



Variation in taxonomic, functional, and phylogenetic diversity of parasites in *Hypostomus* spp. (Loricariidae: Hypostominae) from two Neotropical rivers in Brazil

Atsler Luana Lehun¹ · Aparecida de Fátima Cracco² · Larissa Sbeghen Pelegrini³ · Lidiany Doreto Cavalcanti¹ · Lucas Aparecido Rosa Leite⁴ · João Otávio Santos Silva¹ · Gabriela Cássia Reinas¹ · Gabriela Michelan² · Vanessa Doro Abdallah⁴ · Ricardo Massato Takemoto^{1,2,5}

Received: 31 October 2025 / Accepted: 26 February 2026 / Published online: 10 March 2026
© The Author(s) 2026

Abstract

Understanding how ecological and evolutionary processes shape biodiversity across hierarchical levels is a central goal in ecology, and parasite communities provide a valuable model for investigating assembly rules because they are directly constrained by their hosts. In this study, we investigated how taxonomic (TD), functional (FD), and proxy phylogenetic diversity (PPD) of parasite communities vary across two congeneric fish hosts (*Hypostomus hermanni* and *H. regani*) collected from two rivers (Batalha River and Ivaí River). We quantified diversity at multiple organizational levels, including α -diversity within host individuals, β_1 variation among host individuals within the same host species, β_2 variation between host species, and γ -diversity across habitats. Parasite communities were more similar among host individuals sampled within the same river than between rivers. Alpha diversity differed primarily in TD and FD, with *H. hermanni* from the Batalha River showing the highest values, whereas α PPD showed limited variation among host species. Beta diversity analyses revealed weak departures from random expectations within host species (β_1) but strong differentiation between host species (β_2) across TD, FD, and PPD. Overall, our findings indicate that host species remains a central driver of parasite diversity, while highlighting that taxonomic, functional, and phylogenetic facets respond differently to host and habitat-related factors.

Keywords Parasite community · Fish · River · Alpha diversity · Beta diversity · Host

Introduction

An ecosystem is defined as a set of organisms and the abiotic and biotic environments in which they occur (Begon and Townsend 2021). Within an ecosystem, species interact through shared environments and resources (Schoener 1974); consequently, the search for biodiversity patterns across different spatial and temporal scales, as well as the mechanisms underlying these patterns, is a central goal in ecology (Pennisi 2005). An individual organism, such as a parasite, exists within its host, which in turn is part of a nested hierarchy ranging from the host to the ecological community and ultimately to the broader ecosystem. In this context, parasitism can be viewed as a series of smaller systems embedded within larger ones, allowing parasites to serve as valuable ecological indicators of host biology and ecosystem interactions (Allen and Starr 1982; Horwitz and Wilcox 2005; Marcogliese 2003; Rynkiewicz et al. 2015). Many parasite species are inherited by their

✉ Atsler Luana Lehun
atslerluana@gmail.com

¹ Programa em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá, Maringá, Paraná, Brasil
² Programa de Pós-Graduação em Biologia Comparada, Universidade Estadual de Maringá, Maringá, Paraná, Brasil
³ Instituto de Biociências de Botucatu, Universidade Estadual Paulista, Botucatu, São Paulo, Brasil
⁴ Setor de Parasitologia e Patologia, Universidade Federal de Alagoas, Maceió, Alagoas, Brasil
⁵ Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Maringá, Paraná, Brasil

current hosts from distant ancestors; therefore, closely related hosts may share similar parasite faunas (Lehun et al. 2024; Poulin 2010). However, over evolutionary time, parasite faunas can change through the acquisition of new species and the loss of others because of evolutionary processes (Vickery and Poulin 1998; Poulin 2007, 2014).

The genus *Hypostomus* Lacépède (1803) belongs to the family Loricariidae and is distributed from Central America to South America, with several species recorded in the tributaries of the Paraná, Paraguay, Uruguay, and Amazon basins, thus representing an important component of the Neotropical freshwater ichthyofauna. Members of this family are easily recognizable by their sucker-shaped mouth and body covered in bony plates (Montoya-Burgos 2003; Rocha-Reis et al. 2021). The parasitic fauna associated with *Hypostomus* species includes monopisthocotyleans, digeneans, nematodes, and hirudinea, parasite groups commonly reported in freshwater fishes (Lehun et al. 2020; Takemoto et al. 2009). However, despite the wide distribution and ecological relevance of this genus, the structure of parasite communities and the characteristics of host–parasite interactions in these species remain poorly understood (Pelegriani et al. 2022).

In recent years, ecological research has increasingly highlighted the complex and multidimensional nature of biodiversity, incorporating not only traditional taxonomic approaches but also functional and phylogenetic dimensions, an especially relevant perspective for parasite communities (Llopis-Belenguer et al. 2020). Taxonomic diversity, the most frequently employed metric, refers to the number of species found within a given area (Whittaker et al. 2001). Functional diversity, in turn, captures the range and variability of species' functional traits within an assemblage (Petchey and Gaston 2006; Violle et al. 2007), while phylogenetic diversity reflects the evolutionary relationships among taxa (Faith 1992; Srivastava et al. 2012). Biodiversity can also be examined hierarchically at three complementary scales: within communities (α -diversity), between communities (β -diversity), and across broader regions (γ -diversity) (Crist and Veech 2006; Loreau 2000; Pavoine et al. 2016; Whittaker 1972).

Thus, all components of biodiversity must be considered to improve our understanding of ecosystem processes, as parasite species composition and host–parasite interaction patterns may not show congruent variation across different environmental contexts (Runghen et al. 2021). In this study, we investigated whether taxonomic, functional, and phylogenetic measures of parasite diversity differ between host species of the genus *Hypostomus*. We focused on two phylogenetically close species, *H. hermanni* (Ihering 1905) and *H. regani* (Ihering 1905), collected from different rivers (Montoya-Burgos 2003; Rocha-Reis et al. 2021). We hypothesized that the different facets of parasite diversity

vary between host species (α - and β -diversity) and between habitats (γ -diversity).

Materials and methods

Study area, fish, and parasite collection

The Batalha River is an important tributary of the Tietê River, approximately 167 km long and responsible for about 40% of the water supply of Bauru, São Paulo state, Brazil. In recent decades, it has experienced intense anthropogenic pressures, particularly from agricultural and industrial activities, resulting in environmental degradation, water pollution, and biodiversity loss (Secretaria Municipal do Meio Ambiente 2008). In this study, individuals of *Hypostomus hermanni* and *H. regani* were collected between 2014 and 2016 (SISBIO no. 40998-2; Ethics Committee CEUA/USC no. 3353050417) from two river stretches with distinct limnological characteristics: a lentic stretch used for water intake between Piratininga and Bauru (22° 24' 46" S; 49° 05' 05" W) and a lotic stretch in Reginópolis (21° 53' 17" S; 49° 13' 31" W), where the surrounding area, despite the presence of riparian forest, is strongly influenced by agricultural activities (Fig. 1). Gill nets with internode sizes ranging from 20 to 100 mm were set along the riverbanks or near the bottom overnight and retrieved before dawn, after approximately 10 h of exposure. Captured fish were removed from the nets, anesthetized with a eugenol solution (100 mg L⁻¹ clove oil), and euthanized by spinal cord section. Each one was then placed in a separate plastic bag and frozen for subsequent laboratory analysis.

The Ivaí River is a left-bank tributary of the Paraná River in the state of Paraná, draining approximately 35,845 km² and extending about 685 km in length (Maack 1981). It originates in the municipality of Ivaí at the confluence of the Patos and São João rivers, both located within the Serra da Esperança State Park, along the boundary between the second and third plateaus of Paraná state (Maack 1981; Santos et al. 2008). Specimens of *H. hermanni* and *H. regani* were collected in the Ivaí River between May 2019 and March 2020 (SISBIO no. 66135-3; Ethics Committee CEUA/UEM no. 5073090620) in the municipality of Engenheiro Beltrão (23° 40' 15.4" S 52° 09' 36.6" W, 23° 40' 06.3" S 52° 09' 31.5" W, and 23° 38' 57.7" S 52° 09' 52.7" W) (Fig. 1). Sampling was conducted using gillnets with mesh sizes of 3.0, 5.0, 6.0, and 7.0 cm between knots, which were deployed for 12 h and checked every 6 h. Captured fish were anesthetized with benzocaine, and after the cessation of opercular movements, euthanasia was performed by cranial perforation to ensure brain destruction. Individuals were then stored separately in thermal boxes, transported to the laboratory, and frozen. The number of hosts analyzed,

