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Fish endoparasite metacommunity in environments with different degrees of conservation in the western Brazilian Amazon

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Abstract

Parasite communities correspond to the definition of metacommunity, as species interact and disperse within hosts. The present study evaluated parasite metacommunities in a tropical floodplain. The study was conducted in the Western Amazon around the municipalities of Cruzeiro do Sul, state of Acre, and Guajará, state of Amazonas, Brazil. Six sampling sites were selected and grouped into conserved and degraded environments. Fish were caught between periods of drought and flood, using passive and active sampling methods; in the laboratory, they were measured weighed, and necropsied. Parasites found were fixed, evaluated, and identified. Physical and chemical variables and environmental conservation characteristics were measured in all sites. Diversity index, ANOVA, Tukey, local contribution to beta diversity (LCBD), species contribution to beta diversity by individual species (SCBD), and variance partitioning were summarized. The α species diversity increased in conserved environments and varied between seasonal periods, mainly in detritivorous and omnivorous hosts. Local contributions to beta diversity showed significantly higher values in conserved environments for the endoparasite fauna of piscivorous and omnivorous hosts, indicating that these environments presented unique parasite infracommunities and revealing the conservation status of these environments. Variations in infracommunities were explained mainly by niche-based processes, including environmental conditions, degree of conservation, and host characteristics. Thus, these data will serve as a tool to understand the way parasite communities are structured, which is important information for the management and conservation of aquatic environments.

Keywords LCBD · SCBD · Anthropic factors · Species classification · Abiotic variables · Distribution

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Introduction

Metacommunity theory has demonstrated how local and regional processes interact to structure ecological communities (Leibold et al. 2004; Leibold and Geddes 2005). The concept is based on the distribution of species that can be related to concepts of species classification, dispersion dynamics, mass effect, and neutral model. These paradigms differ in how organisms disperse, in the degree of heterogeneity of local habitat conditions, and in the similarity of species in terms of their niche (Logue et al. 2011) and thus can be used to evaluate the structure of metacommunities (Cottenie 2005; McCauley et al. 2008).

Parasite communities correspond to the definition of metacommunity, as species disperse within hosts (Leibold et al. 2004; Mihaljevic 2012); in the case of some fish endoparasites, metacommunity can be influenced by both host availability, which can influence dispersal, and directly or

indirectly environmental quality, especially in organisms with free-living stages in their life cycle (Marcogliese 2004; Soldánová et al. 2010; Costa et al. 2021). The metacommunity of endoparasites can generally be explained by the concept of species classification or mass effects, in which local factors classify species along an environmental gradient (Cottenie 2005). Most biological communities are structured by these effects, especially when organisms have passive dispersal in aquatic systems (Hoverman et al. 2013). The species classification process emphasizes that differences in habitat patches such as environmental gradients, determine species composition and structure, while dispersal allows communities to track environmental changes (Leibold et al. 2004; Holyoak et al. 2005).

In aquatic ecosystems, the transmission of trophically transmitted fish endoparasites depends on abiotic (environmental parameters, sampling area, hydrological period) and biotic factors (food chain, host characteristics, such as body size, trophic state, and reproductive characteristics) (Olsen 1962; Lizama et al. 2006a, b; Sousa et al. 2012). All these factors can act as structurers of endoparasite metacommunities, as these variables influence the successful colonization and propagation of parasite species in their hosts (Kuris et al. 1980; Combes 2001; Hechinger et al. 2011). However, anthropogenic pressures able to produce changes in aquatic ecosystems may affect the population dynamics of parasites and their hosts (Grönroos et al. 2013; Choudhury et al. 2017; Santoro et al. 2020; 2022). Thus, parasite species diversity, composition, and dominance can be influenced by the homogenization of riparian vegetation, changes in microhabitat composition, and reduction in the water column due to increased sedimentation (Ramalho et al. 2014; Brejão et al. 2018; Virgilio et al. 2018; Souza et al. 2019), which can affect ecological communities and ecosystem health (Urban et al. 2006; Hitt and Angermeier 2011).

These anthropogenic changes prevail at scales ranging from local and landscape to regional and global and can be considered from a metacommunity perspective (Heino 2013). Thus, evaluating the metacommunity of parasites can help to integrate these dynamics on a temporal, local, or regional scale to explore the patterns of composition of these symbiotic communities in space, in addition to helping to assess how environmental degradation can influence biotic interactions and interfere with factors related to the dispersal of these species (Costa et al. 2021). Fish parasites are important and integral elements in aquatic ecosystems in which they drive fundamental ecological processes, for example, contributing to biodiversity, productivity, and food web structure or ecosystem engineering of an environment (Poulin and Morand 1999; Marcogliese 2004). Disturbances in aquatic ecosystems can negatively influence some parasite species and favor others, as environmental impacts often promote changes in the behavior or numbers of organisms (Lafferty 1997; Pietrock and Marcogliese 2003; Blanar et al. 2009). Initially, the beta diversity of endoparasites was considered by the unique pattern each environment can present in terms of species composition, compared to a set of conserved and degraded environments (i.e., LCBD-local contribution to beta diversity) (Legendre and De Cáceres 2013). In addition, alpha diversity descriptors were analyzed, such as diversity and species richness between these environments, and the processes organizing the metacommunity of endoparasites of fish at different trophic levels were investigated. More specifically, the influence of environmental characteristics, human impacts, host characteristics, and spatial factors on the structure of the metacommunity of endoparasites in fish populations from environments with different conservation degrees was evaluated. Thus, the present study aimed to evaluate the structure of the metacommunity of fish endoparasites between conserved and degraded environments in the dry and flood periods.

Initially, the beta diversity of endoparasites was considered from the unique pattern each environment can have in terms of species composition, compared to a set of conserved and degraded environments (i.e., LCBD) (Legendre and De Cáceres 2013). In addition, alpha diversity descriptors such as diversity and species richness among these environments were analyzed and the processes organizing the metacommunity of endoparasites of fish at different trophic levels were investigated. More specifically, the influence of environmental characteristics, human impacts, host characteristics, and spatial factors on structuring the endoparasite metacommunity in fish populations found in environments with different conservation status was evaluated. Thus, the present study aimed to evaluate the structure of the fish endoparasite metacommunity between conserved and degraded environments in the dry and flood periods.

