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ATSLER LUANA LEHUN

Patterns of parasitic infections in fish from a floodplain: use of functional traits and phylogeny from fish and parasites

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutora em Ecologia e Limnologia.
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“Now, here, you see, it takes all the running you can do, to keep in the same place”.
Through the looking glass, Lewis Carroll, 1871.

Padrões de infecções parasitárias em peixes de uma planície de inundação: uso de traços funcionais e filogenia de peixes e parasitas

RESUMO

As características funcionais são as propriedades mensuráveis dos organismos que influenciam seu desempenho por meio de seus efeitos no crescimento, sobrevivência e reprodução individual. Dessa forma, a escolha das características funcionais são essencias para tirar conclusões ecológicas sólidas, bem como prever propriedades do ecossistema e interações entre organismos. A estrutura da comunidade parasitária pode variar ao longo do tempo e do espaço, resultante de variação das características dos hospedeiros, relações filogenéticas e características do ambiente. Estas podem ser examinadas em diferentes níveis de diversidade: alfa (diversidade local) e beta (variação da composição da comunidade entre locais), incluindo múltiplas facetas, como a taxonômica (TD), funcional (FD) e filogenética (PD). Avaliou-se quais características do hospedeiro podem ser determinantes na composição dos parasitas de peixes da planície de inundação do alto rio Paraná; e comparou-se as diferentes facetas da biodiversidade de endoparasitas no nível da unidade amostral (diversidade α ou diversidade parasitária no nível de um hospedeiro individual) e entre unidades amostrais (diversidade de parasitas dentro de (β1) ou entre (β2) indivíduos hospedeiros de uma espécie). A dieta do hospedeiro foi o fator que apresentou maior influência na composição e similaridade dos endoparasitas em peixes da planície de inundação. A diversidade α das espécies de endoparasitas diferiu principalmente em termos de TD e PPD. Quanto à diversidade β, as comunidades parasitárias apresentaram padrões agrupados em diferentes níveis (β1 e β2, respectivamente). Para explicar padrões na diversidade de endoparasitas, as características funcionais e a filogenia de peixes atuam juntas como impulsionadores da estrutura da comunidade parasitária, sendo a dieta um dos principais fatores. E os padrões de montagem nas infracomunidades de endoparasitas de diferentes espécies hospedeiras da planície de inundação refletem as características de suas comunidades componentes e compostas.

Palavras-chave: traços funcionais; diversidade alfa; diversidade beta; dieta; endoparasita; hospedeiro.

Patterns of parasitic infections in fish from a floodplain: use of functional traits and phylogeny from fish and parasites

ABSTRACT

Functional traits are the measurable properties of organisms that influence their performance through their effects on individual growth, survival, and reproduction. Therefore, the choice of functional characteristics is essential for drawing solid ecological conclusions and predicting ecosystem properties and interactions between organisms. The structure of the parasite community can vary over time and space, resulting from variations in host characteristics, phylogenetic relationships, and environmental characteristics. These can be examined at different levels of diversity: alpha (local diversity) and beta (variation in community composition between locations), including multiple facets such as taxonomic (TD), functional (FD), and phylogenetic (PD). We evaluated which host characteristics may be determinant in the composition of fish parasites from the upper Paraná River floodplain; and compared different facets of endoparasite biodiversity at the sampling unit level (α diversity or parasite diversity at the level of an individual host) and between sampling units (parasite diversity within (β1) or between (β2) host individuals of a species). The host's diet was the factor that had the greatest influence on the composition and similarity of endoparasites in floodplain fish. The α diversity of endoparasite species differed mainly in terms of TD and PPD. Regarding β diversity, the parasite communities presented patterns grouped at different levels (β1 and β2, respectively). To explain patterns in endoparasite diversity, functional traits, and fish phylogeny act as drivers of parasite community structure, with diet being one of the main factors. And the assembly patterns in the endoparasite infracommunities of different floodplain host species reflect the characteristics of their component and composite communities.

***Keywords*:** functional traits; alpha diversity; beta diversity; diet; endoparasite; host.

SUMMARY

Tese elaborada e formatada conforme as normas das publicações científicas:

1. *Journal of Fish Biology.* (Os direitos autorais pertencem à revista). O artigo está disponível em: https://doi.org/10.1111/jfb.15576

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1 GENERAL INTRODUCTION

Functional traits are the measurable properties of organisms that influence their performance through their effects on individual growth, survival, and reproduction (Violle et al., 2007). This approach is based on the use of functional traits, which are defined as any measurable biological attribute in an individual that impacts the organism's performance and fitness (Darwin, 1859; McGill et al., 2006; Violle et al., 2007; Laughlin et al., 2020). Thus, the choice of functional characteristics is essential for drawing solid ecological conclusions and predicting ecosystem properties and interactions between organisms, so they must be explicitly related to individual performance (Violle, 2007).

Diversity measures are often associated with environmental and spatial characteristics, aiming to analyze the effects of abiotic and spatial factors on community structure (Legendre et al., 2005). Like free-living species, parasite communities are affected by local environmental and spatial factors (Poulin, 2007; Krasnov, 2008; Krasnov et al., 2019a; 2019b). However, a parasite's environment includes its most important component, its host. Hosts provide parasites with food and places to live and reproduce and often serve as tools for dispersal (Combes, 2001; Poulin, 2007). As a result, parasite diversity is demonstrated to respond to host diversity (Poulin, 2007; Kamiya et al., 2014; Poulin, Morand, 2000).

Among the characteristics of the hosts that can influence the parasite community, diet, trophic level, position in the water column, body size and migratory behavior will mainly determine the composition of endoparasites (Campbell et al., 1980; Poulin, 1997; 2004; Poulin et al., 2011; Jacobson et al., 2019; Poulin, Angeli Dutra, 2021; Cavalcanti et al., 2023; Lehun et al., 2023a). Endoparasites can be acquired through food ingestion, and their transmission occurs along the trophic chain, from one level to another (Poulin, 1995; Lafferty et al., 2008; Benesh et al., 2014). Typically, definitive hosts are located at medium to high trophic levels, thus, fish that occupy the top of the trophic web are expected to be definitive hosts and accumulate a greater wealth of adult parasites (Poulin, 2011; Lehun et al., 2023b), whereas fish that are at the lowest levels of the trophic chain will present a greater composition of endoparasites in intermediate life stages (Marcogliese, 2002; Poulin, 2011; Lehun et al., 2023b). Thus, as the host's dietary preference can be decisive for the level of infection, the position occupied by a fish species in the water column also influences the parasite load, as the fish's diet is based on the resources available in each extract of depth (Campbell et al., 1980; Silva et al., 2021; Cavalcanti et al., 2023).

It is expected that the larger the host's body size, the greater its capacity to support greater abundance and diversity of parasites (an example of the species-area relationship), just as it is also expected that hosts accumulate parasites during their body growth (Poulin, 1997; 2004; Poulin et al., 2003; Lehun et al., 2023b). Migratory species generally have a relatively larger body size when compared to non-migratory species, and this is mainly due to the large investment to achieve greater reproductive success (Jonsson, Jonsson, 1993; Ota et al., 2018). When carrying out these migrations, as they disperse across many environments, they can acquire parasites from various regions, while sedentary species are more restricted to local parasites (Lizama et al., 2005). Furthermore, host phylogeny can determine the richness of parasites accumulated over evolutionary time (Poulin et al., 2011; Paterson et al., 2012), as phylogenetically close hosts tend to have similar physiological and immunological characteristics, which makes them susceptible to the same groups of parasites (Bersier, Kehrli, 2008; Krasnov et al., 2014; Locke et al., 2014), showing greater similarity in parasite composition (Timi et al., 2011).

