Integrity Matters: Riparian Forest Preservation Influences Body Condition and Parasites of Amphibians

Aline Aguiar[1,2*] · Alison C. Wunderlich[1*] · Lucas Henrique dos Santos[2] · Drausio H. Morais[3] · Alba L. Cavalheiro[2] · Célio F. B. Haddad[1]

[1]Universidade Estadual Paulista (UNESP), Instituto de Biociências – Departamento de Biodiversidade e Centro de Aquicultura (CAUNESP), Campus de Rio Claro (SP), Brazil

[2]Universidade Estadual de Londrina (UEL), Centro de Ciências Biológicas –Departamento de Biologia Animal e Vegetal, Londrina (PR), Brazil

[3]Universidade Federal de Uberlândia (UFU), Instituto de Ciências Agrárias (ICIAG) – Campus de Monte Carmelo (MG), Brazil.

Corresponding author

Alison C. Wunderlich

awunderlich@gmail.com

*These authors contributed equally to this manuscript and are co-first authors.

ORCID

Aline Aguiar (https://orcid.org/0000-0003-2727-1348)

Alison Carlos Wunderlich (https://orcid.org/0000-0001-9222-8536)

Lucas Henrique dos Santos (https://orcid.org/0000-0002-5850-0089)

Drausio Honório Morais (https://orcid.org/0000-0002-9866-6008)

Alba L. Cavalheiro (https://orcid.org/0000-0002-5302-9259)

Célio F. B. Haddad (https://orcid.org/0000-0003-1057-5660)

Note: Supplementary data associated with this article.

Abstract

Riparian forests are essential for structure and dynamic of head streams performing an important role in maintaining biodiversity in fragmented forests. Integrity condition influences the stream quality and the distribution of amphibians and their responses to infections. To investigate this premise, we evaluated parasite infection parameters in amphibians through six riparian areas with different integrity levels (low, intermediate and high) in an Atlantic Forest ecosystem. We hypothesized that more preserved forest fragments (high integrity) sustain a high diversity, low abundance, and large proportion of parasite species with complex life cycles. To test this hypothesis, we described the parasite community in *Proceratophrys avelinoi* populations and modeled the forest traits and water abiotic factors as predictor variables on parasite parameter responses. Although the amphibians' populations exhibited a total parasite richness of eight species, our multivariate analysis revealed that only Physalopterinae nematodes showed significant differences between forest fragments; moreover, the overall parasite abundances were affected by abiotic factors. We found that high-integrity fragments not only support parasites with complex life cycles but also improve the host body condition. This contributes to the development of host populations with more energetic investments which are essential to resist and tolerate infections. On the contrary, the concurrent high parasite loads, and reduced body conditions observed in intermediary-integrity areas may lead to a metabolic collapse that threatens long-term population decline. Our results highlight the importance of ecosystem integrity in the riparian forests for providing better resources for amphibians and in overcoming the risk of diseases by helminth parasites.

Keywords Anurans · Helminths · Conservation · Atlantic Forest · Deforestation · Risk rapid assessment

1. Introduction

The riparian forests are associated with water bodies that include parts of terrestrial and aquatic ecosystems and they are essential to regulate the inputs into these environments (Naiman and Décamps, 1997; Turunen et al., 2021; Costa et al., 2026). These forests function as filters for the substances and energy supplied by the surrounding regions (Naiman et al., 1988). Vegetation quality (*e.g.*, composition of plant species) as well as the forest strip width (distance from riverside and forest border) could affect or determine the environmental conditions and local biodiversity (Rodríguez-Mendoza and Pineda, 2010; Kowalska et al., 2021). Thus, these factors are related to the forest integrity and could also affect the water quality, which is essential for maintaining a high biodiversity of species in fragmented forests (Rodríguez-Mendoza and Pineda, 2010; Turunen et al., 2021).

Forest fragmentations have been one of the main disturbances in natural environments which generate cascading events affecting biodiversity and organisms' health (Blaustein et al., 2012; Newbold et al., 2015; Tan et al., 2023). For instance, many amphibian species depend on the riparian forest integrity and the connection between aquatic and terrestrial habitats to complete their life cycles (Becker et al., 2010; Oropeza-Sánchez et al., 2022; Volkmer et al., 2025). In this context, the effects of habitat loss and agrochemical drainage in water bodies have been extensively studied by ecologists and ecotoxicologists using amphibians as models (Blaustein et al., 2012; Bahl et al., 2024; Salinas et al., 2024). For the latest decades, the decline of amphibian populations and their skin sensitivity have gained attention due to the impacts of deforestation, pollutants, and risk of diseases (Blaustein et al., 2012). Then, the environmental changes and their impacts on animal health are the main triggers for the risk of infection diseases such as chytrid fungus, *Ranavirus*, and macroparasites which can promote population decline in amphibians by direct and indirect effects (Koprivnikar et al., 2012; Carvalho et al., 2017; Luedtke et al., 2023; Carvalho et al., 2025). In a recent global amphibian assessment, the authors found that diseases and habitat loss drove 91% of declines for the world's amphibians (Luedtke et al., 2023).

In this way, studies suggest that parameters of parasite communities could reveal habitat integrity and host population health, since parasites as well as the top predators are the first to indicate populational changes (Marcogliese and Cone, 1997; Laurence et al., 2002; Lafferty et al., 2008). Thus, in a pristine environment with high biological diversity it is also expected to have high parasite diversity in low loads (*i.e.*, parasite abundance or intensity of infection) (Marcogliese and Cone, 1997). The biological diversity found in riparian habitats contributes to the success of parasites with complex life cycles such as trematodes which need two or more specific hosts to complete their cycle (Gibb and Hochuli, 2002; Poulin and Cribb, 2002). On the other hand, in areas with low diversity, the intermediate hosts (*e.g.*, different species of invertebrates) may be scarce and the dependent parasites could not complete their cycles resulting in the decrease of parasite competition (Gibb and Hochuli, 2002; Aguiar et al., 2015). In this scenario, generalist parasite species with fewer ecological requirements tend to be more abundant and prevalent, thereby increasing the risk of

infectious diseases in host populations (Marcogliese and Cone, 1997). The changes in the community composition from specialist species to generalist ones result in biotic homogenization that may occur in all communities due to deforestation and other anthropogenic activities (Olden et al., 2004; Laliberté and Tylianakis, 2010).

Herein, we aim to evaluate whether riparian ecosystem factors (abiotic factors of water, forest integrity, and forest strip width) and host traits (size and body condition) can affect richness, diversity, abundance, and community composition of helminth parasites infecting amphibians in an Atlantic Forest region experiencing intense agricultural fragmentation in southern Brazil. To test these effects, we predicted that riparian forest fragments with high integrity would exhibit high diversity, low loads of infection, and increased proportion of parasites with complex life cycle; whereas forest fragments with lower integrity are expected to negatively affect parasite parameters and potentially increase the risk of infectious diseases in amphibian populations.

2. Materials and methods

2.1. Study area and collection of amphibians

Northern Paraná State, in southern Brazil, is characterized by extensive agricultural landscapes dominated by soybean, corn, and wheat cultivation, resulting in intense habitat fragmentation, with the remaining forest cover mostly restricted to small riparian fragments (IPARDES, 2018). However, the original forest cover was Seasonal Semideciduous Forest, a derivation of Atlantic Forest, a *hotspot* with great biological diversity and water sources (Torezan, 2002; Mittermeier et al., 2005).