In this sense, the present study tested the following hypotheses: (i) conserved environments show higher values of α (richness and diversity) and β (i.e., LCBD) diversity of fish endoparasites. A degraded habitat is expected to present a low abundance of infection and low similarity of endoparasite species. Therefore, the high biotic homogenization can influence the increase of tolerant species (Teresa and Casatti 2012). The sites with high species richness and high dissimilarity are typical of conserved environments (Legendre and De Cáceres 2013). The present study also expects (ii) an increase in β diversity of the endoparasite fauna of fish in the dry period in conserved environments, because the isolation of rivers and surrounding environments, during this period, can lead to a stronger relative influence of local factors and limitation of dispersion in communities (Thomaz et al. 2007; Hurd et al. 2016). Furthermore, niche-based processes were expected to influence the endoparasite metacommunity dynamics, so that natural and anthropogenic environmental factors contribute to the explanatory power of species distribution models. Thus, we tested the hypothesis that (iii) during flooding, niche-based processes influenced the metacommunity of endoparasites in omnivorous and detritivorous host species. During this period, there is an expansion of the environment, input of allochthonous material, and increase and recycling of environmental variables (nutrients, oxygen, temperature, and conductivity) in these flooded ecosystems (Junk et al. 1989), which can influence the presence of intermediate parasite hosts, such as plankton and ostracods (Benedito-Cecilio et al. 2000; Boulton 2003), which can be ingested by detritivorous and omnivorous hosts, influencing the parasitic fauna. Finally, we hypothesized that (iv) factors, such as the host characteristic (length, weight, and condition factor) and the degree of conservation of the environment (degraded or conserved), are responsible for the organization of the endoparasite metacommunity during the dry season. During the dry season, many species remain isolated in lakes or small streams due to lower river levels and are subjected to the action of local environmental factors and increased predator activity (Junk et al. 1989). As a consequence, the suitability, characteristics, and behavior of each host during this period can play a key role in the endoparasite community. According to Berkhout et al. (2020), host characteristics have an important role in the probability of infection of parasites with complex life cycles and can be influenced by the environment (Berkhout et al. 2020).

Material and methods

Study area

The study was carried out in the Upper Juruá River region, Western Amazon, around the municipalities of Cruzeiro do Sul, state of Acre, and Guajará, state of Amazonas, Brazil (07° 37' 52" S and 72° 40' 12" W). Six sampling sites were selected in this region and grouped into conserved environments, that is, sites with dense vegetation, but used by man for extraction or use of natural resource, and anthropic environments, which present urban areas, roads, rural areas, and small forest fragments. A rapid protocol was applied to evaluate the conservation status of each environment, according to Callisto et al. (2002). This rapid protocol assesses the characteristics of the level of environmental impacts from human activity, based on the protocol proposed by the Ohio Environmental Protection Agency (U.S. EPA, 1987). The studied environments with anthropic characteristics were (i) downstream and upstream of the Juruá River (7° 40' 34.1" 72° 39' 39.5" W), in which they presented points with a high degree of degradation located in the urban center, highways, and rural areas and preserved fragments, and (ii) Môa River (7° 37' 18" S 72° 47' 47" W), which presented deforested areas with roads, urban part, and presence of pastures, suffers from the effect of removing sand from its remnants, but presented fragments of conserved forests. The conserved environments were (i) Crôa River (7° 71' 48.30" S 72° 53' 34.98" W) with rural areas and logging; the preserved areas are used by the community for ecotourism activities; (ii) Paranã River (7° 17' 13" S 72° 36' 49" W) has areas subjected to logging, but with areas of preserved vegetation where a riverside population lives; and (iii) Gama River (7° 37' 13" S 72° 16' 49" W), an area subjected to logging and farm implantation, but has areas with a high degree of conservation (Fig. 1).

Sampling

Fish were caught (SISBIO 59642–2/2019) from March 2019 to April 2021, during the dry season (May, June, August, and September) and the flood season (February, March, November, and December). In each region of the sub-basins, three conserved and three anthropized sites were selected in an area of 14 km² each, including the main river, lakes, and streams surrounding these areas, and sampled.

Passive fish collections were conducted using 12 gill nets 80 m in length and 3.0 m in height, with a mesh sizes of 1.5 cm, 2.5 cm, 3.5 cm, and 5.5 cm between opposite knots, in areas of rivers, lakes, and streams. Nets were set in the early afternoon, remaining exposed for 24 h. Inspections were carried out every 4 h, in which samples were obtained for the morning, afternoon, and night periods. Active collections were performed with a trawl net of 25 m in length and 2.5 m in height, where nets were trawled along the banks of lakes, rivers, and streams. A 12-m-long and 1.8-m-high cast net was also used for sampling, for 24 h; at every 4 h, six casts were carried out on the bank, six in the water flow, and six in bc (according to Torrente-Vilara et al. 2013; Silvano 2001, 2020), measured, weighed, and necropsied. Some individuals, after biometry evaluation, were fixed in 10% formalin, taken to the laboratory, and deposited in the Fish Collection, Fish Center of the Juruá River Valley (NIVAJ), Federal University of Acre.

Nine species of host fish were selected according to their trophic characteristics, including three piscivorous, three omnivorous, and three detritivorous (Table 1). A total of 405 specimens of detritivorous, 498 omnivorous, and 446 piscivorous were collected and analyzed in all environments and seasonal periods.



Fig. 1 Study area of fish endoparasites in the Western Amazon

Table 1 Weight, length, and feeding habits of endoparasite hosts from the Western Amazon. *Antr.* number of fish species in anthropized sites, *Cons.* number of fish species in conserved sites

Hosts	Antr	Cons	Feeding habit	Weight (g)	Length (cm)
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	69	70	Detritivorous	40.0 ± 4.4	15.0 ± 4.6
Curimatella meyeri Steindachner, 1882	60	75	Detritivorous	90.7 ± 28.8	14.0 ± 1.3
Prochilodus nigricans Spix & Agassiz, 1829	60	71	Detritivorous	56.0 ± 11.4	14.8 ± 12.5
Trachelyopterus galeatus Linnaeus, 1766	70	77	Omnivorous	111.1 ± 0.12	18.4 ± 1.3
Nemadora humeralis Kner, 1855	100	102	Omnivorous	20.0 ± 2.32	11.8 ± 0.69
Ossancora asterophysa Birindelli & Sabaj Pérez, 2011	89	60	Omnivorous	21.8 0.7	12.4 ± 1.11
Hoplias malabaricus Bloch, 1794	78	69	Piscivorous	71.1 ± 90.3	22.5 ± 6.4
Serrasalmus maculatus Kner, 1858	65	66	Piscivorous	310.6 ± 15.6	21.8 ± 1.4
Acestrorhynchus heterolepis Cope, 1878	78	90	Piscivorous	79.25 ± 36.3	20.44 ± 3.5

Endoparasite analysis

For endoparasite collection, a longitudinal ventral incision was made with a scalpel, and the internal organs were removed and individually separated in Petri dishes containing 0.65% physiological saline solution; after being separated, the organs were opened with the help of an insulin needle and analyzed. The endoparasites found were placed in Petri dishes, washed with 0.85% physiological saline solution, and observed under a stereoscopic microscope. The Nematoda, Acanthocephala, Cestoda, and Pentastomida found were fixed in 70% alcohol at 65°C. Digenea were fixed by slight compression between the slide and the coverslip in 70% alcohol. Digenea, Acanthocephala, and Cestoda were stained with Langeron's carmine, dehydrated by an increasing alcohol series, cleared in phenol and beech creosote, and mounted between a slide and a coverslip in Canada balsam (Eiras et al. 2000). Nematoda and Pentastomida were cleared and mounted on semi-permanent slides in phenol. Endoparasites were identified according to Jones et al. (2005), Martins and Yoshitoshi (2003), Moravec (1998), and Yamaguti (1970), in addition to specific literature.