In general, the structure of the parasite community can vary over time and space, resulting from variations in host characteristics, phylogenetic relationships, and environmental characteristics (Poulin, 2004; Locke et al., 2013). These can be examined at different levels of diversity: alpha (local diversity) and beta (variation in community composition between locations) (Whittaker, 1960; 1972; Baselga, 2010; Pavoine et al., 2016), including multiple facets such as the variety of species (TD), functionals (FD) or phylogenetics (PD) (Pavoine, Bonsall, 2011). Therefore, the numerous ways to quantify taxonomic and functional diversity in a set of species often reveal patterns in the biodiversity of communities (Petchey, Gaston, 2002).

Investigating which host characteristics may be determinant in the composition of parasites in a location, as well as incorporating information on the taxonomic, functional, and phylogenetic affiliations of parasites in the host population can clarify the structure of parasite communities. Furthermore, these approaches are important because they provide a representation of local diversity and define the possible patterns of these communities, as well as the use of more sophisticated measures will allow testing hypotheses and theories of parasitism (Guégan et al., 1992; Poulin, 2001; Luque, Poulin 2008; Bellay et al., 2015; Salgado Maldonado et al., 2016). Therefore, the present thesis was prepared in two manuscripts: the first manuscript aims to evaluate whether the functional characteristics of the hosts can determine a pattern of parasitic diversity in fish in the upper River Paraná floodplain; The second manuscript aims to contribute to the knowledge and applicability of the multiple facets of parasite diversity in fish from the upper River Paraná floodplain.

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2 THE FUNCTIONAL TRAITS OF HOST FISH CAN ACT AS GOOD PREDICTORS FOR PARASITE COMPOSITION IN A NEOTROPICAL FLOODPLAIN

Abstract

Parasite diversity can be influenced by the interaction of environmental factors and host traits, but understanding which traits can be decisive for the establishment of the parasite may provide subsidies for a better understanding of the host-parasite relationship. In this study, we investigated whether functional traits, diet, and host phylogeny can predict the similarity of the endoparasite composition of a fish assemblage in a Brazilian floodplain. Of the three evaluated components, the host's diet was the factor that showed the greatest influence on the composition and similarity of endoparasites, demonstrating the highest value of the explanation. The functional traits and phylogeny, despite presenting significant values (unique effect and global effect), showed low explainability in the composition of the endoparasites. When analyzing the joint effects, all components showed significant influence. Hosts that live in the same environment that are phylogenetically related and have a similar ecology have a certain degree of homogeneity in their parasite assemblages and, because they are endoparasites (which are acquired trophically along the chain), diet is the main driver of parasite richness and similarity. Overall, host traits can be one of the main determinants of parasite composition, so studies that address the functional traits of the host provide a representation of local diversity and define the possible patterns of these parasite communities.

Keywords: diet, functional traits, fish, host-parasite relationship, Paraná River.

2.1 Introduction

Interactions between evolutionary and ecological factors are determinants for the composition of the parasite community observed for each host species, and can affect the transmission and establishment of the parasite (Carrassón et al., 2019; Krasnov et al., 2010; Pantoja et al., 2016; Poulin, 2010). Understanding the factors that structure the host species community and relating them to the parasite community composition can generate information for a better understanding of this host–parasite relationship (Lima et al., 2016; Poulin & Leung, 2011; Takemoto et al., 2005).

Fish assemblages harbor a diversity of species of parasites, which can be ecto- or endoparasites, and present strategies in their life cycles to reach their hosts, thus they are able to be monoxenous, carrying out their entire life cycle in a single host, or heteroxenous, using more than one host to complete their cycle (Pavanelli et al., 2013). In these cases, in heteroxenous parasite species, it is thought that the dominant drivers of infracommunities are mainly related to the diversity and abundance of the host community (Baia et al., 2018; Luque & Poulin, 2008; Valtonen et al., 2010) and this makes sense, considering that the hosts serve both as habitat and as dispersal agents of parasites.

In addition to host density, the mechanisms by which hosts can affect the transmission and establishment of endoparasites are mainly related to functional traits and their phylogeny (Vickery & Poulin, 1998). Many studies highlight host body size as a predictor of parasite communities (e.g., Costa et al., 2021; Lizama et al., 2005; Poulin, 1997; Poulin et al., 2011), as it is expected that the larger the host species, the greater its ability to support a greater abundance and diversity of parasites (Lehun et al., 2023; Poulin, 1999). Other studies also highlight the role of the host's diet and trophic level (e.g., Cavalcanti et al., 2023; Lehun et al., 2023; Muñoz et al., 2006; Poulin & Leung, 2011), influencing mainly endoparasites, which can be acquired through food ingestion and their transmission occurs along the trophic chain, from one level to another (Benesh et al., 2014; Poulin, 1995), migratory behavior, considering that migratory species, when dispersed in different environments, can acquire parasites from several regions, while sedentary species are more restricted to local parasites (Criscione et al., 2006; Jacobson et al., 2019; Poulin & Angeli Dutra, 2021; Shaw et al., 2018), and habitat use (e.g., Campbell et al., 1980; Cavalcanti et al., 2023).

The phylogeny of the host can be decisive for a parasite to establish itself in a new environment with new hosts (Streicker et al., 2010). In general, it is expected that evolutionarily similar hosts tend to share more parasite species (Poulin, 2004; Poulin, 2010). However, when comparing different fish species, Poulin (2010) reports that phylogenetic distance may be a poor predictor of parasite community similarity, and suggests that the ecological convergence of host species may be more important than their phylogeny in determining sharing parasites.

Thus, investigating which host traits can be determinant in the composition of parasites in a location can elucidate the structure of parasite communities. Furthermore, these approaches are important because they provide possible patterns of these communities (Bellay et al., 2015; Guégan et al., 1992; Luque & Poulin, 2008; Poulin, 2001; Salgado-Maldonado et al., 2016). In this study, we investigated whether functional traits and phylogeny are good predictors and can determine a pattern in endoparasite communities in a fish assemblage in a floodplain in Brazil. We define three main host components that can influence the parasite community: (1) a functional component, which includes host body size, migratory habit, and habitat use (a position it occupies in the water column); (2) a diet component, which includes trophic category and host trophic level, and (3) a phylogenetic component, which includes the phylogenetic distance of hosts. We predict that hosts that are ecologically or phylogenetically similar tend to share more endoparasite species, showing greater similarity in composition. Among the components, we predict that the diet component is the determining factor for the presence of endoparasites, so fish that belong to the same trophic category will show greater similarity in their parasite composition.

2.2 Material and methods

2.2.1 Parasites

We used a database compiled from studies of endoparasite communities in fish in the upper Paraná River floodplain. A systematic search was conducted for scientific articles indexed in the Web of Science database. The choice of keywords was directly related to the objectives, and followed the following combination of words and arguments: (Parana floodplain OR Parana river) AND (acanthocephala OR cestoda OR digenea OR nematoda OR parasite) AND (fish) AND NOT (snail) AND NOT (anuran). The search was carried out in all years available on the Web of Science.

