Parasitism in heterogeneous landscapes: association between conserved habitats and gastrointestinal parasites in populations of wild mammals.

Brenda Solórzano-García[a]*, Jennifer M. White[bc], Aralisa Shedden[d]

[a] Laboratorio de Parasitología y Medicina de la Conservación, Departamento de Sistemas y Procesos Naturales, ENES – Mérida, UNAM, Km 4.5 Carretera Mérida-Tetiz, Ucú, Yucatán, México.

brenda_solorzano@yahoo.com.mx

[b] Center for Conservation Biology, Department of Biology, University of Washington; Seattle, WA USA.

[c] Current affiliation: A&P/Biology Program Manager; Catalyst Education LLC; jennifer@catalystedu.com

[d]Faculty of Science and Technology, Bournemouth University, Poole, Dorset, BH12 5BB, United Kingdom.

ashedden@bournemouth.ac.uk

***** Corresponding author

Abstract

Parasites constitute essential elements of biodiversity, playing fundamental roles for the functioning and configuration of any ecosystem. The continuous and accelerated human expansion into previously pristine territories is changing landscape structure and climatic regimes that could alter host – parasite dynamics. We explore the influence of landscape structure and habitat quality on gastrointestinal parasites in several species of mammals inhabiting remnants of tall evergreen forest within a matrix of anthropic vegetation. Here, we record 32 taxa of gastrointestinal parasites with nematodes as the most diverse group. Landscape variables such as forest edge density, river density and percentage of conserved habitat were among the best predictors of gastrointestinal parasites. Parasite species richness was higher in conserved habitats, but hosts living in disturbed areas show higher intensity of infection. The results presented here indicate that parasites are susceptible to habitat perturbation. It is pertinent to keep monitoring wildlife health in human dominated landscapes to understand disease dynamics, zoonotic risk, and ecosystem health.

Keywords: functional ecosystem, landscape structure, multiparasitism, parasites.

1. Introduction

The COVID-19 pandemic has evidenced the strong link between animal and human health, and the enormous repercussions that certain human activities can have on a disease dynamics and global welfare. These recent events highlight the importance of monitoring wildlife parasites and pathogens, as well as ecosystem health with the aim of identifying potential disease agents, and elucidating disease evolutionary and ecological processes to pursue planetary health and biodiversity conservation (Glidden et al., 2021). Modern approaches for the study of wildlife and human health, such as One Health, address these global health objectives by including both environmental and ecological components, and human and social factors. By integrating human and non-human disciplines, we hope to improve our understanding of the interactions among human induced changes in habitat, parasites, pathogens and biodiversity (Aguirre et al., 2002; Cunningham et al., 2017; Murray et al., 2018).

Parasites constitute essential elements of biodiversity, playing fundamental roles for the functioning and configuration of any ecosystem. Even though a state free of disease is desired at the individual level, at population and community levels parasites regulate many aspects of their hosts' biology, behavior, demography, predation dynamics, and even host diversity and evolution (Betts et al., 2018; de Thoisy et al., 2021; Marcogliese, 2004). Thus, the presence of parasites is expected in any functional ecosystem (Marcogliese, 2005). The continuous and accelerated human expansion into previously pristine territories is changing landscape configuration, habitat structure, and climatic regimes that could alter ecological interactions such as parasitism. Through directly modifying an ecosystem's species composition, these environmental perturbations could impact the prevalence of parasitic diseases by changing parasite abundance, host densities, or facilitating the exposure to new parasites (Ancillotto et al., 2018; Lafferty and Kuris, 2005). For instance, the emergence of infectious diseases in wildlife and humans has been associated to spillover events between domestic animals and wildlife living in proximity, as well as to human population expansion and encroachment into wildlife habitats exacerbating the contact with zoonotic agents (Daszak et al., 2000).

The responses to environmental changes observed in parasites and parasitic diseases are complex, depending on the type of parasite and the environmental scene that they take place in. Processes of habitat loss and fragmentation could have different effects on the dynamics of parasitic diseases given their impacts on host density. A higher use intensity of the remaining habitat is expected to favor parasite transmission and prevalence by increasing the encounter rate among hosts, and between hosts and parasites (Budria and Candolin, 2014; Lafferty, 2003). For example, higher abundance and parasitic richness has been observed in aquatic amphibians inhabiting ponds in agricultural lands due to changes in water quality that might facilitate the presence of intermediate hosts (Mckenzie, 2007). Likewise, deforestation has contributed to the proliferation of human parasitic diseases in the tropics, such as malaria, leishmaniasis and filariasis, by changing microclimatic and ecological conditions that favor the abundance of vectors, human – animal contact, and water pollution (Patz et al., 2000).

Conversely, environmental perturbation could hinder transmission by isolating host populations, eliminating the parasite´s intermediate hosts, and altering microclimatic conditions that negatively affect the survivorship of a parasite’s free-living stages. Therefore, identifying those environmental and social factors that influence the presence, distribution and transmission of parasites and pathogens across habitat types and species is fundamental to address health issues, especially to decide the best strategies that could aid in the management and prevention of disease while fostering functional ecosystems.

In this study, we explore the influence of landscape structure and habitat quality on the gastrointestinal parasitic frequency and richness in different wild mammal species inhabiting remnants of tall evergreen forest within a heterogeneous landscape dominated by anthropic vegetation. These host species show different life histories and tolerance to habitat perturbation and include: 1) two species of arboreal primates (howler and spider monkeys – *Alouatta palliata* and *Ateles geoffroyi*) that rely on forested land for subsistence; however howler monkeys seem to cope better with habitat fragmentation than spider monkeys (Bicca-Marques, 2003; Ramos-Fernández and Wallace, 2008); 2) one large terrestrial herbivore (tapir – *Tapirus bairdii*), which is associated to waterbodies and constrained to undisturbed habitat (de la Torre et al., 2018; Sánchez-Pinzón et al., 2019); 3) three species of small felids (ocelot, margay and yaguarundi – *Leopardus pardalis, L. wiedii* and *Herpailurus yagouaroundi*); and 4) two apex predators (jaguar and puma – *Panthera onca* and *Puma concolor*) with pumas considered less sensitive to human perturbation than jaguars (De Angelo et al., 2011). All of these species are considered as threatened species by Mexican law (SEMARNAT, 2010).