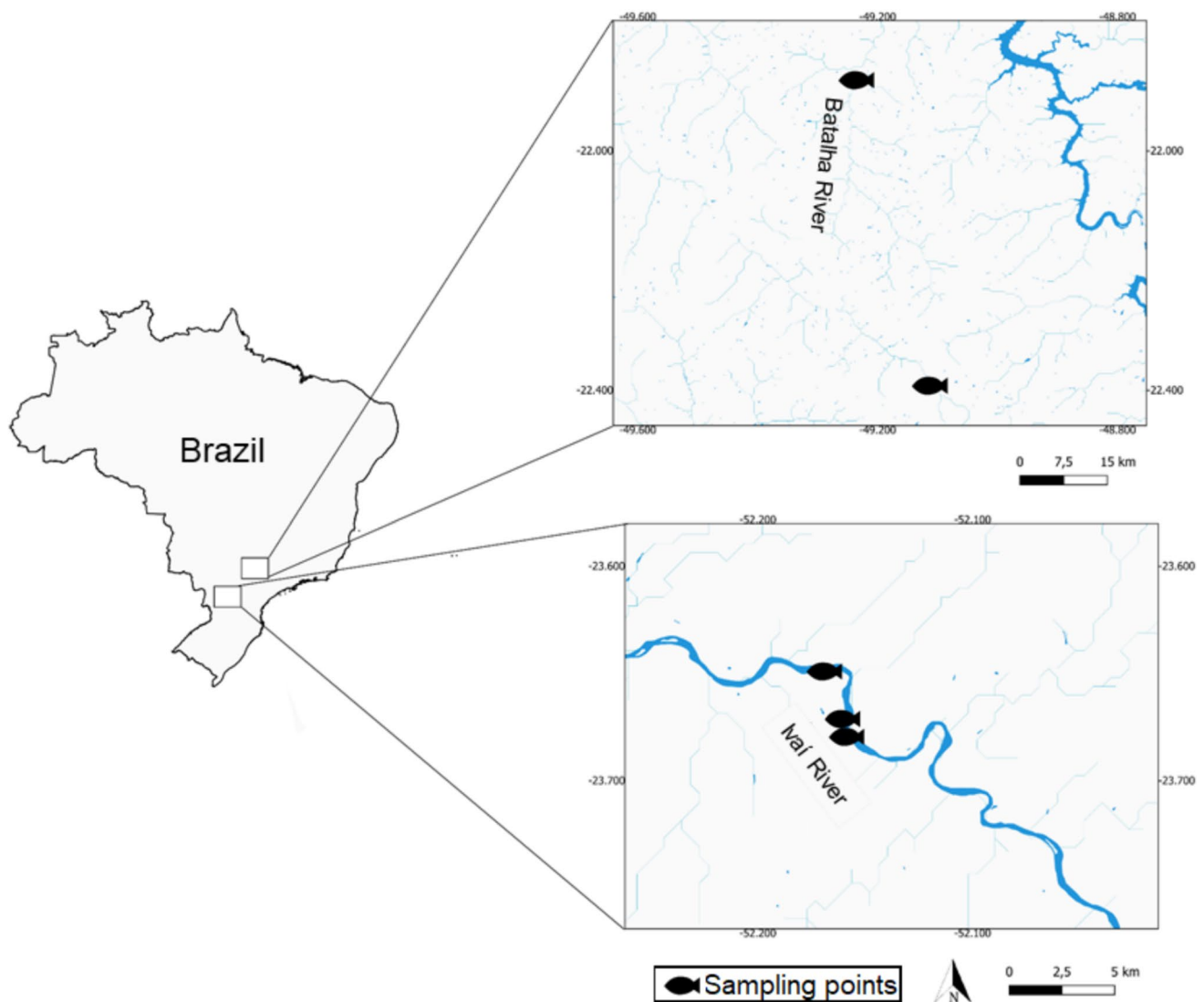


Fig. 1 Map of the location of the Batalha River and the Ivaí River, Brazil, and the sampling points

Table 1 Biometric data of *Hypostomus hermanni* and *H. regani* collected from the Batalha River (São Paulo, Brazil) and the Ivaí River (Paraná, Brazil)

	<i>N</i>	<i>SL</i> ± <i>SE</i> (cm)	<i>W</i> ± <i>SE</i> (g)
Batalha River			
<i>Hypostomus hermanni</i>	31	15.64 ± 0.42	120.27 ± 10.67
<i>Hypostomus regani</i>	60	17.72 ± 0.37	160.45 ± 10.03
Ivaí River			
<i>Hypostomus hermanni</i>	50	16.15 ± 1.64	128.65 ± 43.62
<i>Hypostomus regani</i>	22	23.00 ± 5.15	303.09 ± 218.55

N number of host individuals analyzed, *SL* mean standard length (cm), *W* mean weight (g), *SE* standard error

as well as their standard length and weight, are presented in Table 1.

For necropsy of the hosts and collection of parasites, we followed the methodology proposed by Eiras et al. (2006). Immediately after the frozen fish arrived at the laboratory (the day after capture), the necropsy was started. First, the gill arches were carefully removed and examined with a stereomicroscope in a Petri dish with water. Next, to collect the endoparasites, the visceral cavity of each fish was opened by making a longitudinal incision from the anal region to the anterior portion of the body. This exposed the internal organs, which were placed separately in Petri dishes containing 70% alcohol for individual analysis. The surfaces of the intestine, stomach, gallbladder, heart, and swim bladder were analyzed in situ, then longitudinal cuts were made, and the internal contents were carefully sorted under a

stereomicroscope. The procedures for fixing and preparing the parasite slides followed the methodology described by Eiras et al. (2006). Identification followed Moravec (1998) for Nematoda; Santos et al. (2002), Thatcher (2006), Kohn et al. (2007), Zica et al. (2009, 2011), De Núñez (2017), and Franceschini et al. (2020) for Digenea and Monopisthocotylea; and Damborenea et al. (2020) for Hirudinea.

Data analysis

Although sampling was conducted at different times in the two rivers, the objective of this study was strictly comparative and spatial, aiming to assess differences in parasite community structure in the genus *Hypostomus*. Temporal variation was therefore not considered a primary factor in the analyses.

The prevalence, mean intensity, and mean abundance of each parasite species in each host species were calculated following Bush et al. (1997). Diversity analyses were conducted at different hierarchical levels: α -diversity refers to the diversity contained within a single sampling unit (i.e., an individual host); β -diversity captures the degree of

dissimilarity between sampling units, where β_1 represents differences between hosts within the same population, and β_2 represents differences between hosts from distinct populations; and γ -diversity reflects the overall diversity of the system (Llopis-Belenguer et al. 2019, 2020) (Fig. 2).

For alpha diversity, we examined how different facets of diversity (taxonomic, functional, and phylogenetic) varied across host species. Taxonomic diversity (TD) was quantified using the parasite species abundance matrix. Functional diversity (FD) was estimated from a matrix of parasite functional traits (Thioulouse et al. 2018), including five traits representing morphological, life-history, and behavioral characteristics, following Llopis-Belenguer et al. (2019) and subsequent applications (Krasnov et al. 2021a, b; Sarabeev et al. 2024; Lehun et al. 2025). The traits considered were: (1) life cycle, (2) niche preference, (3) attachment, (4) feeding mode, and (5) body length (Table 2). We calculated interspecific functional distances using the Gower metric (Gower 1971). The resulting distance matrix was then transformed into a Euclidean distance matrix and standardized by dividing all values by the maximum observed distance, constraining the range to 0–1, following Pavoine et al. (2009)

Fig. 2 Representation of parasite diversity across hierarchical levels in *Hypostomus* hosts from the Batalha River and Ivaí River: α represents parasite diversity within individual hosts; β_1 represents variation among individuals within the same population; β_2 represents variation among populations; and γ represents total parasite diversity of the system. Different parasite and host colors indicate distinct species occurring within and across habitats

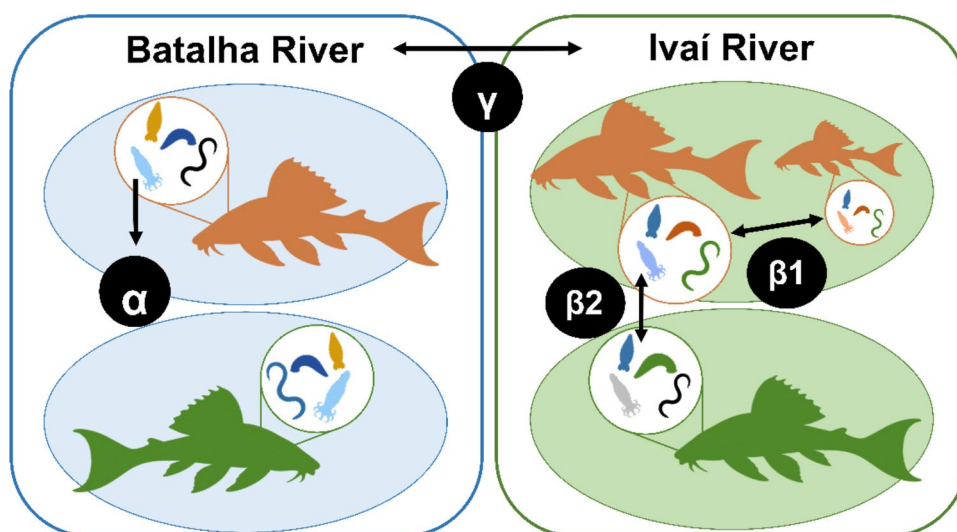


Table 2 Functional traits of parasite species, including traits, type of trait, and type of measurement