During fieldwork, we sampled the "Smooth Horned Frog", *Proceratophrys avelinoi* (Odontophrynidae), from six riparian forest fragments ranked by three integrity levels (high, intermediate, and low integrity) according to the mean of forest strip width and Rapid Ecological Assessment (REA) based on data from Cavalheiro (2018). For conducting the REA and the forest strip width measurements we established four points (P1, P2, P3, and P4) in the stream where P1 is the headwater and the other points are 50 m, 100 m, and 150 m, respectively from the headwater (Fig. 1b). From each point, two perpendicular transects (right and left riverside) were taken in direction to forest edge; additionally, from P1 a third transect was taken upriver, resulting in nine transects towards the edge of each riparian fragment (Fig. 1b). The distances were measured in loco, except for those longer than 100 m which were estimated using Google Earth Pro. Then, we calculated the mean distances for each point considering the three distances from P1 (right, left, and upriver) and the two distances (right and left) from the other points. Thus, the mean of these nine transects represent the forest strip width of a given fragment. Rapid Ecological Assessment (REA) was conducted by Cavalheiro (2018) based on Medeiros and Torezan (2013) to evaluate forest quality considering 11 ecological variables of plant communities which were ranked from 0 to 4 (Table S1). Then, the REA was applied following the nine transects mentioned before (Fig. 1b).

126 To determine the water quality of the streams, we measured the physical-chemical properties of water such as
127 concentrations of nitrate and phosphate, dissolved oxygen, electrical conductivity, and temperature (Table S2). Nitrate
128 (NO3–N) and phosphate (PO4–P) were quantified using a portable photometer (Macherey-Nagel, model PF-12 Plus) and
129 the analyzing kits (Visocolor Eco) 5-84 test for phosphate (detection limits 0.2 mg L−1 e 5.0 mg L−1) and 5-41 test for
130 nitrate (detection limits 1.0 mg L−1 e 14.0 mg L−1); values below the detection limit were considered as a half of it (*i.e.*,
131 0.1 mg L−1 for phosphate and 0.5 mg L−1 for nitrate) (Dinelli et al., 2012). Dissolved oxygen, electrical conductivity,
132 and temperature were measured with Multi-Parameter YSI 85.
133 The six riparian fragments house headwaters which belong to the Tibagi River basin (França, 2002), in the region
134 of Londrina municipality, Paraná State, and they are sparse in the agriculture matrix (Fig. 2); the geographic location of
135 fragments and their traits are given in the Table 1 according to prior research conducted by Cavalheiro (2018). The high-
136 integrity forest fragments are nominated H1 and H2; intermediate-integrity fragments are I1 and I2; and forest fragments
137 with low-integrity are L1 and L2 (Figs. 1a, 2).
138 The voucher specimens of P. avelinoi are deposited in the Coleção Célio F. B. Haddad (CFBH 48941 – 49042),
139 Department of Biodiversity, Institute of Biosciences, São Paulo State University, UNESP campus Rio Claro, São Paulo,
140 Brazil.
141 *2.2. Parasites procedures*
142 Amphibian necropsy was conducted after an overdose of lidocaine (5 mg/g), and then the organs were separated into petri
143 dishes for searching helminth endoparasites. Parasites were collected and cleaned with saline solution (0.9%) and then
144 they were fixed according to specific protocols for each parasite group. Nematodes were fixed using hot ethanol 70%,
145 whereas platyhelminths as digeneans and cestodes were fixed between slides with slight pressure using 90% ethanol or
146 AFA (solution with alcohol, formalin and acetic acid) (Amato et al., 1991). Subsequently, parasite specimens were
147 conserved in bottles with 70% ethanol for posterior slides mounting for morphological analyses and identification. In
148 slides, nematodes were clarified with lactic acid or lactophenol, and digeneans and cestodes were stained with chloridric
149 carmine followed by eugenol in temporary slides (Amato et al., 1991). These slides were analyzed under microscopy
150 using computerized image system Zeiss Axio Shat AX10 for recording and morphometric measurements.
151
152 *2.3. Data analysis*
153 The parasite communities associated with populations of *P. avelinoi* were described by the richness (number of taxa),
154 diversity (Brillouin index according to Magurran, 2004), prevalence, mean abundance, and mean intensity of infection
155 (load parasite) (Bush et al., 1997). The diversity and richness were also estimated for each host individual
156 (infracommunity) and then as the means for the host population (component community). We also analyze the presence

of parasite species that exhibit a complex life cycle which use two or more hosts (heteroxenic cycles) as well as their developmental stage (cyst or adult) found in these frogs.

Body condition was measured according to scaled mass index (SMI) (Peig and Green, 2009; Brodeur et al., 2020) as a health indicator of the amphibians from the six forest fragments. To determine the SMI, we used the formula: SMI = Wi (L0/Li)bSMA. First, we log-transformed the body weight and snout-vent length (SVL) to estimate the β coefficient of the regression, and then calculated Wi and Li as the weight and SVL of each frog specimen, respectively; L0 is the average SVL of the population; and bSMA is the β coefficient (Peig and Green, 2009). We used generalized linear mixed model (GLMM) with a gaussian distribution to compare the SMI among the riparian forest fragments. Before running the GLMM, we combine the two sites of the same fragment level (i.e., low, intermediate and high) to improve the representative of the sample and statistical power.

We also used generalized linear mixed models (GLMMs) with a negative binomial (NB) distribution to examine the relationship between the parameters of parasite infections (i.e. response variables: mean abundance, richness, diversity, life cycles, and developmental stage) as a function to host health (SMI), integrity levels of fragments (i.e., REA and forest width), and abiotic factors (i.e. temperature, dissolved oxygen, electrical conductivity, nitrate, and phosphate). As an alternative distribution to NB, we also used a Conway–Maxwell–Poisson distribution to count data over- (dispersion parameter < 1) or under-dispersion (dispersion parameter > 1) (Sellers and Premeaux, 2021). Previously, we tested for collinearity among predictors using a variance inflation factor (VIF), with the threshold set to VIF < 10, which represents high multicollinearity among predictors (Borcard et al., 2011; Shrestha 2020). The model with the lowest Akaike Information Criterion score and small sample size correction (AICc) was used to select the best model among competing models (Tredennick et al., 2021). All GLMM analyses were conducted in R version 4.4.1 (R Development Core Team 2024), using the lme4 package (Bates et al., 2015).

To verify the similarity among the parasite community compositions of *P. avelinoi* from the six forest fragments and test whether the differences are significant we used nonmetric multidimensional scaling (NMDS) with Bray-Curtis index and ANOSIM (Analysis of Similarities) in PAST (Hammer et al., 2001). Beyond the multivariate distance-based analysis, we also used the manyglm function (mvabund package), which fits a separate GLM to each parasite species, using a common set of explanatory variables (*i.e.* SMI, forest width, REA and abiotic factors). This analysis uses resampling-based hypothesis tests to infer which exploration variables are associated with parasite species abundance (Wang et al., 2024). For all analyses, we used negative binomial distribution and the results were considered significant at $\alpha = 0.05$ using a Likelihood Ratio Test (LRT).

Maps were created using QGIS version 3.34.3 (QGIS Development Team 2024), and graphics were generated with the ggplot2 package (Wickham, 2011).

