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ORIGINAL PAPER

Endoparasite Communities of Fish at Different Trophic Levels in the Western Brazilian Amazon: Human, Environmental and Seasonal Influence

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Abstract

Purpose The composition of the fish parasite community depends on several factors related to the environment, the host and its biology. This study aimed to evaluate the influence of environmental factors in anthropized and conserved areas on the endoparasite community structure in fish at different trophic levels, in addition to verifying that some species of Digenea are indicators of conserved environments.

Methods The study was carried out in the Upper Juruá River region, Western Amazon, Brazil. Six sampling sites were selected in this region and grouped in conserved and degraded environments. Fish were caught from periods of drought and flood, using passive and active sampling methods. Fish collected were measured, weighed, necropsied and the parasites found were counted, fixed, and subjected to morphological analysis. Physical and chemical variables and environmental characteristics were measured in all sites.

Results The present study demonstrated that environmental variables in a floodplain system can influence the richness, diversity, composition and abundance of endoparasites in hosts at different trophic levels. In addition, anthropized environments may favor the abundance of some generalist parasites and present a more homogeneous biota between seasonal periods compared to conserved environments.

Conclusion Study contributed with information supporting the importance of conservation of aquatic environments, and demonstrated that fish parasites can be excellent indicators of environments.

Keywords Environmental indicators · Floodplain · Species composition · Diversity · Abiotic factors

Introduction

Endoparasites are organisms transmitted through a food web involving intermediate, paratenic and/or definitive hosts [1]. Among fish endoparasites, helminths have a direct life cycle and complex life cycle and require multiple hosts at different trophic levels, and thus transmission is dependent on prey-predator relationships [2, 3]. Interactions involving hosts and parasites can provide essential ecosystem functions and services, contributing to biomass flow, food web connectivity and population control, as well as driving the evolution of other species [4–7]. Furthermore, obligatory dependence of parasites on their hosts can make these organisms vulnerable to environmental changes, even before their hosts are at risk of extinction [8, 9]. This is because the composition of the fish endoparasites community depends on several factors related to the environment (low water quality, changes in pH,

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oxygen dissolved level, variations in temperature, water level and seasonality effects) and their hosts (feeding behavior, physiology, age, sex and biology) [10].

Furthermore, seasonality is also an important factor in structuring the parasite community, in the case of the Amazon, periodic floods and droughts are major forces coordinating the lowland systems [11]. Biological and biochemical exchanges occur between aquatic and terrestrial environments determining productivity, reproduction and population dynamics of aquatic organisms, as well as consumer-resource interactions [12]. Thus, understanding how seasonal and environmental variation influences the dynamics of parasite infection is necessary to better understand, for example, the impacts caused by human actions [13, 14].

Anthropic changes are transforming seasonal cycles and environmental characteristics, which can impact host physiology and phenology, on the one hand, and temporal peaks in the epidemiological dynamics of the parasite, on the other [15]. Furthermore, these impacts can be particularly pronounced in aquatic ecosystems [16–19]. Fish parasites can face a dual threat and be directly vulnerable to extinction due to climate change or invasive species and indirectly vulnerable through host co-extinction [20–22]. These organisms also react to different specific environmental conditions, such water quality variation, environmental stress and pollution [23–25].

The choice of hosts to assess the environmental, seasonal and human influence is fundamental to understand how the endoparasite fauna responds to these factors. Thus, selecting hosts with different feeding habits can be important, as the diet of these organisms influences and reflects the presence of endoparasites in environments [26]. For example, detritivorous species consume organic matter, algae, detritus and microorganisms [27] and thus may ingest intermediate hosts of endoparasites [28]. Omnivorous hosts are opportunistic, feeding on a wide variety of items including fish, detritus, crustaceans, seeds, fruits, leaves, insects and mollusks [28, 29], which make them suitable hosts for endoparasites in different environments [30, 31]. However, piscivorous hosts are dominant consumers of intermediate fish within the food web, so they can present a high load of parasites due to their high trophic level [3, 32].

In this context, the present study aimed to evaluate the influence of environmental and seasonal factors in anthropized and conserved areas on the endoparasite community structure in fish at different trophic levels. The following hypotheses were tested: (i) endoparasites show greater species richness and diversity in conserved environments, and greater abundance and dominance in anthropized areas, regardless of trophic characteristics of the hosts. The high diversity of parasites is found in conserved sites, while anthropized environments present a greater abundance of more opportunistic organisms [19, 33, 34]. (ii) Endoparasites found in fish, mainly trematode species (Digenea), are indicators of conserved environments. The disturbance of aquatic environments can negatively influence the intermediate hosts of certain parasites, in addition to inhibiting the reproductive physiology [35] and the encysting process of some helminth species [36], altering the behavior of individuals with free-living stages, such as digeneans, impairing locomotion and the ability to find hosts [37]. (iii) and, drought and flooding periods and environmental characteristics are responsible for influencing the endoparasite community structure in conserved environments. This may occur because the natural floodplain system presents a dynamic structure mainly maintained by fluctuations in the water level, affecting the dynamics of definitive and intermediate hosts, and consequently, the structure and composition of their parasites [11, 38]. However, in anthropized environments, as in the present study, it is expected to find similar temporal distribution patterns in the endoparasite community, because human activities can reduce allochthonous food sources, increase silting, alter the flow and cause eutrophication of aquatic systems [39], negatively affecting rare and more sensitive species and reducing species variability in the community of endoparasites [40].

Materials and Methods

Study Area

The study was carried out in the Upper Juruá River region, Western Amazon, near 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 and grouped in conserved environments, that is, places with dense vegetation, but used by man for extraction or use of natural resources, and anthropized environments, which present urban areas, roads, rural areas and small forest fragments. To categorize the environments, the Rapid Habitat Diversity Assessment was used according to Callisto *et al.* [41] 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 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; 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 assignment of the evaluator. The studied environments with anthropized characteristics were: (i) downstream and (ii) the Juruá River (7°40′34.1″S 72°39′39.5″W), under a high degree of degradation, located in the urban center, highways, rural areas and preserved fragments; and (iii) Môa River (7°37′18″S 72°47′47″W) presented deforested areas with roads, urban part and the presence of pastures, suffers from the effect of removal of 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), which presented rural stretches and logging; the conserved stretches were 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 stretches 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 stretches with a high degree of conservation (Fig. 1).

Sampling

Fish were caught (SISBIO—Authorizations for activities with a scientific purpose 59,642-2/2019) from March 2019 to April 2021, during the periods of drought (May, June, August and September) and flooding (February, March, November and December). In each region of the sub-basins, three conserved and three anthropized sites were selected, the total sampled area was 14 km^2, including the main river, lakes and streams surrounding these areas.

Passive fish collections were conducted using 12 gill nets with 80 m in length and 3.0 m in height, with mesh sizes of 1.5 cm, 2.5 cm, 3.5 cm, 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; nets were trawled along the banks of lakes, rivers and streams. A 12 m in length and 1.8 m in height cast net was also used for sampling, for 24 h; at every 4 h, six casts

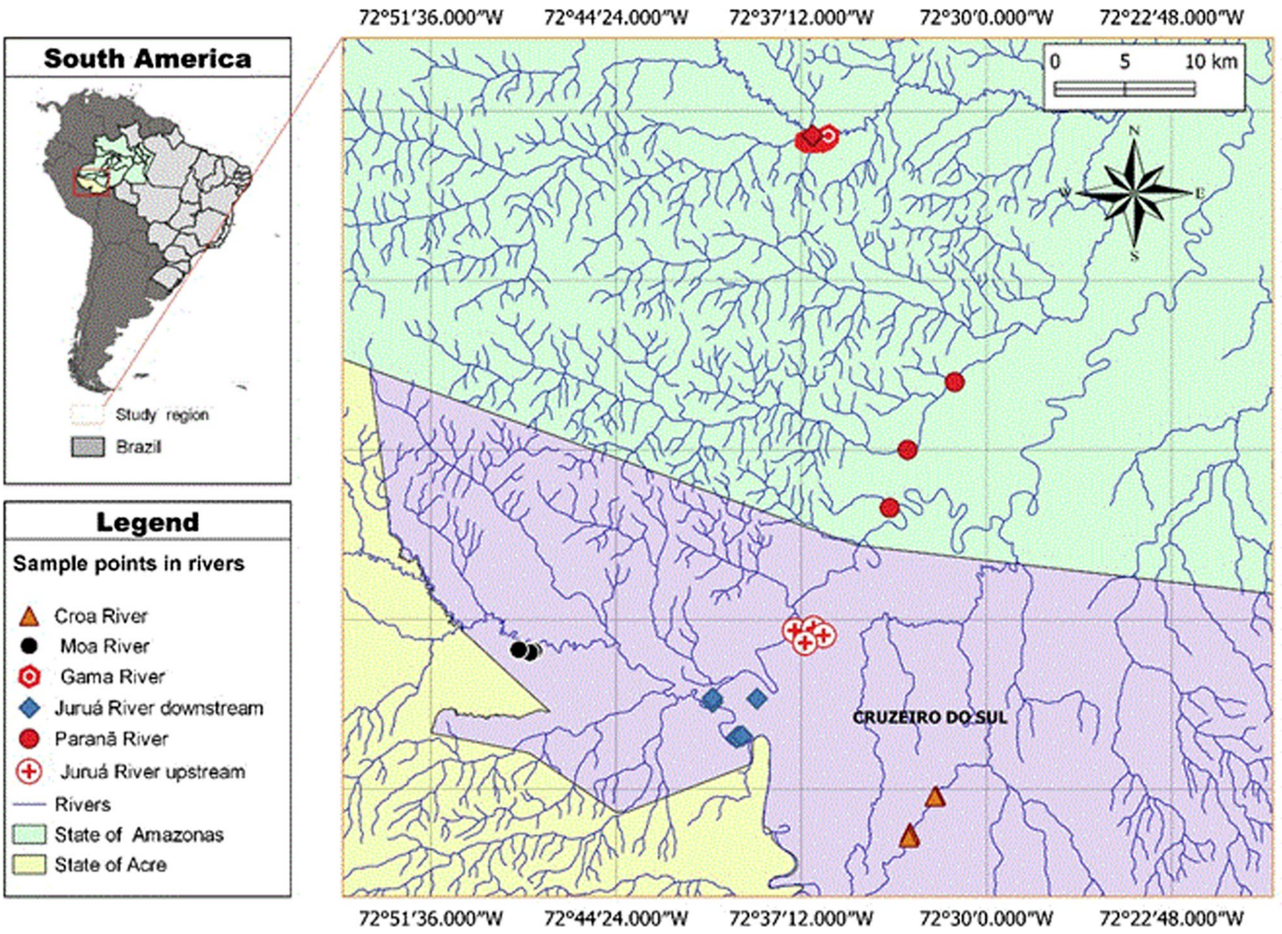

Fig. 1 Sampling sites of fish endoparasites in the Western Amazon, state of Acre, Juruá, Crôa and Môa rivers basins and state of Amazonas, Gama and Paranã river basins

were carried out on the bank, six in the water flow and six in backwater areas.

Fish caught were identified according to literature [27, 42, 43], length (cm), Weight (mg) and necropsied in situ. Some individuals, after biometry evaluation, were fixed in 10% formalin and taken to the laboratory, where they were deposited in the Núcleo de ictiologia do vale do Juruá (NIVAJ), Universidade Federal do Acre.

Twelve species of host fish were selected according to their trophic characteristics found in the literature including [3, 27, 29, 32], three detritivorous, three omnivorous, three piscivorous and three invertivorous (Table 1).