Trait	Type of trait	Type of measurement
Life cycle	Ecological performance	Qualitative (larval or adult)
Niche preference	Ecological performance	Qualitative (site of infestation)
Attachment	Functional trait	Quantitative (continuous standardized linear measurements: sclerotized parts of the haptor; ordinal: number of combs)
Feeding mode	Functional trait	Qualitative (presence or absence of a digestive system—which, although not directly related to the ecological functions of parasites in ecosystems, provides valuable insight into resource acquisition strategies and functional differentiation)
Body length	Functional trait	Quantitative (continuous linear measurements: mean body length)

Adapted from Llopis-Belenguer et al. (2019)

and Llopis-Belenguer et al. (2020). Diversity values were expressed as effective numbers of species, defined as the number of equally abundant species required to produce a given diversity index value (Jost 2006).

For proxy phylogenetic diversity (PPD), we built a taxonomic-based phylogenetic tree using the hierarchical Linnaean classification of each parasite species (species, genus, subfamily, family, suborder, order, and class). Taxonomic information was obtained from the Global Biodiversity Information Facility (GBIF) and World Register of Marine Species (WoRMS) and checked for consistency across taxa. The tree was constructed by converting the taxonomic hierarchy into a phylogenetic framework, where taxa sharing more inclusive ranks were considered more closely related. Pairwise phylogenetic distances among parasite species were then computed by generating a Euclidean distance matrix using the `taxa2dist` function from the `Vegan` Package (Oksanen et al. 2020), and the resulting matrix was standardized to values between 0 and 1. This taxonomic proxy was adopted because a complete molecular phylogeny is not available for all parasite taxa in our dataset, and taxonomic-based distances have been widely used as a surrogate to represent evolutionary relatedness in community-level analyses (see Llopis-Belenguer et al. 2020 for details).

To assess differences in α -diversity, we used linear models with residual randomization to generate empirical sampling distributions for subsequent analyses of variance (ANOVAs), following Collyer and Adams (2018). Univariate α -diversity metrics (TD, FD, and PPD) were log-transformed prior to the analyses. We then fitted one-way models using the `lm.rppp` function in the `RRPP` package and performed type I ANOVAs on the basis of randomized F -statistic distributions, with host species as the grouping factor. When significant differences were detected among host species, we conducted post hoc pairwise comparisons of α TD, α FD, and α PPD among host species using the pairwise function implemented in the `RRPP` package.

We estimated β -diversity (β_1 and β_2) using the equivalent number approach (Ricotta and Szeidl 2009) on the basis of the third formulation of Rao's quadratic entropy proposed by Pavoine et al. (2016). Calculations were performed with the `EqRao` function in the `adiv` package (Pavoine 2018) for taxonomic (TD), functional (FD), and proxy phylogenetic diversity (PPD). To test whether observed β_1 and β_2 values departed from random expectations, we generated 999 permuted β -diversity values using the `rtestEqRao` function (`adiv`) and assessed significance at $p < 0.05$. When significant deviations were detected, we compared observed and permuted values to determine whether parasite communities were more homogeneous than expected (observed < simulated; higher similarity) or more heterogeneous than expected (observed > simulated; higher dissimilarity), following Llopis-Belenguer et al. (2020). We also used

standardized β -diversity values (standardized effect sizes) provided by `EqRao`, calculated as (observed β – mean of randomly simulated β s)/standard deviation of randomly simulated β s, to infer the magnitude and direction of dispersion. Positive standardized values indicate clustering (greater similarity), whereas negative values indicate overdispersion (greater dissimilarity), either within levels of a factor (β_1) or between levels of a factor (β_2) (Head et al. 2018).

To assess parasite diversity, we applied Dual Principal Coordinate Analysis (DPCoA) (Pavoine et al. 2004) to characterize taxonomic, functional, and phylogenetic diversity of parasite infracommunities associated with *Hypostomus* spp. from the Batalha River and the Ivaí River. To evaluate the effects of two cross-classified factors on parasite diversity, we used cross-DPCoA (Pavoine et al. 2013), defining host species as factor *A* and collection site (habitat) as factor *B*. This approach partitions the total variation in parasite diversity into components uniquely attributable to each factor and their shared component. Cross-DPCoA produces an ordination space in which parasite species, infracommunities, and factor levels are represented along principal axes. First, the main ordination is computed considering only factor *A* (host species), while ignoring variation associated with factor *B*. Next, the first version removes the variation explained exclusively by factor *B* (habitat) while retaining the shared variation between factors *A* and *B*. Finally, the second version removes all variation associated with factor *B*, including the shared component between factors *A* and *B* (i.e., their interaction), thereby isolating the diversity structure attributable exclusively to factor *A* (host species).

All analyses were conducted in R (R Core Team 2024) using the `ade4` (Thioulouse et al. 2018), `adiv` (Pavoine 2020), `RRPP` (Collyer and Adams 2018), and `vegan` (Oksanen et al. 2020) packages.

Results

A total of 163 *Hypostomus* spp. individuals were collected. Overall, 21 parasite species were recorded, with parasite assemblages showing broadly similar composition across host species, most being ectoparasites, particularly monopisthocotyleans (Table 3). Fish sampled in the Batalha River exhibited greater parasite richness: *H. hermanni* hosted 11 species, while *H. regani* harbored 12. In this river, the leech *Oligobdella* sp. was the most prevalent parasite in both host species. In contrast, *Hypostomus* spp. collected from the Ivaí River displayed lower richness, with *H. hermanni* hosting four parasite species and *H. regani* five. The most prevalent species in the Ivaí River were *Austrodiplostomum compactum* (Lutz 1928) in *H. hermanni* and *Procamallanus (Procamallanus) annipetterae* Kohn and Fernandes 1988 in *H. regani*.

Table 3 Parasite species and parasitological indices recorded in *Hypostomus hermanni* and *H. regani* from the Batalha River (São Paulo, Brazil) and the Ivaí River (Paraná, Brazil)

