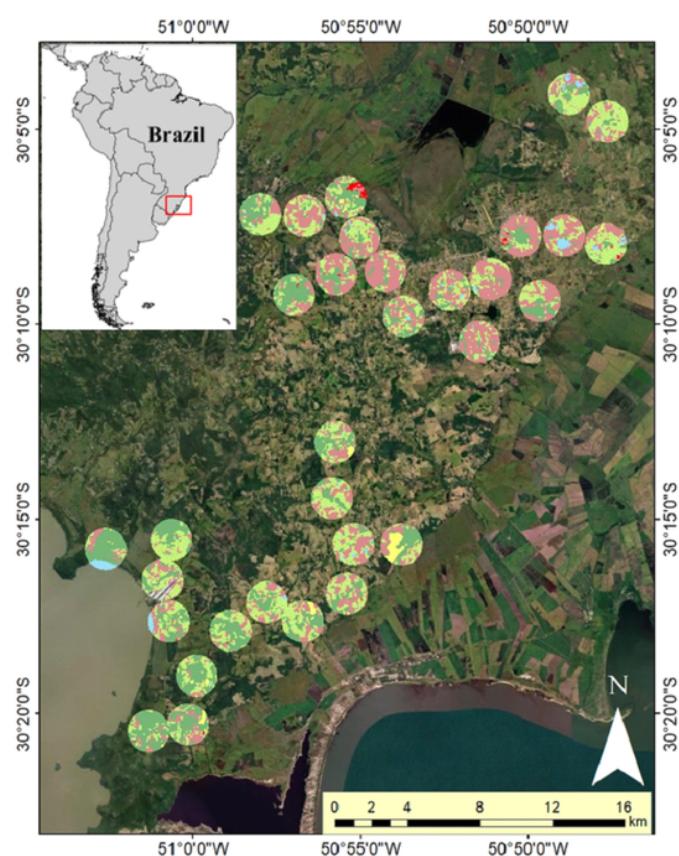
a**b**

Figure 1

Spatial distribution of the (a) 60 study forest fragments (yellow outline) and (b) 32 study patch-landscapes (circles) in Viamão, Rio Grande do Sul state, Brazil. Satellite image source: Imagery (ArcGis)
Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