Collection and Analysis of Parasite

Fish were fresh necropsied for endoparasite collection. Internal organs of fish were removed and individually separated in Petri dishes containing 0.65% sodium chloride solution. Endoparasites were placed in Petri dishes and observed under a stereomicroscope. The Cestoda, Nematoda, Acanthocephala, and Pentastomida found were fixed in 5% formaldehyde and preserved in 70% alcohol at 65 °C. Digenea were fixed by slight compression between the slide and the coverslip in heated 70% alcohol. Digenea, Cestoda and Acanthocephala were stained in Langeron's carmine, dehydrated by an increasing alcohol series, from 70 to 100% alcohol, cleared in phenol and beech creosote, and then mounted between a slide and coverslip in Canada balm. Nematodes and pentastomids were cleared and mounted on semi-permanent slides in phenol. Helminths were identified according to Travassos *et al.* [44], Thatcher [45], Moravec [46], Martins and Yoshitoshi [47], Jones *et al.* [48], Giesen *et al.* [49], and Miller and Cribb [50].

Environmental Variables

The environmental variables (supplementary material 1) pH, electrical conductivity (µS.cm), water temperature (°C), dissolved oxygen (mg.L), 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 using a spectrophotometer, according to the methods proposed by Apha, 2012 [51] 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 fhosphate (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 of the Agência Nacional das águas (ANA), upstream of the sampling sites. Rainfall, temperature and humidity data for the region were obtained from INMET (Instituto Nacional de Meteorologia) data for the years 2019 to early 2021.

Table 1 Weight, number of host species between environments and seasonal periods (F = flooding; D = drought), length and feeding habit of endoparasite hosts, Western Amazon

Hosts	Feeding habit	Anthropized (D)	Conserved (D)	Anthropized (F)	Conserved (F)	Weight (mg)	Length (cm)
Psectrogaster amazonica Eigenmann and Eigenmann, 1889	Detritivorous	45	45	45	45	40.0 ± 4.4	15.0 ± 4.6
Curimatella meyeri Steindachner 1882	Detritivorous	42	42	42	42	90.7 ± 28.8	14.0 ± 1.3
Prochilodus nigricans Spix and Agassiz, 1829	Detritivorous	42	42	42	42	56.0 ± 11.4	14.8 ± 12.5
Trachelyopterus galeatus Linnaeus, 1766	Omnivorous	44	44	44	44	111.1 ± 0.12	18.4 ± 1.3
Nemadora humeralis Kner, 1855	Omnivorous	43	43	43	43	20.0 ± 2.32	11.8 ± 0.69
Ossancora asterophysa Birindelli and Sabaj Pérez 2011	Omnivorous	49	49	49	49	21.8 ± 0.7	12.4 ± 1.11
Hoplias malabaricus Bloch, 1794	Piscivorous	55	55	55	55	71.1 ± 90.3	22.5 ± 6.4
Serrasalmus maculatus Kner, 1858	Piscivorous	51	51	51	51	310.6 ± 15.6	21.8 ± 1.4
Acestrorhynchus heterolepis Cope, 1878	Piscivorous	49	49	49	49	79.25 ± 36.3	20.44 ± 3.5
Laetacara flavilabris Cope, 1870	Invertivorous	40	40	40	40	30.2 ± 0.7	10.2 ± 2.1
Biotodoma cupido Heckel, 1840	Invertivorous	43	43	43	43	24.0 ± 0.72	11.27 ± 1.2
Bujurquina cordemadi Kullander, 1986	Invertivorous	42	42	42	42	52.1 ± 2.3	14.3 ± 3.4

Data Analysis

Prevalence, intensity and mean abundance of endoparasite populations were determined according to Bush *et al*. [52]. The following descriptors, based on the structure of infracommunities, were calculated: abundance, richness, Shannon–Wiener diversity and Berger–Parker dominance. Parametric analysis of variance (ANOVA) was applied to test for significant differences in abundance, richness, diversity, dominance of endoparasites and environmental variables between anthropized and conserved environments in different hydrological periods, the Tukey's post-hoc test was applied to evaluate the difference between the sites. Assumptions of normality and homoscedasticity were met.

Principal Coordinate Analysis (PCoA) was summarized to assess the dissimilarity of endoparasites found in piscivorous, omnivorous, detritivorous and invertivorous host fish, between environments and seasonal periods [53]. A multivariate permutational analysis of variance (PERMANOVA) was performed to assess changes in endoparasite species composition between sampling sites. A total of 999 permutations were run to assess significance, paired PERMANOVA was used to assess for significant differences between sites.

In order to determine which species were indicators of environmental conditions between anthropized and conserved environments, the Indicator Value Index (IndVal) was applied [54]. The indicator value of a species can range from 0 to 100, reaching its maximum when all individuals of a species occur at all sites within a single group, the significance value of the indicator was tested for each species with a test of Monte Carlo with 4999 permutations.

Pearson correlation coefficient "*r*" was estimated to determine possible correlations between physical and chemical variables and the richness, diversity and abundance of endoparasites between the anthropized and conserved sites. To check for differences in physical and chemical variables between environments, during the periods of flooding and drought, and influence on the distribution of endoparasite species, a Canonical Correspondence Analysis (CCA) was performed. Matrices were log-transformed to homogenize the values of the variables, except for pH, and the effect of rare species was not removed, since for parasites, rare species can provide site-specific information. Subsequently, a Monte Carlo test with 999 permutations was run to test the significance of CCA axes [53]. Statistical analyses were performed in software R 3.2.4 (R Development Core Team 2018), using the vegan [55] and permute [56] packages for PCoA and according to the "ADONIS" function of the vegan package [55] for PERMANOVA. The level of statistical significance adopted was $p \leq 0.05$.

Results

Fish Endoparasite Fauna

In total, 5832 endoparasites were found, belonging to 61 species, being 26 Digenea, four Cestoda, 20 Nematoda, nine Acanthocephala, and two Pentastomida,

In conserved environments, during the flooding, a total of 1240 endoparasites belonging to 39 species were found, 11 Digenea, 1 Cestoda, 18 Nematoda, seven Acanthocephala, and two Pentastomida. The highest prevalence was observed for *Dadaytrema oxycephalum* Diesing, 1836, while the highest mean abundance and mean intensity was for C*osmoxynema vianai* Travassos, 1949 and *Cosmoxynemoides aguirrei* Travassos, 1948, in detritivorous fish. As for omnivorous fish, *Sharpilosentis peruviensis* Lisitsyna, Scholz and Kuchta, 2015 was the parasite with the highest prevalence, mean abundance and mean intensity. Among piscivorous, the highest prevalence, abundance and mean intensity were registered for *Prosthenhystera obesa* Diesing, 1850 and *Bellumcorpus majus* Kohn, 1962. Among the invertivorous, *P. obesa* and *Crassicutis cichlasomae* Manter, 1936 were the most prevalent, with greater mean abundance and mean intensity. In conserved environments, during the drought period, 1319 endoparasites belonging to 53 species were observed, including 23 Digenea, four Cestoda, 17 Nematoda, seven Acanthocephala, and two Pentastomida. Among detritivorous hosts, Paramphistomidae gen. sp. and *Cucullanus pinnai pinnai* Travassos, Artigas and Pereira, 1928 were the parasites with the highest prevalence and *C. aguirei*, with the highest prevalence and mean abundance. Among omnivorous hosts, the highest prevalence was observed for *Dadaytremoides parauchenipteri* Lunaschi, 1989, *S. peruviensis* and *D. oxycephalum*. Among piscivorous fish, *Posthodiplostomum* sp. and *Procamallanus inopinatus* Travassos, Artigas and Pereira, 1928 were the most prevalent, and *Austrodiplostomum* sp. showed the highest mean intensity. For the invertivorous species, *C. cichlasomae* and *Clinostomum* sp. were the most prevalent, and *Ithyoclinostomum dimorphum* Diesing, 1850 had the highest mean intensity (Table 2).

In anthropized areas, during the flooding, 1358 endoparasites were collected and during the drought, 1575 were collected. During these two periods, the richness was 27 species, including 11 Digenea, 12 Nematoda and five Acanthocephala. During the flooding, among detritivorous fish, *Gorytocephalus elongorchis* Thatcher, 1979 and *Contracaecum* sp. showed the highest prevalence, intensity and mean abundance. During the drought, *Neoechinorhynchus curemai* Noronha, 1973 was the parasite with the highest prevalence and mean abundance, and *Contracaecum* sp.

Table 2 Parasitic indices of fish endoparasites in anthropized and conserved environments during periods of flooding and drought

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Detritivorous																
Psectrogaster amazonica																
Digenea																
Dadaytrema oxycephalum (Diesing, 1850) Vaz, 1932	30.0	3.0	0.9	36.0	–	–	–	–	–	–	–	–	–	–	–	–
Cestoda																
Monticellia sp.	–	–	–	–	–	–	–	–	5.0	1.5	0.1	3.0	0.0	0.0	0.0	0.0
Nematoda																
Contracaecum sp.	10.0	1.8	0.2	7.0	30.0	1.2	0.3	14.0	–	–	–	–	5.0	11.5	0.1	23.0
Cosmoxynema vianai Travassos, 1949	10.0	18.3	1.8	73.0	–	–	–	–	–	–	–	–	–	–	–	–
Cucullanus pinnai pinnai Travassos, Artigas and Pereira, 1928	5.0	2.0	0.1	4.0	–	–	–	–	22.5	1.2	0.3	11.0	2.5	1.0	0.0	1.0
Ichthyouris laterifilamenta Moravec, Kohn and Fernandes, 1992	–	–	–	–	–	–	–	–	2.5	7.3	1.7	66.0	2.5	3.0	0.1	3.0
Neoparaseuratum travassosi Moravec, Kohn and Fernandes, 1992	20.0	1.4	0.3	11.0	10.0	1.5	0.1	6.0	10.0	1.3	0.1	5.0	2.5	3.0	0.0	3.0
Procamallanus pimelodus Pinto, Fábio, Noronha and Rolas, 1974	–	–	–	–	–	–	–	–	2.5	3.0	0.1	3.0	0.0	0.0	0.0	0.0
Procamallanus inopinatus Travassos, Artigas and Pereira, 1928	20.0	1.1	0.2	9.0	30.0	1.3	0.3	16.0	2.5	2.0	0.1	2.0	12.5	1.2	0.1	6.0
Acanthocephala																
Octospiniferoides incognita Schmidt and Hugghins, 1973	–	–	–	–	–	–	–	–	7.5	1.3	0.1	4.0	–	–	–	–
Curimatella meyeri																
Digenea																
Zonocotyle sp.	–	–	–	–	–	–	–	–	5.0	1.0	0.1	2.0	–	–	–	–
Paramphistomidae gen. sp.	–	–	–	–	–	–	–	–	30.0	3.3	1.0	39.0	–	–	–	–
Nematoda																
Cosmoxynemoides aguirei Travassos, 1949	7.5	15.0	1.1	45.0	–	–	–	–	17.5	10.9	1.9	76.0	–	–	–	–
Cosmoxynema vianai Travassos, 1949	12.5	7.0	0.9	35.0	5.0	6.0	0.1	12.0	–	–	–	–	–	–	–	–
Travnema travnema Pereira, 1938	–	–	–	–	–	–	–	–	2.5	2.0	0.1	2.0	–	–	–	–
Contracaecum sp.	5.0	2.0	0.1	4.0	15.0	2.0	0.2	12.0	5.0	1.5	0.1	3.0	12.5	2.2	0.1	11.0
Acanthocephala																
Gorytocephalus elongorchis Thatcher, 1979	–	–	–	–	40.0	2.8	0.4	45.0	–	–	–	–	2.5	2.0	0.0	2.0
Prochilodus nigricans																
Digenea																
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	5.0	2.0	0.1	4.0	–	–	–	–	–	–	–	–	32.5	2.0	0.3	26.0
Microrchis oligovitellum Lunaschi, 1987	–	–	–	–	7.5	1.0	0.1	3.0	–	–	–	–	5.0	1.0	0.1	2.0
Saccocoelioides magnorchis Thatcher, 1978	5.0	1.0	0.1	2.0	–	–	–	–	17.5	1.1	0.2	8.0	–	–	–	–

Table 2 (continued)