	Batalha River			Ivaí River		
	<i>P</i> %	MA ± SE	MI ± SE	<i>P</i> %	MA ± SE	MI ± SE
<i>Hypostomus hermanni</i>						
Monopisthocotylea						
<i>Trinigyus</i> sp.	61.3	10.9 ± 3.4	16.8 ± 5.0	–	–	–
<i>Trinigyus anthus</i> Franceschini, Acosta, Zago, Müller, and Silva 2020	–	–	–	42	1.08 ± 1.60	2.57 ± 1.50
<i>Unilatus anoculus</i> (Price 1968)	3.2	0.1 ± 0.07	2	–	–	–
<i>Unilatus unilatus</i> Mizelle and Kritsky 1967	35.5	1.9 ± 0.9	4.9 ± 2.0	–	–	–
<i>Phanerothecioides agostinhoi</i> Kritsky, Vianna, and Boeger 2007	48.4	1.8 ± 1.05	3.7 ± 1.2	–	–	–
<i>Phanerothecium spinatoides</i> Kritsky, Vianna, and Boeger 2007	6.4	0.1 ± 0.1	2 ± 1	–	–	–
<i>Phanerothecium spinatus</i> Boeger, Kritsky, and Belmont-Jegu 1994	16.1	1.0 ± 0.5	5 ± 2.3	–	–	–
<i>Phanerothecium spinulatum</i> Kritsky, Vianna, and Boeger 2007	6.4	0.3 ± 0.2	5 ± 2	–	–	–
<i>Phanerothecium deiropedeum</i> Kritsky, Vianna, and Boeger 2007	3.2	0.1 ± 0.07	2	–	–	–
Digenea						
<i>Austrodiplostomum compactum</i> (Lutz 1928)	74.2	2.7 ± 0.5	3.6 ± 0.5	76	10 ± 17.2	13.2 ± 18.7
<i>Tylodelphys</i> sp.	3.2	0.03 ± 0.03	1	–	–	–
Nematoda						
<i>Procamallanus</i> (<i>Procamallanus</i>) <i>annipetterae</i> Kohn and Fernandes 1988	–	–	–	74	2.38 ± 2.32	3.22 ± 2.14
<i>Pseudocapillaria</i> sp.	9.7	0.1 ± 0.07	1.3 ± 0.3	–	–	–
Hirudinea						
<i>Oligobdella</i> sp.	93.6	18.7 ± 3.1	20.6 ± 3.3	–	–	–
<i>Placobdella</i> sp.	–	–	–	66	2.02 ± 2.55	3.06 ± 2.59
<i>Hypostomus regani</i>						
Monopisthocotylea						
<i>Trinigyus</i> sp.	80	23.7 ± 3.6	29.7 ± 4.1	–	–	–
<i>Trinigyus anthus</i>	–	–	–	68	7.04 ± 8.75	10.3 ± 8.85
<i>Unilatus anoculus</i>	5	0.3 ± 0.2	5.3 ± 1.5	–	–	–
<i>Unilatus unilatus</i>	38.3	1.8 ± 0.4	4.7 ± 0.6	13	0.18 ± 0.5	1.33 ± 0.57
<i>Phanerothecioides agostinhoi</i>	60	3.9 ± 0.9	6.4 ± 1.3	–	–	–
<i>Phanerothecium caballeri</i> Kritsky and Thatcher 1977	1.7	0.02 ± 0.01	1	–	–	–
<i>Phanerothecium deiropedeum</i>	8.3	0.2 ± 0.1	1.8 ± 0.8	–	–	–
<i>Phanerothecium spinatoides</i>	3.3	0.1 ± 0.07	3.5 ± 0.7	–	–	–
<i>Phanerothecium spinatus</i>	11.7	0.4 ± 0.1	3.0 ± 0.6	–	–	–
<i>Phanerothecium spinulatum</i>	10	0.3 ± 0.1	2.5 ± 0.6	–	–	–
Digenea						
<i>Austrodiplostomum compactum</i>	33.3	0.6 ± 0.1	1.7 ± 0.3	68.2	3.5 ± 4.73	5.13 ± 4.95
<i>Austrodiplostomum mordax</i> Szidat and Nani 1951	1.7	0.02 ± 0.01	1	–	–	–
Nematoda						
<i>Procamallanus</i> (<i>Procamallanus</i>) <i>annipetterae</i>	–	–	–	90.9	5.23 ± 4.83	5.75 ± 4.75
<i>Rhabdochona</i> sp.	1.7	0.1 ± 0.06	4	–	–	–
Hirudinea						
<i>Oligobdella</i> sp.	100	32.7 ± 3.8	32.7 ± 4	–	–	–
<i>Placobdella</i> sp.	–	–	–	72.7	4.5 ± 7.29	6.19 ± 7.96

P %, prevalence; MA, mean abundance; SE, standard error; MI, mean intensity

Taxonomic and functional α -diversity of parasites varied significantly among *Hypostomus* species (ANOVA: TD: $F = 7.833$, $p = 0.001$; FD: $F = 7.267$, $p = 0.001$; Fig. 3). In contrast, phylogenetic α -diversity showed no significant

differences between host species (ANOVA: PPD: $F = 1.322$, $p = 0.274$; Fig. 3).

For the β_1 level, parasite communities of host individuals of the same species (within host species) tended to be more

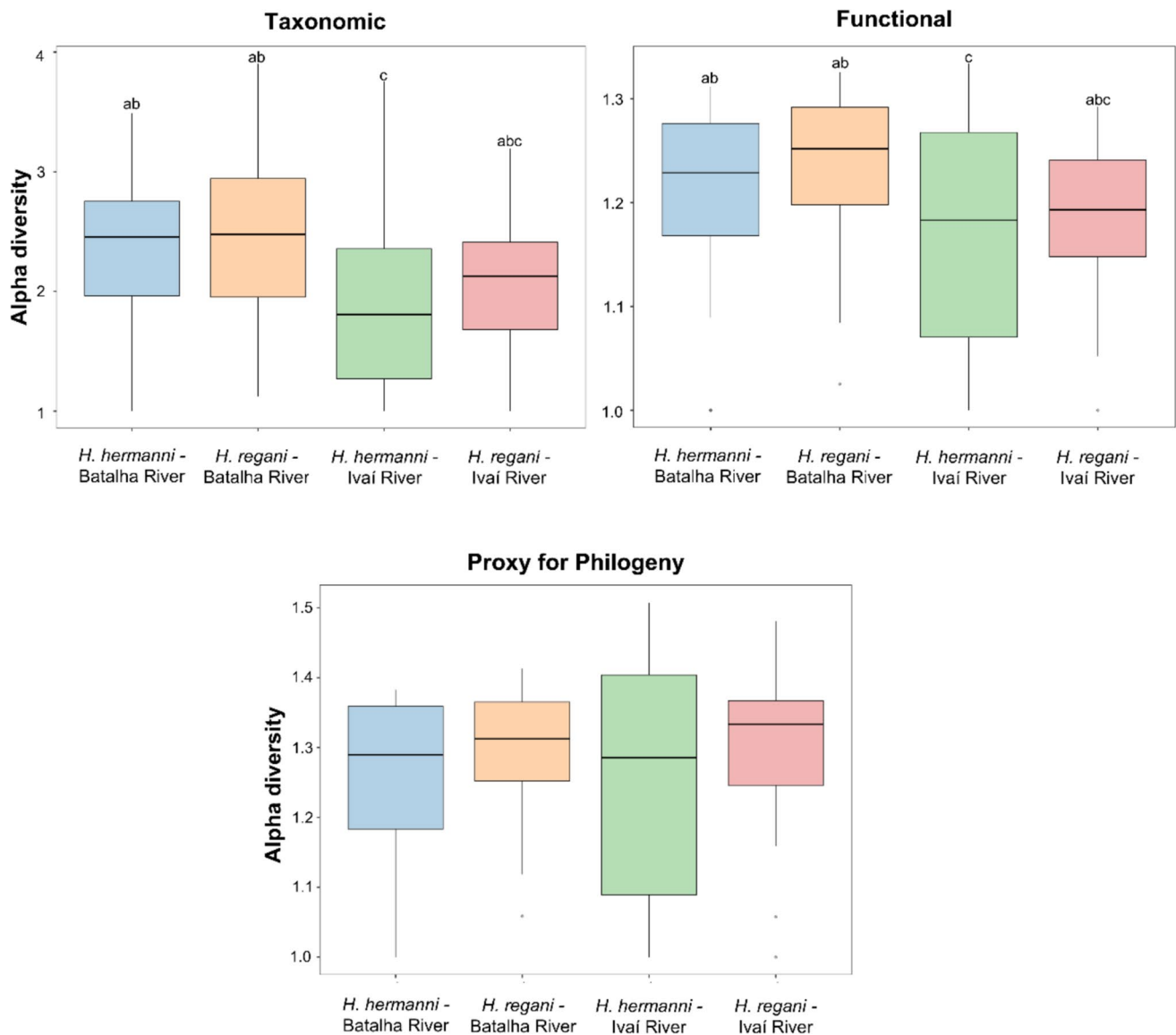


Fig. 3 Parasite α -diversity in terms of taxonomic (TD), functional (FD), and proxy phylogenetic diversity (PPD) for each host individual of *Hypostomus hermanni* and *H. regani* sampled in the Batalha River and the Ivaí River

Table 4 Statistical results of β -diversity partitioning for taxonomic (TD), functional (FD), and proxy phylogenetic diversity (PPD) at two organizational levels: β_1 (variation among host individuals within the same host species) and β_2 (variation between host species)

	β_1			β_2		
	TD	FD	PPD	TD	FD	PPD
Obs	0.33	0.22	0.26	0.12	0.02	0.04
<i>p</i> -value	0.19	0.77	0.8	0.001	0.001	0.001
Std. Obs.	-1.26	0.25	0.25	25.7	10.7	13.3

Obs. indicates the observed β value; *p*-value indicates the significance of the deviation from random expectations ($p < 0.05$); and Std. Obs. indicates the standardized effect size, calculated from the distribution of simulated β values

similar (Table 4), as positive values of $\beta 1$ -TD, $\beta 1$ -FD, and $\beta 1$ -PPD indicate that parasite species tended to be clustered within host species. At the $\beta 2$ -level (between host species), parasite communities differed significantly from randomness in TD, FD, and PPD, indicating that similarity between infracommunities was lower than simulated values (Table 4) and that community structure was clustered at this level of the organizational scale. Analyzing the cross-effect (host species and habitat), it was demonstrated that the largest proportion of the taxonomic, functional, and phylogenetic diversity of the entire parasite assemblage was associated with the effect of diversity in each infracommunity (i.e., host individual), followed by the cross-effect between the two factors and the host species (Table 5). The parasite communities of the host species of *Hypostomus* spp. showed an overlap in taxonomic, functional, and proxy diversity for phylogeny. However, the host species and habitat are significant predictors for the taxonomic and functional diversity of the parasite communities (Fig. 4).