188

189 **3. Results**

190 We collected 98 specimens of *P. avelinoi* from six forest fragments in the north of Paraná State, Brazil (Table 2). The
191 parasite community associated with these populations was composed predominantly by nematodes (Cosmocercidae,
192 Physalopterinae, *Raillietnema* sp., *Raillietnema spectans*, and *Rhabdias* sp.); however, we found two species of digenetic
193 trematodes (*Gorgoderina* sp. 1 and *Gorgoderina* sp. 2) and an encysted cestode (*Spirometra* sp.) (Table 3). Nonetheless,
194 the parasite richness and diversity varied across the fragments as did other overall parameters of parasitism, such as
195 prevalence, mean abundance, and mean intensity of infection (Table 2). Both intermediate forest fragments, I1, and I2,
196 presented respectively the highest richness (six parasite taxa) and the highest diversity (Brillouin index 0.71). The overall
197 prevalences of parasitism were similar among the six fragments ranging from 83.33% (I2) to 100% (H1 and L1); the
198 highest mean abundance was in I1 (8.88 ± 0.77) followed by H1 (8.33 ± 3.18), while intensity of infection was higher in
199 I2 (9.40 ± 2.25) followed by I1 (9.06 ± 0.77) (Table 2).

200 Nematodes cosmocercids were present in all frog populations in the present study (Table 3); since only female
201 cosmocercids with similar morphological characteristics were recovered, species-level identification was not possible.
202 Larvae of Physalopterinae were found in three frog populations (H2, I1, and I2), as well as *Raillietnema* sp. (I1, I2, and
203 L1) and the encysted cestode *Spirometra* sp. (H2, I1, and L1) (Table 3). *Raillietnema spectans* (I1), *Rhabdias* sp. (L1),
204 *Gorgoderina* sp. 1 (I1), and *Gorgoderina* sp. 2 (L2) were exclusive of their respective frog population. Cosmocercids
205 showed high infection intensity values in most frog populations, ranging from 8.36 ± 0.78 (I1) to 3.17 ± 0.75 (L2);
206 however, *Raillietnema* sp. (I2) and *Gorgoderina* sp. 2 (L2) also have considerable mean infection intensity values, 15 and
207 7 (± 6.00), respectively (Table 3).

208 We found a lower significant difference on the scaled mass index (SMI) in individuals of low habitat integrity
209 (GLMM: estimate ± SE: 2.27 ± 0.070: $p < 0.001$), compared to individuals of high habitat integrity (GLMM: estimate ±
210 SE: 2.63 ± 0.071; $p < 0.001$; Fig. 3).

211 Results of generalized linear mixed models describing the relationship between parasite abundance, parasite
212 richness, and parasite diversity (Brillouin index) are described in Table 4. Our models retained predictors with VIFs < 10
213 only (*i.e.* forest width, NO3-N, and PO4-P were excluded). Of three analyzed models, parasite abundance showed a
214 significant difference in relation to temperature (GLMM: estimate ± SE: –1.109 ± 0.384, $p = 0.003$), dissolved oxygen
215 (GLMM: estimate ± SE: –0.512 ± 0.206, $p = 0.012$), and electrical conductivity (GLMM: estimate ± SE: –0.013 ± 0.004,
216 $p = 0.005$). Significant effects of the predictors were not found on the model of parasite richness and diversity (Table 4),
217 life cycle (GLMM: estimate ± SE: –0.022 ± 0.258, $p = 0.930$), and developmental stages (GLMM: estimate ± SE: 2.23 ±
218 1.69, $p = 0.188$). Abiotic factors of water stream (Table S2) such as temperature ranged from 21.05 ºC (H1 – high integrity)

219 to 22.70 ºC (L1 – low integrity), while dissolved oxygen ranged from 5.61 mg L-1 (L1 – low integrity) to 9.60 mg L-1
220 (I2 – intermediary integrity), and electrical conductivity ranged from 36.05 µS (H1 – high integrity) to 164,0 µS (L1 –
221 low integrity).

222 Multivariate distance-based analysis revealed that the conditions of habitat integrity could explain the variation of
223 the parasite community (Fig. 4). First, the structure of NMDS space (Stress = 0.1916; i.e., < 0.2 provides a good
224 representation in reduced dimensions) showed some differences in parasite species distribution among the six frog
225 populations, and the differences were confirmed by ANOSIM ($R = 0.116$; $p = 0.0404$). Overall, our multivariate model-
226 based analysis also showed differences in the parasite community composition on different forest fragments ($LRT = 53.24$, $p = 0.011$). In addition, we found that only a species of nematode, Physalopterinae gen. sp., showed significant
227 differences in relation to forest fragments ($LRT = 14.76$, $p = 0.038$).
228
229

230 **4. Discussion**

231 Overall, our findings reveal that riparian forest integrity affects helminth parasite communities in the anuran
232 *Proceratophrys avelinoi* across six forest fragments in southern Brazil's Atlantic Forest. Our analyses have shown
233 significant differences in the composition of parasite communities from these forest fragments. We found that
234 Physalopterinae nematodes differ significantly across fragments. These nematodes were not observed in low-integrity
235 forest fragments since their complex life cycle requires a high diversity of hosts (invertebrates and vertebrates as birds,
236 reptiles, or mammals), a condition not expected in degraded habitats. Our results also show that the abiotic factors
237 influence parasite abundances, and that high-integrity fragments are associated with complex life cycle parasites and
238 better host body condition, while intermediate-integrity areas show the worst combination of high parasite loads and poor
239 host condition.

240 However, according to our models, temperature, dissolved oxygen, and electrical conductivity were the only
241 factors that negatively affected parasite abundance, while richness and diversity of parasites were not influence of the
242 predictor tested *(i.e.*, abiotic factors, Rapid Ecological Assessment, and frogs' SMI – Scaled Mass Index). In the low-
243 integrity fragments, higher temperatures and reduced parasite abundance could be related to an increased feeding rate on
244 the parasites' free-living stages by their predators. According to Thieltges et al. (2008), parasite numbers decreased as the
245 temperature increased with the presence of predators of parasites' free-living stages; on the other hand, parasite numbers
246 increased under the same conditions when the predators were absent. The authors argued that high temperatures increase
247 predators' feeding rates, resulting in reduced parasite numbers. Low concentration of dissolved oxygen may stem from
248 high temperature, intense light, and ultraviolet radiation due to forest cover loss, which promotes eutrophication and
249 biodiversity loss. These combined factors reduce the viability of free-living stages of parasites. The increased electrical

conductivity observed in water bodies within low-integrity fragments may be attributed to the runoff of agrochemicals, which easily reaches the streams due to the reduced buffering capacity of narrowed riparian forests (Allan, 2004; Sweeney and Newbold, 2014). Numerous pollutants are known to disrupt host-parasite dynamics through diverse routes, as well as the survivals of free-living stages of parasites (Poulin, 1992; Pietrock and Marcogliese, 2003). These results reinforce that parasite communities and host-parasite dynamics are shaped by both environmental conditions and local biodiversity acting in concert. For instance, one would expect increased numbers of infective stages as temperatures rise if other biotic factors were absent, as typically found in natural environments (Thieltges et al., 2008).