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Cestoda																
Proteocephalus sp.	–	–	–	–	–	–	–	–	7.5	1.0	0.1	3.0	–	–	–	–
Nematoda																
Spinitectus asperus Travassos, Artigas and Pereira, 1928	7.5	1.0	0.1	3.0	–	–	–	–	5.0	1.0	0.1	2.0	–	–	–	–
Procamallanus inopinatus Travassos, Artigas and Pereira, 1928	–	–	–	–	5.0	1.5	0.1	3.0	2.5	1.0	–	1.0	20.0	1.5	0.2	12.0
Acanthocephala																
Quadrigyrus sp.	7.5	1.0	0.1	3.0	–	–	–	–	2.5	2.0	0.1	2.0	–	–	–	–
Rhadinorhynchus sp.	2.5	2.0	0.1	2.0	0.0	0.0	0.0	0.0	10.0	2.0	0.2	8.0	–	–	–	–
Neoechinorhynchus curemai Noronha, 1973	5.0	3.0	0.2	6.0	27.5	2.8	0.3	31.0	12.5	2.8	0.4	14.0	100.0	3.1	1.0	123.0
Pentastomidae																
Sebekia oxycephalum Diesing, 1836	5.0	2.0	0.1	4.0	–	–	–	–	12.5	2.0	0.3	10.0	–	–	–	–
Omnivorous																
Trachelyopterus galeatus																
Digenea																
Genarchella genarchella Travassos, Artigas and Pereira, 1928	4.4	1.0	0.0	2.0	–	–	–	–	8.9	1.0	0.1	4.0	–	–	–	–
Doradamphistoma parauchenipteri (Lunaschi, 1989) Pantoja, Scholz, Luque and Jones, 2019	26.7	2.0	0.5	24.0	53.3	2.0	0.5	48.0	51.1	2.0	1.0	46.0	24.4	2.0	0.2	22.0
Cestoda																
Cangatiella arandasi Pavanelli and Santos, 1990	–	–	–	–	–	–	–	–	8.9	1.0	0.1	4.0	–	–	–	–
Endorchis sp.	2.2	1.0	0.0	1.0	–	–	–	–	8.9	1.5	0.1	6.0	–	–	–	–
Nematoda																
Cucullanus brevispiculus Kohn and Fernandes, 1993	4.4	1.0	0.0	2.0	–	–	–	–	28.9	1.0	0.3	13.0	–	–	–	–
Contracaecum sp.	–	–	–	–	11.1	1.0	0.1	5.0	–	–	–	–	13.3	1.8	0.1	11.0
Hysterothylacium sp.	11.1	1.0	0.1	5.0	–	–	–	–	8.9	1.0	0.1	4.0	–	–	–	–
Cucullanus pimelodellae Moravec, Kohn and Fernandes, 1993	–	–	–	–	4.4	1.0	0.0	2.0	–	–	–	–	13.3	1.0	0.1	6.0
Procamallanus peraccuratus Pinto 1976	4.4	1.5	0.1	3.0	0.0	0.0	0.0	0.0	26.7	1.1	0.3	13.0	0.0	0.0	0.0	0.0
Nemadora humeralis																
Digenea																
Phyllodistomum sp.	–	–	–	–	8.9	1.0	0.1	4.0	–	–	–	–	6.7	1.7	0.1	5.0
Diplostomum sp.	–	–	–	–	13.3	3.0	0.1	18.0	–	–	–	–	15.6	2.4	0.2	17.0
Clinostomum sp.	–	–	–	–	4.4	2.0	0.0	4.0	–	–	–	–	20.0	1.2	0.2	11.0
Doradamphistoma bacuense Thatcher, 1999	11.1	2.0	0.2	10.0	–	–	–	–	13.3	2.0	0.3	12.0	–	–	–	–
Prothenhystera obesa	–	–	–	–	24.4	2.0	0.2	22.0	–	–	–	–	8.9	2.0	0.1	8.0

Table 2 (continued)

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Dadaytrema oxycephalum	26.7	1.8	0.5	21.0	–	–	–	–	20.0	1.3	0.3	12.0	–	–	–	–
Nematoda																
Cucullanus pinnai pinnai	26.7	1.1	0.3	13.0	–	–	–	–	20.0	1.0	0.2	9.0	4.4	1.0	0.0	2.0
Contracaecum sp.	–	–	–	–	17.8	1.4	0.2	11.0	–	–	–	–	24.4	1.1	0.2	12.0
Procamallanus pimelodus Pinto, Fabio, Noronha and Rolas, 1976	24.4	1.0	0.2	11.0	–	–	–	–	20.0	1.2	0.2	11.0	–	–	–	–
Pseudoproleptus sp.	6.7	1.3	0.1	4.0	–	–	–	–	8.9	1.0	0.1	4.0	–	–	–	–
Ichthyouris laterifilamenta Moravec, Kohn and Fernandes, 1992	–	–	–	–	20.0	4.2	0.2	38.0	–	–	–	–	22.2	3.4	0.2	34.0
Neoparaseuratum travassosi Moravec, Kohn and Fernandes, 1992	–	–	–	–	20.0	1.0	0.2	9.0	–	–	–	–	15.6	2.0	0.2	14.0
Rondonia rondoni Travassos 1920	–	–	–	–	4.4	17.0	0.0	34.0	–	–	–	–	0.0	0.0	0.0	0.0
Cosmoxynemoide aguirei Travassos, 1949	–	–	–	–	24.4	4.1	0.2	45.0	–	–	–	–	26.7	3.6	0.3	43.0
Acanthocephala																
Sharpilosentis peruviensis Lisitsyna, Scholz and Kuchta, 2015	28.9	5.0	1.4	65.0	17.8	4.3	0.2	34.0	51.1	3.8	1.9	87.0	26.7	5.8	0.3	69.0
Ossancora asterophysa																
Digenea																
Phyllodistomum sp.	–	–	–	–	4.4	1.0	0.0	2.0	8.9	1.0	0.1	4.0	–	–	–	–
Clinostomum sp.	–	–	–	–	17.8	1.5	0.2	12.0	–	–	–	–	26.7	2.7	0.3	32.0
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	17.8	2.0	0.4	16.0	6.7	2.0	0.1	6.0	15.6	2.0	0.3	14.0	20.0	2.0	0.2	18.0
Austrodiplostomum sp.	–	–	–	–	24.4	8.0	0.2	88.0	–	–	–	–	28.9	7.2	0.3	93.0
Dadaytrema oxycephalum (Diesing, 1850) Vaz, 1932	26.7	2.8	0.8	34.0	–	–	–	–	51.1	2.9	1.5	66.0	4.4	4.0	0.0	8.0
Acanthostomum sp.	20.0	1.2	0.2	11.0	–	–	–	–	24.4	1.0	0.2	11.0	2.2	1.0	0.0	1.0
Dadayius sp.	2.2	1.0	0.0	1.0	–	–	–	–	2.2	1.0	0.0	1.0	–	–	–	–
Phyllodistomum wallacei Pérez-Ponce de León, Martínez-Aquino and Mendoza-Garfias, 2015	15.6	1.6	0.2	11.0	–	–	–	–	26.7	1.3	0.4	16.0	–	–	–	–
Cestoda																
Travassiella jandia (Woodland, 1934) de Chambrier, Scholz and Kuchta, 2014	4.4	1.0	0.0	2.0	–	–	–	–	2.2	1.0	0.0	1.0	–	–	–	–
Nematoda																
Contracaecum sp.	–	–	–	–	8.9	3.0	0.1	12.0	2.2	1.0	0.0	1.0	8.9	2.3	0.1	9.0
Cosmoxynema viana Travassos, 1949	13.3	5.7	0.8	34.0	37.8	2.6	0.4	44.0	20.0	1.3	0.3	12.0	24.4	1.4	0.2	15.0
Cosmoxynemoides aguirrei Travassos, 1949	–	–	–	–	24.4	1.0	0.2	11.0	–	–	–	–	51.1	2.4	0.5	55.0
Cucullanus pimelodellae Moravec, Kohn and Fernandes, 1993	2.2	1.0	0.0	1.0	2.2	1.0	0.0	1.0	4.4	1.0	0.0	2.0	2.2	1.0	0.0	1.0
Cucullanus pinnai pinnai Travassos, Artigas and Pereira, 1928	15.6	1.1	0.2	8.0	–	–	–	–	6.7	1.7	0.1	5.0	6.7	1.3	0.1	4.0
Cystidicoloides vaucheri Petter, 1984	2.2	1.0	0.0	1.0	–	–	–	–	6.7	1.0	0.1	3.0	–	–	–	–
Ichthyouris laterifilamenta Moravec, Kohn and Fernandes 1992	17.8	1.5	0.3	12.0	–	–	–	–	4.4	2.0	0.1	4.0	24.4	1.1	0.2	12.0

Table 2 (continued)

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Neoparaseuratum travassosi Moravec, Kohn and Fernandes, 1992	4.4	2.0	0.1	4.0	2.2	2.0	0.0	2.0	26.7	1.9	0.5	23.0	8.9	1.3	0.1	5.0
Procamallanus inopinatus Travassos, Artigas and Pereira, 1929	4.4	1.5	0.1	3.0	17.8	2.0	0.2	16.0	2.2	2.0	0.0	2.0	26.7	2.0	0.3	24.0
Pseudoproleptus sp.	2.2	1.0	0.0	1.0	–	–	–	–	4.4	2.0	0.1	4.0	–	–	–	–
Acantocephala																
Sharpilosentis peruviensis Lisitsyna, Scholz and Kuchta, 2015	33.3	3.7	1.2	56.0	24.4	4.0	0.2	44.0	20.0	2.1	0.4	19.0	28.9	2.6	0.3	34.0
Piscivorous																
Hoplias malabaricus																
Digenea																
Posthodiplostomum sp.	26.2	1.2	0.3	13.0	–	–	–	–	35.7	2.2	0.8	33.0	–	–	–	–
Austrodiplostomum sp.	–	–	–	–	35.7	6.6	0.4	99.0	–	–	–	–	52.4	4.5	0.5	98.0
Clinostomum sp.	–	–	–	–	4.8	1.5	0.0	3.0	4.8	2.0	0.1	4.0	26.2	1.1	0.3	12.0
Ithyoclinostomum dimorphum (Diesing, 1850) Witenberg, 1925	–	–	–	–	28.6	4.7	0.3	56.0	–	–	–	–	26.2	2.9	0.3	32.0
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	54.8	2.0	1.1	46.0	–	–	–	–	26.2	2.0	0.5	22.0	–	–	–	–
Nematoda																
Procamallanus (S.) inopinatus Travassos, Artigas and Pereira, 1928	4.8	2.0	0.1	4.0	28.6	2.0	0.3	24.0	11.9	2.0	0.2	10.0	28.6	2.0	0.3	24.0
Pseudoproleptus sp.	2.4	2.0	0.0	2.0	4.8	2.0	0.0	4.0	–	–	–	–	–	–	–	–
Paraseuratum soaresi Fabio, 1982	4.8	1.0	0.0	2.0	2.4	1.0	0.0	1.0	–	–	–	–	4.8	1.5	0.0	3.0
Contracaecum sp.	4.8	2.0	0.1	4.0	16.7	1.7	0.2	12.0	4.8	2.0	0.1	4.0	19.0	2.0	0.2	16.0
Procamallanus pimelodus Pinto, Fabio, Noronha and Rolas, 1976	4.8	2.0	0.1	4.0	2.4	2.0	0.0	2.0	4.8	2.0	0.1	4.0	14.3	2.0	0.1	12.0
Cucullanus pinnai pinnai Travassos, Artigas and Pereira, 1928	4.8	1.5	0.1	3.0	–	–	–	–	9.5	0.5	0.0	2.0	9.5	2.0	0.1	8.0
Acanthocephala																
Quadrigyrus Machadoi Fabio, 1983	7.1	1.3	0.1	4.0	9.5	0.8	0.1	3.0	11.9	2.0	0.2	10.0	7.1	2.7	0.1	8.0
Neochinorhynchus sp.	2.4	2.0	0.0	2.0	2.4	3.0	0.0	3.0	9.5	1.5	0.1	6.0	7.1	2.0	0.1	6.0
Hirudina																
Glossiphonidae gen. sp.	7.1	1.0	0.1	3.0	4.8	1.0	0.0	2.0	–	–	–	–	7.1	1.0	0.1	3.0
Placobdella sp.	2.4	1.0	0.0	1.0	2.4	1.0	0.0	1.0	–	–	–	–	–	–	–	–
Serrasalmus maculatus																
Digenea																
Austrodiplostomum sp.	2.4	13.0	0.3	13.0	28.6	6.5	0.3	78.0	4.8	17.0	0.8	34.0	35.7	6.6	0.4	99.0
Allocreadium sp.	11.9	1.0	0.1	5.0	–	–	–	–	14.3	1.2	0.2	7.0	–	–	–	–
Diplostomum sp.	7.1	2.0	0.1	6.0	–	–	–	–	14.3	2.0	0.3	12.0	–	–	–	–
Nematoda																
Procamallanus inopinatus Travassos, Artigas and Pereira, 1928	9.5	2.0	0.2	8.0	35.7	1.5	0.4	23.0	7.1	1.7	0.1	5.0	38.1	1.1	0.4	18.0