Discussion

Parasite communities of *Hypostomus* spp. showed greater similarity among individuals collected within the same habitat than among individuals from different habitats, indicating that spatial context contributes to parasite community structure. At the same time, the host species also played an important role, as α -diversity differed among host species in both taxonomic (α TD) and functional (α FD) dimensions. In contrast, proxy phylogenetic α -diversity (α PPD) showed little variation among hosts. Together, these results suggest that parasite assemblages vary across host species and habitats mainly through changes in species composition and functional strategies, while their phylogenetic structure remains more conserved.

The higher α TD observed for *H. hermanni* from the Batalha River was largely driven by ectoparasite-rich infracommunities, particularly monopisthocotyleans of the family Gyrodactylidae. Monopisthocotyleans are often host-specific (Thatcher 2006), and host–parasite associations

are expected to reflect long-term coevolutionary dynamics (Poulin 2004, 2010). Consequently, parasite assemblages may show limited species sharing among hosts, especially when infestations are dominated by highly host-specific taxa (Krasnov et al. 2012). In addition, parasites typically exhibit aggregated distributions, with a few hosts harboring many parasites while most hosts carry few or none (Poulin et al. 2013). Such aggregation can increase among-host heterogeneity within a given host species and habitat, thereby contributing to within-population variation in community composition.

Functional diversity helped clarify that differences between host species and between habitats can reflect not only taxonomic turnover but also shifts in the ecological strategies represented within parasite communities. The α FD patterns indicate that parasite communities can differ functionally between hosts, which is consistent with the idea that traits related to transmission, attachment, microhabitat use, and resource acquisition influence parasite establishment and coexistence. Parasite assemblages within hosts may include functionally distinct taxa, even within the same host individual, suggesting that niche differentiation in microhabitat use and feeding strategies can reduce direct overlap and facilitate coexistence (Poulin 1997; Schluter 2000). Conversely, when communities show limited functional differentiation despite taxonomic variation, this suggests functional redundancy, whereby different species perform similar ecological roles (Moreno-García and Baiser 2021). Therefore, FD can provide mechanistic insights beyond TD by revealing that host- and habitat-associated changes involve shifts in functional strategies, rather than only changes in taxonomic diversity.

The characterization of functional diversity in parasitology remains in its early stages (Llopis-Belenguer et al. 2019). Parasite traits may be more informative than taxonomic diversity in predicting performance within communities; however, trait-based approaches are still constrained by several limitations. First, the number of functional traits available in literature is restricted, and in this study, only five traits could be incorporated, which inevitably reduces the explanatory power and resolution of functional analyses (Dallas et al. 2017). Thus, functional patterns should be interpreted cautiously, as limited trait coverage may reduce the sensitivity to detecting functional turnover among assemblages and may increase apparent functional redundancy across communities. This limitation is compounded by the absence of standardized and comprehensive trait databases for parasites, unlike what is available for plants, birds, or fishes (see Cornelissen et al. 2003; Petchey and Gaston 2002; Stewart et al. 2022; Stuart-Smith et al. 2013; Villéger et al. 2010), making cross-study comparisons difficult and limiting the development of broader predictive frameworks. Moreover, many relevant functional traits, such as a reproductive organ, seasonality in reproduction, degree

Table 5 Percentage contributions of taxonomic (TD), functional (FD), and proxy phylogenetic diversity (PPD) components of β -diversity in parasite infracommunities, partitioned among the effects of host individual (HI), host species (HS; *Hypostomus hermanni* and *H. regani*), habitat (HA; Batalha River and Ivaí River), and their interaction (HS $\times$ HA)

Diversity	HI	HS	HA	HS $\times$ HA
TD	68.9	11.73	9.48	9.87
FD	71.05	4.99	2.34	21.6
PPD	71.04	5.3	3.37	20.27

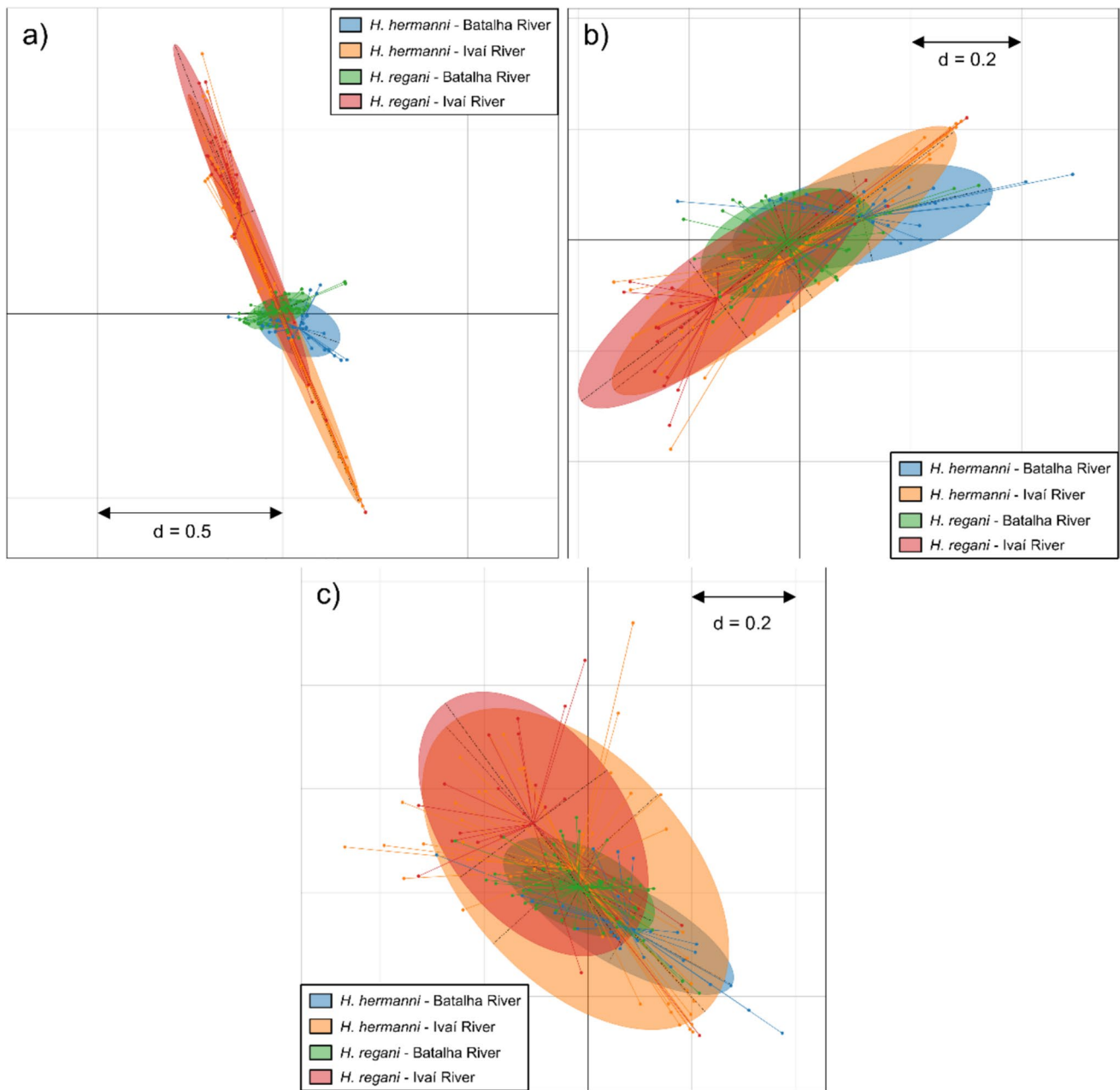


Fig. 4 Centroid positions of parasite species in three diversity spaces: **a** taxonomic (TD), **b** functional (FD), and **c** proxy phylogenetic (PPD). Ordinations were generated using the first version of the crossed-DPCoA, with host species (*Hypostomus hermanni* and *H. regani*) and habitat (Batalha River and Ivaí River) included as cross-

classified factors. Ellipse width and height represent the variance of individual coordinates along each axis, and ellipse slope reflects the covariance between axes. Parameter d indicates the side length of the gray squares in the background grid

of sexual dimorphism, and geographic range size or range latitude (Llopis-Belenguer et al. 2019), remain challenging to quantify, as they often require experimental approaches or invasive observations that are not easily standardized. Additionally, some parasite groups exhibit low morphological variability, which may lead to functional redundancy and reduce the sensitivity of FD metrics to detecting differences among communities (Krasnov et al. 2024; Krasnov

and Khokhlova 2025; Mouillot et al. 2013). Future research should therefore expand the range and quality of trait information to advance our understanding of parasite community structure and better evaluate the ecological roles and ecosystem services associated with parasite diversity (Mouillot et al. 2013; Petchey and Gaston 2002).