Environmental variables

The environmental variables (supplementary material 1) pH, electrical conductivity (μ S•cm⁻¹), water temperature (°C), dissolved oxygen (mg \cdot L⁻¹), turbidity (NTU), total dissolved solids (TDS), and chlorophyll α were measured during the 24 h of collection in the margin, middle, and bottom regions using a multiparameter probe. A Secchi disk was used to measure the transparency (cm) and depth profiles (m) of aquatic environments. Water samples for physical-chemical analysis were taken using a Van Dorn bottle and stored for analysis. Analyses of physical and chemical variables were carried out in a spectrophotometer, according to the methods proposed by Apha (2012) for analysis of zinc (zinc method), nitrite (N 202 (1-naphthyl)-ethylenediamine (NTD) method), nitrate (N-(1-naphthyl)-ethylenediamine (NTD) method), total nitrogen (persulfate method), ammonia nitrogen (indophenol method), total phosphate (ascorbic acid and molybdenum blue method), and soluble orthophosphate (ascorbic acid and molybdenum blue method).

The water level and river flow were measured using rulers from the stations (1370000 and 13180000) of the National Water Agency (ANA), upstream of the sampling sites. Rainfall, temperature, and humidity data for the region were obtained from INMET data for the years 2019 to early 2021.

Variables indicating the degree of conservation

In order to assess the degree of conservation of the environments, some biotic factors were considered and measured, such as the ETP (Ephemeroptera-Trichoptera-Plecoptera) index, aquatic insect richness, fish species richness, EVI (Enhanced Vegetation Index), and NDVI (Normalized Difference Vegetation Index), in addition to the area of dense forest and bare soil in the study region. Furthermore, a Protocol for Rapid Assessment of Habitat Diversity was applied to assess the structural characteristics of each environment.

Collections of aquatic insects were carried out in 100 m along each region of the sampling sites, encompassing the banks and the bottom of the rivers using a D-net sampler for 10 min per sampling. Insects were collected, sorted, and stored in 70% alcohol. Insects were identified at the family level according to Pes et al. (2005), and Hamada et al. (2014). The species richness of aquatic insects and the families Ephemeroptera, Plecoptera, and Trichoptera (EPT) was measured and used as environmental indicators (Supplementary Material 1).

Fish species richness was also used as an environmental conservation variable, where a total of 10,716 fish were collected, belonging to eight orders, 32 families, and 216 species. In this sense, the present study determined the species richness of the fish community in each sampling environment (Supplementary Material 1) and the values were used to indicate the quality of each environment, according to Casatti and Ortigossa (2021) and Vieira and Shibatta (2007).

To seasonally analyze the values of vegetation indices, the average value of the NDVI and EVI images from the MODIS/Terra sensor was obtained. The product MOD13A1 collection 5 was used, which are compositions every 16 days, with 250 m spatial resolution. Images used were obtained between January 2019 and April 2021. The NDVI was acquired DVI = (NIR - RED)/(NIR + RED), where NIR is near-infrared reflectance and RED is red reflectance. The EVI is calculated EVI = G (NIR - R)/(L + NIR + C1RED + C2BLUE), where in the blue band, L is the adjustment factor for ground, with a constant value equal to 1; C1 and C2 are adjustment coefficients for the effect of atmosphere aerosol, with constant values equal to 6 and 7.5, respectively; and G is the gain factor, with a value equal to 2.5 (Justice et al. 1998). Both the EVI and NDVI ranged from -1 to 1 (Supplementary material 1). Samples of 4 pixels were collected in the areas of each river for analysis.

In this study, variations in the area of vegetation cover area or open field in square meters of the sampling sites were measured using data from the Sentinel-2 satellite and the Normalized Difference Vegetation Index (NDVI) during the period from 2019 to 2021. For this, the Google Earth Engine (GEE) was used. After coding the GEE and building the NDVI for several months, the constructed maps were converted to ArcGIS 10.6.1.

The Rapid Habitat Diversity Assessment was used according to Callisto et al. (2002) for each sampling site. This Rapid Habitat Diversity Assessment protocol assesses the characteristics of stream sections and the level of environmental impacts from human activity, based on the protocol proposed by the Ohio Environmental Protection Agency (U.S. EPA, 1987). This document is represented by 10 (ten) parameters: 1, type of occupation of the watercourse banks (main activity); 2, erosion near and/or on the banks of the river, silting in its bed; 3, anthropogenic changes; 4, vegetation cover on the bed; 5, odor in the water; 6, oiliness of the water; 7, water transparency; 8, sediment odor (bottom); 9, oiliness of the bottom; and 10, type of bottom. Each parameter has 3 criteria for assigning the score, which can be 4, 2, or 0 points, depending on environmental conditions and the assignment of the evaluator (Table 2; Supplementary material 1).

Spatial variables

Spatial variables were generated by principal coordinates of neighbor matrix analysis (Borcard and Legendre 2002). This method involves two steps: (i) modification of the distance matrix between sites. After determining the distance between sites, a truncation distance must be defined, above which any distance between pairs of sites is considered equal to four times the truncation distance; (ii) application of a principal coordinate analysis on the modified distance matrix. The principal coordinates obtained were considered predictor spatial variables (spatial filters) used in ordination or multiple regression analysis.

Host characteristic variables

Values of standard length (Ls) and weight (Wt) of each host were fitted to the Wt/Ls relationship (Wt=a•Ltb), and the values of regression coefficients a and b were estimated. Values of a and b were used in the estimates of the expected values of weight (We), through the equation We=a•Ltb. In this way, the relative condition factor (Kn) was calculated, which corresponds to the quotient of the observed to the expected weight for a given length (Kn=Wt/We) (Le Cren 1951).

Data analysis

Alpha diversity was measured by the number of species in each assemblage and by the Shannon–Wiener index. The number of endoparasite individuals was also calculated for each environment and host according to the trophic category. To check for differences in α diversity and species abundance between anthropized and conserved sites in seasonal periods, a two-way ANOVA and Tukey's test were summarized. These variables showed homoscedasticity (Levene) and normality (Shapiro–Wilk).

Beta diversity was obtained through LCBD (local contribution to beta diversity) and SCBD (species contribution to beta diversity by individual species). LCBD describes the uniqueness of each set of habitats in a region, where it was calculated from the species abundance matrix using the Bray–Curtis dissimilarity coefficient (Legendre and De Cáceres 2013). The LCBD and SCBD values were calculated for each environment and seasonal period from the Hellinger transformed-species composition matrices; all calculations were made using the R beta.div function (Legendre and De Cáceres 2013).

To test the differences in LCBD and SCBD values between the environments, in the different seasonal periods, the parametric analysis of variance ANOVA was used followed by Tukey's post hoc multiple comparison test. These variables showed homoscedasticity (Levene) and normality (Shapiro–Wilk).