Table 2 (continued)

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Contracaecum sp.	4.8	2.0	0.1	4.0	38.1	1.1	0.4	18.0	7.1	2.7	0.2	8.0	40.5	1.2	0.4	21.0
Procamallanus peraccuratus Pinto, Fábio, Noronha and Rolas, 1976	9.5	1.0	0.1	4.0	2.4	1.0	0.0	1.0	9.5	1.0	0.1	4.0	2.4	1.0	0.0	1.0
Ichthyouris laterifilamenta Moravec, Kohn and Fernandes 1992	31.0	1.9	0.6	25.0	4.8	1.0	0.0	2.0	26.2	2.0	0.5	22.0	–	–	–	–
Neoparaseuratum travassosi Moravec, Kohn and Fernandes, 1992	2.4	1.0	0.0	1.0	–	–	–	–	26.2	1.0	0.3	11.0	4.8	1.0	0.0	2.0
Acestrorhynchus heterolepis																
Digenea																
Dadaytrema oxycephalum (Diesing, 1850) Vaz, 1932	28.6	2.3	0.7	28.0	–	–	–	–	11.9	3.6	0.4	18.0	–	–	–	–
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	28.6	2.0	0.6	24.0	4.8	2.0	0.0	4.0	19.0	2.0	0.4	16.0	2.4	1.0	0.0	1.0
Bellumcorpus majus Kohn, 1962	35.7	4.5	1.6	67.0	11.9	2.4	0.1	12.0	26.2	4.1	1.1	45.0	7.1	6.0	0.1	18.0
Nematoda																
Contracaecum sp.	2.4	3.0	0.1	3.0	28.6	1.1	0.3	13.0	7.1	2.3	0.2	7.0	2.4	3.0	0.0	3.0
Pseudoproleptus sp.	14.3	1.5	0.2	9.0	9.5	2.0	0.1	8.0	4.8	2.5	0.1	5.0	–	–	–	–
Procamallanus inopinatus Travassos, Artigas and Pereira, 1928	26.2	1.2	0.3	13.0	14.3	1.3	0.1	8.0	28.6	1.2	0.3	14.0	9.5	1.5	0.1	6.0
Invertivorous																
Laetacara flavilabris																
Digenea																
Crassicutis cichlasomae Manter, 1936	37.5	3.0	1.1	45.0	5.0	4.0	0.1	8.0	55.0	4.0	2.2	88.0	5.0	1.5	0.1	3.0
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	7.5	2.0	0.2	6.0	–	–	–	–	27.5	2.0	0.6	22.0	2.5	2.0	0.0	2.0
Crassicutis manteri Pantoja, Scholz, Luque and Perez–Ponce de León, 2021	30.0	1.8	0.6	22.0	27.5	1.5	0.3	16.0	5.0	2.0	0.1	4.0	22.5	2.0	0.2	18.0
Clinostomum sp.	20.0	1.1	0.2	9.0	–	–	–	–	27.5	2.0	0.6	22.0	–	–	–	–
Nematoda																
Cosmoxynemoides aguirrei Travassos, 1949	30.0	8.2	2.5	98.0	37.5	5.2	0.4	78.0	27.5	9.0	2.5	99.0	30.0	4.7	0.3	56.0
Procamallanus peraccuratus Pinto, Fábio, Noronha and Rolas, 1976	5.0	1.0	0.1	2.0	57.5	2.0	0.6	46.0	5.0	2.0	0.1	4.0	27.5	2.0	0.3	22.0
Biotodoma cupido																
Digenea																
Genarchella isabellae Lamothe–Argumedo, 1977	27.5	1.0	0.3	11.0	–	–	–	–	12.5	1.0	0.1	5.0	–	–	–	–
Thometrema sp.	15.0	1.2	0.2	7.0	–	–	–	–	22.5	1.2	0.3	11.0	–	–	–	–
Crassicutis cichlasomae Manter, 1936	30.0	2.8	0.9	34.0	5.0	4.0	0.1	8.0	27.5	2.8	0.8	31.0	–	–	–	–
Nematoda																
Procamallanus peraccuratus Pinto, Fábio, Noronha and Rolas,	12.5	1.2	0.2	6.0	27.5	1.1	0.3	12.0	2.5	1.0	0.0	1.0	–	–	–	–
Procamallanus inopinatus Travassos, Artigas and Pereira, 1928	27.5	1.1	0.3	12.0	2.5	2.0	0.0	2.0	37.5	1.2	0.5	18.0	2.5	1.0	0.0	1.0
Acanthocephala																
Neochinorhynchus sp.	10.0	1.8	0.2	7.0	5.0	1.5	0.1	3.0	2.5	1.0	0.0	1.0	20.0	1.5	0.2	12.0

Table 2 (continued)

Species	Flooding								Drought							
	Conserved				Anthropized				Conserved				Anthropized			
	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP	P %	IM	MA	TNP
Bujurquina cordemadi																
Digenea																
Crassicutis manteri Pantoja, Scholz, Luque and Perez–Ponce de León, 2021	30.0	1.8	0.6	22.0	2.5	1.0	0.0	1.0	27.5	1.8	0.5	20.0	5.0	1.0	0.1	2.0
Clinostomum sp.	10.0	1.3	0.1	5.0	2.5	1.0	0.0	1.0	30.0	1.0	0.3	12.0	5.0	1.5	0.1	3.0
Prosthenhystera obesa (Morrendo, 1850) Travassos, 1922	40.0	2.0	0.8	32.0	5.0	2.0	0.1	4.0	27.5	2.0	0.6	22.0	2.5	2.0	0.0	2.0
Ithyoclinostomum dimorphum (Diesing, 1850) Witenberg, 1925	5.0	17.0	0.9	34.0	57.5	5.3	0.6	121.0	5.0	16.5	0.8	33.0	45.0	5.4	0.5	98.0
Bellumcorpus majus Kohn, 1962	5.0	4.0	0.2	8.0	5.0	6.0	0.1	12.0	2.5	7.0	0.2	7.0	27.5	6.0	0.3	66.0
Nematoda																
Contracaecum sp.	–	–	–	–	10.0	2.0	0.1	8.0	5.0	2.0	0.1	4.0	30.0	1.9	0.3	23.0
Acanthocephala																
Neochinorhynchus sp.	27.5	2.1	0.6	23.0	5.0	3.0	0.1	6.0	2.5	1.0	0.0	1.0	–	–	–	–
Pentastomidae																
Subtriquetra subtriquetra Diesing, 1836	2.5	8.0	0.2	8.0	–	–	–	–	5.0	6.0	0.3	12.0	–	–	–	–

P% Prevalence, *MI* mean intensity, *MA* mean abundance, *TNP* number of parasites analyzed per environment and seasonal period, Juruá valley, Western amazon had the highest mean intensity. Among omnivorous hosts, *D. parauchenipteri* and *C. viana* were the most prevalent species with the highest mean abundance, and *Rondonia rondoni* Travassos, 1920 presented the highest mean intensity during the flooding. In the drought, *Austrodiplostomum* sp. and *S. peruviensis* were the parasites with the highest prevalence, abundance and mean intensity. *P. inopinatus*, *Contracaecum* sp., *B. majus* and *Austrodiplostomum* sp. were the most prevalent endoparasite species during the flooding and drought among piscivorous fish. In both periods, *Austrodiplostomum* sp. showed the highest mean intensity. Among the invertivorous, in both periods, *Procamallanus peraccuratus* Pinto, Fabio, Noronha and Rolas, 1976 and *I. dimorphum* were the parasites with the highest prevalence and mean abundance (Table 2).

For the endoparasite fauna of detritivorous hosts, species richness was significantly higher in conserved environments (ANOVA $p = 0.003$). The difference occurred between the environments in the drought (Tukey-$p = 0.002$) and in the flooding (Tukey-$p = 0.003$) season. The same was observed in omnivorous fish (ANOVA $p = 0.004$) between environments in different seasonal periods (Drought: Tukey-$p = 0.02$; Flooding: Tukey-$p = 0.001$). For piscivorous and invertivorous, the difference in richness (ANOVA $p = 0.01$) occurred during the drought between anthropized and conserved environments (Tukey-$p = 0.01$) (Table 3). Differences in the number of individuals of endoparasites were found between anthropized and conserved environments in the fauna of detritivorous (ANOVA $p = 0.02$), omnivorous (ANOVA-$p = 0.002$) and piscivorous (ANOVA $p = 0.02$) fish. For detritivorous, the difference occurred between environments during the flooding season (Tukey-$p = 0.001$) and between anthropized areas in the drought and flooding season (Tukey-$p = 0.02$). For omnivorous and piscivorous, the difference in abundance of endoparasites was observed between conserved and anthropized environments in the flooding season (Tukey-$p < 0.05$) and between conserved environments, in the flooding, and the anthropized environments, in the drought (Tukey-$p < 0.05$) (Table 3). The lowest diversity of endoparasites in detritivorous fish was verified in the drought in anthropized environments and showed a significant difference (ANOVA $p = 0.001$) from conserved environments in both seasonal periods (Tukey-$p < 0.05$), there was also a difference in diversity between anthropized environments in the drought and flooding season (Tukey-$p < 0.05$). For piscivorous hosts, the difference was seasonal (ANOVA $p = 0.002$), between the drought and flooding environments (Tukey-$p = 0.001$). As for invertivorous fish, the diversity of endoparasites was different between anthropized and conserved environments during flooding (Tukey-$p = 0.001$) and drought (Tukey-$p = 0.004$) (Table 3). For endoparasite dominance, the difference was

Table 3 Mean and standard deviation of richness, number of individuals, diversity and dominance of fish endoparasites, in conserved and disturbed environments in the periods of flooding and drought

Parameters	Drought anthropized	Drought conservation	Flood anthropized	Flood conservation	ANOVA -F	p
Detritivorous						
Species richness (S)	11	17*	9	14*	5.6	0.003
Individuals number (n)	444*	475	376*	382*	3.8	0.02
Shannon–Wiener diversity (H)	1.68 ± 0.10*	1.97 ± 0.11*	1.58 ± 0.10*	1.67 ± 0.15*	5.3	0.001
Berger-Parker dominance	0.37 ± 0.05	0.36 ± 0.05	0.44 ± 0.06	0,45 ± 0.06	0.65	0.772
Omnivorous						
Species richness (S)	12*	15*	19*	12*	4.6	0.004
Individuals number (n)	274*	570*	425*	552*	3.7	0.003
Shannon–Wiener diversity (H)	1.98 ± 0.01	2.0 ± 0.05	2.44 ± 0.04	2.01 ± 0.01	0.98	0.543
Berger-Parker dominance	0.28 ± 0.03	0.34 ± 0.02	0.18 ± 0.02	0.23 ± 0.02	0.05	0.876
Invertivorous						
Species richness (S)	6*	12*	7*	6*	3.56	0.01
Individuals number (n)	332	127	233	91	1.23	0.24
Shannon–Wiener diversity (H)	0.99 ± 0.06*	2.12 ± 0.07*	1.23 ± 0.08*	1.62 ± 0.08*	3.25	0.01
Berger-Parker dominance	0.63 ± 0.03*	0.19 ± 0.03*	0.57 ± 0.04*	0.37 ± 0.06*	2.56	0.02
Piscivorous						
Species richness (S)	10*	15*	12	13	3.32	0.01
Individuals number (n)	208*	445*	289*	162*	2.23	0.02
Shannon–Wiener diversity (H)	1.95 ± 0.11*	2.33 ± 0.06*	2.3 ± 0.05*	1.87 ± 0.13*	4.8	0.001
Berger-Parker dominance	0.33 ± 0.04	0.20 ± 0.02	0.16 ± 0.02*	0.33 ± 0.03*	5.1	0.001

*$p < 0.05$

detected in piscivorous (ANOVA $p=0.001$) and invertivorous (ANOVA $p=0.02$) hosts. In piscivorous hosts, the difference was observed between anthropized and conserved environments during the flooding, whereas for invertivorous, the dominance was higher in anthropized environments compared to conserved environments in both periods (Tukey-$p<0.05$) (Table 3).