Unlike α TD and α FD, α PPD did not vary substantially among host species, suggesting that parasite

infracommunities were broadly similar in their phylogenetic structure across hosts. This pattern may reflect turnover among closely related parasite taxa, consistent with phylogenetic conservatism in parasite lineages and traits, and/or limited resolution inherent to taxonomic proxies when molecular phylogenies are incomplete. Even when phylogenetic differences are not detected at the α level, the inclusion of proxy phylogenetic structure remains informative because many parasite traits and host–parasite associations are shaped by evolutionary history and often exhibit phylogenetic signal (Westoby et al. 1995; Luque et al. 2004; Poulin et al. 2011).

Beta diversity patterns further clarified how parasite communities changed across different levels of organization. Within host species (β_1), parasite assemblages tended to show relatively high similarity among individual hosts. In contrast, among host species (β_2), parasite communities differed significantly from random expectations in taxonomic, functional, and proxy phylogenetic dimensions, indicating pronounced differentiation among host species at broader organizational scales. Thus, host-related attributes, together with spatial variation between habitats, were the most important factors explaining variation in parasite assemblages (Brian and Aldridge 2023; Martins et al. 2021). In general, several key factors and processes, which are not mutually exclusive, may drive variation in beta diversity (Astorga et al. 2014). These patterns are consistent with deterministic processes associated with host filtering and compatibility constraints, combined with spatial effects that influence transmission and dispersal opportunities (Astorga et al. 2014; Chase 2010; Legendre and De Cáceres 2013). In parasitic systems, especially for taxa with complex life cycles, spatial differences in host availability and environmental conditions can strongly affect encounter rates and the persistence of parasites across habitats.

The cross-DPCoA analysis highlighted the combined influence of host species and habitat on parasite community structure. Most of the overall variation in parasite assemblages was associated with differences among individual infracommunities, indicating strong among-host heterogeneity. Importantly, the interaction between host species and habitat contributed substantially to the taxonomic, functional, and phylogenetic structuring of parasite communities, suggesting that the effect of the host can vary depending on the environmental context (Dallas and Presley 2014). This habitat-dependent host effect indicates that host-related processes operate in conjunction with spatial constraints that influence parasite transmission and local assembly dynamics (Blasco-Costa et al. 2015; Costa et al. 2021).

Although the initial objective of this study was to spatially compare parasite communities of *Hypostomus* spp. in two Neotropical rivers, it is important to acknowledge the lack of environmental variables measured simultaneously

with fish sampling, as well as the fact that sampling periods differed between rivers. Thus, interannual variation in environmental conditions may have contributed to the observed differences in parasite community structure between habitats, especially because most taxa recorded were ectoparasites (mainly monopisthocotyleans), which are often considered sensitive indicators of environmental conditions owing to their direct life cycle and high reproductive rates, allowing rapid responses to changes in aquatic environments (Jerônimo et al. 2022; Lafferty and Kuris 1999; Marcogliese 2025). Unmeasured abiotic factors such as water temperature, turbidity, flow regime, dissolved oxygen, and habitat complexity may have differed between rivers and years and could have influenced parasite transmission, persistence, and encounter rates. Therefore, the higher similarity of parasite infracommunities within the same habitat and the differences observed between rivers may reflect not only spatial segregation and host-related filters but also unmeasured environmental variation across sampling years. In addition, host-related attributes (e.g., length, weight, diet, behavior, and habitat use) may indirectly mediate environmental effects by altering exposure to infective stages and shaping transmission pathways (Lehun et al. 2024). Future studies should integrate abiotic and biotic components to better elucidate the mechanisms shaping infection patterns and to identify key determinants underlying taxonomic, functional, and phylogenetic structuring, even in seemingly homogeneous systems (Cohen et al. 2016; Bolnick et al. 2020; Vigneault et al. 2025).

Taken together, our results indicate that host species remains a central driver of parasite diversity, but we expand this pattern by demonstrating that taxonomic, functional, and phylogenetic dimensions of diversity respond in distinct ways to both host- and site-related factors. By integrating TD, FD, and PPD within the same analytical framework, our study reveals that parasite assemblages are structured by a combination of host specificity, functional niche differentiation, and shared evolutionary history (processes that cannot be detected when only taxonomic information is considered). In general, hosts are expected to harbor an aggregated parasite fauna, and intrahost speciation or co-occurrence of parasites across different host species may contribute to clustering or coexistence patterns, reinforcing the role of deterministic processes linked to host traits and environmental conditions in shaping infracommunity composition (e.g., Spickett et al. 2017). This multidimensional perspective provides a conceptual advance by indicating that the degree to which the host shapes parasite communities depends on the facet of diversity examined, highlighting that functional and phylogenetic structure may remain stable even when taxonomic turnover is high. The acquisition or loss of parasites during periods of geographic isolation further

illustrates how host-related filters structure parasite communities, emphasizing that hosts act as primary ecological filters determining parasite presence or absence (Poulin 2007). More broadly, our findings underscore that integrating functional and phylogenetic information yields a more mechanistic understanding of how parasite communities assemble across space and closely related host species, contributing to a broader understanding of how parasite diversity varies across regions and host taxa.

Acknowledgments We would like to thank the Conselho Nacional de Desenvolvimento Científico (CNPq) e Tecnológico and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a postdoctoral scholarship, the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) and the Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos e Continentais (PEA) for logistical support.

Author contributions Atsler Luana Lahun was responsible for data analysis and interpretation and for writing the article. Aparecida de Fátima Cracco was responsible for data collection. Larissa Sbeghen Pelegrini and Lucas Aparecido Rosa Leite were responsible for data collection and writing the article. Gabriela Cássia Reinas, Gabriela Michelin, João Otávio Santos Silva, and Lidiany Doreto Cavalcanti were responsible for writing the article. Vanessa D. Abdallah and Ricardo Massato Takemoto were responsible for supervising the study. All authors read and approved the final manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). A.L.L. was awarded a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Data availability The data supporting the results will be made available.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval The procedures for capture, collection, and transportation of biological material were authorized by IBAMA (SISBIO no. 40998-2 and SISBIO no. 66135-3) and Ethics Committee CEUA/USC no. 3353050417 and Ethics Committee CEUA/UEM no. 5073090620.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Allen TF, Starr TB (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago
- Astorga A, Death R, Paavola R, Chakraborty M, Muotka T (2014) Habitat heterogeneity drives the geographical distribution of beta diversity: the case of New Zealand stream invertebrates. *Ecol Evol* 4:2693–2702. <https://doi.org/10.1002/ece3.1124>
- Begon M, Townsend CR (2021) Ecology: from individuals to ecosystems. Wiley, Chichester
- Blasco-Costa I, Rouco C, Poulin R (2015) Biogeography of parasitism in freshwater fish: spatial patterns in hot spots of infection. *Ecography* 38:301–310. <https://doi.org/10.1111/ecog.01020>
- Bolnick DI, Reserits EJ, Ballare K, Stuart YE, Stutz WE (2020) Scale-dependent effects of host patch traits on species composition in a stickleback parasite metacommunity. *Ecology* 101:e03181. <https://doi.org/10.1002/ecy.3181>
- Brian JJ, Aldridge DC (2023) Factors at multiple scales drive parasite community structure. *J Anim Ecol* 92:377–390. <https://doi.org/10.1111/1365-2656.13853>
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83:575–583. <https://doi.org/10.2307/3284227>
- Chase JM (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391. <https://doi.org/10.1126/science.1187820>
- Cohen JM, Civitello DJ, Brace AJ, Feichtinger EM, Ortega CN, Richardson JC, Sauer EL, Liu X, Rohr JR (2016) Spatial scale modulates the strength of ecological processes driving disease distributions. *Proc Natl Acad Sci USA* 113:E3359–E3364. <https://doi.org/10.1073/pnas.15216571>
- Collyer ML, Adams DC (2018) RRPP: an R package for fitting linear models to high-dimensional data using residual randomization. *Methods Ecol Evol* 9:1772–1779. <https://doi.org/10.1111/2041-210X.13029>
- Cornelissen JH, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Ter Steege H, Morgan HD, Van Der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust J Bot* 51(4):335–380. <https://doi.org/10.1071/BT02124>
- Costa APL, Takemoto RM, Lizama MDLAP, Padial AA (2021) Metacommunity of a host metapopulation: explaining patterns and structures of a fish parasite metacommunity in a Neotropical floodplain basin. *Hydrobiologia* 848:5103–5118. <https://doi.org/10.1007/s10750-021-04695-7>
- Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species–area relationships: unifying α -, β - and γ -diversity with sample size and habitat area. *Ecol Lett* 9:923–932. <https://doi.org/10.1111/j.1461-0248.2006.00941.x>
- Dallas T, Presley SJ (2014) Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* 123:866–874. <https://doi.org/10.1111/oik.00707>
- Dallas T, Park AW, Drake JM (2017) Predictability of helminth parasite host range using information on geography, host traits and parasite community structure. *Parasitology* 144:200–205. <https://doi.org/10.1017/S0031182016001608>
- Damborenea C, Rogers DC, Thorp JH (eds) (2020) Thorp and Covich's freshwater invertebrates: volume 5: keys to neotropical and antarctic fauna. Academic Press, Cambridge
- De N  n  z MO (2017) Redescription of *Austrodiplostomum compactum* (Trematoda: Diplostomidae) from its type host and locality in Venezuela, and of *Austrodiplostomum mordax* from Argentina. *J Parasitol* 103:497–505. <https://doi.org/10.1645/16-128>