We conducted a gastrointestinal parasitic survey and modelled the presence of parasites and multiparasitism as a function of different environmental and anthropic variables; furthermore, we assessed if such patterns are species-specific or rather general across mammals. We expect parasitism in species relatively tolerant to the anthropic landscape (such as howler monkeys and large felids) to be less influenced by landscape composition, than those mostly constraint to conserved habitat (such as spider monkeys and tapir). We also expect to find a higher parasitic richness in more conserved areas, whereas host living in more disturbed areas will show greater intensity of infections. Except for monkeys, parasitic information for these mammal species is not abundant. Hence, this study provides parasitological information regarding wild populations of these species of mammals and contributes to the understanding on how parasitic associations are responding to environmental changes and habitat transformation, to determine the possible implications for wildlife and ecosystem health in the region.

2. Materials and Methods

2.1 Study site and collection of samples

The Uxpanapa Valley is located in the south of Veracruz state, southeastern Mexico. It is part of the Selva Zoque region, one of the largest northernmost relicts of tall evergreen forest in the country, home to vast biodiversity. Processes of deforestation and habitat transformation began in the region in the 1970´s (Hernández-Gómez, 2014; Velasco-Toro, 1993) and today the Uxpanapa Valley consists of a heterogeneous landscape of forest fragments, secondary vegetation, and anthropogenic land-cover such as agricultural land and pastures for livestock, as well as paved roads and villages.

We employed non-invasive techniques to collect fecal samples from different species of mammals including primates, tapir, and several wild felids in a total of 45 locations (Fig. 1). Primate groups were detected via their morning calls or by direct sighting; fresh fecal samples were collected right after deposition and placed in 50 ml tubes with 4% formalin. For tapir and wild felids sampling we employed a wildlife scat detection dog from the Conservation Canines program at University of Washington (Wasser et al., 2004). We conducted two surveys per locality each of 6 – 20 km circular transects. Surveys often followed human or game trails, but also included off-trail and road-side portions. Samples were preserved in 4% formalin for parasitological analysis. In the case of felids, a piece of the scat was kept frozen for genetic confirmation of host species through mitochondrial DNA sequencing. The ATP6 region (approximately 175 base pairs) was able to distinguish all sympatric carnivore species (data not shown). Additionally, host hair found in the scats (ingested during auto-grooming) was used to support the felid species ID. We collected a total of 247 samples, 55 from howler monkeys in 18 localities; 68 from spider monkeys in 23 localities, 25 samples from tapir in 6 localities; 22 from small felids in 16 localities, and 77 large felids samples in 27 localities (39 were confirmed jaguar*,* 18 were confirmed puma, and 20 samples were confirmed large felids, but we could not discriminate between jaguar and puma). For each collected sample, we registered host species, habitat type, habitat condition, geographic location, as well as host sex and group size only for primates. All surveys were conducted with permission of local landowners.

2.2 Coproparasitological examinations

Preserved samples were examined for parasite eggs under direct light microscopy (10x, 40x, 100x) using flotation in saturated sodium chloride solution, and simple sedimentation techniques (for complete protocols see Greiner and McIntosh, 2009). Both procedures were performed for each collected sample to avoid missing parasites with different egg densities. The identification of parasites was based on egg morphology, shape, size, and color. For each type of host, we estimated the percentage of positive samples (number of samples containing any parasite taxa divided by the total number of examined samples); prevalence (number of hosts infected with a particular parasite species, divided by the number of hosts examined -Bush et al., 1997), prevalence 95% CI employing the R package epiR (Stevenson and Sergeant, 2022) and parasite richness (number of parasitic taxa identified). We also calculated parasite eggs per gram (EPG) of fecal material (Stoll, 1930) to explore the relationship between habitat quality and intensity of infection. Mean intensity of infection and 95% CI were estimated in Quantitative Parasitology (QP web) (Reiczigel et al., 2019). We acknowledge that EPG is not an accurate measure of parasite burden (Gillespie, 2006); nonetheless this is the best proxy to an intensity of infection measurement when employing non-invasive techniques for parasitological diagnosis.

2.3 Landscape metrics

We used a supervised classification of five multispectral SPOT 5 satellite images (5 bands, 10m resolution) of the Uxpanapa Valley with six vegetation classes: 1) primary forest, 2) mature secondary forest, 3) secondary forest, 4) grassland, 5) agriculture, and 6) urban (C. A. Muñoz-Robles, unpublished data). The image processing was conducted using PCI Geomatica 12 software (PCI Geomatics 2011). We also employed cartographic layers of villages, rivers, and roads (1:250,000 – 2010) from the Mexican National Institute of Geography, Statistics and Informatics (INEGI). We created two different sized buffers around the sampling point for each species of mammal; one comparable in size with the reported home range of each species, and a larger buffer almost twice the home range size to assess the robustness of results and potential sensitivity to the fact that a fecal sample may not have been collected at the center point of the mammals' home range (Vanderwaal et al., 2015). (Tables S1 – S3). In those cases where two or more buffers overlapped, the corresponding samples were then considered as part of the same buffer. We estimated landscape structure in each buffer based on five parameters: i) proportion of vegetation types (in percentage); ii) percentage of conserved habitat (primary plus mature secondary forest); iii) edge density (i.e., length of all conserved forest borders); iv) road density; and v) river density. Also, the distance to nearest town was calculated for each sampling point. Parameters of landscape structure for each buffer were estimated using the landscape vector overlay tools in LecoS 3.0 plugin (Jung, 2016) and the Quantum GIS 3.14 software (mean landscape statistics for each buffer size are shown in Tables S1 – S3).