We found 12,299 articles, as reported in Figure 1. As the objective was to select only studies carried out in the upper Paraná River floodplain, we first restricted it to studies carried out in Brazil, which were original and parasitology research. Subsequently, we restricted it to studies carried out by Pavanelli and Takemoto, as they were the only authors who carried out studies in this area. In total, 79 articles were evaluated, and of these, only 23 were included in our study. As eligibility criteria, we only selected studies that provided data on all endoparasite species found in a sample of individual hosts of the same species, where identification occurred at the genus and/or species level and the methods used in each survey follow procedures standardized parasitological tests (Eiras et al., 2006). Taxonomic description articles were not considered. We extracted the following information: (1) analyzed host species; (2) sampling year; (3) number of fish analyzed; (4) sampling effort; (5) total parasite richness; and (6) the mean abundance of each endoparasite. The articles that did not present the mean abundance values of the genus/species of parasites were calculated according to Bush et al. (1997). For the articles that presented more than one record for the same parasite genus, we summed the mean abundance. The genus/species of parasites and their respective hosts were validated according to Gbif.org (2023) and Ota et al. (2018). In total, 28 hosts presented their complete endoparasitic fauna (see Data S1).

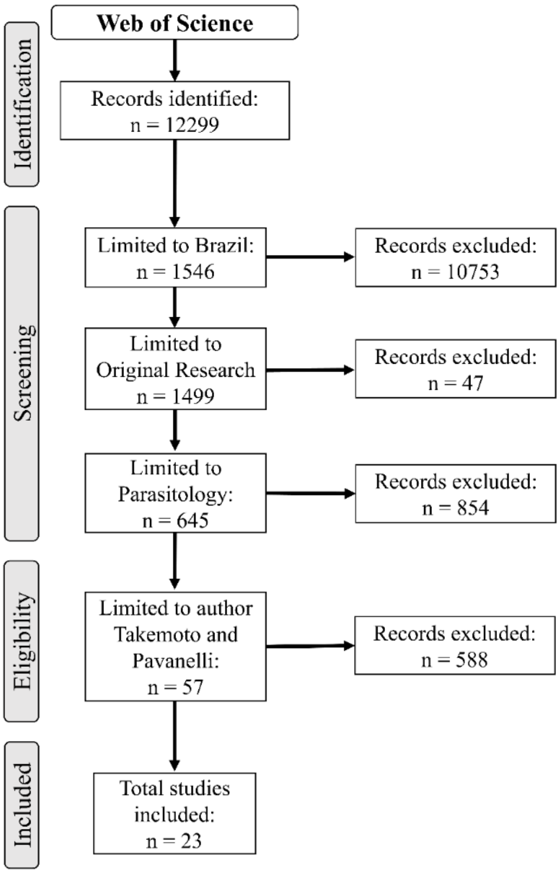

FIGURE 1 Inclusion and exclusion criteria for studies in our systematic search (Moher et al., 2015).

We used the presence of the parasite at the genus level to limit any inaccuracies associated with misidentifications. We emphasize that in our study, the sampling effort was not treated as a variable, since the analyses did not focus on how many species were found, but on the presence of these in each species of fish in the given period that the study was carried out (see Luque & Poulin, 2004; Poulin & Leung, 2011).

2.2.2 Fish functional traits

2.2.2.1 Functional component

Functional traits are defined as biological characteristics that influence the performance of the organism (Díaz et al., 2013; Petchey & Gaston, 2006). For this study we selected body length, use of habitat and whether or not the species exhibits migratory behavior.

The standard mean body length (mm) is defined as the length from snout to tail, without considering the caudal fin. In special cases, such as Gymnotiformes, the total length was considered, and in Myliobatiformes the diameter of the disc was considered (Graça & Pavanelli, 2007).

Migration is related to the strategy used to complete the life cycle and is an important feature in the life history of tropical fish (Myers, 1949). Species have been classified into migratory (perform large migrations to reproduce) and sedentary (perform small migrations or do not use this strategy) (Agostinho et al., 2003; Duponchelle et al., 2021; see Oliveira et al. (2018) and Table S2 for details).

In the use of habitat, the species were classified according to the position in the water column that they use most during their life cycle. We classify them as: (I) pelagic (occupying the pelagic portion of the water column, mainly the clear upper waters); (II) benthopelagic (occupying the benthic portion of the water column, occasionally making inroads into pelagic waters); and (III) demersal (strictly occupying the fund) (see Oliveira et al. (2018) and Table S2 for details).

2.2.2.2 Phylogeny component

We recorded the phylogeny of fish species according to Ota et al. (2018) and created a paired Euclidean distance matrix between fish species using the taxa2dist function of the vegan package (Oksanen et al., 2020). The resulting distance matrix was divided by its maximum to limit the cell values between 0 and 1. A principal coordinate analysis (PCoA) was performed (Gower, 1966) and then the first two axes were used as a proxy for phylogenetics to estimate the phylogenetic distance between host species.

2.2.2.3 Diet component

The trophic category of the species was defined according to food preferences and was classified into: (I) detritivore (feeds on detritus or particles deposited on the bottom); (II) herbivore (feeds on plants or algae); (III) insectivore (feeds on insects, usually adults); (IV) omnivorous (feeds on various items); and (V) piscivorous (feeds on fish or fish parts) (Abujanra et al., 2009; Angelini & Agostinho, 2005; Delariva et al., 2013; Hahn et al., 2004; Russo, 2004). The trophic level is defined as the number of energy-transfer steps between the basal resources and the position of the fish in the food chain, but, as we did not have measurements of real networks, the trophic level was estimated by FishBase (Froese & Pauly, 2021). Table 1 summarizes the functional traits used in this study for all fish species.

TABLE 1 Standard length, functional traits, and phylogeny of fish species of the upper river Paraná floodplain.