- Eiras JC, Takemoto RM, Pavanelli GC (2006) Métodos de estudo e técnicas laboratoriais em parasitologia de peixes, 2 rd. Eduem, Maringá
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Franceschini L, Acosta AA, Zago AC, Müller MI, Da Silva RJ (2020) *Trinigyrrus* spp. (Monogenea: Dactylogyridae) from Brazilian catfishes: new species, molecular data and new morphological contributions to the genus. *J Helminthol*. <https://doi.org/10.1017/S0022149X20000097>
- Gower JC (1971) A general coefficient of similarity and some of its properties. *Biometrics* 27:857–871. <https://doi.org/10.2307/2528823>
- Head CE, Koldewey H, Pavoine S, Pratchett MS, Rogers AD, Taylor ML, Bonsall MB (2018) Trait and phylogenetic diversity provide insights into community assembly of reef-associated shrimps (Palaeomonidae) at different spatial scales across the Chagos Archipelago. *Ecol Evol* 8:4098–4107. <https://doi.org/10.1002/ece3.3969>
- Horwitz P, Wilcox BA (2005) Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *Int J Parasitol* 35:725–732. <https://doi.org/10.1016/j.ijpara.2005.03.002>
- Jerônimo GT, da Cruz MG, Bertaglia EDA, Furtado WE, Martins ML (2022) Fish parasites can reflect environmental quality in fish farms. *Rev Aquac* 14:1558–1571. <https://doi.org/10.1111/raq.12662>
- Jost L (2006) Entropy and diversity. *Oikos* 113:363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kohn A, Fernandes BMM, Cohen SC (2007) South American trematodes parasites of fishes. Imprinta Express, Rio de Janeiro
- Krasnov BR, Khokhlova IS (2025) Decomposition of functional beta, but not alpha, diversity detects deviations from the “host-diversity-begets-parasite-diversity” rule in flea-mammal associations. *Parasitol Res* 124:80. <https://doi.org/10.1007/s00436-025-08527-8>
- Krasnov BR, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R (2012) Compositional and phylogenetic dissimilarity of host communities drives dissimilarity of ectoparasite assemblages: geographical variation and scale-dependence. *Parasitology* 139:338–347. <https://doi.org/10.1017/S0031182011002073>
- Krasnov BR, Spickett A, Junker K, Van der Mescht L, Matthee S (2021a) Functional and phylogenetic uniqueness of helminth and flea assemblages of two South African rodents. *Int J Parasitol* 51:865–876. <https://doi.org/10.1016/j.ijpara.2021.02.003>
- Krasnov BR, Vinarski MV, Korralo-Vinarskaya NP, Shenbrot GI, Khokhlova IS (2021b) Spatial and temporal variation of compositional, functional, and phylogenetic diversity in ectoparasite infracommunities harboured by small mammals. *Parasitology* 148:685–695. <https://doi.org/10.1017/S0031182021000299>
- Krasnov BR, Stanko M, Vinarski MV, Korralo-Vinarskaya NP, Khokhlova IS (2024) Variation of functional diversity structure measured as combined species dominance, functional diversity, and functional redundancy in two taxa of ectoparasitic arthropods at two spatial scales: host-associated, ecological, and geographic effects. *Parasitology* 151:1570–1579. <https://doi.org/10.1017/S0031182024001483>
- Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnol Oceanogr* 44:925–931. https://doi.org/10.4319/lo.1999.44.3_part_2.0925
- Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol Lett* 16:951–963. <https://doi.org/10.1111/ele.12141>
- Lehun AL, Hasuiki WT, Silva JOS, Ciccheto JRM, Michelan G, Rodrigues ADFC, Nicola DN, Lima LD, Correia AN, Takemoto RM (2020) Checklist of parasites in fish from the upper Paraná River floodplain: an update. *Rev Bras Parasitol Vet* 29:e008720. <https://doi.org/10.1590/S1984-296120200066>
- Lehun AL, Muniz CM, Silva JOS, Cavalcanti LD, Takemoto RM (2024) The functional traits of host fish can act as good predictors for parasite composition in a Neotropical floodplain. *J Fish Biol* 104:206–215. <https://doi.org/10.1111/jfb.15576>
- Lehun AL, Cavalcanti LD, Casali GP, Silva JOS, Michelan G, Balbuena JA, Takemoto RM (2025) Host fishes shape the taxonomic, functional, and phylogenetic diversity of endoparasite communities in a Neotropical floodplain. *Hydrobiologia* 852:1973–1985. <https://doi.org/10.1007/s10750-024-05791-0>
- Llopis-Belenguer C, Balbuena JA, Lange K, de Bello F, Blasco-Costa I (2019) Towards a unified functional trait framework for parasites. *Trends Parasitol* 35:972–982. <https://doi.org/10.1016/j.pt.2019.09.003>
- Llopis-Belenguer C, Pavoine S, Blasco-Costa I, Balbuena JA (2020) Assembly rules of helminth parasite communities in grey mullets: combining components of diversity. *Int J Parasitol* 50:1089–1098. <https://doi.org/10.1016/j.ijpara.2020.06.006>
- Loreau M (2000) Are communities saturated? On the relationship between α , β and γ diversity. *Ecol Lett* 3:73–76. <https://doi.org/10.1046/j.1461-0248.2000.00127.x>
- Luque JL, Mouillot D, Poulin R (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* 128:671–682. <https://doi.org/10.1017/S0031182004005050>
- Maack R (1981) Geografia física do Estado do Paraná, 2nd edn. José Olympio, Rio de Janeiro
- Marcogliese DJ (2003) Food webs and biodiversity: are parasites the missing link? *J Parasitol* 89:106–113
- Marcogliese DJ (2025) Climate change and parasitism in aquatic ecosystems. In: Smit NJ, Sures B (eds) *Aquatic parasitology: ecological and environmental concepts and implications of marine and freshwater parasites*. Springer, Cham. https://doi.org/10.1007/978-3-031-83903-0_22
- Martins PM, Poulin R, Gonçalves-Souza T (2021) Drivers of parasite β -diversity among anuran hosts depend on scale, realm and parasite group. *Philos Trans R Soc Lond B Biol Sci* 376:20200367. <https://doi.org/10.1098/rstb.2020.0367>
- Montoya-Burgos JI (2003) Historical biogeography of the catfish genus *Hypostomus* (Siluriformes: Loricariidae), with implications on the diversification of Neotropical ichthyofauna. *Mol Ecol* 12:1855–1867. <https://doi.org/10.1046/j.1365-294X.2003.01857.x>
- Moravec F (1998) Nematodes of freshwater fishes of the neotropical region. Academia, Prague
- Moreno-García P, Baiser B (2021) Assessing functional redundancy in Eurasian small mammal assemblages across multiple traits and biogeographic extents. *Ecography* 44:320–333. <https://doi.org/10.1111/ecog.05312>
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28(3):167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Stevens MHH, Wagner H (2020) Vegan: community ecology package. R Package, Version 2, pp 3–4. <http://cran.r-project.org/web/packages/vegan>
- Pavoine S (2018) adiv: analysis of Diversity. R package. Available from the Comprehensive R Archive Network (CRAN). <https://CRAN.R-project.org/package=adiv>
- Pavoine S (2020) adiv: an R package to analyse biodiversity in ecology. *Methods Ecol Evol* 11:1106–1112. <https://doi.org/10.1111/2041-210X.13430>
- Pavoine S, Dufour AB, Chessel D (2004) From dissimilarities among species to dissimilarities among communities: a double principal