Pearson correlation coefficient (r) was estimated to assess whether the LCBD patterns of the flooding and drought periods were correlated. Correlation was also used to assess the relationship between LCBD and species richness; the Shapiro–Wilk *W*-test was used to test normality.

To explain the response matrices, four prediction matrices were used, being the fish host (rows) by their characteristics of weight (g), length (cm), and relative condition factor (columns); fish host (rows) by environmental variables (columns); fish host (rows) by latitude and longitude of sampling site (columns); and fish host (rows) by degree of environmental conservation (columns). The host characteristics

 Table 2
 Protocol for the Rapid Habitat Diversity Assessment in areas of basins, modified from the Ohio Environmental Protection Agency protocol (U.S. EPA, 1997). Four points—natural situation; 2 and 0 indicate mild or altered situations

Score					
4 points	2 points	0 points			
Natural vegetation	Pasture/agriculture field	Residential/commercial/industrial			
Absent	Moderate	Accentuated			
Absent	Changes of domestic origin	Changes of industrial/urban origin			
Total	Partial	Absent			
None	Sewage	Oil			
Absent	Moderate	Abundant			
None	Sewage	Oil			
Transparent	Turbid	Opaque			
Absent	Moderate	Abundant			
Gravel	Sand	Mud			
	Score 4 points Natural vegetation Absent Absent Total None Absent None Transparent Absent Gravel	Score4 points2 pointsA pointsPasture/agriculture fieldAbsentModerateAbsentChanges of domestic originTotalPartialNoneSewageAbsentModerateNoneSewageTransparentTurbidAbsentModerateGravelSand			

were transformed into a Gower distance matrix and ordered by a principal coordinate analysis (PCoA). Environmental variables were associated with hosts according to the site/ period in which the host was sampled. If more than one host was sampled simultaneously, values of environmental variables were repeated. All PCoA axes with positive eigenvalues were used to compose summary matrices of host characteristics and environmental variables. A spatial matrix was composed by applying PCNM (principal coordinates of neighbor matrices) (Borcard and Legendre 2002) in geographic coordinates of the sampled environments in which the host individuals occurred. Therefore, spatial variables represent individual dispersion hypotheses. Similarly for the environmental matrix, if two or more individuals were sampled at the same site, the PCNM values were repeated.

Then, a variation partitioning procedure based on a partial redundancy analysis pRDA (Borcard et al. 1992) was used separately for the endoparasites of piscivorous, detritivorous, and omnivorous species in each flooding and dry season, using the four above-mentioned prediction matrices. Only the most important predictor variables from each matrix were filtered using forward selection, and the significance of the pRDA components was evaluated after 999 permutations. In pRDA, large fractions shared between PCNM and an environmental matrix may indicate spatial autocorrelation of environmental predictors. To clarify this phenomenon, we tested spatial autocorrelation on environmental variables using the Moran I coefficient. Few variables showed spatial autocorrelation, which anticipates a low shared fraction of PCNMs and environmental predictors in the explanation of endoparasite metacommunities. All analyses were conducted using "vegan" (Oksanen 2016), "metacom" (Dallas 2014), and "betapart" (Baselga and Orme 2012) in software R (R Core Team, 2020).

Results

α and β diversity

A total of 4958 endoparasites belonging to 61 species were recorded, being 26 Digenea, 20 Nematoda, nine Acanthocephala, four Cestoda, and two Pentastomida. Endoparasites of omnivorous fish presented a total of 870 individuals belonging to 17 species during the dry season, and in the flooding period, 1143 individuals were recorded, of 24 species. For detritivorous hosts, 755 individuals were collected, 14 species during the flooding season, while in the dry season, 913 individuals belonging to 20 species of endoparasites. In the case of piscivorous endoparasites, 512 individuals belonging to 24 species were found during the flood and 765 individuals and 22 species during the dry season (Supplementary material 1). The number of individuals was higher (ANOVA p = 0.02) in the endofauna of omnivorous parasites during the dry season between conserved and anthropized environments (Tukey p = 0.01). Endoparasites of insectivorous also showed a significant difference in the number of species (ANOVA p = 0.01), mainly in anthropized environments (Tukey p = 0.02) (Fig. 2).

In general, α diversity (species richness and diversity) was higher in conserved environments for detritivorous, omnivorous, and piscivorous in both seasonal periods (Figs. 3 and 4). The present study showed a difference in species richness (ANOVA p = 0.01) and diversity (ANOVA p = 0.02) of endoparasites in omnivorous and piscivorous hosts in the flood season (ANOVA p = 0.01), where the values were higher in conserved environments (Tukey p < 0.05). During the dry season, the endoparasite fauna of omnivorous (ANOVA p = 0.01), piscivorous (ANOVA p = 0.01), and detritivorous (ANOVA p = 0.02) fish showed a difference in species richness, which was higher in conserved environments (Tukey p < 0.05). As for diversity (ANOVA; p =0.01), the difference occurred between environments during the flood season (Tukey p < 0.05). During the dry season, only the diversity of endoparasites of omnivorous (ANOVA p = 0.01) and piscivorous (ANOVA F = 3.75; p = 0.002) fish was significantly higher in conserved environments (Tukey p < 0.05).

During drought and flooding, environments with LCBD values greater than 0.18 were significant, such as conserved environments in the parasite fauna of piscivorous and omnivorous fish and anthropized environments in the endoparasite fauna of detritivorous fish (Fig. 5).

During the dry period in anthropized environments, LCBD was negatively correlated with the endoparasite species richness in piscivorous fish (r = -0.78; p = 0.001) and positively with the endoparasite species richness in omnivorous fish (r = 0.89; p = 0.002). There was no relationship between the LCBD and the α diversity of endoparasites in conserved environments in the periods of flooding and drought (p > 0.05). The abundance of individuals also showed no correlation with the LCBD in any environment between the hydrological periods.

Values of LCBD in the parasite fauna of detritivorous fish during the dry season were significantly correlated with the LCBD of the flooding season in conserved (r=0.86; p=0.01) and anthropized (r=0.98; p=0.001) environments. The same pattern was observed for the endofauna of parasites of piscivorous and omnivorous fish between the flooding (conserved environments: r=0.78, p=0.02; anthropized: r=0.77, p=0.01) and the drought (conserved environments: r=0.88, p=0.002; anthropized: r=0.97, p=0.001).

Among endoparasites of detritivorous hosts in conserved environments, in both periods, Cosmoxynema



Fig. 2 Mean and standard deviation of the number of individuals of endoparasites, between anthropized and conserved environments during periods of drought and flooding. A–D Omnivorous; B–E piscivo-

rous; C–F detritivorous. P, conserved environments; A, anthropized environments. A–C Drought; D–F flooding

vianai, Neoparaseuratum travassosi, Cosmoxynemoides aguirei, and Travnema travnema were contributors to the β diversity (SCBD), and Zonocotyle sp. and Paramphistomidae gen. sp. were the species related to β diversity during the flood, while Saccocoelioides magnerchis during the drought. In anthropized environments, Contracaecum sp. and Neoechinorhynchus curemai contributed to β diversity of endoparasites in both periods, while Monticellia sp. and Cucullanus pinnai, contributed only during the drought (Table 3).