Host	Standard length	Migration	Water column position	Family	Trophic category	Trophic level
***Acestrorhynchus lacustris* (Lütken, 1875)**	150	Sedentary	Benthopelagic	Acestrorhynchidae	Piscivore	3.6
***Astyanax lacustris* (Lütken, 1875)**	79.9	Sedentary	Benthopelagic	Characidae	Omnivore	2.9
***Auchenipterus osteomystax* (Miranda Ribeiro, 1918)**	191	Sedentary	Pelagic	Auchenipteridae	Insectivore	3.3
***Brycon orbignyanus* (Valenciennes, 1850)**	270	Migratory	Benthopelagic	Bryconidae	Insectivore	2.8
***Cichla kelberi* Kullander & Ferreira, 2006**	190	Sedentary	Benthopelagic	Cichlidae	Piscivore	4.4
***Cichla piquiti* Kullander & Ferreira, 2006**	240	Sedentary	Benthopelagic	Cichlidae	Piscivore	4.2
***Gymnotus* spp.**	240	Sedentary	Benthopelagic	Gymnotidae	Omnivore	3.3
***Hemisorubim platyrhynchos* (Valenciennes, 1840)**	470	Migratory	Demersal	Pimelodidae	Piscivore	4.5
***Iheringichthys labrosus* (Lütken, 1874)**	200	Sedentary	Benthopelagic	Loricariidae	Invertivore	2.7
***Leporinus friderici* (Bloch, 1794)**	189.2	Migratory	Benthopelagic	Anostomidae	Omnivore	2.6
***Leporinus lacustris* Campos, 1945**	200	Sedentary	Benthopelagic	Anostomidae	Omnivore	2.7
***Loricariichthys platymetopon* Isbrücker & Nijssen, 1979**	210	Sedentary	Demersal	Loricariidae	Detritivore	2.3
***Megaleporinus obtusidens* (Valenciennes, 1836)**	190.8	Migratory	Benthopelagic	Anostomidae	Omnivore	2.6
***Metynnis lippincottianus* (Cope, 1870)**	149.3	Sedentary	Pelagic	Serrasalmidae	Herbivore	2.9
***Plagioscion squamosissimus* (Heckel, 1840)**	330	Sedentary	Pelagic	Sciaenidae	Piscivore	3.7
***Potamotrygon cf. falkneri* Castex & Maciel, 1963**	400	Sedentary	Demersal	Potamotrygonidae	Piscivore	3.2
***Prochilodus lineatus* (Valenciennes, 1836)**	495.2	Migratory	Benthopelagic	Prochilodontidae	Detritivore	2.2
***Pseudoplatystoma corruscans* (Spix & Agassiz, 1829)**	675	Migratory	Demersal	Pimelodidae	Piscivore	4
***Rhaphiodon vulpinus* Spix & Agassiz, 1829**	480	Migratory	Pelagic	Cynodontidae	Piscivore	3.8
***Salminus brasiliensis* (Cuvier, 1816)**	500	Migratory	Benthopelagic	Bryconidae	Piscivore	3.6
***Serrasalmus maculatus* Kner, 1858**	157.2	Sedentary	Pelagic	Serrasalmidae	Piscivore	3.8
***Serrasalmus marginatus* Valenciennes, 1837**	160.2	Sedentary	Pelagic	Serrasalmidae	Piscivore	3.8

2.2.3 Data analysis

The variation partitioning analyses (PV) assessed the influence of the three sets of predictors on the endoparasites composition. The three sets of PV predictors were functional (medium body size, migratory behavior, and use of habitat), phylogeny (a proxy for phylogenetic), and diet (which included trophic guild and trophic level). The Hellinger transformation was applied to the parasite abundance matrix. This transformation was necessary because species abundance data (in particular, with the presence of many rare species) can cause distortions in ordering methods based on Euclidean distance (Legendre & Gallagher, 2001). Subsequently, we applied the Euclidean distance index to calculate the similarity between the host species. No transformation was applied to the predictor variables, since most were categorical, and trophic level and standard length (continuous variables) were included in different predictor components, not requiring standardization of their effects. Distance-based redundancy analysis (dbRDA) was used to visualize the composition of endoparasites, restricted by the predictor variables of the PV components when considered significant in their unique effect. Analyses were performed using the vegan package (Oksanen et al., 2020) and ggplot2 (Wickham, 2011) in R software (R Core Team, 2022).

2.3 Results

The results of the variation partition analysis showed that the diet (21.7%) and functional traits (6.9%) of the hosts presented the highest percentages of the variation explained for the composition of the endoparasites (Figure 2). It was also possible to find an influence, even if low, on the phylogeny of the hosts (5.9%). The three host components presented significant values for both the unique and the global effect (Table 2).

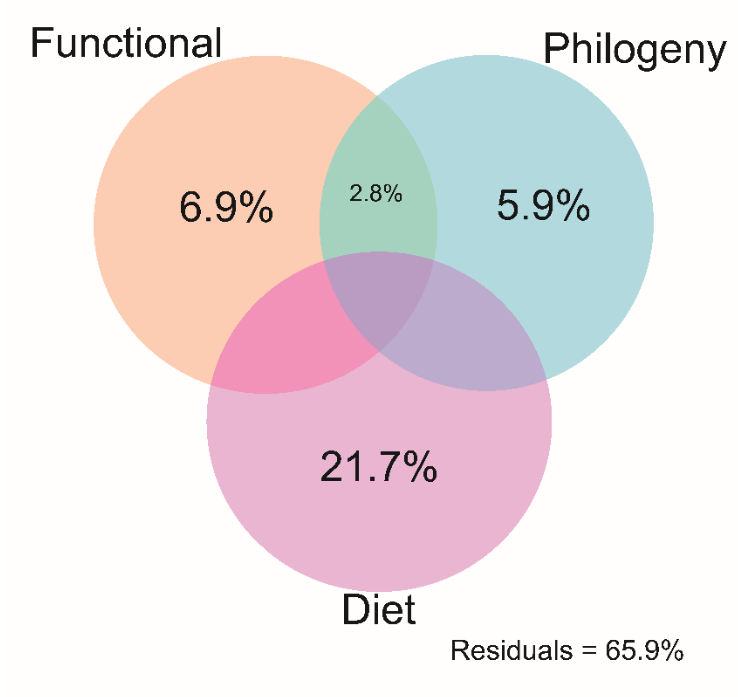

FIGURE 2 Variation partitioning analyses predictor components of the endoparasite composition in fish. The figure corresponds to percentages (zero or negative values are omitted). The analyze used three sets of predictors: functional traits; phylogeny; and diet.

TABLE 2 Variation partitioning analyses of predictors set on the composition of the parasite in fish hosts. The explained variation (R^2 adj) and corresponding P value are shown.

Response variable	**Factors**	**R^2_{adj} overall**	**P**	**R^2 adj unique**	**P**
Endoparasites composition in hosts	Functional Traits	0.073	0.004	0.069	0.023
	Phylogeny	0.059	0.002	0.059	0.015
	Diet	0.183	0.001	0.217	0.001

Among the functional traits (F = 1.53, Pr[>F] = 0.004, restricted proportion = 21%; Figure 3), despite the low percentage of explanation, benthopelagic fish showed similarity in parasitic composition, demonstrating segregation in the multivariate space. Fish with larger body sizes and migrants, such as *Prochilodus lineatus*, *Pseudoplatystoma corruscans*, and *Salminus brasiliensis*, also showed a tendency towards similarity in the composition of the parasitic fauna.