Contrary to our predictions, parasite richness and diversity were not highest in the high-integrity forests. Moreover, frogs from high- and intermediary-integrity forests exhibited the highest parasite loads compared to frogs from low-integrity fragments. Additionally, the highest proportions of parasites with heteroxenous life cycle (i.e., Physalopterinae gen. sp., *Spirometra* sp., *Gorgoderina* spp.) were observed in parasite communities from high-integrity forests (2/3 species – 67%), followed by intermediary-integrity forests (3/6 species – 50%), and low-integrity forests (2/5 species – 40%) (Table 3). These results highlight the importance of considering both the species composition in the parasite communities and the life cycle attributes of parasites. Parasites with heteroxenous life cycle require more than one specific host to complete their development, necessitating high levels of biodiversity among invertebrates (usually as intermediate hosts) and vertebrates—such as birds, reptiles, and mammals—that serve as definitive hosts (Anderson, 2000; Aguiar et al., 2021). In contrast, parasites with monoxenous life cycles (i.e., Cosmocercidae, *Raillietnema* spp. and *Rhabdias* sp.) require only a single host and are generally considered generalist species (Smyth, 1994; Anderson, 2000). The frogs in this study act as intermediate hosts for Physalopterinae species and *Spirometra* sp., which complete their cycles in other vertebrates (Anderson, 2000; Mueller, 1974). These findings corroborate our premise regarding the presence of heteroxenous parasites in areas of high biological diversity and reinforce previous studies (*e.g.*, Marcogliese and Cone, 1997; McKenzie, 2007; Rohr et al., 2020).

Areas of greater biodiversity not only support parasites with complex life cycles but also enhance host health (*e.g.*, body condition) by providing better natural resources. This fosters the development of host populations with greater energetic reserves, which are essential for resisting and tolerating infections (Read et al., 2008; Rohr et al., 2010). Resistance comprises host mechanisms—such as immune response—that decrease parasite fitness and prevent infection establishment, while tolerance reduces the damage caused by infection without affecting parasite fitness (Read et al., 2008; Medzhitov et al., 2012; Knutie et al., 2017). Frogs from the high-integrity areas exhibited significantly greater body condition (*i.e.*, SMI) than those from other areas and harbored high parasite loads, which could be sustained by tolerant mechanisms given their presumably superior energetic condition. Similarly, mechanisms of resistance to colonization by parasites may explain the low richness and diversity of parasites found in these frogs. Hosts with better body condition

in the infection inception exhibit reduced parasite loads due to their capacity to invest energy in immune responses that resist infection (Read et al., 2008). Once infection is established, these hosts can tolerate higher parasite loads, as supporting metabolic damage is more energetically feasible than resisting, which requires high energetic demands (Knutie et al., 2017). According to Boots et al. (2009), the type of host defense (resistance or tolerance) and its associated costs are linked to traits of both the host and the parasite, thereby influencing this ecological dynamic.

Although resistance and tolerance are context-dependent mechanisms (Medzhitov et al., 2012; McCarville and Ayres, 2018), these findings highlight the risk of infectious diseases and consequent population declines in intermediary and low-integrity forests. In intermediate-integrity areas, the concurrent high parasite loads and reduced body conditions (SMI) may lead to metabolic collapse, endangering population declines in long-term. In contrast, in the low-integrity fragment, frogs' reduced body condition renders them unable to tolerate high parasite loads, which would be fatal. Therefore, the surviving populations—and thus our field samples—consist predominantly of individuals with low parasite burdens.

In conclusion, our study demonstrates that changes in forest fragmentation and abiotic factors influence host–parasite interactions and host body condition, and that the consequences of these alterations may be detrimental, potentially leading to severe impacts on amphibian populations. Many threats (deforestation, pollution, pesticides, habitat loss) have been reported to biodiversity, especially to amphibians, highlighting the importance to understanding and anticipating the potential effects on the risk of infection diseases (Thieltges et al., 2008; Johnson et al., 2013; McCallum, 2015; Rohr et al., 2020). Moreover, other studies (*e.g.*, Baxter et al., 2005; Bowler et al., 2012; Turunen et al., 2021) advocate the importance of riparian forests in the ecosystem dynamics and mitigating ecological degradation. Therefore, the present study reinforces these predictions and shows consistently through field findings the outcomes on amphibian populations and their parasites under changes of habitat integrity in riparian forests.

Statements and Declarations

Supplementary Information

The online version contains supplementary material available at a link.

Author contributions

AA and DHM conceived the idea, executed field collections, and performed parasitological procedures in laboratory. AA and ACW analyzed, interpreted the data, and wrote the manuscript. ALC, JMDT and CFBH participated in conceiving the idea and revised the final manuscript. All authors critically revised the final manuscript version, provided editorial advice, and approved it for publication.

Funding Financial

Support was provided by the São Paulo State Research Foundation (FAPESP grant no. 2018/25554-2 to A.A. and 2017/16650-5 to A.C.W.) and A.C.W acknowledges support through postdoctoral fellowships from UNESP/PROPE (#13/2022 and #05/2024).

Data availability

Data supporting the findings of this study are available upon request from the corresponding author.

Declarations

Conflict of interest

The authors declare no competing interests.

Ethical approval

This study was conducted under the following permits (SISBio #69194-1, CEUA-Unesp 3042, 19/2019).

Acknowledgements

We acknowledge the colleagues who helped in fieldwork, especially Prof. Dr. Gustavo M. Teixeira and Dr. Nick T. Narezzi. We also acknowledge the funding agencies for financial support provided by the São Paulo State Research Foundation (FAPESP #2018/25554-2 to A.A. and #2017/16650-5 to A.C.W.) and support from UNESP/PROPe (#13/2022 and #05/2024 to A.C.W).

References

Aguiar, A., Morais, D.H., Silva, L.A.F., Anjos, L.A., Foster, O.C., Silva, R.J., 2021. Biodiversity of anuran endoparasites from a transitional area between the Atlantic Forest and Cerrado biomes in Brazil: new records and remarks. Zootaxa 4948, 1–41. https://doi.org/10.11646/zootaxa.4948.1.1

Aguiar, A., Toledo, G.M., Anjos, L.A., Silva, R.J., 2015. Helminth parasite communities of two *Physalaemus cuvieri* Fitzinger, 1826 (Anura: Leiuperidae) populations under different conditions of habitat integrity in the Atlantic Rain Forest of Brazil. Braz. J. Biol. 75, 963–968. https://doi.org/10.1590/1519-6984.03614

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. 35, 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122

Amato, J.F.R., Boeger, W., Amato, S.B., 1991. Protocolos para laboratório: coleta e processamento de parasitos de pescado. UFRRJ, Seropédica.

Anderson, R.C., 2000. Nematode parasites of vertebrates: their development and transmission, 2nd edn. CAB Publishing, London. https://doi.org/10.1079/9780851994215.0000

Bahl, M.F., Costa, C.S., Demetrio, P.M., Loughlin, T.M.M., Arruti, M.E., Brodeur., J.M.C., Natale, G.S., 2024. Integration of a battery of biomarkers to evaluate the health status of field-collected frogs of *Leptodactylus luctator* living in ecosystems with different anthropogenic disturbances. Sci. Total. Environ. 933, 173174. https://doi.org/10.1016/j.scitotenv.2024.173174

Bates, D., Mächler, 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

Baxter, C.V., Fausch, K.D., Saunders, W.C., 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. 50, 201–220. https://doi.org/10.1111/j.1365-2427.2004.01328.x

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Prado, P.I., 2010. Habitat split as a cause of local population declines of amphibians with aquatic larvae. Conserv. Biol. 24, 287–294. https://doi.org/10.1111/j.1523-1739.2009.01324.x

Blaustein, A.R., Gervasi, S.S., Johnson, P.T.J., Hoverman, J.T., Belden, L.K., Bradley, P.W., Xie, G.Y., 2012. Ecophysiology meets conservation: understanding the role of disease in amphibian population declines. Philos. Trans. R. Soc. B. 367, 1688–1707. https://doi.org/10.1098/rstb.2012.0011

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical ecology with R. Springer.