- coordinate analysis. *J Theor Biol* 228:523–537. <https://doi.org/10.1016/j.jtbi.2004.02.014>
- Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118:391–402. <https://doi.org/10.1111/j.1600-0706.2008.16668.x>
- Pavoine S, Blondel J, Dufour AB, Gasc A, Bonsall MB (2013) A new technique for analysing interacting factors affecting biodiversity patterns: crossed-DPCoA. *PLoS ONE* 8(1):e54530. <https://doi.org/10.1371/journal.pone.0054530>
- Pavoine S, Marcon E, Ricotta C (2016) ‘Equivalent numbers’ for species, phylogenetic or functional diversity in a nested hierarchy of multiple scales. *Methods Ecol Evol* 7(10):1152–1163. <https://doi.org/10.1111/2041-210X.12591>
- Pelegrini LS, Leite LA, Giao T, Bueno RM, Serrano TD, da Silva RJ, Abdallah VD (2022) Diversity, similarity, and host–parasite relationships in parasitic infracommunities of *Hypostomus* spp. from the Tietê-Batalha river basin, southeastern Brazil. *Stud Neotrop Fauna Environ* 57(3):301–313. <https://doi.org/10.1080/01650521.2020.1870033>
- Pennisi E (2005) What determines species diversity? *Science* 309(5731):90. <https://doi.org/10.1126/science.309.5731.90>
- Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecol Lett* 5(3):402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9(6):741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Poulin R (1997) Species richness of parasite assemblages: evolution and patterns. *Annu Rev Ecol Syst* 28:341–358. <https://doi.org/10.1146/annurev.ecolsys.28.1.341>
- Poulin R (2004) Macroecological patterns of species richness in parasite assemblages. *Basic Appl Ecol* 5(5):423–434. <https://doi.org/10.1016/j.baae.2004.08.003>
- Poulin R (2007) Are there general laws in parasite ecology? *Parasitology* 134(6):763–776. <https://doi.org/10.1017/S00311820060002150>
- Poulin R (2010) Decay of similarity with host phylogenetic distance in parasite faunas. *Parasitology* 137:733–741. <https://doi.org/10.1017/S0031182009991491>
- Poulin R (2014) Parasite biodiversity revisited: frontiers and constraints. *Int J Parasitol* 44(9):581–589. <https://doi.org/10.1016/j.ijpara.2014.02.003>
- Poulin R, Krasnov BR, Mouillot D, Thieltges DW (2011) The comparative ecology and biogeography of parasites. *Philos Trans R Soc B* 366(1576):2379–2390. <https://doi.org/10.1098/rstb.2011.0048>
- Poulin R, Krasnov BR, Pilosof S, Thieltges DW (2013) Phylogeny determines the role of helminth parasites in intertidal food webs. *J Anim Ecol* 82(6):1265–1275. <https://doi.org/10.1111/1365-2656.12101>
- R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Ricotta C, Szeidl L (2009) Diversity partitioning of Rao’s quadratic entropy. *Theor Popul Biol* 76:299–302. <https://doi.org/10.1016/j.tpb.2009.10.001>
- Rocha-Reis DA, Pasa R, Kavalco KF (2021) High congruence of karyotypic and molecular data on *Hypostomus* species from Brazilian southeast. *Org Divers Evol* 21(1):135–143. <https://doi.org/10.1007/s13127-021-00478-z>
- Runghen R, Poulin R, Monlleó-Borrull C, Llopis-Belenguer C (2021) Network analysis: ten years shining light on host–parasite interactions. *Trends Parasitol* 37(5):445–455. <https://doi.org/10.1016/j.pt.2021.01.005>
- Rynkiewicz EC, Pedersen AB, Fenton A (2015) An ecosystem approach to understanding and managing within-host parasite community dynamics. *Trends Parasitol* 31(5):212–221. <https://doi.org/10.1016/j.pt.2015.02.005>
- Santos ML, Stevaux JC, Gasparetto NVL, Souza Filho EE (2008) Geologia e Geomorfologia da Planície Aluvial do Rio Ivaí em seu Curso Inferior. *Rev Bras Geomorfol* 9(1):23–34. <https://doi.org/10.20502/rbg.v9i1.98>
- Santos RS, Pimenta FDA, Martins ML, Takahashi HK, Marengoni NG (2002) Metacercárias de *Diplostomum* (*Austrodiplostomum*) *compactum* Lutz, 1928 (Digenea, Diplostomidae) em peixes do rio Paraná, Brasil: prevalência, sazonalidade e intensidade de infecção. *Acta Sci Biol Sci* 24:475–480. <https://doi.org/10.4025/actasciobiolsci.v24i0.2350>
- Sarabeev V, Balbuena JA, Oros M, Domnich V, Sueiro RA, Leiro JM, Ovcharenko M (2024) Symbiotic species diversity can explain invasion success and host–parasite system stability: the case of gammarid hosts. *Ecosphere* 15(7):e4946. <https://doi.org/10.1002/ecs2.4946>
- Schluter D (2000) Ecological character displacement in adaptive radiation. *Am Nat* 156(S4):S4–S16. <https://doi.org/10.1086/303412>
- Schoener TW (1974) Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185(4145):27–39. <https://doi.org/10.1126/science.185.4145.27>
- Secretaria Municipal do Meio Ambiente (2008) Diagnóstico ambiental e dos recursos hídricos do município de Bauru: Relatório final. Bauru, Brazil
- Spickett A, Junker K, Krasnov BR, Haukisalmi V, Matthee S (2017) Intra- and interspecific similarity in species composition of helminth communities in two closely-related rodents from South Africa. *Parasitology* 144(9):1211–1220. <https://doi.org/10.1017/S003118201700049X>
- Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecol Lett* 15(7):637–648. <https://doi.org/10.1111/j.1461-0248.2012.01795.x>
- Stewart PS, Voskamp A, Santini L, Biber MF, Devenish AJ, Hof C, Willis SG, Tobias JA (2022) Global impacts of climate change on avian functional diversity. *Ecol Lett* 25(3):673–685. <https://doi.org/10.1111/ele.13830>
- Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill AN, Kininmonth ST, Airoidi L, Becerro MA, Campbell SJ, Dawson TP, Navarrete SA, Soler GA, Strain EMA, Willis TJ, Edgar GJ (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501(7468):539–542. <https://doi.org/10.1038/nature12529>
- Takemoto RM, Pavanelli GC, Lizama MdLLA, Lacerda ACF, Yamada FH, Moreira LHA, Ceschini TL, Bellay S (2009) Diversity of parasites of fish from the Upper Paraná River floodplain, Brazil. *Braz J Biol* 69:691–705. <https://doi.org/10.1590/S1519-69842009000300025>
- Thatcher VE (2006) Amazon fish parasites, 2nd edn. Pensoft Publishers, Sofia, Bulgaria, p 508
- Thioulouse J, Dray S, Dufour AB, Siberchicot A, Jombart T, Pavoine S (2018) Multivariate analysis of ecological data with ade4. Springer, New York. <https://doi.org/10.1007/978-1-4939-8850-1>
- Vickery WL, Poulin R (1998) Parasite extinction and colonization and the evolution of parasite communities: a simulation study. *Int J Parasitol* 28(5):727–737. [https://doi.org/10.1016/S0020-7519\(98\)00036-8](https://doi.org/10.1016/S0020-7519(98)00036-8)
- Vigneault J, Binning SA, Harvey É (2025) Local environment and sampling bias drive parasite prevalence estimates in freshwater fish communities. *Oikos* 2025:e11196. <https://doi.org/10.1002/oik.11196>

- Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol Appl* 20(6):1512–1522. <https://doi.org/10.1890/09-1310.1>
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116(5):882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Westoby M, Leishman MR, Lord JM (1995) On Misinterpreting the 'Phylogenetic Correction'. *J Ecol* 83(3):531–534. <https://doi.org/10.2307/2261605>
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21(2–3):213–251. <https://doi.org/10.2307/1218190>
- Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 28(4):453–470. <https://doi.org/10.1046/j.1365-2699.2001.00563.x>
- Zica EOP, Brandão H, Zawadzki CH, Nobile AB, Carvalho ED, da Silva RJ (2011) The occurrence of *Austrodiplostomum compactum* (Lutz, 1928) (Digenea: Diplostomidae) metacercariae in the eyes of loricariid fish (Siluriformes: Osteichthyes: Loricariidae) from Brazil. *J Helminthol* 85(1):73–79. <https://doi.org/10.1017/S0022149X10000271>
- Zica EOP, Santos KR, Ramos IP, Zanatta AS, Carvalho ED, Silva RJ (2009) First case of infection of *Austrodiplostomum compactum* (Digenea: Diplostomidae) metacercariae in *Hypostomus regani* (Siluriformes: Loricariidae). *PPanamJAS* 4:35–38

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.