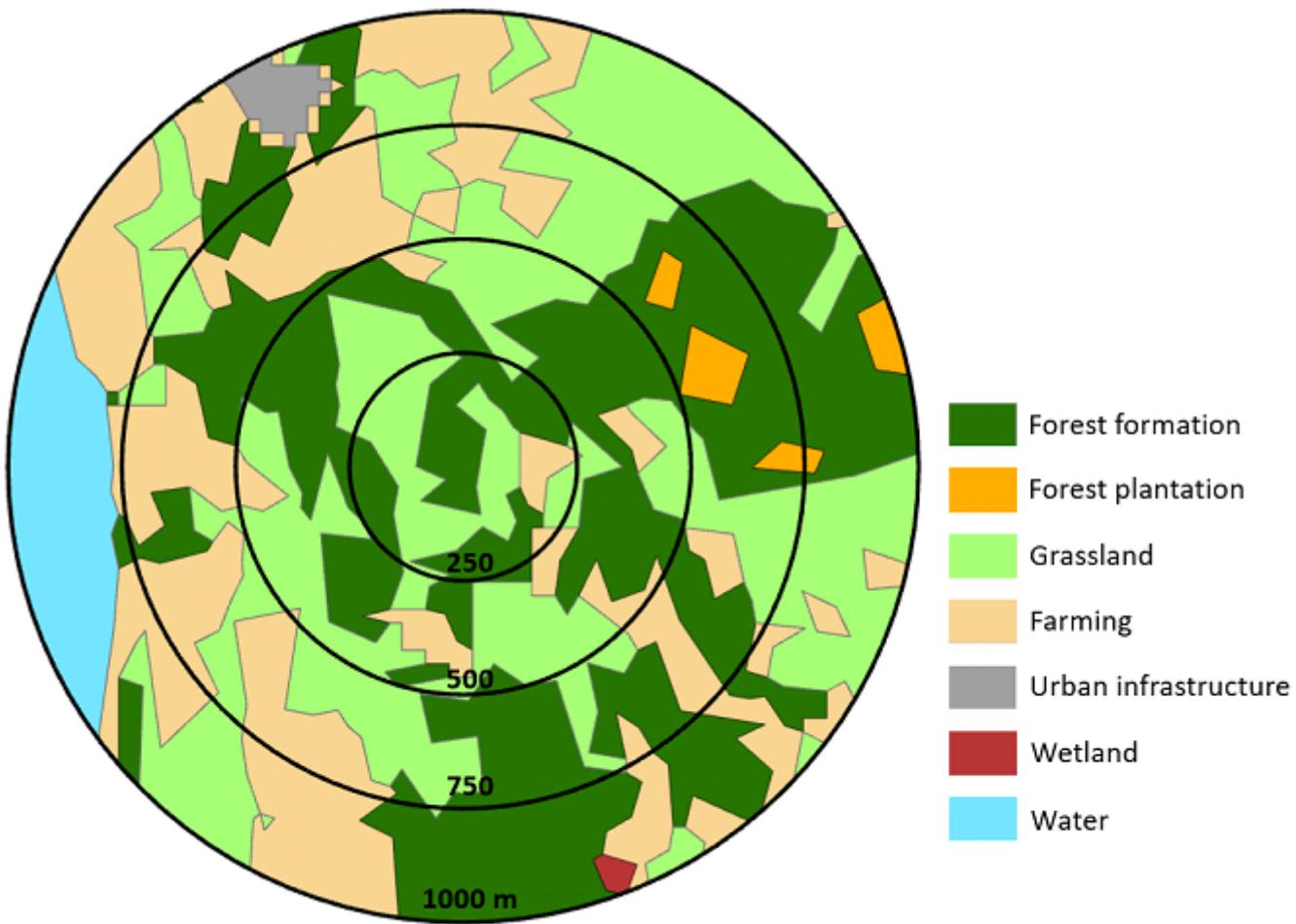


Figure 2

Scheme of a patch-landscape with the 250-, 500-, 750- and 1,000-m radii from the centroid (the center of the focal forest fragment where the fecal samples were collected) and the classification of the types of land cover