Boots, M., Best, A., Miller, M.R., White, A., 2009. The role of ecological feedbacks in the evolution of host defence: what does theory tell us? Philos. Trans. R. Soc. B. 364, 27–36. https://doi.org/10.1098/rstb.2008.0160

Bowler, D.E., Mant, R., Orr, H.G., Hannah, D.M., Pullin, A.S., 2012. What are the effects of wooded riparian zones on stream temperature? Environ. Evid. 1, 1–9. https://doi.org/10.1186/2047-2382-1-3

Brodeur, J.C., Damonte, M.J., Candioti, J.V., Poliserpi, M.B., D'Andrea, M.F., Bahl, M.F., 2020. Frog body condition: basic assumptions, comparison of methods and characterization of natural variability with field data from *Leptodactylus latrans*. Ecol. Indic. 112, 106098. https://doi.org/10.1016/j.ecolind.2020.106098

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.

Carvalho, T., Becker, G.C., Toledo, L.F., 2017. Historical amphibian declines and extinctions in Brazil linked to chytridiomycosis. Proc. Biol. Sci. 284:20162254. https://doi.org/10.1098/rspb.2016.2254

Carvalho, T., Falconi, N., White, T. et al., 2025. The role of seasonal migration in predicting amphibian population persistence across fragmented tropical landscapes: an individual-based model. Biodivers. Conserv. 34, 1291–1310. https://doi.org/10.1007/s10531-025-03016-x

Cavalheiro, A.L., 2018. Florestas ripárias na paisagem agrícola do norte do Paraná, Brasil: relação com a qualidade da água em nascentes. Dissertation, PhD thesis. Available at: https://sucupira-legado.capes.gov.br/sucupira/public/consultas/coleta/trabalhoConclusao/viewTrabalhoConclusao.jsf?popup=true&id_trabalho=7122045

Costa, V.M., Gavioli, F.R., Alves-dos-Santos, H.L.R. et al., 2026. Conservation and restoration of riparian zones: impacts of legal and land use changes. Perspect. Ecol. Conserv. https://doi.org/10.1016/j.pecon.2026.02.003

Dinelli, E., Lima, A., Albanese, S., Birke, M., Cicchella, D., Giaccio, L., Valera, P., De Vivo, B., 2012. Comparative study between bottled mineral and tap water in Italy. J. Geochem. Explor. 112, 368–389.

França, V. 2002. O rio Tibagi no contexto hidrográfico paranaense. In: Medri ME, Bianchini E, Shibatta OA, Pimenta JA (eds) A bacia do rio Tibagi. M.E. Medri, Londrina, pp 45–61.

Gibb, H., Hochuli, D.F., 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol. Conserv. 106, 91–100. https://doi.org/10.1016/S0006-3207(01)00232-4

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.

IPARDES, 2018. Caderno estatístico município de Londrina. Available at: https://www.google.com.br/search?ei=kNqzWsqkMtH9wATMvI_ACA&q=ipardes+londrina (Accessed 13 March 2018)

Johnson, P.T.J., Preston, D.L., Hoverman, J.T., Richgels, K.L.D., 2013. Biodiversity decreases disease through predictable changes in host community competence. Nature 494, 230–234. https://doi.org/10.1038/nature11883

Knutie, S.A., Wilkinson, C.L., Wu, Q.C., Ortega, C.N., Rohr, J.R., 2017. Host resistance and tolerance of parasitic gut worms depend on resource availability. Oecologia 183, 1031–1040. https://doi.org/10.1007/s00442-017-3822-7

Koprivnikar, J., Marcogliese, D.J., Rohr, J.R., Orlofske, S.A., Raffel, T.R., Johnson, P.T.J., 2012. Macroparasite infections of amphibians: what can they tell us? EcoHealth 9, 342–360. https://doi.org/10.1007/s10393-012-0785-3

Kowalska, A., Affek, A., Wolski, J., Regulska, E., Kruczkowska, B., Zawiska, I., Kołaczkowska, E., Baranowski, J., 2021. Assessment of regulating ES potential of lowland riparian hardwood forests in Poland. Ecol Indic 120:106834. https://doi.org/10.1016/j.ecolind.2020.106834

Lafferty, K.D., Allesina, S., Arim, M. et al., 2008. Parasites in food webs: the ultimate missing links. Ecol. Lett. 11, 533–546. https://doi.org/10.1111/j.1461-0248.2008.01174.x

Laliberté, E., Tylianakis, J.M., 2010. Deforestation homogenizes tropical parasitoid–host networks. Ecology 91, 1740–1747. https://doi.org/10.1890/09-1328.1

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Luedtke, J.A., Chanson, J., Neam, K. et al., 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature 622, 308–314. https://doi.org/10.1038/s41586-023-06578-4

Magurran, A.E., 2004. Measuring biological diversity. Oxford University Press, Oxford.

Marcogliese, D.J., Cone, D.K., 1997. Parasite communities as indicators of ecosystem stress. Parasitologia 39, 227–232.

McCallum, H.I., 2015. Lose biodiversity, gain disease. Proc. Natl. Acad. Sci. USA 112, 8523–8524. https://doi.org/10.1073/pnas.1506279112

McCarville, J.L., Ayres, J.S., 2018. Disease tolerance: concept and mechanisms. Curr. Opin. Immunol. 50, 88–93. https://doi.org/10.1016/j.coi.2017.12.003

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

Medeiros, H.R., Torezan, J.M., 2013. Evaluating the ecological integrity of Atlantic Forest remnants by using rapid ecological assessment. Environ. Monit. Assess. 185, 4373–4382. https://doi.org/10.1007/s10661-012-2875-7

Medzhitov, R., Schneider, D.S., Soares, M.P., 2012. Disease tolerance as a defense strategy. Science 335, 936–941. https://doi.org/10.1126/science.1214935

Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, J., Mittermeier, C.G., Lamoreux, J., Fonseca, G.A.B., 2005. Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Washington, DC.

Mueller, J.F., 1974. The biology of *Spirometra*. J. Parasitol. 60, 3–14.

Naiman, R.J., Décamps, H., Pastor, J., Johnston, C.A., 1988. The potential importance of boundaries of fluvial ecosystems. J. North. Am. Benthol. Soc. 7, 289–306.

Naiman, R.J., Décamps, H., 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Syst. 28, 621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621

Newbold, T., Hudson, L.N., Hill, S.L.L. et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. Trends. Ecol. Evol. 19, 18–24. https://doi.org/10.1016/j.tree.2003.09.010

Oropeza-Sánchez, M.T., Suazo-Ortuño, I., Benítez-Malvido, J., 2022. Amphibian richness along modified riparian areas of central Mexico: conservation priorities. Ecol. Process. 11, 63. https://doi.org/10.1186/s13717-022-00408-7

Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative. Oikos 118, 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

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

Poulin, R., 1992. Toxic pollution and parasitism in freshwater fish. Parasitol. Today 8, 58–61.