2.4 Data analyses

To explore the association between landscape structure with gastrointestinal parasitism we built a series of models, employing different types of predictor and response variables. First, we performed generalized linear mixed models (GLMMs) fitted by maximum likelihood (Adaptive Gauss-Hermite Quadrature) to assess the effect of landscape structure on the presence/absence of parasites. We also built separate models for each of the most prevalent taxa of parasites in each species of mammal. Spatial metrics characterizing landscape structure within home range buffers were included as fixed effects, and buffer ID was included as random effect. The presence of parasites was modeled using a logit-link function with binomial distribution. To avoid multicollinearity, we removed variables with a Pearson's correlation coefficient above 0.4 (Shrestha, 2020; Vatcheva et al., 2016). We built models of all possible combinations for a maximum of three predictors. Best-fitting models were selected using the Akaike Information Criterion corrected for small samples (AICc) retaining all models with with Δ AICc >2. Odds ratios (OR) and 95% confidence interval (95% CI) were calculated, as well as marginal and conditional R^2 (Nakagawa and Schielzeth, 2013).

Second, to test the relationship between landscape structure and multiparasitism, we employed generalized linear models (GLMs) using parasite richness per buffer (the number of different parasite taxa found in all samples belonging to the same buffer) as response variable and the landscape metrics with $r < 0.4$ as predictors. Models were fit using Poisson distribution, best-fitting models were selected through the AICc criterion, and quality of fit was estimated through Nagelkerke's pseudo R^2 (Nagelkerke, 1991). GLMMs and GLMs analyses were repeated using the larger buffer.

Finally, to assess the effects of habitat quality on gastrointestinal parasitism, we ran GLMs with binomial distribution using as predictor categorical variables of habitat condition (conserved vs disturbed) and presence/absence of parasites as response variable. Conserved habitat was defined as those buffers with a primary forest cover of ≥ 60%. We constructed contingency tables and estimated the odds ratio and the Phi coefficient (ϕ) to assess the association between habitat quality and parasitism. The relationship between habitat quality and mean intensity of infection was explored through a U-test comparing parasite burden (EPG) in conserved versus disturbed habitats

Statistical analyses were carried out in R, through libraries PerformanceAnalytics (Peterson and Carl, 2020), lme4 (Bates et al., 2015); best models were selected with MuMIn (Barton, 2020); odds ratios and quality of fit measurements were obtained with SjPlot (Lüdecke, 2021); Phi coefficient was estimated in epitools (Aragon, 2020); and regression plots were built with Sjplot and ggplot2 (Wickham, 2016).

1. Results

3.1 Parasite prevalence and richness

The studied mammal populations in the Uxpanapa Valley showed 57% of the samples positive for at least one taxa of gastrointestinal parasite, representing 141 positive cases out of 247 samples. Tapir showed the highest overall parasitism with 80% of positive to at least one parasite species, followed by primates with 64% positive samples, small felids (50%) and large felids (40%) (Tables S4 – S6). Primates were parasitized by at least 7 parasite taxa (5 taxa in howler monkeys, and 7 taxa in spider monkeys); tapir was parasitized by 13 parasite taxa, while felids were parasitized by 16 taxa (Tables S4 – S6). Parasites of the genus *Strongyloides* were among the most prevalent in primates and felids, while parasites belonging the family Trichostrongylidae were the most prevalent in tapir samples.

3.2 Landscape structure and gastrointestinal parasitism

A greater likelihood of infection with parasites was observed in howler monkeys living in areas with less proportion of mature secondary forest (β= -6.62, OR= 0 – 0.20, P= 0.009) and less edge density (β= -0.13, OR= 0.80 – 0.96, P =0.006) (Fig. 2). A negative association with edge density was also observed for the presence of nematodes (β= -0.17, OR= 0.75 – 0.95, P= 0.004), particularly *Trypanoxyuris* sp. (β= -0.21, OR= 0.69 – 0.94, P= 0.007) (Table S7). For spider monkeys, the probability of overall parasitism and infection for *Strongyloides* sp. was greater in areas with high proportion of conserved habitat (β= 0.51, OR= 1.18 – 2.31, P= 0.003; and β= 0.59, OR= 1.13 – 2.87, P= 0.01) and less proportion of grassland (β= -9.77, OR= 0 – 0.04, P= 0.003) (Fig. 2, Tables S8). Likewise for tapir, presence of parasites was inversely related to edge density, particularly for parasites of the family Trichostrongylidae (β= -0.26, OR=0.60 – 0.99, P= 0.04) and *Kililuma* sp. (β= -0.25, OR= 0.61 – 1, P= 0.05) (Fig. 3, Table S9).

For small felids the best predictor was distance to nearest town, with higher probability of parasitism at longer distances, followed by a higher infection in areas with less edge density; however, none of the observed associations were statistically significant (P > 0.05) (Fig. 4, Table S10). For large felids in general, variables such as road density (β= 0.43, OR= 1.06 – 2.21, P =0.02), and distance to nearest town (β= 0.69, OR= 1.07 – 3.70, P= 0.03), along with river density (β= -2.47, OR=0.01 – 0.61, P =0.02), were also good predictors of presence of parasites. (Fig. 4, Table S11). For jaguars, less parasitism and infection for cestodes was observed in areas with higher river density (β= -1.10, OR= 0.13 – 0.84, P= 0.02; and β= -2.03, OR= 0.02 – 0.85, P =0.03) (Fig. 4, Table S12); while for puma none of the tested models performed better that the other, resulting in non-significant associations (Table S13).