The species that indicated the β diversity (SCBD) of the endoparasite fauna of omnivorous fish in conserved environments in both periods were *Dadaytremoides parauchenipteri* and *Ichthyouris laterifilamenta*; during the flood, they were *Gernachella gernachella* and *Cucullanus brevispiculus*, and during the drought, the nematodes *Neoparaseuratum travassosi* and *Cosmoxynemoides aguirei*. In anthropized environments, *Sharpilosentis peruviensis* and *Cangatiella arandasi* contributed to β diversity in both periods and *Procamallanus inopinatus*, *Proteocephalus jandia*, *Hysterothylacium* sp. contributed during the flood, and *Cangatiella arandasi* during the drought (Table 3).

For the endoparasite fauna of piscivorous fish, during the flood, *Austrodiplostomum* sp., *Allocreadium* sp., and

Contracaecum sp. significantly contributed to the β diversity (SCBD) of conserved environments. In the drought, *Bellum-corpus majus* and *Quadrigyrus machadoi* were the species that contributed to these environments. In anthropized environments, *Pseudoproleptus* sp., *Procamallanus* (*S.*) *pimelo-dus*, and *Cucullanus pinnai* contributed to the β diversity during both periods, *Photodiplostomum* sp. during the flood and *Dadaytrema oxycephalum* and *Paraseuratum soaresi*, during the drought (Table 3).

Metacommunity structuring elements

According to the global models, the four sets of predictors were significantly associated with fish endoparasite composition (p < 0.05) (Tables 4, 5 and 6).

During the flood, the environment (26%) best explained the variation in endoparasite composition in omnivorous fish, followed by the degree of conservation (11%) (Fig. 6A). The selected environmental variables were chlorophyll α and total nitrogen; the explanatory variable related to the degree of conservation was the richness of endoparasites in the environment (Table 4). During the drought, the host trait was the variable that better explained the composition of



Fig.3 Mean and standard deviation of the number of species (α diversity) of endoparasites, between anthropized and conserved environments during periods of drought and flooding. **A–D** Omnivorous;

B–E piscivorous; **C**–F detritivorous. P, conserved environments; A, anthropized environments. **A**–**C** Drought; **D**–F flooding

endoparasites in omnivorous fish, in which the total length and the relative condition factor were the related variables (Fig. 6B and Table 4).

During the flood, environmental variables and the host traits were the fractions that best explained the composition of species of detritivorous fish, being the water temperature and the ammonia content the explanatory variables of the environment and the total length, the characteristic of hosts that influenced endoparasites (Fig. 6C and Table 5). In turn, during the drought, the host traits and the degree of conservation were the factors that influenced the endoparasites, and the related variables were fish length, fish weight, and richness of fish hosts and endoparasites in the environment (Fig. 6D and Table 5).

For piscivorous fish, the environmental fraction was the one that best explained the distribution of endoparasites during the flood, and in the drought, the host traits best explained endoparasite distribution (Fig. 6E, F). The environmental variables chlorophyll α , phosphorus, and phosphate were the most explanatory variables during the flood; and total weight and the condition factor were the most explanatory variables during the drought (Table 6).

Discussion

α and β diversity

As expected, the study indicated that the α diversity of fish endoparasites increased in conserved environments and varied between hydrological periods; this pattern was observed both in host fish of lower and intermediate trophic levels such as detritivorous and omnivorous, as well as in high trophic levels, like piscivorous. These results may reflect the quality of these environments, as a high species richness of endoparasites may reflect the diversity of intermediate and definitive hosts in an ecosystem such as plankton, crustaceans, mollusks, and birds. According to Hudson et al. (2006), a fauna with high species richness and diversity of endoparasites may indicate environments that maintain a complex trophic web, in which this factor is an important indicator of quality, functionality, and resilience of ecosystems (Marcogliese 2005).

The study demonstrated that the local contribution to the beta diversity of endoparasites was high in conserved environments. This may indicate that these environments presented uniqueness in their parasite infracommunities, revealing their degree of conservation. Legendre and De



Fig. 4 Mean and standard deviation of Shannon–Wiener diversity of endoparasites, between anthropized and conserved environments during periods of drought and flooding. A–D Omnivorous; B–E piscivo-

rous; **C–F** detritivorous. P, conserved environments; A, anthropized environments. **A–C** Drought; **D–F** flooding

Cáceres (2013) indicated that environments that are home to high species richness can present a high degree of conservation. The advantage of a high diversity of endoparasites in conserved environments is possibly because these organisms represent an important regulator of ecosystems. According to some studies, parasites influence the flow of energy through the ecosystem (Britton and Andreou 2016; Vannatta and Minchella 2018) and contribute to the structure and complexity of the food web (Lafferty et al. 2006; Lafferty 2008; Dunne et al. 2013) in addition to acting as important ecosystem engineers (Hatcher et al. 2012). Thus, these parasites can play influential roles in the functioning, structure, and stability of a balanced ecosystem (Hudson et al. 2006; Lafferty 2008). In the present study, the species of parasites that acted as indicators of conserved environments were organisms that depend on at least three hosts to complete their life cycle and exhibit free-living stages of their life cycle in the environment. Like the digeneans Genarchella genarchella, Dadaytremoides parauchenipteri, and Allocreadium sp., these organisms depend on arthropods and mollusks and have fish as their final hosts (Martorelli 1989; Ditrich et al. 1997; Petkevičiūtė et al. 2023). The complex life cycle of these organisms involves transmission patterns related to habitat,

to abiotic and biotic conditions, and especially to the different host species (SHOOP, 1988; Wood et al., 2022). In this sense, some studies use these parasites to indicate environmental conditions, climate change, and anthropogenic impacts (Hechinger et al. 2011; Johnson and Paull 2011; Poulin et al. 2019). Disturbances in environmental factors can influence some digenean species, causing stress in freeliving larvae, as well as the desiccation of eggs and, therefore, causing the mortality of these organisms (Hubbell, 2011; Franzova et al. 2019).

However, the present study also showed digenetic species that contributed as indicators of anthropized environments, such as the metacercariae of *Posthodiplostomum* sp., *Austrodiplostomum* sp., and *Clinostomum* sp. Species of families Diplostomidae and Clinostomidae are considered generalist species in terms of intermediate hosts, colonizing species of mollusks and fish that are opportunistic and adaptable to environmental variations, which would facilitate their distribution in these environments. For example, mollusk *Biomphalaria* acts as the first host of these digeneans (Lima et al., 2019; Tavares-Dias et al., 2021). According to Aragão (1987), these organisms can spread in areas that have suffered deforestation, in addition to the increase in temperature and rainfall related to anthropogenic global changes, which



Fig. 5 Local contribution to beta diversity (LCBD) for periods of drought and flooding and sampled environments. A–D Omnivorous; B–E piscivorous; C–F detritivorous. P, conserved environments; A, anthropized environments. A–C Drought; D–F flooding

can also influence the increase of this organism (Marengo, 2014) and consequently of these endoparasites. The same is reported for *Hoplias malabaricus*, an opportunistic fish species that serves as an intermediate or paratenic host for these metacercariae (Virgilio et al. 2023). In addition, a study showed that environmental variations, such as the increase in temperature in aquatic environments, favor the development of free-living larvae of Diplostomidae and Clinostomidae species (Souza et al. 2012; Silva et al. 2022).