Poulin, R., Cribb, T.H., 2002. Trematode life cycles: short is sweet? Trends Parasitol. 18, 176–183. https://doi.org/10.1016/S1471-4922(02)02262-6

R Core Team, 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: https://www.R-project.org/

Read, A.F., Graham, A.L., Råberg, L., 2008. Animal defenses against infectious agents: is damage control more important than pathogen control? PLoS Biol 6:2638–2641. https://doi.org/10.1371/journal.pbio.1000004

Rodríguez-Mendoza, C., Pineda, E., 2010. Importance of riparian remnants for frog species diversity in a highly fragmented rainforest. Biol. Lett. 6, 781–784. https://doi.org/10.1098/rsbl.2010.0334

Rohr, J.R., Raffel, T.R., Hall, C.A., 2010. Developmental variation in resistance and tolerance in a multi-host–parasite system. Funct. Ecol. 24, 1110–1121. https://doi.org/10.1111/j.1365-2435.2010.01709.x

Rohr, J.R., Civitello, D.J., Halliday, F.W., Hudson, P.J., Lafferty, K.D., Wood, C.L., Mordecai, E.A., 2020. Towards common ground in the biodiversity–disease debate. Nat. Ecol. Evol. 4, 24–33. https://doi.org/10.1038/s41559-019-1060-6

Salinas, Z.A., Babini, M.S., Bionda, C.L., Martino, A.L., Lajmanovich, C.R., 2024. Agroecosystems under conventional and organic management: hematological analysis of anuran for environmental health assessment. Environ. Adv. 15, 100508. https://doi.org/10.1016/j.envadv.2024.100508

Sellers, K.F., Premeaux, B. 2021. Conway–Maxwell–Poisson regression models for dispersed count data. WIREs Comput Stat 13, e1533.

Shrestha, N., 2020. Detecting multicollinearity in regression analysis. American Journal of Applied Mathematics and Statistics 8, 39–42. https:// doi. org/ 10. 12691/ ajams - 8- 2- 1

Smyth, J.D., 1994. Introduction to animal parasitology. Cambridge University Press, London.

Sweeney, B.W., Newbold, J.D., 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: a literature review. J. Am. Water Resour. Assoc. 50, 560–584. https://doi.org/10.1111/jawr.12203

Tan, W.C., Herre, A., Rödder, D., 2023. A global analysis of habitat fragmentation research in reptiles and amphibians: what have we done so far? Biodivers. Conserv. 32, 439–468. https://doi.org/10.1007/s10531-022-02530-6

Thieltges, D.W., Jensen, K.T., Poulin, R., 2008. The role of biotic factors in the transmission of free-living endohelminth stages. Parasitology 135, 407–426. https://doi.org/10.1017/S0031182007000248

Torezan, J.M.D., 2002. Nota sobre a vegetação da bacia do rio Tibagi. *In*: Medri ME, Bianchini E, Shibatta OA, Pimenta JA (eds) A bacia do rio Tibagi. M.E. Medri, Londrina, pp 103–107.

Tredennick, A.T., Hooker, G., Ellner, S.P., Adler, P.B., 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology102(6), e03336. 10.1002/ecy.3336

Turunen, J., Elbrecht, V., Steinke, D., Aroviita, J., 2021. Riparian forests can mitigate warming and ecological degradation of agricultural headwater streams. Freshw, Biol. 66, 785–798. https://doi.org/10.1111/fwb.13678

Volkmer, G., Biasotto, L.D., Thiesen, Brum, F. et al., 2025. Conservation beyond protected areas: what is known about amphibians in agroforests? Biodivers. Conserv. 34, 4157–4187. https://doi.org/10.1007/s10531-025-03184-w

Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., Warton, D., 2024. mvabund: statistical methods for analysing multivariate abundance data. R package version 4.2.6.

Wickham, H., 2011. ggplot2. Wiley Interdiscip. Rev. Comput. Stat. 3, 180–185. https://doi.org/10.1002/wics.147

Figure captions

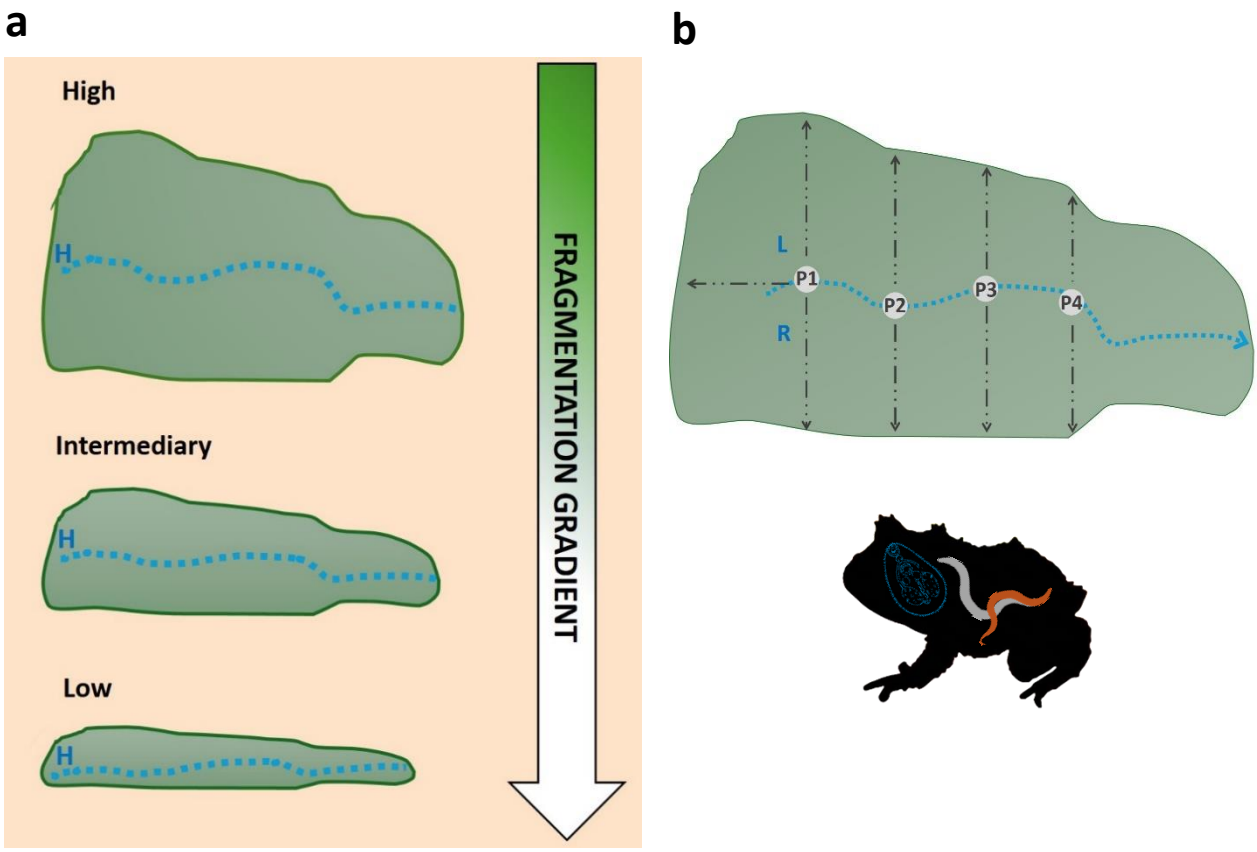
Fig. 1 a) Diagram of forest fragments representing the three integrity levels (high, intermediate, and low) where amphibians were collected and analyzed for helminth parasites. Riparian forests are the green area in an agriculture matrix (beige area) from the present study, north of Paraná state, Brazil. Blue dashed lines mean the streams with headwater (H). **b)** Diagram representing the nine transects (dark dashed lines) from the points (P1, P2, P3, and P4) from the riverside right (R) and left (L) to determine the mean of forest strip width. P1 is the headwater, and the following points are 50 m from each other to downstream in the river's course (blue dashed line).