3.3 Landscape structure and multiparasitism

Areas with greater proportion of conserved vegetation were associated with higher parasitic richness in all sampled mammals except howler monkeys (Fig. 5); although the significance of such association was not ubiquitous (Table S14). In howler monkeys, greater parasite richness was associated with greater proportion of grassland (β= 2.41, P= 0.01), less proportion of mature secondary forest (β= -3.29, P= 0.05) and less edge density (β= -0.06, P= 0.05). Parasite richness in spider monkeys was better predicted by road density (β= -0.05, P= 0.25) and the proportion of conserved habitat (β= 0.05, P= 0.45), with a weak non-statistically significant association. For tapir, higher parasite richness was associated with less proportion of mature secondary forest (β= -7.61, P= 0.01), a greater proportion of conserved habitat and primary forest (β= 1.42, P= 0.01; and β= 0.13, P= 0.04) and less edge density (β= -0.09, P= 0.01). In small felids, high parasite richness was found in areas with less proportion of grassland (β= -12.8, P= 0.06). Likewise, parasite richness in large felids was associated with less proportion of secondary forest (β= -3.60, P= 0.006), greater proportion of conserved habitat (β= 0.16, P= 0.02), and lower river density (β= -0.47, P= 0.02). Particularly for jaguar, river density was the best predictor of parasite richness, although non-significant (β= -0.45, P= 0.07), while for puma none of the tested models performed better than the others or resulted in a significant prediction of parasite richness.

The results of the GLMM assessing the effects of landscape structure on parasitism and multiparasitism were maintained when considering the expanded buffer zone, showing the same patterns of associations between predictor variables and parasitism as those found in the home range buffers for all species of mammals. This suggests robustness of the observed effects of the different predictors.

3.4 Habitat quality and gastrointestinal parasitism

A non-significant association was found when independently assessing the risk of parasitism and habitat quality (conserved vs disturbed) for each mammal (Fig. S1), except in the case of spider monkeys where a moderate positive association between habitat quality and parasitism was found (ϕ= 0.32 p = 0.016), with less positive samples in disturbed habitat (β= -1.70, OR= 0.18, P =0.013) (Fig 6). This association between habitat quality and parasitism was also observed when analyzing all hosts species together (ϕ= 0.25 p = 0.00), with samples from disturbed habitats 65% less probable of having parasites than those from conserved habitats (β= -1.04, OR= 0.35, $P < 0.001$) (Fig. 6). When comparing intensity of parasitic infection between conserved versus disturbed habitat, there was a general tendency to present higher egg density on disturbed habitats (Fig. 6 B – H) (Table S16); however, none of these differences were significant when running the U-test.

2. Discussion

In this study we present data on the parasitic fauna of several species of mammals inhabiting remnants of tall evergreen forest within a matrix of anthropic vegetation, and we assess the effects of landscape structure on gastrointestinal parasitism and parasite species richness. Populations of mammals in this region showed moderate levels of parasitism with more than half of the samples positive for at least one taxa of parasites. We recorded 32 taxa of gastrointestinal parasites, with nematodes as the most diverse group. Richness data might be underestimated, because in some cases, morphological examinations of parasite eggs shed in feces only allowed diagnosis to the genus or even family levels.

Landscape structure had strong effects on parasite infection. The best predictors of gastrointestinal parasites varied between mammals in accordance with their tolerance to disturbed habitats and include forest edge density, percentage of conserved habitat and river density. Primates and tapir, which highly rely on forest cover, were more likely to be parasitized in areas with less forest fragmentation and larger proportion of conserved habitat. Particularly, for spider monkeys which are highly vulnerable to habitat loss (Shedden et al., 2022), parasitism was better predicted by the amount of conserved habitat. Furthermore, for large felids, which can easily move through this heterogeneous landscape, likelihood of parasitism was negatively associated to variables related to human presence such as road density, distance to nearest town and river density. A moderate negative correlation was observed between river density and habitat conservation (data not shown), with higher river density in places with less amount of conserved habitat, suggesting that the presence of rivers may encourage human activity in the area, hence habitat perturbation.

As part of the biological diversity and as components of any functional ecosystem, parasites are expected to be present in conserved habitats where they find suitable environmental and ecological conditions for their survival and transmission (Lafferty and Kuris, 2005; Marcogliese, 2005). Microclimatic conditions required for the survival of parasites have been reported to become increasingly hostile when approaching the edge between forest and agricultural lands. Particularly, the low humidity and higher temperatures of these border zones could negatively affect the viability of parasites' infective stages such as eggs (Escorcia-Quintana, 2014). Habitat fragmentation and the resulting edge effect could be hindering parasite survival in highly fragmented habitats resulting in lower parasite infection than more conserved areas (Budria and Candolin, 2014) .

As expected, multiparasitism was associated to landscape composition, with higher parasite species richness in areas with larger proportion of conserved habitat in almost all host species. Given the vast diversity of life history strategies of parasites, the reliance on different intermediate hosts to complete their life cycles, the variety of transmission dynamics, and free-living stages that could persist either in the water or in the soil, parasites are considered bioindicators of environmental quality (Sures et al., 2017; Vidal-Martínez et al., 2010). Since a single species of parasite could be associated to a series of different host species through its life cycle (vectors, intermediate hosts and reservoir hosts), the presence of a variety of parasites is only possible in ecosystems with high biodiversity. Furthermore, some parasites can be highly susceptible to toxins and pollutants especially during their free-living stages (Pietrock and Marcogliese, 2003); thus, a habitat free of contaminants is require for many parasites to persist (Lafferty and Kuris, 2005).

Notably, in howler monkeys multiparasitism showed an inverse association of higher parasite richness in less forested areas. This trend has been also reported in *Alouatta guariba* groups inhabiting fragmented forest in Brazil, with higher parasite richness in small forest fragments and less forest cover (Klain et al., 2021); however, lower parasite richness has been reported in *Alouatta palliata* groups living in more disturbed forests (Cristobal-Azkarate et al., 2010), whereas others found no relationship between parasite richness and forest perturbation in *Alouatta pigra* (Martínez-Mota et al., 2018). Most of the parasites found in the surveyed howler groups during the present study have a direct life cycle; the ability of howler monkeys to cope with habitat perturbation and persist in forest fragments (Bicca-Marques et al., 2020; Cristobal-Azkarate and Dunn, 2013) could result in higher population densities in habitat remnants facilitating the direct transmission of their parasites. More studies are needed to understand the confounding effects that habitat perturbation, host ecology and behavior, and parasite transmission mode could be having on parasite richness and prevalence in howler monkey groups living in heterogenous landscapes.