The species composition of endoparasites in omnivorous, piscivorous (Fig. 2), detritivorous and invertivorous fish (Fig. 3) showed variability between environments in different sampling season. In endoparasites of piscivorous (PCoA: $p=0.001$) fish, differences were detected between conserved and anthropized environments during the flooding (PCoA: $p=0.01$); conserved environments in the flooding and anthropized in the drought (PCoA: $p=0.002$). *Gorytocephalus elongorchis* (IndVal = 0.682; $p=0.02$), *G. genarchella* (IndVal = 0.612; $p=0.02$) and *A. compactum* (IndVal = 0.732; $p=0.03$) were the indicator species of conserved environments, which influenced the variations.

For omnivorous hosts, there was also a difference in endoparasite composition (PCoA: $p=0.001$), the difference occurred between environments in the flooding (PCoA:$p=0.01$), the conserved environments in the flooding and anthropized environments in the drought (PCoA:$p=0.002$). The indicator species influencing the variability between environments were *P. inopinatus* (IndVal = 0.698; $p=0.02$), *A. compactum* (IndVal = 0.567; $p=0.02$), in anthropized environments, *C. pinnai* (IndVal = 0.582; $p=0.02$) and *Contracaecum* sp. (IndVal = 0.657; $p=0.01$) in conserved environments.

For detritivorous hosts, the difference occurred (PCoA:$p=0.001$) between anthropized and conserved environments in flooding (PCoA:$p=0.02$) and drought (PCoA: $p=0.01$) periods. The species that indicated this variability were *P. inopinatus* (IndVal = 0.763; $p=0.03$) and *Monticellia* sp. (IndVal = 0.687; $p=0.02$), in anthropized areas and *N. travassossi* (IndVal = 0.568; $p=0.01$) and *C. pinnai* (IndVal = 0.654; $p=0.01$) in conserved environments.

As for endoparasites in invertivorous fish, the differences occurred (PCoA: $p=0.001$) between environments during the flooding (PCoA: $p=0.03$), conserved environments during the flooding and anthropized environments during the drought (PCoA: $p=0.02$) and between environments during the drought (PCoA: $p=0.01$). Endoparasite species influencing this variation were *P. peraccuratus* (IndVal = 0.622; $p=0.01$), *C. manteri* (IndVal = 0.622; $p=0.02$) and *C. cihlasomae* (IndVal = 0.672; $p=0.03$) in conserved environments, *I. dimorphum* (IndVal = 0.592; $p=0.03$) and *Contracaecum* sp. (IndVal = 0.692; $p=0.03$) in anthropized environments.

Species Composition and Environmental Variables

Variables of electrical conductivity, pH, TDS, nitrite, nitrate, orthophosphate, zinc, phosphate, phosphorus, chlorophyll α and nitrogen variables were higher in anthropized environments. And dissolved oxygen presented higher content in

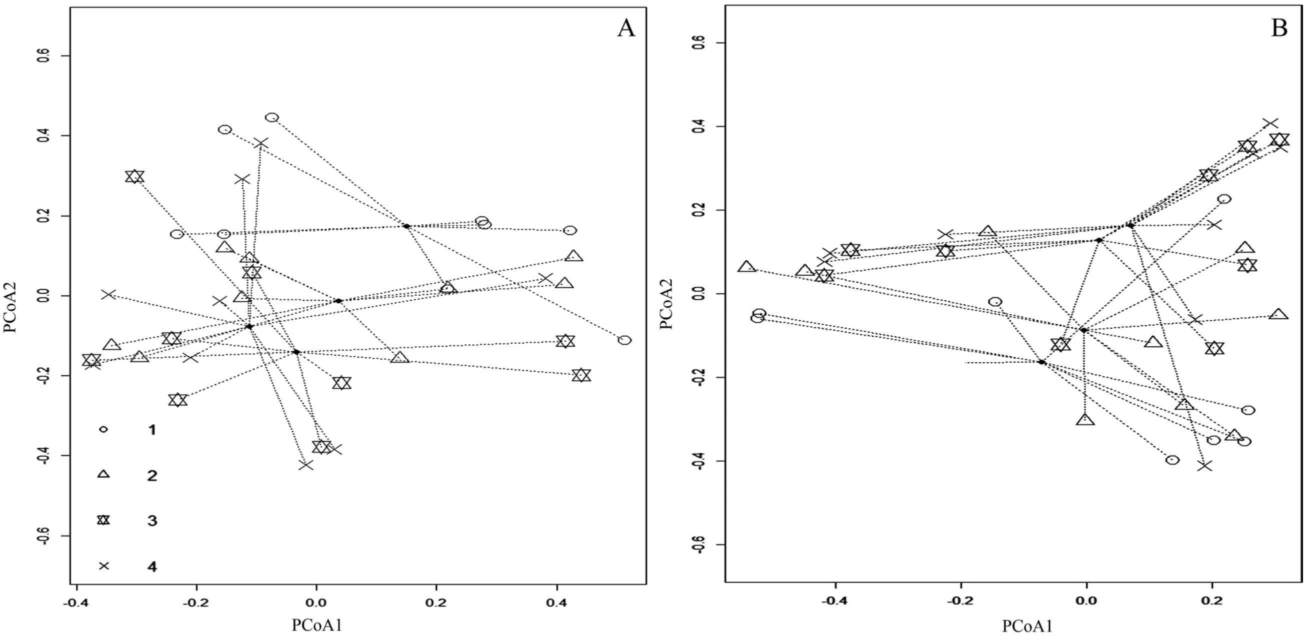

Fig. 2 Principal coordinate analysis (PCoA) showing the variability in species composition of endoparasites of omnivorous and piscivorous fish between conserved and anthropized sampling sites in the periods of flooding and drought. **A** Piscivorous; **B** omnivorous. 1—Conserved environment (Flooding); 2—conserved environment (Drought); 3—anthropized environment (Flooding); 4—anthropized environment (Drought)

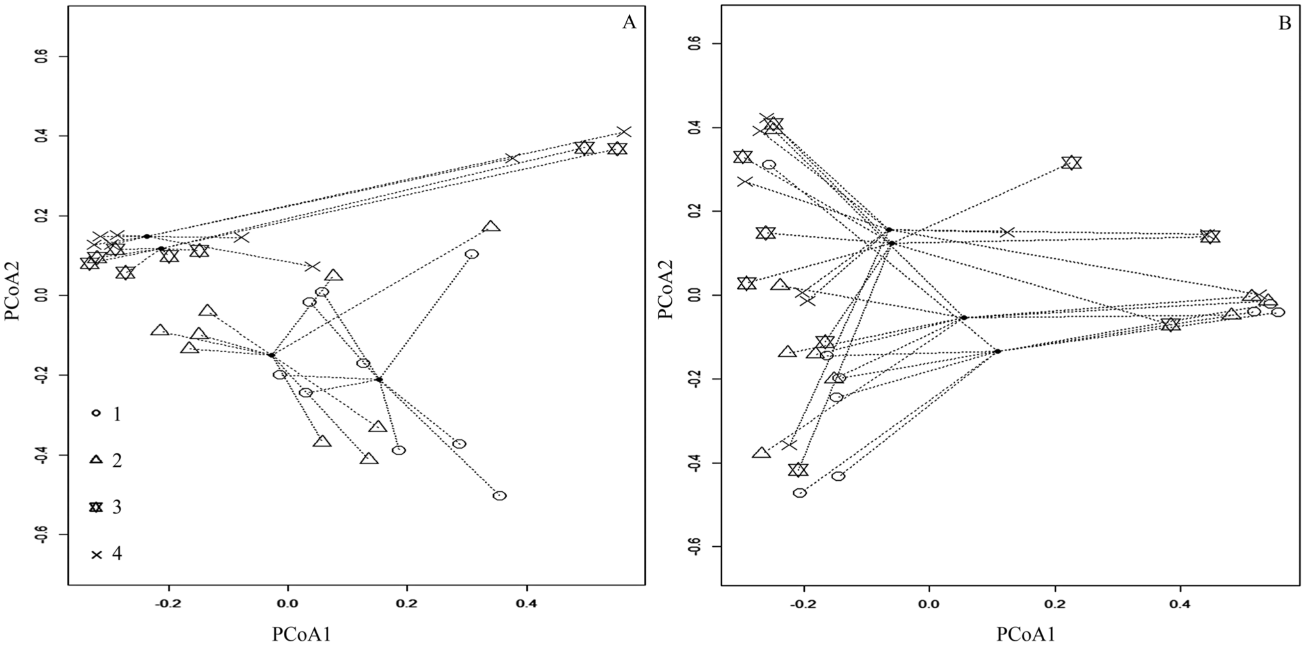

Fig. 3 Principal coordinate analysis (PCoA) showing the variability in species composition of endoparasites of detritivorous and invertivorous fish between conserved and anthropized sampling sites in the periods of flooding and drought. **A** Invertivorous; **B** detritivorous. 1—Conserved environment (Flooding); 2—conserved environment (Drought); 3—anthropized environment (Flooding); 4—anthropized environment (Drought)

conserved environments. As for the level and flow of water, values were high during the flooding in all environments (supplementary material 1).

During the flooding season, richness and diversity of endoparasites in piscivorous fish showed a positive correlation with chlorophyll α and the level of dissolved oxygen and a negative correlation with river flow in conserved environments. In the same seasonal period, in anthropized environments, the oxygen level showed a correlation with richness, diversity and abundance of endoparasites. During the drought, in anthropized environments, pH and TDS showed a positive correlation with the endoparasite abundance in piscivorous hosts. For the invertivorous fauna, in conserved environments, during the flooding, richness and diversity of species indicated a correlation with oxygen and river water level, in addition, the species diversity showed a positive relationship with Chlorophyll α, and the richness, a negative correlation with water flow. The endoparasite abundance was also negatively correlated with zinc levels in these environments during the flooding period, and with chlorophyll α in the drought.

In anthropized areas, during the drought, the levels of dissolved oxygen were correlated with the richness and abundance of endoparasites in invertivorous fish (Table 4). Total nitrogen showed a positive correlation with the richness and diversity of endoparasites of omnivorous hosts, in anthropic environments in the drought, and a negative correlation in conserved environments during the flooding (Table 4). Total phosphorus showed a positive correlation with richness and abundance of endoparasites in omnivorous hosts in the drought, and a negative correlation with diversity in conserved environments during the flooding (Table 4). This environment during the flooding also showed a correlation between the abundance of endoparasites and the levels of dissolved oxygen. For detritivorous, richness, diversity and abundance of endoparasites showed negative relationships with chlorophyll α, conductivity, river water level, water flow, zinc and nitrogen during drought in anthropized environments (Table 4). In conserved environments, during the flooding, the diversity of endoparasites in detritivorous fish was negatively related to total phosphorus and during the drought, to zinc concentration (Table 4).