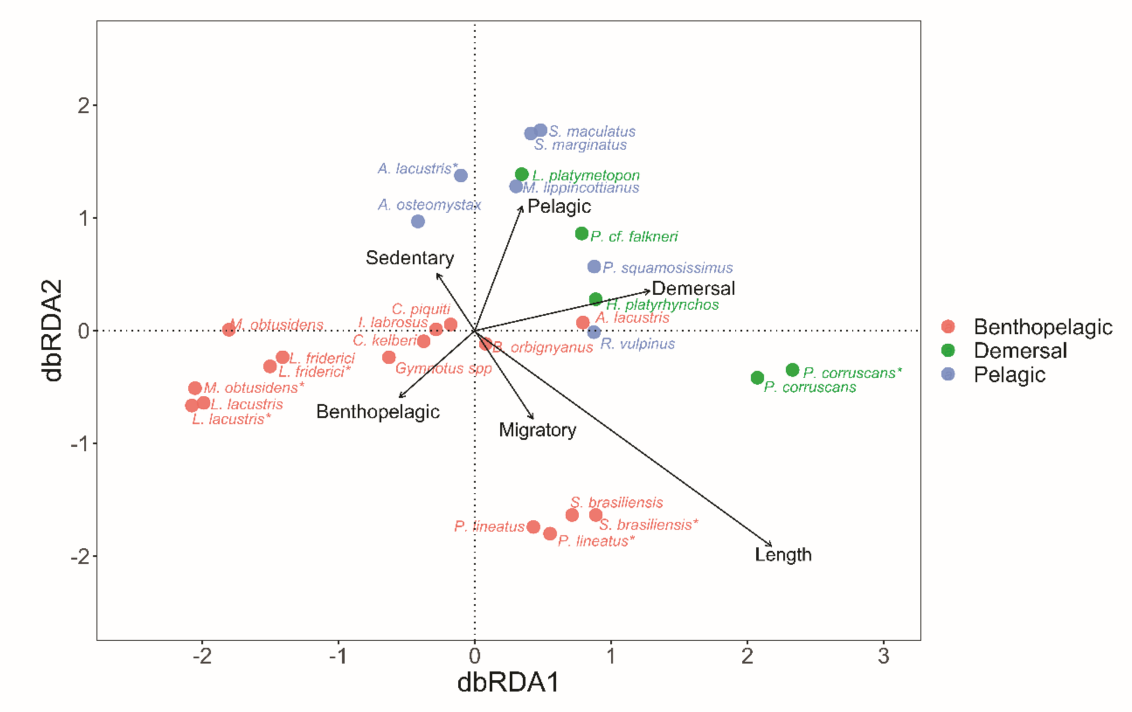

FIGURE 3 Distance-based redundancy analysis (dbRDA) ordering for the host water column position component.

*Hosts who submitted more than one floodplain study were marked with an asterisk.

In the phylogeny component, representatives of the Anostomidae and Auchenipteridae families showed clear segregation in the multivariate space (F = 2.58, Pr[>F] = 0.001, restricted proportion = 70.6%; Figure 4). Species from the families Serrasalmidae and Bryconidae showed similarity in parasitic composition and showed some similarity with the families Curimatidae and Sciaenidae (closer in space). The other families are positioned along the dbRDA1 axis in the opposite direction for Bryconidae, Curimatidae, Sciaenidae, and Serrasalmidae, and in the opposite direction to the dbRDA2 axis for Anostomidae.

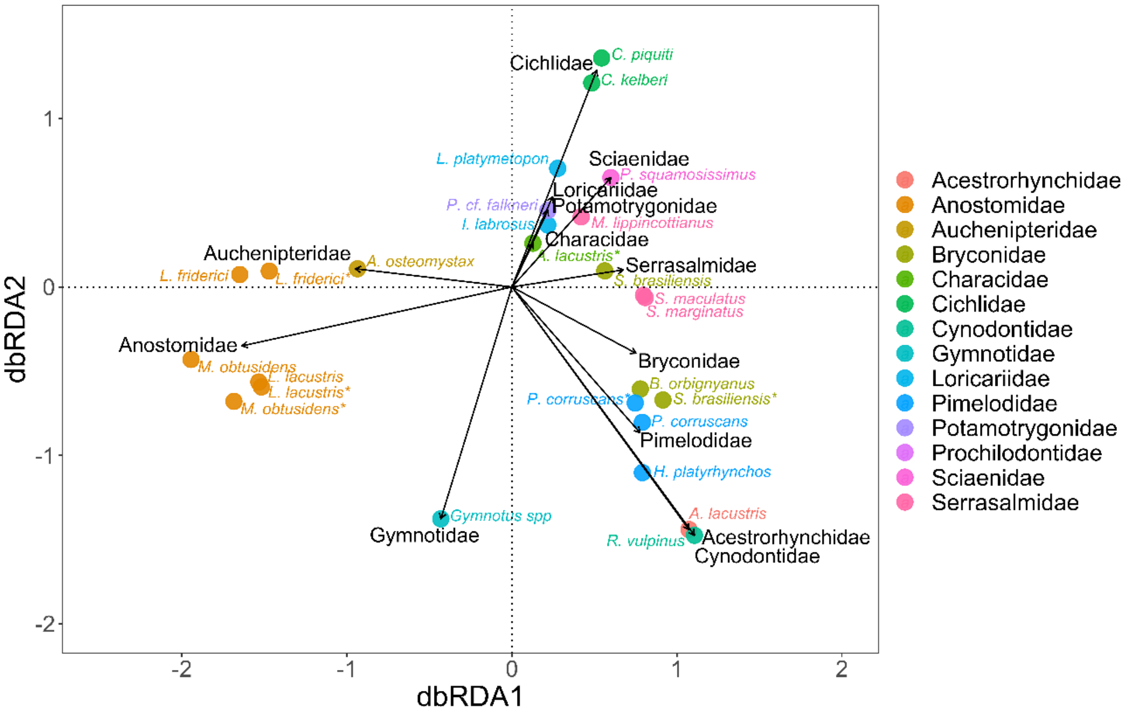

FIGURE 4 Distance-based redundancy analysis (dbRDA) ordering for the host phylogeny component.

*Hosts who submitted more than one floodplain study were marked with an asterisk.

In the diet component, detritivores, piscivores, and omnivores fish species showed segregation, but the percentage of explanation was low (F = 2.06, Pr[>F] = 0.001, restricted proportion = 31.9%; Figure 5). Insectivorous species showed similarity with piscivorous species (closer in space), while invertivores, herbivores, and detritivores species were positioned along the dbRDA1 axis in the opposite direction about piscivores.

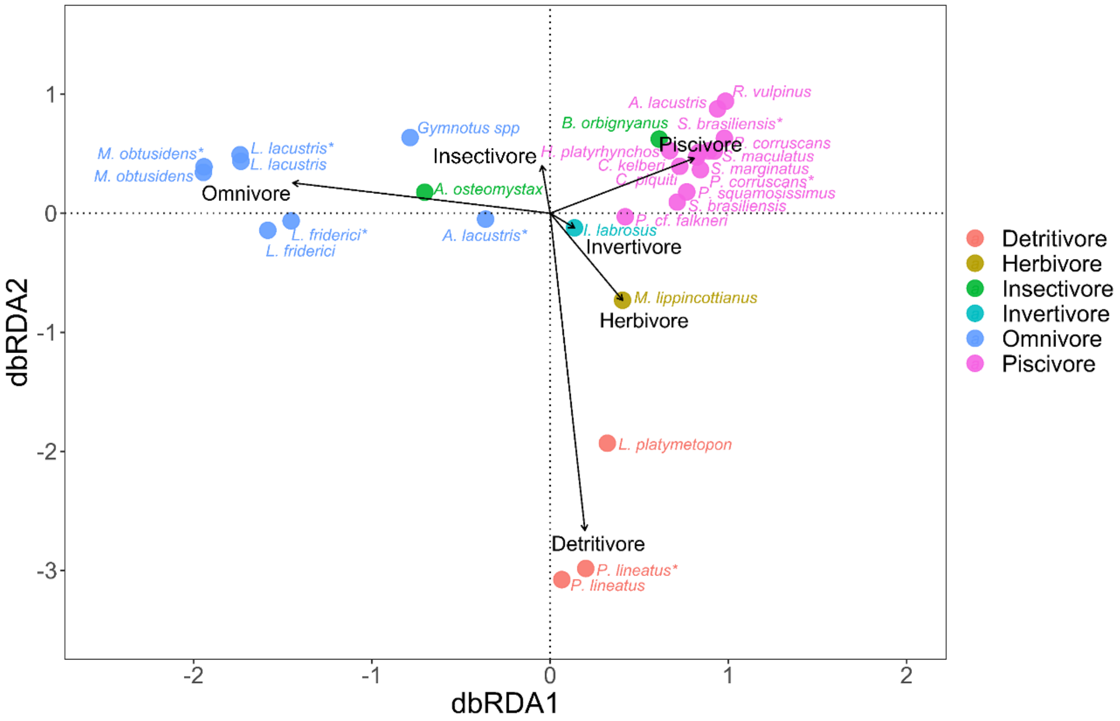

FIGURE 5 Distance-based redundancy analysis (dbRDA) ordering for the host trophic category component.