Regarding the risk of gastrointestinal parasitism in relation to habitat quality, no differences were observed in terms of the percentage of parasitized hosts between conserved and disturbed habitats, except for spider monkeys which showed lower risk of parasitism in more disturbed areas.

Nonetheless, higher egg density (EPG) was observed for many parasite species in disturbed versus conserved habitats. This higher intensity of infection by fewer parasite species in disturbed habitats, suggests that higher diversity of parasites in conserved habitats does not necessarily lead to a higher risk of parasitism for individual hosts. Higher intensity of infection in disturbed areas could be related to a host's poor physical condition due to higher stress, deficient nutrition and loss of genetic diversity, making them more vulnerable to parasitic diseases and leading to a spiral of population decline (Arroyo-Rodríguez and Dias, 2010; Budria and Candolin, 2014; Messina et al., 2018).

Moreover, in anthropic landscapes such as this one, the remnants of forest constitute the main habitat for most wild mammals. The crowding effect, with higher hosts densities due to an increase in the intensity of use of these remnants of forest could be facilitating the transmission of certain parasites (Bonnell et al., 2018) as may be the case for howler monkeys in this study. Less parasite diversity in these disturbed areas could also signify less interspecies competition for host infection; therefore, those few parasite species that better cope with habitat perturbation can proliferate (Johnson et al., 2013; Johnson and Hoverman, 2012). Increasing biodiversity and connectivity in fragmented landscapes could have a variety of effects on parasitic disease dynamics, including possible negative outcomes suggested in previous studies (Halsey, 2019; Huang et al., 2016); nonetheless, the ecological and evolutionary benefits conferred by a more conserved and connected habitat seem to outweigh the parasite transmission concern (Johnson and Thieltges, 2010; Jousimo et al., 2014; Keesing et al., 2006; Mccallum and Dobson, 2002).

It is well known that opportunity for zoonosis and cross transmission is greater in the interface between humans, domestic animals, and wildlife (de Thoisy et al., 2021; Vanhove et al., 2020; White and Razgour, 2020). Rural anthropic landscapes where human encroachment into wild areas is constantly growing, as the case of our study site, constitute ideal models for the study of the parasitic communities of these three entities from the ecological and evolutionary perspective. In all the species of wild mammals surveyed, we registered several taxa of parasites that could be shared between wildlife and humans, or between wildlife and domestic animals. For example, strongyloidiasis, caused by soil-transmitted helminths of the genus *Strongyloides*, is considered a neglected tropical disease due to its effects on human health (Olsen et al., 2009; WHO, 2021). Eggs of *Strongyloides* were observed in both primates and felids in our study area and were the most prevalent parasite in this survey. Likewise, species of *Ancylostoma*, *Toxocara* and *Spirocerca* are common parasites of dogs and domestic cats (Bowman et al., 2002; Saari et al., 2019), and were also found in wild felid scats. Determination of the transmission potential and zoonotic origin of these parasites needs to be appropriately verified, by adding diagnosis and molecular information of the parasites from humans and domestic animals in the region. However, it is clear from this study, that landscape structure and human activity influence in a complex manner parasitism in wildlife.

3. Conclusion

The results presented here indicate that parasites are susceptible to habitat perturbation. Habitat loss and fragmentation negatively affect the presence of parasites and parasite richness, while egg density suggested higher intensity of infections in hosts living in disturbed areas. Habitat transformation could have complex effects on parasite – host dynamics, depending on the host’s tolerance to perturbation and human presence. For those host relaying on forest cover, habitat loss changes could concentrate host activities and parasite occurrence into the remaining habitat possibly facilitating parasite transmission. On the other hand, highly tolerant hosts will be more exposed to parasitic contamination from humans and domestic fauna facilitating parasite cross-transmission and zoonosis. Conservation actions that aim to increase habitat amount and connectivity could aid in maintaining ecosystem biodiversity and possibly dilute parasitism. It is pertinent to keep monitoring wildlife health in human dominated landscapes to understand disease dynamics, zoonotic risk, and ecosystem health in modified landscapes.

Funding

This work was supported by CONACyT in Mexico and the Veracruz State Government (Grant Number 108990). The UW Department of Biology Riddiford-Truman graduate–student award to JMW used to partially fund travel of the CK9 team.

CRediT authorship contribution statement

Brenda Solórzano-García: Conceptualization, field work, data analysis, writing. **Jennifer M. White:** field work, data analysis, writing – review and editing. **Aralisa Shedden:** field work, writing – review and editing.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgements

We acknowledge the working dog Scooby, of the UW Conservation Canines, for his tireless energy and contribution to a good-natured field team. We thank all the local people for their hospitality and help during field work. We sincerely thank Cristina Mac Swiney, Ernesto Rodríguez Luna, Jurgi Cristóbal Azkárate, Jacob Dunn and Samuel Wasser for their valuable support. David Osorio and the CNHE-IB-UNAM aided us with parasite identification. Finally, we thank the anonymous reviewers whose suggestions help to improve this manuscript

References

Aguirre, A.A., Ostfeld, R.S., Tabor, G.M., House, C., Pearl, M.C. (Eds.), 2002. Conservation Medicine: Ecological Health in Practice. Oxford University Press.

Ancillotto, L., Studer, V., Howard, T., Smith, V.S., McAlister, E., Beccaloni, J., Manzia, F., Renzopaoli, F., Bosso, L., Russo, D., Mori, E., 2018. Environmental drivers of parasite load and species richness in introduced parakeets in an urban landscape. Parasitol. Res. 117, 3591–3599. https://doi.org/10.1007/s00436-018-6058-5

Aragon, T.J., 2020. epitools: Epidemiology Tools.