The ordination indicated that between environments, the first two axes explained 76.7% distribution of the endoparasite fauna in invertivorous fish. The main environmental variables indicating the correlation between sampling sites and the parasite endofauna were conductivity, oxygen, pH, TDS and zinc. Dissolved oxygen and pH influenced species composition in anthropized and conserved environments, where the related species were *S. peruvensis* and *C. manteri* in conserved environments, whereas *I. laterifilamenta* and *C. aguirre*, in anthropized environments. Conductivity, TDS and zinc negatively influenced the anthropized sites

Table 4 Values of Pearson's r correlation coefficient between richness, diversity and abundance of endoparasite species and environmental variables

Host/period	Chlo	Cond	Ox	pH	TDS	Temp	W_L	Flo	Nit	Zin	TP
S_Pisc_F_Antro	0.22	0.11	0.86*	0.11	0.12	0.24	0.22	0.26	0.11	0.08	0.08
S_Pisc_D_Antro	− 0.12	0.12	0.19	0.21	0.11	0.12	0.45	− 0.41	0.22	− 0.22	0.22
S_Pisc_F_Conser	0.61*	0.24	0.80*	0.13	0.11	0.22	0.21	− 0.82*	0.26	0.22	0.26
S_Pisc_D_Conser	0.01	0.22	0.33	0.11	0.26	0.26	0.35	− 0.12	0.11	0.12	0.11
H'_Pisc_F_Antro	0.11	0.26	0.89*	0.10	0.11	0.11	0.12	− 0.11	0.11	0.09	0.11
H'_Pisc_D_Antro	0.22	0.11	0.13	0.33	0.11	0.11	0.16	0.34	0.23	0.25	0.23
H'_Pisc_F_Conser	0.68*	0.15	0.83*	0.11	0.08	0.23	0.11	− 0.85*	0.25	0.21	0.05
H'_Pisc_D_Conser	0.21	0.11	0.45	0.11	− 0.11	0.25	0.18	0.33	0.11	0.11	0.008
N_Pisc_F_Antro	0.11	0.22	0.74*	0.10	0.21	0.11	0.22	− 0.12	0.008	0.33	0.008
N_Pisc_D_Antro	0.10	0.11	0.44	0.83*	0.67*	0.008	0.11	− 0.32	0.09	0.11	0.25
N_Pisc_F_Conser	0.33	0.09	0.12	0.11	0.09	0.11	0.008	− 0.11	0.33	0.22	− 0.11
N_Pisc_D_Conser	0.11	0.15	0.24	0.21	0.12	0.12	0.16	− 0.16	0.12	0.12	− 0.16
S_Inver_F_Antro	0.23	0.13	0.05	0.008	0.008	0.23	0.11	0.11	0.15	0.15	0.11
S_Inver_D_Antro	0.12	0.11	− 0.67*	0.16	0.11	0.12	0.18	0.33	0.15	0.15	0.33
S_Inver_F_Conser	0.22	0.23	0.82*	0.12	0.12	0.35	0.61*	− 0.68*	0.11	0.11	0.09
S_Inver_D_Conser	− 0.12	0.25	0.11	0.23	0.15	0.23	0.13	0.32	− 0.02	− 0.02	0.15
H'_Invert_F_Antro	− 0.22	0.11	0.23	0.12	0.15	0.35	0.11	0.12	0.26	0.11	0.13
H'_Inver_D_Antro	0.04	0.008	0.008	0.35	0.11	0.12	0.23	0.24	0.09	0.13	0.11
H'_Inver_F_Conser	0.60*	0.07	0.68*	0.23	− 0.02	0.16	0.65*	− 0.24	0.05	0.11	0.23
H'_Inver_D_Conser	0.13	0.18	0.09	0.24	− 0.16	0.11	0.23	0.11	0.33	0.18	0.22
N_Inver_F_Antro	0.15	0.16	0.12	0.22	0.33	0.18	0.22	0.22	0.24	0.11	− 0.12
N_Inver_D_Antro	0.11	0.11	0.80	0.11	0.15	0.65*	0.12	0.11	0.09	0.16	0.11
N_Inver_F_Conser	0.05	0.27	0.15	0.13	0.17	0.11	0.11	0.09	0.11	− 0.65*	0.17
N_Inver_D_Conser	0.58*	0.33	0.06	0.07	0.12	0.12	0.12	0.15	0.11	0.11	0.21
S_Oniv_F_Antro	0.11	0.16	0.44	0.03	0.22	0.14	0.22	0.13	− 0.02	− 0.02	0.11
S_Oniv_D_Antro	0.17	0.12	0.25	0.08	0.08	0.11	0.08	0.11	0.59*	− 0.16	0.70*
S_Oniv_F_Conser	0.22	0.12	0.39	0.05	0.06	0.16	0.06	0.23	− 65*	0.33	− 0.16
S_Oniv_D_Conser	0.21	0.22	0.03	0.06	0.15	0.17	0.15	0.22	0.15	0.15	0.17
H'_Oniv_F_Antro	0.11	0.08	0.12	0.11	0.24	0.18	0.24	0.21	0.17	0.17	0.22
H'_Oniv_D_Antro	0.21	0.06	0.22	0.03	0.34	0.11	0.34	0.11	0.62*	0.12	0.15
H'_Oniv_F_Conser	0.13	0.15	0.08	0.15	0.22	0.24	0.22	0.21	− 0.59*	0.22	− 0.60*
H'_Oniv_D_Conser	0.04	0.24	0.06	0.24	0.11	0.12	0.17	0.13	0.08	0.08	0.34
N_Oniv_F_Antro	0.05	0.23	0.15	0.08	− 0.02	0.16	0.18	0.04	0.06	0.06	0.22
N_Oniv_D_Antro	0.18	0.22	0.24	0.21	0.008	0.11	0.11	0.05	0.21	0.27	0.66*
N_Oniv_F_Conser	0.11	− 0.12	0.61*	0.18	0.33	0.45	0.24	0.18	0.21	0.33	0.23
N_Oniv_D_Conser	0.23	0.11	0.11	− 0.02	− 0.02	0.44	0.06	0.11	0.04	0.16	0.44
S_Detrit_F_Antro	0.16	0.17	0.22	0.33	0.11	0.12	0.18	0.09	0.18	0.09	0.43
S_Detrit_D_Antro	− 0.65*	− 0.61*	0.11	0.21	0.23	0.11	− 0.74*	− 0.77*	− 0.74*	− 0.66*	0.21
S_Detrit_F_Conser	0.11	0.22	0.09	0.23	0.21	0.08	0.22	− 0.12	− 0.02	0.22	0.12
S_Detrit_D_Conser	0.17	0.23	0.15	0.22	0.08	0.07	0.23	− 0.11	0.008	0.23	0.34
H'_Detrit_F_Antro	0.11	0.43	0.13	0.09	0.06	0.01	0.43	0.34	0.33	0.43	0.34
H'_Detrit_D_Antro	− 0.60*	− 0.62*	0.11	0.23	0.11	0.12	− 0.75*	− 0.75*	− 0.72*	− 0.65*	0.23
H'_Detrit_F_Conser	0.44	0.24	0.23	0.15	0.13	0.1	0.11	− 0.32	0.11	− 0.58*	− 0.23
H'_Detrit_D_Conser	0.43	0.12	0.18	0.153	0.18	0.33	− 0.02	0.11	0.23	0.21	− 0.12
N_Detrit_F_Antro	0.42	0.22	0.45	0.23	0.08	0.13	0.008	0.11	0.21	0.21	0.22
N_Detrit_D_Antro	− 0.65*	− 0.66*	0.08	0.37	0.11	0.11	− 0.69*	− 0.70*	− 0.78*	− 0.66*	0.62*
N_Detrit_F_Conser	0.12	0.11	0.33	0.24	0.11	0.37	0.11	0.21	0.23	0.18	0.21
N_Detrit_D_Conser	0.10	0.11	0.11	0.13	0.23	0.11	0.23	− 0.11	− 0.61*	0.22	0.22

Chlo Chlorophyll α, *Cond* electrical conductivity, *Ox* dissolved oxygen, *TDS* total dissolved solids, *Temp* temperature, *W_L* water level, *Flo* flow, *Nit* nitrogen, *Zinc* zinc, *TP* total phosphorus. S Richness, H' Diversity, *N* number of species, *Pisc* piscivorous, *Inset* invertivorous, *Oni* omnivorous, *Detrit* detritivorous, *Antro* anthropized environment, *Conser* conserved environment, *F* flooding, *D* drought

*$p < 0.05$

between the two periods, in which the correlated parasite was *I. dimorphum* (Fig. 4; Table 5).

The two ordination axes explained 71.1% distribution of endoparasites found in omnivorous hosts, influenced by conductivity, temperature, TDS and zinc, in anthropized areas, mainly during the drought period. The related species were *D. oxycephalum* and *P. peraccuratus*. Species distribution was also positively influenced by total phosphorus and negatively influenced by oxygen level, water flow and river water level in conserved areas in both periods the main correlated species were *R. rondoni*, *P. obesa* and *Contracaecum* sp. (Fig. 5; Table 5).

The ordination axes explained 61.4% distribution of the endoparasite fauna in detritivorous hosts. The chlorophyll α content, conductivity, zinc, TDS and temperature were the environmental variables that influenced the distribution in anthropized areas during the periods of flooding and drought, in which *P. inopinatus* and *Monticellia* sp. were the species that influenced this correlation (Fig. 6; Table 5).

For the distribution of endoparasites in piscivorous hosts, the axes explained 72.0% variation, influenced by the environmental variables chlorophyll α, conductivity, TDS and temperature. *Posthodiplostomum* sp. was the main correlated species in anthropized areas (Fig. 7; Table 5).

The Monte Carlo test applied to ordination axes showed that the correlation between environmental variables and the species involved was significant for the set of CCA axes ($p < 0.001$).