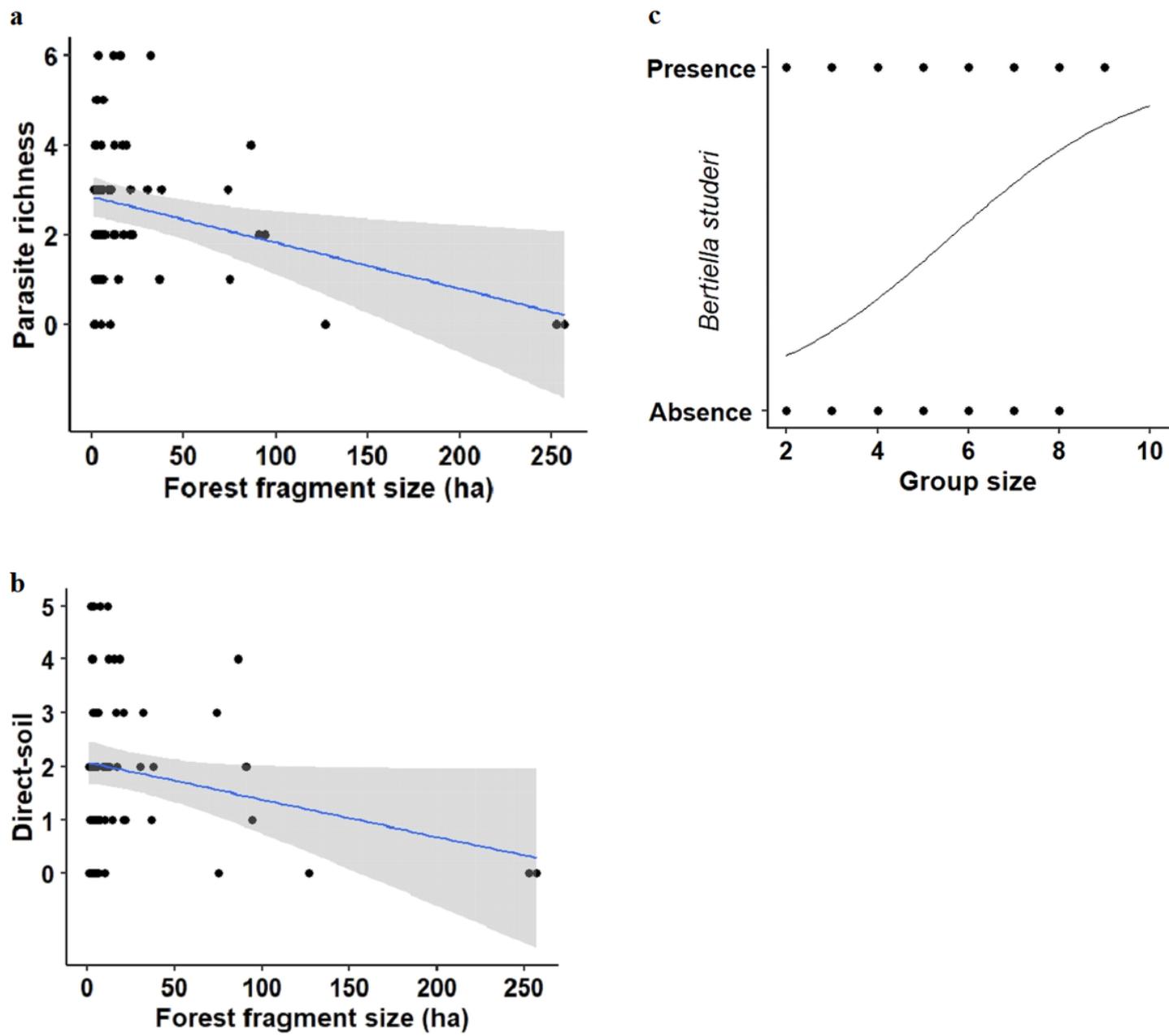


Figure 3

Relationship between (a) patch (forest fragment) size and overall parasite richness of howler monkeys at the patch-scale, (b) patch (forest fragment) size and the richness of direct-soil parasites and (c) group size and the occurrence of indirect-intermediate host parasites. The blue lines represent the linear mixed models and the shaded areas represent the 95% confidence intervals

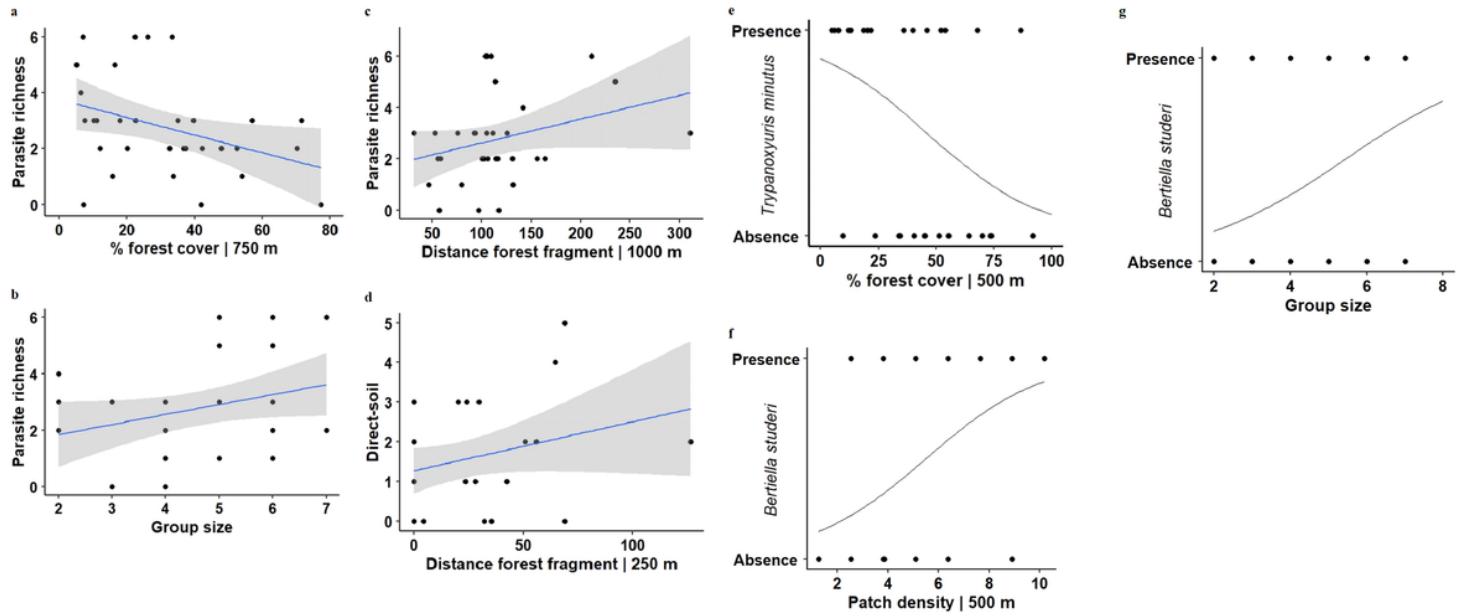


Figure 4

Relationship between (a) forest cover and overall parasite richness of howler monkeys at the patch-landscape-scale, (b) group size and overall parasite richness, (c) mean Euclidean distance to the nearest forest fragment and overall parasite richness, (d) mean Euclidean distance to the nearest forest fragment and the richness of direct-soil parasites, (e) forest cover and the occurrence of direct-arboREAL parasites, (f) patch density and the occurrence of indirect-intermediate host parasites and (g) group size and the occurrence of indirect-intermediate host parasites. The blue lines represent the linear mixed models and the shaded areas represent the 95% confidence intervals

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [KlainetalSupplementaryMaterialLandscapeEcology.docx](#)