Arroyo-Rodríguez, V., Dias, P.A.D., 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am. J. Primatol. 72, 1–16. https://doi.org/10.1002/ajp.20753

Barton, K., 2020. MuMIn: Multi-Model Inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Betts, A., Gray, C., Zelek, M., MacLean, R.C., King, K.C., 2018. High parasite diversity accelerates host adaptation and diversification. Science (80-.). 360, 907–911. https://doi.org/10.1126/science.aam9974

Bicca-Marques, J., Chaves, O., Hass, G., 2020. Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence? Am. J. Primatol. 84, e23089. https://doi.org/10.1002/ajp.23089

Bicca-Marques, J.C., 2003. How do Howler Monkeys Cope with Habitat Fragmentation?, in: Marsh, L.K. (Ed.), Primates in Fragments: Ecology and Conservation. Kluwer Academics/Plenum Publishers, New York, pp. 283–303. https://doi.org/10.1007/978-1-4757-3770-7

Bonnell, T.R., Ghai, R.R., Goldberg, T.L., Sengupta, R., Chapman, C.A., 2018. Spatial configuration becomes more important with increasing habitat loss: a simulation study of environmentally-transmitted parasites. Landsc. Ecol. 33, 1259–1272. https://doi.org/10.1007/s10980-018-0666-4

Bowman, D.D., Hendrix, C.M., Lindsay, D.S., Barr, S.C., 2002. Feline clinical parasitology. Iowa State University Press, Iowa.

Budria, A., Candolin, U., 2014. How does human-induced environmental change influence host-parasite interactions? Parasitology 141, 462–474. https://doi.org/10.1017/S0031182013001881

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83, 575–583.

Cristobal-Azkarate, J., Dunn, J.C., 2013. Lessons from Los Tuxtlas: 30 years of research into primates in fragments, in: Marsh, L.., Champan, C.A. (Eds.), Primates in Fragments: Complexity and Resilience. Springer Science-Bussiness Media, New York, pp. 75–88. https://doi.org/10.1007/978-1-4614-8839-2

Cristobal-Azkarate, J., Hervier, B., Vegas-Carrillo, S., Osorio-Sarabia, D., Rodriguez-Luna, E., Vea, J.J., 2010. Parasitic infections of three mexican howler monkey groups (*Alouatta palliata mexicana*) exposed to differing degrees of habitat disturbance in fragmented forests. Primates 51, 231–239.

Cunningham, A.A., Daszak, P., Wood, J.L.N., 2017. One health, emerging infectious diseases and wildlife: Two decades of progress? Philos. Trans. R. Soc. B Biol. Sci. 372. https://doi.org/10.1098/rstb.2016.0167

Daszak, P., Cunningham, A.A., Hyatt, A.D., 2000. Emerging infectious diseases of wildlife - Threats to biodiversity and human health. Science (80-.). 287, 443–449. https://doi.org/10.1126/science.287.5452.443

De Angelo, C., Paviolo, A., Di Bitetti, M., 2011. Differential impact of landscape transformation on pumas (*Puma concolor*) and jaguars (*Panthera onca*) in the Upper Paraná Atlantic Forest. Divers. Distrib. 17, 422–436. https://doi.org/10.1111/j.1472-4642.2011.00746.x

de la Torre, J.A., Rivero, M., Camacho, G., Álvarez-Márquez, L.A., 2018. Assessing occupancy and habitat connectivity for Baird’s tapir to establish conservation priorities in the Sierra Madre de Chiapas, Mexico. J. Nat. Conserv. 41, 16–25. https://doi.org/10.1016/j.jnc.2017.10.004

de Thoisy, B., Duron, O., Epelboin, L., Musset, L., Quénel, P., Roche, B., Binetruy, F., Briolant, S., Carvalho, L., Chavy, A., Couppié, P., Demar, M., Douine, M., Dusfour, I., Epelboin, Y., Flamand, C., Franc, A., Ginouvès, M., Gourbière, S., Houël, E., Kocher, A., Lavergne, A., Le Turnier, P., Mathieu, L., Murienne, J., Nacher, M., Pelleau, S., Prévot, G., Rousset, D., Roux, E., Schaub, R., Talaga, S., Thill, P., Tirera, S., Guégan, J.F., 2021. Ecology, evolution, and epidemiology of zoonotic and vector-borne infectious diseases in French Guiana: Transdisciplinarity does matter to tackle new emerging threats. Infect. Genet. Evol. 93. https://doi.org/10.1016/j.meegid.2021.104916

Escorcia-Quintana, M., 2014. Efecto del borde selva-pastizal sobre el desarrollo del parásito gastrointestinal *Trypanoxyuris* sp. del mono aullador de manto (*Alouatta palliata mexicana*) en Los Tuxtlas, Veracruz, México. Universidad Veracruzana, Mexico.

Gillespie, T.R., 2006. Noninvasive assessment of gastrointestinal parasite infections in free-rangingpPrimates. Int. J. Primatol. 27, 1129–1143. https://doi.org/10.1007/s10764-006-9064-x

Glidden, C.K., Nova, N., Kain, M.P., Lagerstrom, K.M., Skinner, E.B., Mandle, L., Sokolow, S.H., Plowright, R.K., Dirzo, R., De Leo, G.A., Mordecai, E.A., 2021. Human-mediated impacts on biodiversity and the consequences for zoonotic disease spillover. Curr. Biol. 31, R1342–R1361. https://doi.org/10.1016/j.cub.2021.08.070

Greiner, E.C., McIntosh, A., 2009. Collection methods and diagnostic procedures for primate parasitology, in: Huffman, M.A., Chapman, C.A. (Eds.), Primates Parasite Ecology. The Dynamics and Study of Host-Parasite Relationships. Cambridge University Press, pp. 3–27.

Halsey, S., 2019. Defuse the dilution effect debate. Nat. Ecol. Evol. 3, 145–146. https://doi.org/10.1038/s41559-018-0764-3

Hernández-Gómez, I., 2014. Evaluación de la transformación del paisaje para la determinación de áreas prioritarias de conservaciónen la región de Uxpanapa, Veracruz. Universidad Veracruzana.