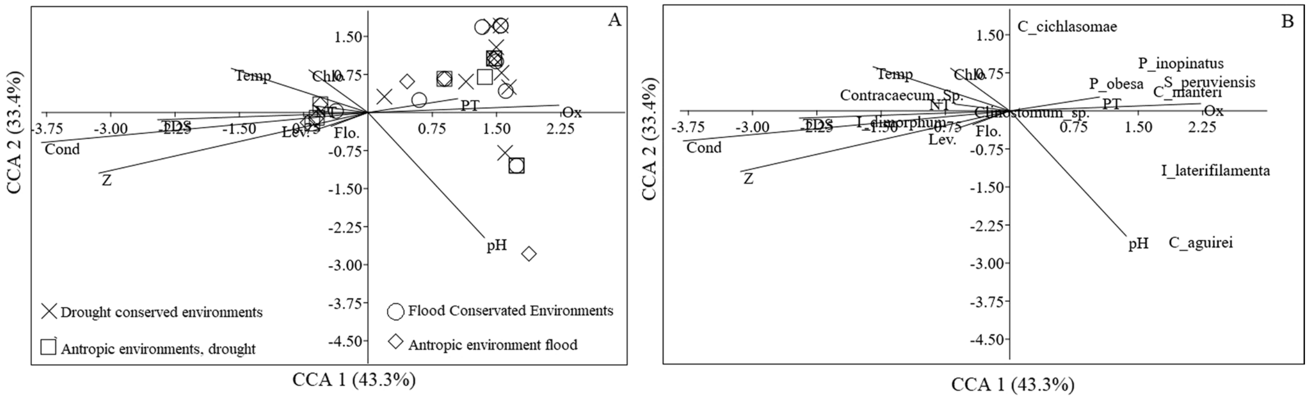

Fig. 4 Ordination of environments and species of endoparasites in invertivorous hosts by Canonical Correspondence Analysis (CCA). **A** Ordination of environments between seasonal periods and limnological characteristics. **B** Ordination of species and limnological characteristics. *Chlo* chlorophyll α; *Temp* temperature; *Cond* conductivity; *Ox* oxygen; *TDS* total dissolved solids; *TP* total phosphorus; *Z* zinc

Table 5 Influence of environmental variables on the distribution of parasite species in CCA biplot

Parameters	Insectivorous		Omnivorous		Detritivorous		Piscivorous	
	F	*p*	F	*p*	F	*p*	F	*p*
Chlorophyll	0.160	0.308	0.878	0.390	**2.190**	**0.010**	**1.980**	**0.010**
Conductivity	**2.290**	**0.030**	**3.990**	**0.001**	**2.440**	**0.001**	**2.010**	**0.001**
Oxygen	**3.440**	**0.002**	0.354	0.727	0.881	0.923	1.382	0.333
pH	**2.990**	**0.002**	0.224	0.825	1.283	0.084	0.477	0.236
TDS	**3.110**	**0.001**	**3.240**	**0.001**	**2.040**	**0.001**	**2.150**	**0.001**
Temperature	0.315	0.168	**2.990**	**0.002**	**1.990**	**0.020**	**2.010**	**0.000**
Nitrite	0.249	0.194	0.354	0.727	1.295	0.472	0.354	0.817
Nitrate	0.142	0.176	0.224	0.825	1.017	0.798	0.543	0.228
Ammonia	0.115	0.740	1.227	0.090	2.625	0.990	1.239	1.055
Orthophosphate	0.532	0.487	1.267	0.072	0.135	0.104	0.147	1.139
Zinc	**3.220**	**0.001**	**2.880**	**0.003**	**2.070**	**0.010**	0.158	0.585
Phosphate	0.637	0.214	0.237	0.608	0.108	0.518	0.108	0.518
PT	0.396	0.634	1.555	1.559	0.108	0.518	0.108	0.518
NT	0.271	0.644	0.354	0.817	0.514	0.722	0.514	0.722
Level	0.175	0.611	0.543	0.228	1.820	2.569	1.162	0.086
Flow	0.141	0.242	1.239	1.055	0.044	0.891	0.220	0.079

$p < 0.05$ are marked in bold

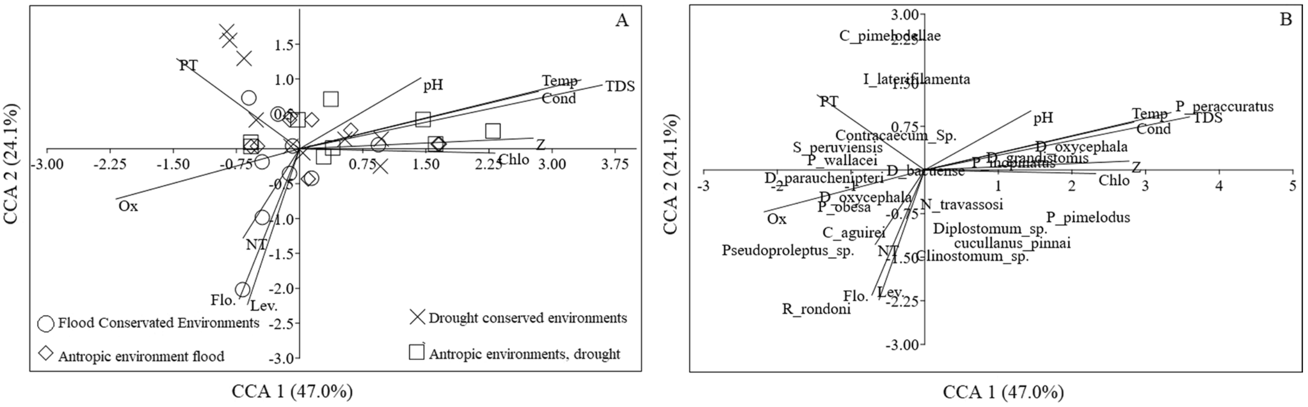

Fig. 5 Ordination of environments and species of endoparasites in omnivorous hosts by Canonical Correspondence Analysis (CCA). **A** Ordination of environments between seasonal periods and limnological characteristics. **B** Ordination of species and limnological characteristics.; *Chlo* chlorophyll *α*; *Cond* conductivity; *Ox* oxygen; *TDS* total dissolved solids; *Temp* temperature; *Lev* river level; *Flo* flow; *NT* total nitrogen; *PT* total phosphorus; *Z* zinc

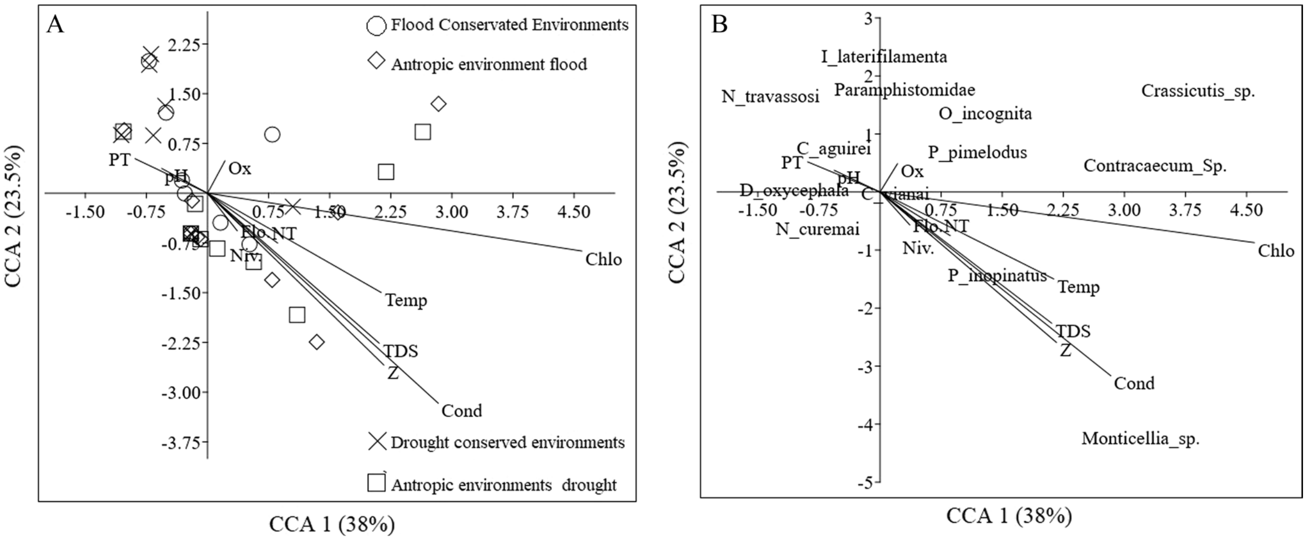

Fig. 6 Ordination of environments and species of endoparasites in detritivorous hosts by Canonical Correspondence Analysis (CCA). **A** Ordination of environments between seasonal periods and limnological characteristics. **B** Ordination of species and limnological characteristics. *Chlo* chlorophyll α; *Cond* conductivity; *Ox* oxygen; *TDS* total dissolved solids; *Temp* temperature; *Lev* river level; *Flo* flow; *NT* total nitrogen; *PT* total phosphorus; *Z* zinc

Discussion

Richness, Diversity, Abundance and Composition of Endoparasites

The present study showed a greater richness and diversity of endoparasites in conserved environments, whereas anthropized environments presented a greater abundance and lower richness of endoparasites in hosts at different trophic levels. In response to human activities, fish parasite communities may increase or decrease in prevalence, abundance and diversity [57]. According to Marcogliese [58], diversity and richness of endoparasite species can reduce in response to environmental degradation. These reductions in parasite richness are believed to parallel the loss of species diversity with free-living stages, such as Digenea, and part of the populations of intermediate hosts that are impacted by environmental changes [19, 25]. Lafferty [57], predicted that some Digenea species may be sensitive to anthropic disturbances, which may explain the greater richness of these endoparasites in conserved environments when compared to the anthropized environments of the present study.

The results also supported the hypothesis that conserved areas present a variation in the richness of taxa between

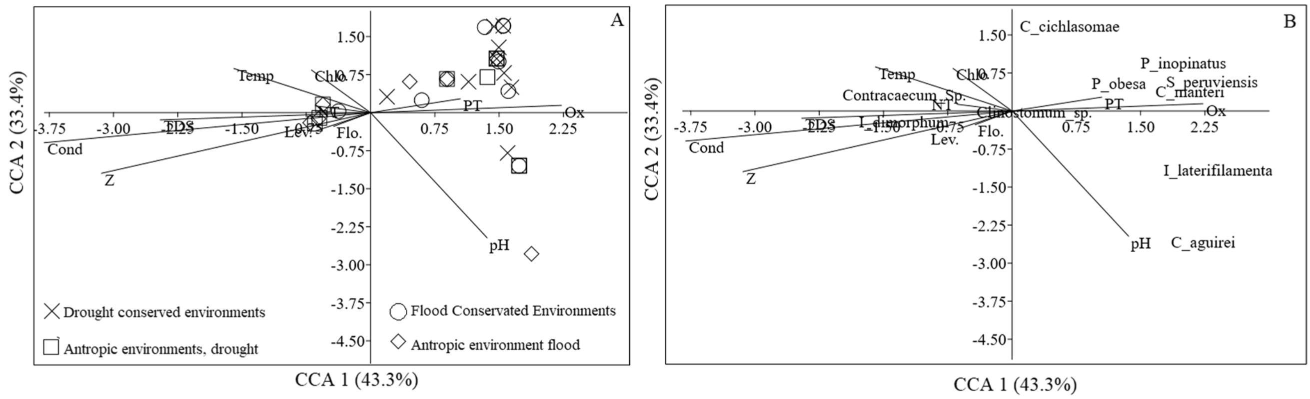

Fig. 7 Ordination of environments and species of endoparasites in piscivorous hosts by Canonical Correspondence Analysis (CCA). **A** Ordination of environments between seasonal periods and limnological characteristics. **B** Ordination of species and limnological characteristics. *Chlo* chlorophyll α; *Cond* conductivity; *Ox* oxygen; *TDS* total dissolved solids; *Temp* temperature; *Flo* flow; *NT* total nitrogen; *PT* total phosphorus; *Z* zinc

the seasonal periods. The study indicated that the greatest richness of Digenea was found during the drought period and decreased during the flooding, when Nematoda was the taxon with the highest species richness. In anthropized areas, the richness of endoparasites remained constant between the two seasonal periods. This is probably related to the fact that in conserved natural environments, the flood regime directly or indirectly influences the distribution of species, influencing the increase or decrease in richness of certain aquatic organisms [11], such as fish parasites. According to Yamada *et al*. [59], it is possible that the flooding conditions imposed on ecosystems may lead to differences in the levels of parasite infections, depending on the taxonomic group and the availability of intermediate and/or definitive hosts. The flooding period may favor the life cycle of some parasites, such as nematodes [60], as infections by some nematode species during this period may be associated with the seasonal dietary composition of their hosts [46, 61]. The fact that drought favors some species of digeneans may be related to the transportation of small, mobile, parasite-free stages out of the aquatic ecosystem by large floods, due to increased water flow, and thus reducing the richness of these parasites [62, 63]. In addition, during the dry season, the reduction in river water level increases the density of invertebrate and fish communities [64]. This can induce the overlap of intermediate and definitive hosts in a shrunken environment [65], facilitating the transmission of parasites with complex life cycles, such as digeneans [60]. However, in anthropized environments, environmental conditions may not be favorable for the occurrence of certain species of parasites. Because, in addition to environmental degradation reducing the host fauna, it can negatively influence the biotic characteristics of ecosystems, allowing only the presence of opportunistic, generalist species with low host specificity, which manage to complete their life cycle in both seasonal periods [66, 67], which may explain the low variation in species richness in these environments.