*Hosts who submitted more than one floodplain study were marked with an asterisk.

2.4 Discussion

We demonstrated that of the three components analyzed, the host's diet was the factor that presented the greatest influence on the composition and similarity of endoparasites in fish from the upper Paraná River floodplain, demonstrating the highest percentage of explanation. The functional traits and phylogeny, despite presenting significant values (unique effect and global effect), demonstrated low explainability in the composition of endoparasites, and around 65.9% of the variation was unexplained.

The low explainability of the effect of fish functional traits on parasite composition can be explained due to the wide taxonomic diversity of parasites that the floodplain presents (Lehun et al., 2020; Silva et al., 2021; Takemoto et al., 2009). For this reason, although hosts have similar ecology and phylogeny, it is not always sufficient to predict the presence of the parasite in a given host. In principle, similarity in species composition along any dimension that characterizes some kind of separation between parasite communities decreases as the distance between them increases, and the greater the parasite specificity, the fewer parasite species were shared by the species hosts (Locke et al., 2013; Pérez-del-Olmo et al., 2009; Poulin, 2003, 2005). Furthermore, some errors may have contributed to the relatively poor patterns observed in our study, for example, some parasite records may be incomplete for some fish species, and inadequate sampling of fish may have reflected uneven sampling effort. Thus, when we chose to analyze the genus level of the parasite, it should have limited any inaccuracy associated with misidentification (Bennett et al., 2022; Walther et al., 1995).

Even with the low percentage of explanation, the influence of functional traits and host phylogeny are considered the main predictors of the presence/absence of a given parasite species. Closely related host species, which utilize immunological defenses and face similar risks of acquiring the same parasite species, should have similar parasite fauna to unrelated host species (Poulin, 2010). For endoparasites, most infections depend on the consumption of infected intermediate hosts, therefore the invertebrate fauna present at the site reflect the characteristics of the habitat and are important factors in determining the composition of the parasitic fauna (Marcogliese, 2002; McDevitt-Galles et al., 2018; Shaw & Dobson, 1995).

Some studies demonstrate a direct relationship between the host's diet and the parasitic fauna, mainly hosts that feed on invertebrates and other fish (high trophic levels), as they have a greater richness of parasites compared to other types of diets (Choudhury & Dick, 2000). However, although they seem to be dominant consumers among fish, in our study piscivores showed similar parasite composition to herbivores and insectivores, and this similarity occurs due to the accumulation of infectious stages that can be acquired along the food chain by hosts (Marcogliese, 2002). Omnivorous fish have a greater trophic range, which is diverse and less specialized than for fish with more restricted diets, therefore they would have access to a greater number and diversity of parasites (Amarante et al., 2015), which would also influence similar species composition. Detritivore fish, on the other hand, presented a different composition of parasites when compared to fish of other trophic categories. This says a lot about the ecology of the hosts, as they have demersal habits and strictly occupy the bottom, with access to the highest density of invertebrates, which facilitates the transmission of parasites (Campbell et al., 1980; Dogel, 1961; Klimpel et al., 2006; Marcogliese, 2002).

Although fish at high trophic levels are parasitized by species considered rare, they harbor a greater number and proportion of parasites, especially those that largely dominate assemblages, such as generalist parasites (Lehun et al., 2023; Timi et al., 2011). In our study, we did not demonstrate the direct influence of the trophic level on the composition of parasites, but the trophic positions of the hosts within a food chain are considered important since the parasitic fauna is positively related to the position of the host network, and preferentially exploit hosts species highly connected at higher trophic positions (Bellay et al., 2020; Chen et al., 2008; Poulin, 1997, 2004).

This interspecific variation in the composition of endoparasites also depends on the characteristics of the parasite and the host, which in turn is mediated by the phylogeny of the host (Lima-Junior et al., 2012). We observed that phylogenetically close hosts are more tolerant of sharing parasitic species and the phylogeny also points to the unique role of some families of fish species in the food web. Although the fish species of the Anastomidae family showed different behaviors, such as *L. lacustris* being markedly sedentary and *L. friderici* migratory, the parasite composition is similar, as these species learned similar habits, confirming that daisies can determine similarity in infracommunities (Guidelli et al., 2006). Thus, phylogeny influences the trophies that arise as a consequence of inherited sets of behavior and morphology (Krasnov et al., 2012; Naisbit et al., 2012), and these parasite specializations and immunity to their hosts motivate the hypothesis that happy and strong phylogenetic relationships between species are expected (Bellay et al., 2015; Krasnov et al., 2012; Lima-Junior et al., 2012).

Differences in interspecific host traits should therefore lead to exposure to increasingly different subsets of the total parasite species assemblage, and similarity in parasite assemblages should decrease due to trophic differences between fish species (Timi et al., 2010). Although host functional traits were not a good predictor of species composition similarity, their effect can be significant when analyzed in conjunction with other predictors. For example, the position of the water column occupied by fish can predict their foraging strategies and diet (Nelson et al., 2016; Werner et al., 1983; Woodstock et al., 2020), and is therefore associated with the similarity of parasitic communities.

Similar to habitat use, host distribution (i.e., biogeographical factors) directly affects the influence on the diversification of parasite assemblages (Luque & Poulin, 2008). Host mobility includes two components: host movement over large areas and between different habitats (migration), and local movement over small areas (Kennedy et al., 1986). Fish migratory patterns have the potential to influence parasite acquisition, as fish moving between different habitats are likely to encounter different parasites associated with different fish species (Paterson et al., 2012; Rochat et al., 2021). Although migration is not a determinant of species composition and the similarity of parasitic infracommunities, host mobility may be closely associated with diets, such as geographic distribution and prey availability (Kennedy et al., 1986).

In summary, diet, functional traits, and phylogeny can act together as drivers of parasite community structure, and diet has proven to be one of the main factors. However, even if the components are explainable, they may not always be good predictors to determine a pattern in parasitic communities. Our results are restricted to an ecosystem that in turn is highly influenced by a subset of characteristics of the area and even if the hosts are ecologically and phylogenetically close, each parasite species may respond differently in each host.