A large part of the nematode species that were indicators of conserved areas in the study were parasites of the order Oxyurida. These organisms have a free-living stage, are host specialists, and have a direct life cycle (Moravec and Prouza 1995). These species are suggested to be important indicators of the state of aquatic environments, as they may be susceptible to sudden environmental changes (Khan and Thulin 1991), as observed with some monoxenic parasites when exposed to anthropic conditions (Sures et al. 2017). The indicators of anthropogenic areas were Cucullanus pinai and Procamallanus inopinatus; these parasites are host generalists, colonizing organisms with a high degree of adaptation to environmental variables, such as microcrustaceans (Moravec 1998; Moreira et al. 2009) and Chironomidae larvae (Moreira et al. 2009; Brasil et al. 2019; Gomes et al. 2020; de Almeida Pinto et al. 2021; Azevêdo et al.

2022). Furthermore, both C. pinai and P. inopinatus lack specificity regarding their host fish, in which these parasites can parasitize a variety of species (Virgilio et al., 2022). This indicates that the environmental conditions of these ecosystems are somehow adequate to complete the life cycle of these organisms, in addition to helping in the dominance of these nematodes in fish. Cestoda species of Protocephalidae and Acanthocephala of the family Diplosentidae were also considered important indicators of anthropogenic areas in the present study. These parasites lose their digestive system and feed by diffusion in the intestine of their hosts, which may indicate a high adaptation between some species of cestodes and acanthocephalans and their opportunist and generalist fish hosts. In fact, some species of cestodes and acanthocephalans have already been used as bioindicators of environmental impacts; they were considered in some studies as environmental filters, where they can accumulate significant amounts of metals in their tissues, reducing the accumulation of these pollutants by their hosts (Huspeni and Lafferty 2004; Nachev and Sures 2016). In addition, some studies indicate that these endoparasites have species resistant to environmental variations and pollutants (Hanzelová, 1992; Reis et al. 2017; Duarte et al. 2020). In this way, they can become sentinels by indicating the environmental quality and become useful in the assessment Table 3SCBD values forconserved and anthropizedenvironments, between theperiods of flooding and drought

Order/species	Flooding	Drought	Flooding	Drought
	Conserved	Conserved	Anthropized	Anthropized
Detritivorous				
Digenea				
Dadaytrema oxycephalum	0.0435	0.0192	-	-
Zonocotyle sp.	0.1405*	-	-	-
Paramphistomidae gen. sp.	0.1147*	0.0052	-	-
Prothenhystera obesa	0.0235	-	-	-
Microrchis oligovitellum	-	-	-	0.0687
Saccocoelioides magnerchis	-	0.1166*	-	-
Nematoda				
Contracaecum sp.	0.0505	0.0320	0.2000*	0.2588*
Cosmoxynema vianai	0.2006*	0.1706*	-	-
Cucullanus pinnai	0.0130	0.0091	-	0.2610*
Ichthyouris laterifilamenta	0.1097	0.1229*	-	-
Neoparaseuratum travassosi	0.1902*	0.1783*	-	-
Procamallanus pimelodus	0.0492		-	-
Procamallanus inopinatus	0.0188	0.0205	0.0200	0.0336
Cosmoxynemoides aguirei	0.1674*	0.1849*	-	0.0299
Travnema travnema	0.1791*	0.1791*	-	-
Acanthocephala				
Octospiniferoides incognita	-	0.1012	-	-
Neoechinorhynchus curemai	0.0276	0.0260	0.3421*	0.2183*
Gorytocephalus elongorchis	-	0.1012	-	-
Cestoda				
<i>Monticellia</i> sp.	-	-	-	0.137*
Omnivorous				
Digenea				
Genarchella genarchella	0.220*	-	-	-
Dadaytremoides parauchenipteri	0.169*	0.151*	0.0072	0.0302
Phyllodistomum sp.	-	-	0.0072	0.0096
Displostomumsp.	0.0108	-	-	0.0024
<i>Clinostomum</i> sp.	-	0.0122	-	0.0560
Doradamphistoma bacuense	-	0.0224	-	0.0120
Prothenhystera obesa	-	0.0122	-	0.0025
Dadaytrema oxycephalum	0.0965	0.0542	0.0182	0.0481
Austrodiplostomumsp.	_	-	0.0388	0.0746
Acanthostomum sp.	-	-	-	0.0099
Dadayius sp.	-	-	-	0.140*
Phyllodistomum wallacei	-	0.0022	-	0.0416
Nematoda				
Cucullanus brevispiculus	0.214*	-	-	-
<i>Contracaecum</i> sp	0.1204	0.0784	-	0.0120
Hysterothylacium sp.	-	-	0.182*	0.0558
Cucullanus pimelodellae	0.0519	-	_	0.0289
Procamallanus peraccuratus	0.0023	-	0.0404	_
Procamallanus pimelodus	0.0271	0.0130	-	0.0048
Neoparaseuratum travassosi	0.0622	0.204*	0.0274	0.0079
Rondonia rondoni Travassos	-	0.1368	-	-
Cosmoxynemoide aguirei	0.0325	0.1845*	-	0.0389
Cucullanus pinnai pinnai	-	0.0257	-	0.0024
Cystidicoloides vaucheri	-	-	-	0.0099

Table 3 (continued)

Table 4 Explanatory variables

variation partitioning (adjusted

redundancy analysis (pRDA) in

omnivorous fish endoparasites

retained by the forward selection procedure and

 R^2) resulting from partial

Order/species	Flooding	Drought	Flooding	Drought
	Conserved	Conserved	Anthropized	Anthropized
Ichthyouris laterifilamenta	0.1803*	0.1813*	0.0652	0.0973
Procamallanus inopinatus	-	0.0337	0.1346*	0.0143
Pseudoproleptus aguirei	0.0325	-	-	-
Acanthocephala				
Sharpilosentis peruviensis	0.0150	0.0179	0.1303*	0.1822*
Cestoda				
Cangatiella arandasi	-	-	0.1355*	0.1355*
Proteocephalus jandia	-	-	-	0.1898*
Piscivorous				
Digenea				
Photodiplostomum sp.	-	-	0.3161*	-
Austrodiplostomum sp.	-	-	0.1549*	-
Clinostomum sp.	-	-	-	0.1438*
Ithyoclinostomum dimorphum	0.0608	0.0608	-	0.0219
Allocreadium sp.	0.2500*	-	-	-
Diplostomumsp.	0.0402	-	-	-
Dadaytrema oxycephalum	0.0174	0.0402	0.0575	0.2563*
Bellumcorpus majus	0.0528	0.1528*	-	-
Nematoda				
Pseudoproleptus sp.	0.0164	0.0484	0.1845*	0.1845*
Paraseuratum soaresi	-	-	-	0.2200*
Contracaecum sp.	-	-	-	0.0381
Procamallanus nimelodus	0.0688	0.0581	0 1816*	0 2257*