Huang, Z.Y.X., Van Langevelde, F., Estrada-Peña, A., Suzán, G., De Boer, W.F., 2016. The diversity-disease relationship: Evidence for and criticisms of the dilution effect. Parasitology 143, 1075–1086. https://doi.org/10.1017/S0031182016000536

Johnson, P.T.J., Hoverman, J.T., 2012. Parasite diversity and coinfection determine pathogen infection success and host fitness. Proc. Natl. Acad. Sci. U. S. A. 109, 9006–9011. https://doi.org/10.1073/pnas.1201790109

Johnson, P.T.J., Preston, D.L., Hoverman, J.T., LaFonte, B.E., 2013. Host and parasite diversity jointly control disease risk in complex communities. Proc. Natl. Acad. Sci. U. S. A. 110, 16916–16921. https://doi.org/10.1073/pnas.1310557110

Johnson, P.T.J., Thieltges, D.W., 2010. Diversity, decoys and the dilution effect: How ecological communities affect disease risk. J. Exp. Biol. 213, 961–970. https://doi.org/10.1242/jeb.037721

Jousimo, J., Tack, A.J.M., Ovaskainen, O., Mononen, T., Susi, H., Tollenaere, C., Laine, A.L., 2014. Ecological and evolutionary effects of fragmentation on infectious disease dynamics. Science (80-.). 344, 1289–1293. https://doi.org/10.1126/science.1253621

Jung, M., 2016. LecoS - A python plugin for automated landscape ecology analysis. Ecol. Inform. 31, 18–21. https://doi.org/10.1016/j.ecoinf.2015.11.006

Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. Ecol. Lett. 9, 485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x

Klain, V.F., Mentz, M.B., Bustamante-Manrique, S., Bicca-Marques, J.C., 2021. Habitat patch size and landscape structure influence, although weakly, the parasite richness of an arboreal folivorous-frugivorous primate in anthropogenic landscapes. Res. Sq. 1–25. https://doi.org/https://doi.org/10.21203/rs.3.rs-509824/v1 License:

Lafferty, K., 2003. Is disease increasing or decreasing, and does it impact or maintain biodiversity? J. Parasitol. 89(Suppl.), S101–S105.

Lafferty, K.D., Kuris, A.M., 2005. Parasitism and environmental disturbances, in: Thomas, F., Renaud, F., Guégan, J. (Eds.), Parasitism and Ecosystems. Oxford University Press, pp. 113–123.

Lüdecke, D., 2021. sjPlot: Data Visualization for Statistics in Social Science.

Marcogliese, D.J., 2005. Parasites of the superorganism: Are they indicators of ecosystem health? Int. J. Parasitol. 35, 705–716. https://doi.org/10.1016/j.ijpara.2005.01.015

Marcogliese, D.J., 2004. Parasites: Small Players with Crucial Roles in the Ecological Theater. Ecohealth 1, 151–164. https://doi.org/10.1007/s10393-004-0028-3

Martínez-Mota, R., Pozo-Montuy, G., Bonilla-Sánchez, Y.M., Gillespie, T.R., 2018. Effects of anthropogenic stress on the presence of parasites in a threatened populations of black howler monkeys (*Alouatta pigra*) in southern Mexico. 2Therya 9, 161–169. https://doi.org/DOI: 10.12933/therya-18-572 ISSN 2007-3364

Mccallum, H., Dobson, A., 2002. Disease , habitat fragmentation and conservation. Proc. R. Soc. B 269, 2041–2049. https://doi.org/10.1098/rspb.2002.2079

Mckenzie, V.J., 2007. Human land use and patterns of parasitism in tropical amphibian hosts. Biol. Conserv. 137, 102–116. https://doi.org/10.1016/j.biocon.2007.01.019

Messina, S., Edwards, D.P., Eens, M., Costantini, D., 2018. Physiological and immunological responses of birds and mammals to forest degradation: A meta-analysis. Biol. Conserv. 224, 223–229. https://doi.org/10.1016/j.biocon.2018.06.002

Murray, K.A., Olivero, J., Roche, B., Tiedt, S., Guégan, J.F., 2018. Pathogeography: leveraging the biogeography of human infectious diseases for global health management. Ecography (Cop.). 41, 1411–1427. https://doi.org/10.1111/ecog.03625

Nagelkerke, N.J., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Olsen, A., van Lieshout, L., Marti, H., Polderman, T., Polman, K., Steinmann, P., Stothard, R., Thybo, S., Verweij, J.J., Magnussen, P., 2009. Strongyloidiasis - the most neglected of the neglected tropical diseases? Trans. R. Soc. Trop. Med. Hyg. 103, 967–972. https://doi.org/10.1016/j.trstmh.2009.02.013

Organization, W.H., 2021. Stongyloidiasis [WWW Document]. Control Neglected Trop. Dis. URL https://www.who.int/teams/control-of-neglected-tropical-diseases/soil-transmitted-helminthiases/strongyloidiasis (accessed 6.1.22).

Patz, J.A., Graczyk, T.K., Geller, N., Vittor, A.Y., 2000. Effects of environmental change on emerging parasitic diseases. Int. J. Parasitol. 9, 1–11.

Peterson, B.G., Carl, P., 2020. PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis.

Pietrock, M., Marcogliese, D.J., 2003. Free-living endohelminth stages: At the mercy of environmental conditions. Trends Parasitol. 19, 293–299. https://doi.org/10.1016/S1471-4922(03)00117-X

Ramos-Fernández, G., Wallace, R.B., 2008. Spider monkey conservation in the twenty-first century: recognizing risks and opportunities, in: Campbell, C.J. (Ed.), Spider Monkeys: Behavior, Ecology and the Evolution of the Genus Ateles. Cambridge University Press, pp. 351–376. https://doi.org/10.1017/cbo9780511721915.013

Reiczigel, J., Marozzi, M., Fabian, I., Rozsa, L., 2019. Biostatistics for parasitologists – a primer to Quantitative Parasitology. Trends Parasitol. 35, 277–281.

Saari, S., Näreaho, A., Nikander, S., 2019. Canine parasites and parasitic diseases. Academic Press.