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3 VARIATION IN THE TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY OF FISH ENDOPARASITES FROM A NEOTROPICAL FLOODPLAIN

Abstract

1. Today, it is widely recognized that biodiversity is multifaceted in taxonomic (TD), functional (FD), and phylogenetic (PD) diversity, as well as diversity change can also be expressed at different spatial levels (α and β diversity). Parasite communities offer excellent models for studying the assembly rules of diversity facets at different levels of organization, however, little is known about the patterns of compositional similarity in host assemblages, mainly because parasite species depend on the occurrence of their respective host species.
2. We evaluated whether the taxonomic, functional and proxy for phylogenetic diversity of endoparasites differ among fish species from the upper Paraná River floodplain. We compared the different facets of biodiversity (TD, FD, and PPD) at the sampling unit level (α diversity or parasite diversity at the level of a host individual) and among sampling units (parasite diversity within (β1) or between (β2) host individuals of a species).
3. We found that the α-diversity of the infracommunities was strongly affected by the host species, and we found differences mainly at the level of TD and PPD. At the β1 level, parasitic communities of fish of the same species tended to be more similar. At the β2 level, the parasitic communities differed significantly from randomness, indicating that the similarity of the infracommunities was lower than the simulated values.
4. These results suggest that the composition of endoparasite infracommunities, in terms of species and phylogeny, is strongly affected by the characteristics of the host species.
5. The assembly patterns in infracommunities of endoparasites of the different host species of the floodplain mirror the characteristics of their component and component communities, and because they are endoparasites, factors linked to the hosts are decisive, mainly because they depend on trophic interactions to achieve their transmission.

Keywords: alpha diversity, beta diversity, facets of diversity, Paraná river, parasites.

3.1 Introduction

Species diversity is the most commonly used representation of ecological diversity, and refers to the variety of all living forms on the planet (Wilson, 1988; Whittaker et al., 2001; Magurran, 2021) and is often equated with a total number of species present in an ecosystem (Connell, 1978; Gotelli & Colwell, 2001). However, when characterizing biodiversity only by species richness, other types of variability that living beings exhibit are neglected (Pavoine & Bonsall, 2011; Mace et al., 2012), which may not adequately describe the community.

Today, widely recognized that biodiversity is multifaceted in additional dimensions beyond taxonomic diversity (TD), such as functional diversity (FD) and phylogenetic diversity (PD) (Hooper et al., 2005; Cardoso et al., 2014). Functional diversity incorporates species-specific characteristics and allows us to explain the differences between species in their ecological characteristics, being a key factor to understand ecosystem functioning (Naeem et al., 2003; Hooper et al. 2005; Cadotte et al., 2011; Petchey & Gaston, 2002). Phylogenetic diversity quantifies the variation in the evolutionary relationship between species, which represents the breadth of evolutionary history in a community (Webb et al., 2002; Schweiger et al., 2008; Schweiger et al., 2018). In this sense, biodiversity is not only focused on species richness, but also on the ecological functions performed by species and on evolutionary history (Diniz-Filho et al., 2013).

Diversity change can also be expressed at different spatial or temporal levels (Pavoine et al., 2009), thus, in addition to investigating the different facets of community diversity within locations (α diversity) (Magurran, 2021), it is also necessary to characterize the variation in species composition between communities (β-diversity) (Whittaker, 1960; Anderson et al., 2011; Hawkins et al., 2015). Parasitic communities offer excellent models to study the assembly rules of diversity facets at different levels of organization (Llopis-Belenguer et al., 2020), however, little is known about the patterns of compositional similarity in host assemblages, mainly because parasite species depend on the occurrence of their respective host species (Clark et al., 2018).

Primarily, the parasite diversity is determined by the encounter and host compatibility filters (Combes, 2001). The first filter is directly related to the possibility of encounters between the parasite and its host so that certain attributes of the hosts can make them more exposed to parasites. At this point, host traits such as population density, mobility, and body size may correlate with the likelihood that parasites and hosts will encounter each other (Anderson & May, 1978; Arneberg et al., 1998; Morand & Poulin, 1998; Patterson & Ruckstuhl, 2013). The second filter, or compatibility filter, delimits which hosts can be used by the parasites, as several species have immunological, physiological, and behavioral barriers to defend against parasitism (Combes, 2001; Locke et al., 2010). Thus, these existing parasite-host associations are the result of antagonistic interactions, whose coevolution led to close reciprocal adaptations that allow parasites to exploit specific biological characteristics of their hosts to ensure their transmission, survival, and maintenance of viable populations (Marcogliese, 2004; Timi & Poulin, 2020).

We selected seven phylogenetically disparate fish species from the upper Paraná River floodplain. We considered whether the incorporation of functional and phylogenetic diversity measures, in addition to traditional measures of taxonomic diversity in endoparasites, differs among host species. We compared different facets of biodiversity at the sampling unit level (α diversity or parasite diversity at the level of an individual host) and between sampling units (that is, diversity of parasites within (β1) or between (β2) host individuals of a species). For α diversity, we expect differences mainly at the level of TD and PPD, due to the taxonomic and phylogenetic differences of parasite species between host species. For the β1 level, we expect TD, FD, and PPD diversity to be clustered and similar within each host species. For the β2 level, we expect TD, FD, and PPD to vary between hosts, presenting overdispersed and different patterns between host species.

3.2 Material and Methods

3.2.1 Study area

The upper Paraná River floodplain (22°40'–22°50'S and 53°15'–53°40'W) is located between the Itaipu reservoir (downstream) and the Sérgio Motta dam (locally known as Porto Primavera; upstream). It is considered the last dam-free stretch of the Paraná River, is approximately 250 km long, and covers an area of 5,268 km^2 (Figure 1) (Agostinho et al., 2004; Thomaz et al., 2004; 2007). Its ichthyofauna is composed of approximately 200 species distributed in 126 genera, 41 families, and 10 orders (Ota et al., 2018). The wide variety of habitats and the high biodiversity in the floodplain favor the high diversity of parasites that use fish as intermediate or definitive hosts (Pavanelli et al., 1997).