Pseudoproleptus sp.	0.0164	0.0484	0.1845*	0.1845*
Paraseuratum soaresi	-	-	-	0.2200*
Contracaecum sp.	-	-	-	0.0381
Procamallanus pimelodus	0.0688	0.0581	0.1816*	0.2257*
Cucullanus pinnai	-	-	0.2243*	0.1786*
Ichthyouris laterifilamenta	0.2132*	0.1731	-	-
Acanthocephala				
Quadrigyrus Machadoi	0.0089	0.1350*		0.0759
Neochinorhynchus sp.	0.0484	0.0096		0.0829

Values in bold indicate p < 0.05

RDA model Selected variables (forward selection) Adj R² Overall Host trait Total length, condition factor (Kn) 0.15* Chlorophyll α, conductivity, TDS, temperature 0.14*Environment Degree of conservation Endoparasite richness, fish species richness, bare soil area 0.16* 0.03* Space 1, 2 Null model 0.34* Flooding 0.09* Host trait Condition factor (Kn) Environment Chlorophyll α, nitrogen 0.26* Degree of conservation Endoparasite richness 0.11*0.02* Space 1, 2 Null model 0.48* Drought Host trait Total length, condition factor (Kn) 0.13* 0.00* Environment Chlorophyll α , conductivity, TDS 0.04* Degree of conservation Fish species richness, dense vegetation, EVI Space 1 0.01*

*p < 0.05

Table 5 Explanatory variablesretained by the forwardselection procedure andvariation partitioning (adjusted R^2) resulting from partialredundancy analysis (pRDA) forendoparasites in detritivorousfish

RDA model	Variables retained by forward selection	Adj R ²
Overall		
Host traits	Total length, total weight	0.25*
Environmental	Chlorophyll α , conductivity, TDS	0.24*
Degree of conservation	Endoparasite richness, fish species richness	0.16*
Spatial	1, 2, 3	0.03*
Null model		0.38*
Flooding		
Host traits	Total length	0.18*
Environmental	Temperature and ammonia	0.17*
Degree of conservation	Endoparasite richness, EVI	0.04*
Spatial	1, 2	0.04
Null model		0.61*
Drought		
Host traits	Total length, total weight	0.11*
Environmental	Conductivity	0.07*
Degree of conservation	Endoparasite richness, fish species richness	0.10*
Spatial	1, 3	0.03
Null model		0.66

*p < 0.05

Table 6 Explanatory variablesretained by the forwardselection procedure andvariation partitioning (adjusted R^2) resulting from partialredundancy analysis (pRDA) forendoparasites in piscivorous fish

RDA model	Variables retained in forward selection	Adj R ²
Overall		
Host traits	Total length, total weight, condition factor (Kn)	0.21*
Environmental	Chlorophyll α, conductivity, TDS	0.19*
Degree of conservation	Endoparasite richness, fish species richness, bare soil, degree of conservation, dense vegetation, EVI	0.16*
Spatial	1, 3, 4	0.13*
Null model		0.42
Flooding		
Host traits	Condition factor, total weight	0.05*
Environmental	Chlorophyll α, phosphorus, phosphate	0.09*
Degree of conservation	Endoparasite richness, EVI, dense vegetation	0.01
Spatial	1, 3	0.01
Null model		0.084
Drought		
Host traits	Condition factor, total weight	0.08*
Environmental	Chlorophyll α, conductivity, TDS	0.01
Degree of conservation	Endoparasite richness, fish species richness, dense vegetation	0.01
Spatial	1, 3	0.01
Null model		0.84

**p* < 0.05

of environmental risks, especially in the development of pollution contingency (Sures et al. 2017). Thus, the results suggest that, as environments with a level of anthropization become less rich in parasite species, they also tend to have more tolerant parasite species. This can be explained by the occurrence of a disturbance related to significant

variations in biotic factors. For example, studies point out that anthropogenic changes can influence the increase of some host species, which are called "winners," while those that decrease can be called "loser" species (Jones and Cheung 2015; Poloczanskae et al., 2013). According to the theory, if a parasite with a complex life cycle is colonizing



Fig. 6 Results of pRDA-based variation partitioning to explain variation in endoparasite infracommunities of A, B omnivorous; C, D detritivorous; and E, F piscivorous floodplain, during A, C, D flooding and B, D, F drought

a "winner" host, it can benefit and manage to survive. But if a parasite is on a "loser" host, a decline in that organism can reduce parasite transmission and even drive these organisms to local extinction. Moreover, significant variations in abiotic factors in an ecosystem can also be negative for parasite transmission (Legendre and Cáceres 2013; Pajuen et al. 2017; Borges et al. 2020), in which the responses of parasite communities may vary depending on the type and intensity of the stressor, the life cycle, and the time of exposure of these organisms to the environment (Marcogliese 2004)

In this sense, anthropization is associated with a reduction in some specialist parasite species (Marcogliese 2004) and an increase in other, more opportunistic species (MacKenzie et al. 1995; Mackenzie 1999; Wood et al., 2022). This could be detrimental to the functioning of the ecosystem and the health of living organisms since the increased occurrence of some parasite species such as some larvae of the families Clinostomidae and Anisakidae at high levels of abundance can cause the death of the host fish (Pinheiro et al. 2019; Tavares-Dias et al., 2021). Furthermore, they transmit diseases to humans who consume these raw or undercooked fish. Thus, our results indicate that the loss of diversity of specialist parasites and the increase of generalists can have critical impacts on the function of ecological communities, as suggested by several studies (Clavel et al. 2010; Li et al. 2020; McKinney & Lockwood 1999; Olden 2006; Olden & Rooney 2006).

Metacommunity structuring elements

The present study revealed that environmental conditions and host traits were the main factors explaining changes in the composition of endoparasites in all hosts, regardless of trophic category. These variations in infracommunities were mainly explained by processes based on niches including environmental conditions, degree of conservation of the environment, and the host traits, which showed variation between hydrological periods. It was recorded that the endoparasite communities (considering all taxa) were explained by environmental factors during the flooding period. Thus, the results are in line with the growing body of evidence for aquatic environments (e.g., Cottenie 2005; Heino et al. 2015), which has indicated the importance of species classification in community structure (Van der Gucht et al. 2007). If community composition is primarily predicted by environmental variables, then mechanisms related to niches are considered the main drivers of metacommunities, and species are classified among habitats (Heino and Mykra 2008). Community-level analyses have indicated in some studies the importance of local environmental factors in mediating host-parasite interactions (Lima-Junior et al. 2021).