Fig. 2 Map of South America and the region north of Paraná State, Brazil, showing the six sites of riparian forest fragments. Dots refer to sites in high integrated forests (H1 and H2), triangles refer to intermediate forests (I1 and I2), and diamonds refer to low integrity level (L1 and L2).

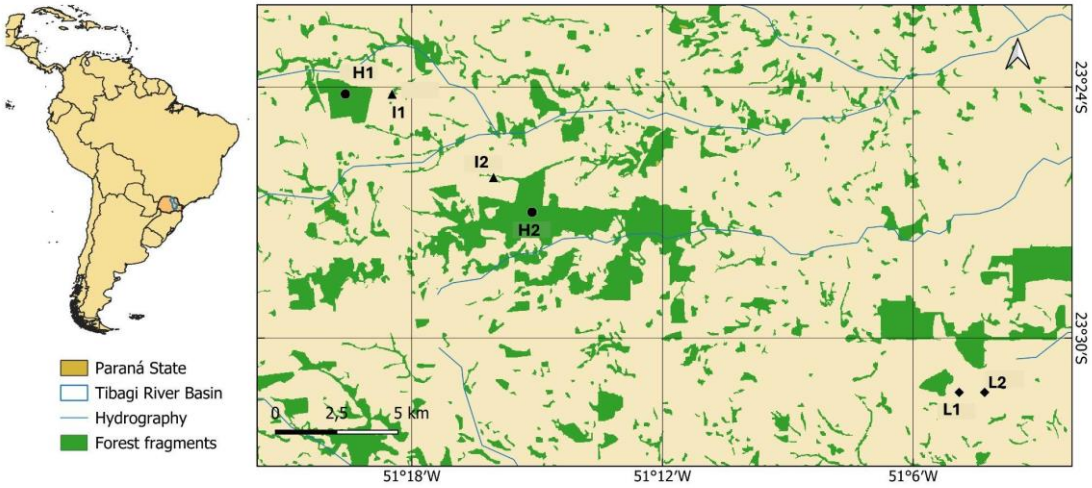
Fig. 3 Variation of the scaled mass index (SMI) among the low-integrity (L1 and L2), intermediate-integrity (I1 and I2), and high-integrity fragments (H1 and H2). Box-and-whisker plots represent the median, interquartile range, and minimum and maximum values.

Fig. 4 Non-parametric multidimensional scaling (NMDS) ordinations of parasite communities of *P. avelinoi* frogs from the six forest fragments. Forest fragments: high integrity - H1 (dark green) and H2 (light green), intermediate integrity - I1 (purple) and I2 (light blue), and low integrity - L1 (orange) and L2 (yellow).

Fig. 1


a
High
H
Intermediary
H
Low
H
FRAGMENTATION GRADIENT
b
L
P1
P2
P3
P4
R

564 **Fig. 2**



565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584

Fig. 3

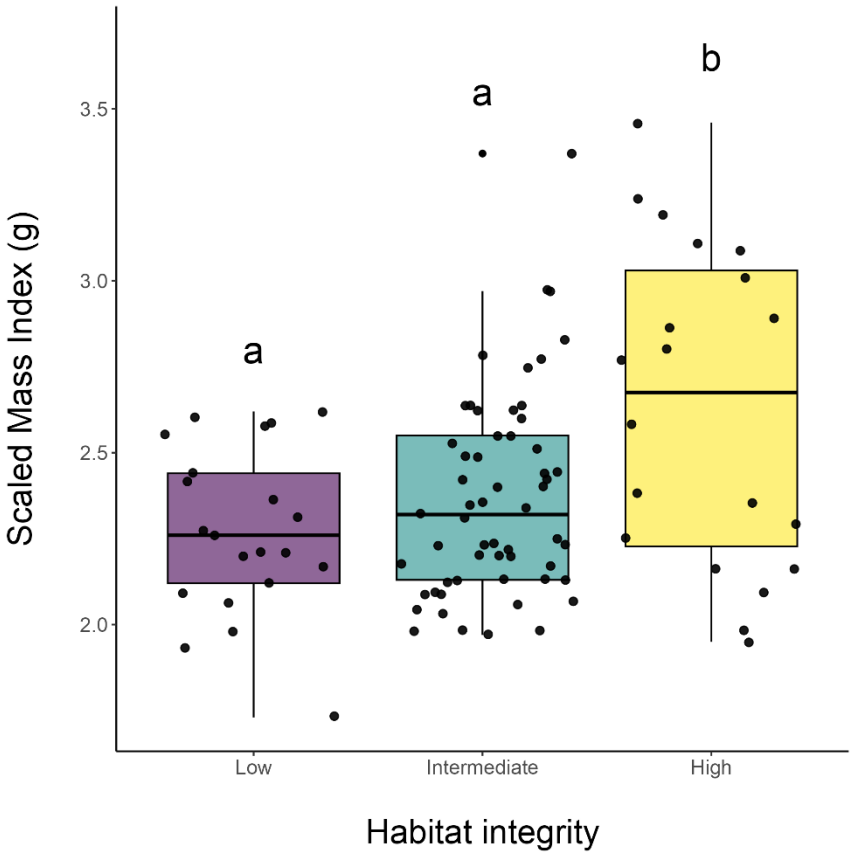

Scaled Mass Index (g)
3.5
3.0
2.5
2.0
a
a
b
Low
Intermediate
High
Habitat integrity

Fig. 4

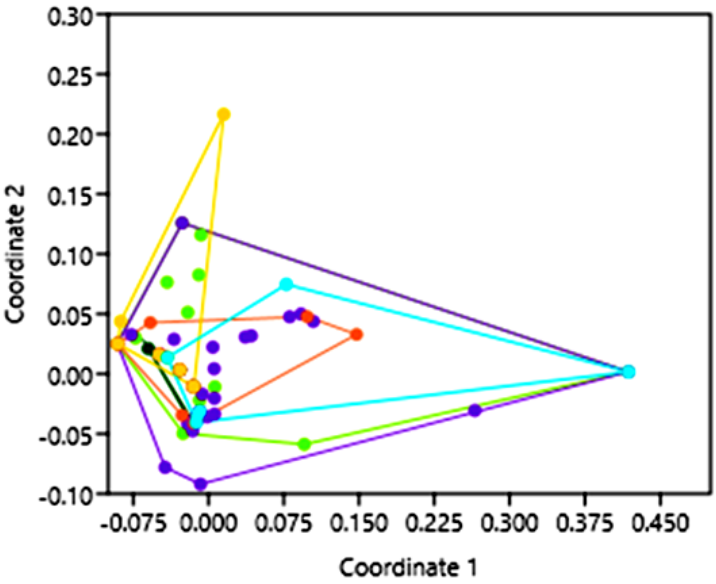

0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
Coordinate 2
-0.075
0.000
0.075
0.150
0.225
0.300
0.375
0.450
Coordinate 1

Table 1 Geographic location and traits of riparian forest fragments from north of Paraná State, Brazil. Forest strip width is given as mean and meters (m), and REA (Rapid Ecological Assessment) represents the scores of the quality forest. Forest fragments are L1 and L2 (low-integrity), I1 and I2 (intermediate-integrity), and H1 and H2 (high-integrity).