The present study showed a contrast in the endoparasite fauna of detritivorous fish between conserved and anthropized environments, where there was a higher prevalence of Digenea in conserved environments, mainly species of the family Cladorchiidae. As this group of hosts ingest large amounts of organic matter from the sediment [68], they may have ingested some of these organisms in the free-living stage [6]. These endoparasites of the family Cladorchiidae encyst in vegetation until they are predated upon by potential definitive hosts, for example, herbivorous, detritivorous and omnivorous fish [45]. Nevertheless, in anthropized environments during periods of flooding and drought, detritivorous hosts showed higher prevalence, abundance and intensity of infection by *G. elongorchis* and *N. curemai*, in addition to *Contracaecum* sp.. This does not mean that these endoparasite species occur in these hosts only in anthropized environments, as these parasites are commonly found in Prochilodontidae and Curimatidae fish in conserved areas, as observed here and in other studies [69–71]. In fact, the present study demonstrated that anthropic activities can induce an imbalance in the infection by certain species of endoparasites. This is because, in anthropized systems, the high input of nutrients can lead to a disproportionate growth of intermediate hosts, such as ostracods, and increase parasitic infection by acanthocephalans [72–75]. Furthermore, it can result in an increase in *Contracaecum* populations in wild fish populations [76, 77].

Endoparasites of omnivorous hosts indicated similar prevalence in conserved and anthropized environments, during the flooding period. However, there was greater abundance and intensity of infection of *R. rondoni* nematodes in anthropized areas. This parasite is known to occur in different fish species and river systems at high intensities [78–80].

They are viviparous parasites and their direct life cycle can allow the dissemination of numerous eggs with several filaments and larvae in the marginal vegetation of water bodies [81]. As anthropized aquatic environments can favor the dissemination of some species of aquatic plants [82], these micro-habitats become environments favorable to the reproduction of these nematodes, which can colonize omnivorous fish that forage in these environments [83].

On the other hand, endoparasites in piscivorous and invertivorous hosts showed high richness and diversity in the drought season in conserved environments. During the drought, invertebrate and fish communities may present higher diversity due to the reduction of river levels and hydrological disconnection of some environments in floodplain areas [64]. This can induce an increase in density, overlapping of intermediate and definitive hosts in a reduced environment [65], facilitating the transmission of parasites with a complex life cycle [60]. In anthropized environments, especially during the drought season, there was an increase in the dominance of endoparasites in piscivorous and invertivorous hosts. An expected pattern in these areas, as environmental degradation induces a change in community structure towards dominance of tolerant species [84, 85]. Thus, richness decreases as a result of the disappearance of taxa as the level of environmental degradation increases and the number of sensitive species is reduced, while the number of tolerant species may increase [19, 57].

The piscivorous and invertivorous host fish showed high prevalence and mean abundance of *Posthodiplostomum* sp. and *Clinostomum* sp. in conserved environments and *Austrodiplostomum* sp. and *I. dimorphum* in anthropized areas. Although studies indicate that water quality is an important factor for the infection of parasite species of the family Diplostomidae [86] *Austrodiplostomum* sp. stood out in the present study for being present in both conserved and anthropized environments. Other factors may be influencing these metacercariae in these environments, first is the generalist characteristic of these species, as the ability to infect different hosts can facilitate the permanence and proliferation of these parasites under adverse environmental conditions [31, 87, 88]. The second factor may be related to the increase in parasite load of metacercariae in eutrophic environments, as the concentration of nutrients in this region can influence the increase of some species of tolerant invertebrates that serve as food for intermediate hosts of these species [89].

Adult digeneans, such as *P. obesa*, *C. cichlasomae*, *D. parauchenipteri* and *B. majus*, found in piscivorous, omnivorous and invertivorous fish occurred, mainly in conserved environments. This suggests that these environments present autogenic endoparasite species and these fish may be playing an important role as definitive hosts. However, in all anthropized areas of the present study, *P. obesa*, *C. cichlasomae* were not observed, which may suggest that some autogenic species may be more susceptible to local extinction [90]. For example, a study showed that *P. obesa* disappeared after anthropic actions in the Paraná River [59], that is, the increase in anthropization can destabilize the parasite community, mainly some autogenic species. Because these organisms complete their entire life cycle within the limits of an aquatic ecosystem, and may not be able to colonize other environments in time, as in the case of allogenic species [91].

The composition of endoparasites in piscivorous, omnivorous, invertivorous and detritivorous hosts were dissimilar between anthropized and conserved areas in different seasonal periods. Thus, it was evidenced that the seasonality influenced the endoparasite community, as suggested in other fish parasite studies [92–94]. It is well established that the hydrological regime and the degree of environmental conservation are important factors in controlling environmental heterogeneity, and consequently in organizing communities in floodplain systems [95, 96].

The indicator endoparasite species influencing the variation in the infracommunity of omnivorous and detritivorous hosts were *P. inopinatus* in anthropized environments and *C. pinnai pinnai*, in conserved environments during the flooding period. These nematode species were also found in fish species from the Amazon region, mainly during the flooding period [97–99]. This may occur because during flooding and flood in the Amazon, environmental conditions are more favorable for some aquatic organisms, so there are a large number of individuals influencing the occurrence of infective larval forms in their hosts [100]. The endoparasite *P. inopinatus* is a generalist species found in different families of fish at different trophic levels, including detritivorous and omnivorous species, which ingest a wide variety of food items [101, 102]. This species has already been found infecting *Astyanax paranae* Eigenmann, 1914 only in highly polluted areas, indicating that this nematode can be used as a bioindicator of anthropized areas [103]. The nematode *C. pinnai pinnai* may also have low host specificity, and can parasitize several fish species [79, 80, 104]. It can be found in omnivorous or invertebrate-predator fish that feed mainly on aquatic insects [105]. As the diversity and richness of aquatic insects are greater in conserved environments [106], this may justify the presence of this Nematoda in these places.

Gorytocephalus elongorchis and *G. genarchella* were the indicator species contributing to the variation of endoparasite fauna in piscivorous hosts in conserved rivers during flooding. The endoparasite *C. maintaini* contributed to the dissimilarity of the parasite endofauna of invertivorous, also in conserved environments. This may indicate that these species found environmental conditions, as well as intermediate and definitive hosts, to complete their life cycles. The transmission of endoparasites with a complex life cycle and free-living stage can be considered a good environmental indicator for these environments [18, 58, 107, 108].

Environmental Variables and Endoparasites

The present study indicated the variation in environmental factors during the hydrological cycle periods influenced the richness, diversity, composition and abundance of the endoparasite fauna of fish between environments with different degrees of conservation.

The variation in chlorophyll α in environments of the present study, influenced the diversity, richness and abundance of endoparasites of piscivorous and invertivorous hosts in conserved environments. This environmental factor also determined the variation in the composition of endoparasites in piscivorous hosts. The presence of chlorophyll α in floodplains indicates a good source of phytoplankton contributing to the diet of diverse organisms, such as zooplankton, containing abundant species of diatoms and green algae [109–111]. Aquatic insects feed on plankton and attract intermediate consumer fish, which serve as food for piscivorous fish. Birds consume piscivorous fish, and so endoparasites can complete their life cycle. This means that environmental factors, such as chlorophyll α, model host assemblages which in turn contribute to the maintenance of parasite assemblages [112]. Nevertheless, in anthropized environments of the present study, chlorophyll α showed high concentration and negative correlation with the richness and diversity of endoparasites in detritivorous hosts, as well as the high concentration of nitrogen, total phosphorus and zinc. The diversity and richness of endoparasites in omnivorous fish also responded negatively to the concentration of phosphorus and nitrogen in the environments of this study. In fact, it has been suggested that unfavorable environmental conditions affect some species of parasites in anthropized environments with excess chlorophyll α, nitrogen, phosphorus, among other nutrients [33, 113].

The composition of some species of detritivorous, piscivorous, invertivorous and omnivorous parasites in the present study were influenced by the high concentration of total solids (TDS), temperature and electrical conductivity in anthropized environments. High conductivity occur in environments with high TDS concentration and temperature, and indicate disturbed environments [114]. According to [115, 116], waters with high conductivity are more productive and, therefore, harbor some invertebrates that are intermediate hosts for endoparasites and allow some species to succeed. In addition, the higher temperature during drought in anthropized environments may favor the development of certain metacercariae species [117, 118] as observed in the present study, where the metacercariae *I. dymorfum* and *Posthodiplostomum* sp. were related to these environments and environmental factors.

The present study indicated that pH was more alkaline in anthropized areas during the drought period, and influenced the abundance of parasites in piscivorous hosts and the composition of endoparasites in invertivorous species. Where the nematodes *C. aguirre* and *P. inopinatus* were the most correlated endoparasite that influenced this correlation. In floodplain regions, studies on anthropized aquatic environments indicated that pH increases during algal blooms in dry season due to photosynthesis, which may result in increased nutrient release [119, 120]. This may favor the presence of some species of copepods, which are intermediate hosts of endoparasites such as *C. aguirre* and *P. inopinatus* [102, 106, 121, 122], which may explain this relationship. The present study also showed that zinc found in anthropized areas influenced the composition of endoparasites in omnivorous, invertivorous and detritivorous hosts. Some studies have shown that zinc generate a direct negative effect, especially in parasite-free life stages [123, 124].

The increase in the level of dissolved oxygen positively influenced the diversity and richness of endoparasites in piscivorous and insectivorous hosts, and also the abundance of parasites of omnivorous fish in anthropized environments during the flooding season. The flood pulse influences the abiotic environment, mainly oxygen levels [125], which is one of the environmental parameters exerting a direct effect on fish growth and production and an indirect effect on nutrient [126]. This may justify its positive correlation with the richness and diversity of endoparasites in several studies [127, 128]. This variable also explained the species composition of endoparasites of omnivorous and invertivorous in conserved environments in periods of drought and flooding, in which *C. manteri, D. oxycephalum* and *P. obesa* were the affected parasites. Dissolved oxygen can contribute to the life cycle of Digenea species by aiding the energy metabolism of these organisms [129–131].

The rise in river water level and flow negatively influenced the richness and diversity of endoparasites in piscivorous hosts, and positively in invertivorous fish. The diversity of zooplankton and other invertebrates is greater during the flooding, and provides fish with better feeding conditions [60, 68]. This may have influenced the fauna of invertivorous in the present study. These hosts belong to the family Cichlidae, according to Tavares-Dias *et al.* [60], some species of this family had higher helminth infections during the flooding due to increased availability of food resources. This influenced the increased ingestion of infectious stages of these trophically transmitted endoparasites. Regarding endoparasites of piscivorous hosts, the present study suggests that the reduction in richness and diversity in these hosts should be associated with a reduction in the consumption of some species of parasitized fish. According to Luz-Agostinho *et al*. [132], during the flooding, the dispersion of aquatic biota occurs by increasing the water level reducing the concentration of prey, such as fish at lower trophic levels, and thus reducing food consumption for these piscivorous fish. As a result, the hydrological cycle should affect interspecific relationships, particularly predation. Thus, flooding increases the number of shelters and reduces the density of prey, which can influence the fauna of parasites trophically transmitted to piscivorous hosts.

Conclusions

In conclusion, endoparasites showed higher species richness and diversity in conserved environments and greater abundance and dominance in anthropized areas. The periods of drought and flooding were responsible for influencing the endoparasite community structure in conserved environments. In anthropized areas, the distribution patterns of the endoparasite community between seasonal periods were similar. In addition, Digenea species were indicators of conserved environments, and the more generalist metacercariae were indicators of anthropized environments. Environmental and host variables in a floodplain system can influence the richness, diversity, composition and abundance of endoparasites in hosts at different trophic levels.

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Declarations

Conflict of interest The authors declare that they have no confict of interest.

Ethical Approval We certify that Fish species reported in the study is not threatened, and all procedures were approved by the ethics committee of the institution where the study was conducted.

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