The study showed that the environmental components explained the species composition of fish endoparasites during the flood period. Environmental factors such as chlorophyll α and nitrogen influenced the endoparasite species composition in omnivorous fish and water temperature and ammonia in detritivorous fish; and chlorophyll α , phosphorus, and phosphate influenced the parasite fauna in piscivorous fish. The presence of phosphate and nitrogen compounds and chlorophyll α indicates the concentration of nutrients in the environment and the primary productivity of the aquatic ecosystem (Santos et al. 2008; Arrieira et al., 2016; Gomes et al. 2020). These environmental factors may vary during the flood period, in floodplains (Thomaz et al. 2007; Padial et al. 2009), in which there may be an increase in the concentration of these nutrients (Simões et al. 2012) and influence primary productivity in this region (Junk et al. 1989; Neiff 1990; Bonnet et al. 2017; Amaral et al. 2018). Thus, the presence of these factors in floodplains may indicate a good source of phytoplankton, with abundant species of diatoms and green algae (KECKEIS, 2003; KISS, 1987; LEWIS et al., 2001), which serve as food for primary hosts of endoparasites such as zooplankton and aquatic arthropods (Baranyi et al. 2002; Ondrackonvá et al. 2004; Lansac-Tôha et al. 2009). Consequently, these infected organisms can be consumed by detritivorous and omnivorous fish, which serve as food for piscivorous. Birds consume piscivorous fish, and thus, endoparasites manage to complete their life cycle. This means that environmental factors such as chlorophyll α , phosphorus, and nitrogen shape host assemblages, which in turn contribute to the maintenance of parasite assemblages (Berkhout et al. 2020).

In this sense, the study suggests that the concentration of total nitrogen, total phosphorus, phosphate, ammonia, and chlorophyll α during the flood period may influence the transmission of some endoparasite species, contributing to the fauna of these organisms. The study demonstrated that some digenetic species of the families Zonocotylidae and Derogenidae occurred only during the flood, in detritivorous and omnivorous fish. Studies have shown a relationship between the concentration of total nitrogen, total phosphorus, and chlorophyll α with the presence of digenetic endoparasites and nematodes, inferring that these variables favored the presence of intermediate hosts for these species (Adamba et al. 2020; Lima—Junior et al., 2021; Virgilio et al. 2023).

The environmental conservation degree factor influenced the endoparasite community of omnivorous hosts during the flood and detritivorous fish, during the drought. The conservation factor can also be considered a local factor, as it takes into account the variables indicating the environmental quality, so our results suggest that environmental filters and anthropogenic factors may be important in modeling the distribution of endoparasite assemblages. Human actions can influence endoparasite species due to the complex life cycle of these organisms, since depending on the degree of environmental degradation, intermediate, paratenic, and definitive hosts may disappear and thus prevent the development of some endoparasite species (Sures et al. 2017). Variables such as fish species richness and endoparasites were important environmental indicators and influenced the infracommunity of endoparasites of detritivorous and omnivorous hosts. This may indicate that the greater richness of fish hosts influences the community structure of these organisms. Many studies have reported a positive relationship between host and parasite richness in well-sampled and conserved habitats (Luque et al. 2017). A meta-analysis confirmed that this relationship is very strong and universally observed in various host and parasite taxa (Luque and Poulin 2008). In addition, variables indicating the conservation of the surrounding vegetation, such as the dense area of vegetation cover and EVI, also influenced the endoparasite fauna of omnivorous and detritivorous hosts. This indicates that vegetation can offer favorable resources for the fauna of intermediate hosts and the environmental quality and thus maintain the transmission of several species of endoparasites. The removal of vegetation in these areas is an important factor to be considered, as it can influence the transport of nutrients and pollutants to the aquatic ecosystem and change the health of organisms as well as the dynamics of energy flow (Oliveira et al. 2018). In this aspect, the surrounding vegetation plays an important mitigating role, mainly by intercepting sediments, fertilizers, and pesticides that drain into water bodies (Bortozolo et al. 2014; Teresa et al. 2015).

The present study revealed that during the drought, the host traits were the factor that structured the endoparasite infracommunity. According to Costa et al. (2021), host traits explain the variation in the parasite community in fish, depending on the infection strategy and hydrological regime in the floodplain. The variables selected by the infracommunity of endoparasites in detritivorous fish were the total length and the relative condition factor. And for structuring the endoparasite fauna in omnivorous fish, it was the total weight and length, and for the parasite infracommunity in piscivorous fish, it was the weight and the condition factor. Several host-associated biological factors can influence the likelihood of parasite infection on a

local scale, such as the condition factor that indicates good body condition (Johnson et al. 2013; Richgels et al. 2013). Furthermore, body size characteristics are indeed commonly related to parasite species (Vidal-Martínez and Poulin 2003; Poulin and Leung 2011). The large size of the host body supports greater mobility and resource use and therefore exposure to a more diverse parasite fauna; length is also related to age and feeding rate, the main source of infection of endoparasites (Combes 2020; González and Poulin 2005). A study reported that hosts collected in the dry season were larger and heavier, indicating a more intense feeding during this season and consequently an increase in endoparasite fauna (de Melo Hoshino and Tavares-Dias 2019).

As in the present study, several metacommunity studies show the lowest explained variation of correlated matrices compared to the unexplained fraction (Mozzaquattro et al. 2020). This may be related to the complexity of ecological communities and the various interaction mechanisms explaining ecological patterns (Low-Décarie et al. 2014). More extensive sampling along an ecological gradient can improve explanatory power (Heino et al. 2015). Nevertheless, the results of the present study allowed to identify the (relatively) most important determinants of species composition in endoparasite communities. As expected, local factors related to the niche, such as environment, degree of conservation, and host traits explained more about infracommunity structuring and relative abundance than spatial variables, such as PCNM 1, 2, 3, and 4, which explained the species composition of endoparasites, by only 3% in the flooding and 11%, in the drought.

In this sense, the present study generated a database indicating how the α and β diversity of endoparasites can serve to determine the influence of anthropization on these aquatic environments. In addition, in conserved environments, there were a high species richness and composition of endoparasites, whereas, in anthropized environments, there were a reduction in sensitive species and an increase in generalist and opportunistic parasite species. Conserved sites contribute to a high species richness and composition, and in anthropized environments, there may be a reduction in more sensitive species and an increase in more generalist species. Further, it was evidenced that niche-related factors contributed to the endoparasite metacommunity distribution, in which environmental factors (Fig. 6, Tables 4, 5 and 6) influenced species during river level rise and host traits were important during the dry season. Nevertheless, the explanation for the patterns related to host traits may be more complex, involving other variables not measured in the present study. However, the data used allowed to explain that host traits represented the factor that best explained the species composition of endoparasites during the dry season. Thus, these data can serve as science-based management tools to investigate how parasite communities are structured in aquatic ecosystems, in addition to helping future studies involving the parasite-host-environment relationship.

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Declarations

Ethics approval All the procedures performed in the study were in accordance with the study registered in the Biodiversity Authorization and Information System (SISBIO 59642–2/2019).

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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