Forest fragments	Geographic coordinates	Surrounding	Forest strip width (m)	REA
L1	23°30'59,07"S; 51° 4'58,60"O	agricultural	0	0
L2	23°31'4,28"S; 51° 4'29,56"O	agricultural	1	1
I1	23°24'11,00"S; 51°18'31,47"O	agricultural	31	17
I2	23°26'6,21"S; 51°16'21,87"O	agricultural	32	16
H1	23°24'6,84"S; 51°19'29,91"O	forest	647	25
H2	23°27'5,13"S; 51°15'17,81"O	forest	1284	35

Table 2 Overall parasite parameters of *Proceratophrys avelinoi* populations from the six riparian forest fragments, North of Paraná State, Brazil. Number of anurans (n), prevalence (P%), mean abundance (AM), range, mean intensity of infection (MII), standard error (SE), richness and diversity (Brillouin index) of parasite taxa.

Integrity level	Fragments	P (%)	AM (±SE)	Range (min-max)	MII (±SE)	Richness	Diversity
High	**H1** (n= 3)	100	8.33 (± 3.18)	2–12	8.33 (± 3.18)	1	0
	H2 (n= 17)	94.12	4.53 (± 1.11)	1–20	4.81 (± 1.14)	3	0.58
Intermediate	**I1** (n= 51)	98.04	8.88 (± 0.77)	1–29	9.06 (± 0.77)	6	0.63
	I2 (n= 6)	83.33	7.83 (± 2.41)	3–15	9.40 (± 2.25)	3	0.71
Low	**L1** (n= 14)	100	4.43 (± 0.78)	1–11	4.43 (± 0.78)	4	0.48
	L2 (n= 7)	100	4.71 (± 1.49)	1–13	4.71 (± 1.49)	2	0.62

Table 3 Parasites and infection parameters of *Proceratophrys avelinoi* populations from the riparian forest fragments, North of Paraná State, Brazil. Forest fragments are H1 and H2 (high-integrity), I1 and I2 (intermediate-integrity), and L1 and L2 (low-integrity). Prevalence (P%), mean abundance (AM), mean intensity of infection (MII), standard error (SE), range and site of infection per parasite. BR (brain), CAV (body cavity muscle), LE (leg muscle), LI (large intestine), LU (lungs), MES (mesentery), SI (small intestine), ST (stomach), and UB (urinary bladder). #Monoxenic life cycle; *Heteroxenic life cycle.

Fragments	Parasites	P%	AM (±SE)	MII (±SE)	Range (min-max)	Site of infection
H1	Cosmocercidae gen. sp.#	100	8.33 (± 3.18)	8.33 (± 3.18)	2–12	LI
H2	Cosmocercidae gen. sp. #	76.47	3.53 (± 1.15)	4.61 (± 1.37)	1–20	LI, SI
	Physalopterinae gen. sp. (larvae)*	35.29	0.82 (± 0.33)	2.33 (± 0.56)	1–5	ST
	Spirometra sp. (encysted)*	11.76	0.18 (± 0.13)	1.5 (± 0.5)	1–2	BR, LE
I1	Cosmocercidae gen. sp. #	88.24	7.37 (± 0.79)	8.36 (± 0.78)	1–29	LI, SI
	Physalopterinae gen. sp.* (larvae)	3.92	0.08 (± 0.06)	2.00 (± 1.00)	1–3	ST
	Raillietnema sp. #	9.80	0.80 (± 0.36)	8.2 (± 1.02)	5–11	LI, SI
	Raillietnema spectans#	1.96	0.06 (± 0.06)	3	1	LI, SI
	Gorgoderina sp. 1*	3.92	0.12 (± 0.08)	3.00 (± 0.00)	3	UB
	Spirometra sp.* (encysted)	17.65	0.45 (± 0.20)	2.56 (± 0.82)	1–7	LE, MES, CAV
I2	Cosmocercidae gen. sp. #	66.67	5.00 (± 1.97)	7.50 (± 1.85)	3–12	LI, SI
	Physalopterinae gen. sp.*	16.67	0.33 (± 0.33)	2	2	ST
	Raillietnema sp. #	16.67	2.50 (± 2.50)	15	15	LI, SI
L1	Cosmocercidae gen. sp. #	85.71	3.71 (± 0.86)	4.33 (± 0.88)	1–11	LI, SI
	Raillietnema sp. #	14.29	0.57 (± 0.44)	4.00 (± 2.00)	2–6	SI
	Rhabdias sp. #	7.14	0.07 (± 0.07)	1	1	LU
	Spirometra sp.*	7.14	0.07 (± 0.07)	1	1	CAV
L2	Cosmocercidae gen. sp. #	85.71	2.71 (± 0.78)	3.17 (± 0.75)	1–5	LI, SI
	Gorgoderina sp. 2*	28.57	2.0 (± 1.84)	7.00 (± 6.00)	1–13	UB

Table 4 Results of generalized linear mixed models describing the relationship between parasite abundance, parasite richness, and parasite diversity (Brillouin index) as a function of host health (SMI), integrity levels of fragments (i.e. REA: Rapid Ecological Assessment), and abiotic factors (i.e. temperature, dissolved oxygen: DO, and electrical conductivity: EC). Parameter estimates, standard error (SE), Wald z-values, and *P*-value, 95% confidence interval (Lower and Upper) are provided for each predictor and model. Bold values and the confidence intervals (CI) that exclude zero indicate significant variables (n = 98)

Model	Parameter estimate	SE	Wald *z*-value	*P*-value	95% CI	
					Lower	Upper
Parasite abundance						
Intercept	31.287	9.133	3.425	**0.001**	**13.385**	**49.189**
SMI	0.224	0.233	0.961	0.336	-0.233	0.683
REA	0.023	0.054	0.425	0.670	-0.083	0.130
Temperature	-1.109	0.384	-2.889	**0.003**	**-1.863**	**-0.356**
DO	-0.512	0.206	-2.485	**0.012**	**-0.915**	**-0.108**
EC	-0.013	0.004	-2.788	**0.005**	**-0.023**	**-0.004**
Parasite richness						
Intercept	-0.917	12.692	-0.072	0.942	-25.794	23.958
SMI	0.167	0.295	0.567	0.571	-0.411	0.746
REA	0.007	0.078	0.090	0.929	-0.146	0.160
Temperature	0.073	0.534	0.137	0.891	-0.974	1.121
DO	-0.098	0.292	-0.336	0.737	-0.672	0.475
EC	-0.002	0.006	-0.392	0.695	-0.015	0.010
Parasite diversity						
Intercept	0.157	2.222	0.071	0.944	-4.198	4.512
SMI	0.060	0.055	1.095	0.274	-4.790	1.691
REA	0.010	0.014	0.717	0.473	-1.821	3.923
Temperature	0.001	0.094	0.009	0.993	-1.839	1.857
DO	-0.021	0.048	-0.445	0.657	-1.170	7.379
EC	-0.001	0.001	-0.683	0.494	-2.958	1.429