Sánchez-Pinzón, K., Reyna-Hurtado, R., Meyer, N.F.V., 2019. Moon light and the activity patterns of baird’s tapir in the Calakmul region, Southern Mexico. Therya 11, 137–142.

https://doi.org/10.12933/therya-20-654

SEMARNAT, 2010. NormaOficial Mexicana NOM-059-ECOL-2010, protección ambiental-especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo., in: Diario Oficial de La Federación. Jueves 30 de diciembre de 2010, México.

Shedden, A., Dunn, J.C., Martínez-Mota, R., Cristobal-Azkarate, J., Gillingham, P., MacSwiney-González, C., Newton, A., Rodríguez-Luna, E., Korstjens, A., 2022. Forest maturity has a stronger influence on the prevalence of spider monkeys than howler monkeys in an anthropogenically impacted rainforest landscape. Primates. https://doi.org/10.1007/s10329-022-00980-8

Shrestha, N., 2020. Detecting multicollinearity in regression analysis. Am. J. Appl. Math. Stat. 8, 39–42. https://doi.org/10.12691/ajams-8-2-1

Stevenson, M., Sergeant, E., 2022. epiR: Tools for the analysis of epidemiological data.

Stoll, N.R., 1930. On methods of counting nematode ova in sheep dung. Parasitology 22, 116–136. https://doi.org/10.1017/S0031182000010969

Sures, B., Nachev, M., Selbach, C., Marcogliese, D.J., 2017. Parasite responses to pollution: what we know and where we go in ‘Environmental Parasitology.’ Parasites and Vectors 10, 1–19. https://doi.org/10.1186/s13071-017-2001-3

Vanderwaal, K.L., Windels, S.K., Olson, B.T., Vannatta, J.T., Moen, R., 2015. Landscape influence on spatial patterns of meningeal worm and liver fluke infection in white-tailed deer. Parasitology 142, 706–718. https://doi.org/10.1017/S0031182014001802

Vanhove, M.P.M., Thys, S., Decaestecker, E., Antoine-Moussiaux, N., De Man, J., Hugé, J., Keune, H., Sterckx, A., Janssens de Bisthoven, L., 2020. Global change increases zoonotic risk, COVID-19 changes risk perceptions: a plea for urban nature connectedness. Cities Heal. 00, 1–9. https://doi.org/10.1080/23748834.2020.1805282

Vatcheva, K.P., Lee, M., McCormick, J.B., Rahbar, M.H., 2016. Multicollinearity in regression analyses conducted in epidemiologic studies. Epidemiol. Open Access 06, 1–20. https://doi.org/10.4172/2161-1165.1000227

Velasco-Toro, J., 1993. Los estudios Botánicos en Uxpanapa previos al reacomodode la población Chinanteca. La Cienc. y el Hombre1 15, 27–39.

Vidal-Martínez, V.M., Pech, D., Sures, B., Purucker, S.T., Poulin, R., 2010. Can parasites really reveal environmental impact? Trends Parasitol. 26, 44–51. https://doi.org/10.1016/j.pt.2009.11.001

Wasser, S.K., Davenport, B., Ramage, E.R., Hunt, K.E., Parker, M., Clarke, C., Stenhouse, G., 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Can. J. Zool. 82, 475–492. https://doi.org/10.1139/Z04-020

White, R.J., Razgour, O., 2020. Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change. Mamm. Rev. 50, 336–352. https://doi.org/10.1111/mam.12201

Wickham, H., 2016. ggplot2 – Elegant Graphics for Data Analysis, 2nd ed. Springer-Verlag, New York.

Figure Legends

Fiq. 1. Collecting sites at the Uxpanapa Valley, southeastern Mexico. Colors indicate land cover types. Different footprints indicate type of host mammal sampled.

Fig. 2. **Landscape structure predictors of gastrointestinal parasitism in primates** at the Uxpanapa Valley southeastern Mexico. A) Top models ranked by AIC, rows represent individual models and columns represent predictor variables; significant associations are marked with ● ($P \leq 0.05$); cells colored according to odds ratio. R^2 expressed marginal R^2 / conditional R^2. B) Graphs of the significant relationships between landscape variables and presence of parasites in howler and in spider monkeys (C). Shading indicates 95% CI around the regression line.

Fig. 3. **Landscape structure predictors of gastrointestinal parasitism in tapir** at the Uxpanapa Valley southeastern Mexico. A) Top models ranked by AIC, rows represent individual models and columns represent predictor variables; significant associations are marked with ● ($P \leq 0.05$); cells colored according to odds ratio. R^2 expressed marginal R^2 / conditional R^2. B) Relationship between presence of Trichostrongylidae and *Kiluluma* sp. and edge density. Shading indicates 95% CI around the regression line.

Fig. 4. **Landscape structure predictors of gastrointestinal parasitism in wild felids** at the Uxpanapa Valley southeastern Mexico. A) Top models ranked by AIC, rows represent individual models and columns represent predictor variables; significant associations are marked with ● ($P \leq 0.05$); cells colored according to odds ratio. R^2 expressed marginal R^2 / conditional R^2. B) Relationship between the presence of parasites and river density in jaguar, and C) the relationship between landscape variables and the presence of cestodes in large felids. Shading indicates 95% CI around the regression line.

Fig. 5. Landscape structure and multiparasitism in wild mammals at the Uxpanapa Valley southeastern Mexico. A) Top models ranked by AIC, rows represent individual models and columns represent predictor

variables; significant associations are marked with ● ($P \leq 0.05$); cells colored according to values of Nagelkerke's R^2. B) Graphs of the significant relationships between landscape variables and richness of parasites in howler monkeys; C) tapir; and D) large felids. Shading indicates 95% CI around the regression line.

Fig. 6. Habitat quality and gastrointestinal parasitism in wild mammals at the Uxpanapa Valley in southeastern Mexico. A) Forest plot for the odds ratio of parasitism in disturbed habitat for each mammal host, error bars represent 95% CI; asterisks denote significant values ($P \leq 0.05$). B - H) Boxplots of parasite's egg density in disturbed versus conserved habitat in (B) howler monkeys, (C) spider monkeys, (D) small felids, (E) jaguar, (F) puma, (G) large felids, and (H) tapir