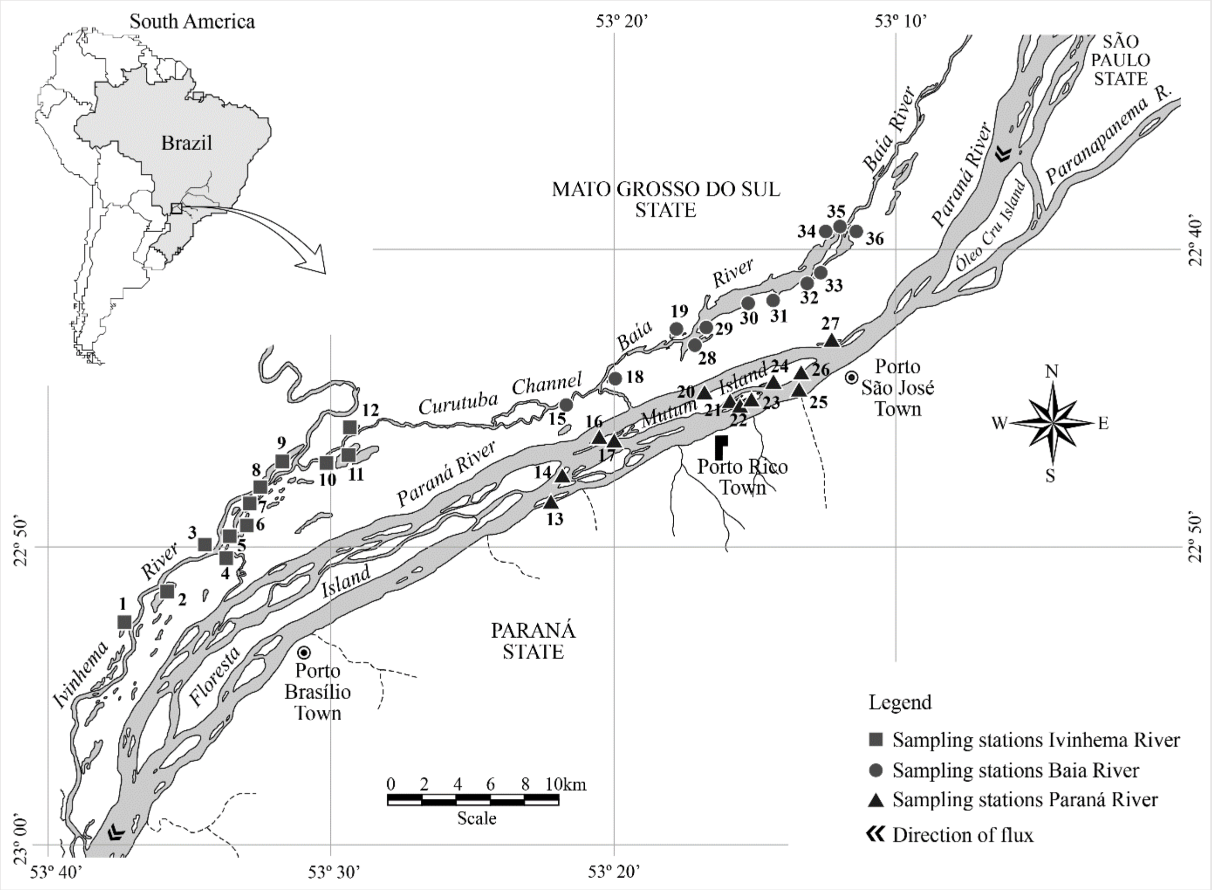

Figure 1: Upper Paraná River floodplain.

*Nupelia field laboratory: Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura. Author: Jaime Luiz Lopes Pereira, 2020.

3.2.2 Data collect

Individuals of *Acestrorhynchus lacustris* (Lütken, 1875), *Leporinus lacustris* Amaral Campos, 1945, *Prochilodus lineatus* (Valenciennes, 1836), *Schizodon borelli* (Boulenger, 1900), *Serrasalmus maculatus* (Kner, 1858), *Steindachnerina insculpta* (Fernández-Yépez, 19 48) and *Trachelyopterus galeatus* (Linnaeus, 1766) were collected in the floodplain of the upper Paraná River, Long Term Ecological Research Site (LTER-CNPq, site 6), between September 2016 and July 2017. The choice of these species was determined based on their taxonomic differences, as it allows us to test whether host factors can select different parasitic life strategies. The capture was carried out with gillnets and afterward, the fish were anesthetized with eugenol (Resolution N^{o}. 1000/12, Federal Council of Veterinary Medicine) and identified (Ota et al., 2018). Necropsy procedures of hosts and collection, conservation, and preparation of parasites were performed according to Eiras et al. (2006). Parasites were identified following

Yamaguti (1958), Travassos et al. (1969), Schmidt (1986), and Moravec (1998). The dataset includes 110 host individuals and an abundance of 25 parasite species. Data on the prevalence, mean intensity, and mean abundance of parasite species in each host species are available in the supplementary material.

3.2.3 Functional traits of parasites (FD)

Functional traits are defined as biological characteristics that influence the organism's performance (Petchey and Gaston, 2002; Díaz et al., 2013), and in this study, functional traits are related to morphology, behavior, and life history. We used five functional traits based on the list developed by Llopis-Belenguer et al. (2019): life stage found in the host (life cycle), organ where the parasite was found in the host (niche space), organ of attachment, presence/absence of digestive system and average body length available in the literature.

We constructed a matrix of parasite functional traits (function dist.ktab from the ade4 package) (Thioulouse et al., 2018) and calculated a Gower’s distance (Gower, 1971) between species. This distance allows the combination of several types of traces (continuous and categorical). Then, we transform the Gower’s distance matrix of Euclidean pairwise distances (lingoes function of the ade4 package) and divided the resulting matrix by its maximum to bound values between 0 and 1 (Pavoine et al., 2009; Llopis-Belenguer et al., 2020).

3.2.4 Proxy for phylogenetic diversity (PPD)

We recorded the seven taxonomic levels (species, genus, subfamily, family, suborder, order, and class), and created a Euclidean pairwise distance matrix between parasite species (tax2dist function from the vegan package) (Oksanen et al., 2019). We divided the resulting distance matrix by its maximum to bound the cell values between 0 and 1. This distance matrix was used as a Proxy for Phylogenetic Diversity (PPD) to estimate the phylogenetic distance between parasite species (Llopis-Belenguer et al., 2020).

3.2.5 Data analysis

Following the approach proposed by Llopis-Belenguer et al. (2020), we analyzed and compared TD, FD, and PPD of the parasitic communities of the seven host species.

We measured the diversity α (function dpcoa from the ade4 package) and transformed these values into their equivalent numbers (Jost, 2006). We test the effects of host species on each facet of α diversity (function lm.rrpp from the RRPP package; Collyer and Adams, 2018), which runs a linear model by residual randomization and provides empirical sampling distributions for additional ANOVAs. Following Collyer and Adams (2018), univariate α values were log-transformed. We then performed ANOVAs (type I sums of squares) using random distributions of the F-statistics (Collyer and Adams, 2018) for TD, FD, and PPD, separately. When significant, pairwise comparisons of α TD, FD, and PPD between host species were performed (pairwise function of the RRPP package). To evaluate whether there was a difference between α TD, α FD and α PPD for each host species, we performed the Kruskal-Wallis test with univariate log α values.

We calculated diversity β at two different organizational levels under the context of the Rao index of diversity (Pavoine et al., 2016). β1 represents the dissimilarity in parasite diversity among individuals of the same host species and β2 represents the dissimilarity in parasite diversity among different host species. In both cases, we calculated the β diversities under the equivalent number approach (Ricotta and Szeidl, 2009), using the third proposition of the Rao index of diversity in Pavoine et al. (2016) (EqRao function of the adiv package; Pavoine, 2020), developed specifically for unbalanced samplings. We compared each of the β1 and β2 diversities of TD, FD, and PPD with 999 randomly simulated permutations of β1 and β2 (βs) (function rtestEqRao from the adiv package), to establish whether the observed values differed significantly from those randomly simulated ($p<0.05$). When significant, we compare the observed and simulated values of β1 and β2, determining whether they are more similar (the observed value is less than the simulated values) or more different (the observed value is greater than the simulated values) (Llopis-Belenguer et al., 2020). Finally, we use standardized β1 and β2 defined as follows:

$$standardised\ \beta 1\ and\ \beta 2\ = \frac{(\text{observed } \beta - \text{mean of randomly simulated } \beta s)}{\text{standard deviation of randomly simulated } \beta s}$$

to indicate whether TD, FD, and PPD are overdispersed (negative standardised β) or clustered (positive standardised β) (Head et al., 2018). The analyzes were performed in the R software (R Core Team, 2022).

3.3 Results

A summary of the results of the ANOVA of the effect of host species on the three facets of infracommunity α-diversity is presented in Table 1. We found significant differences in terms of α TD and α PPD of parasites between fish species. The α FD diversity did not differ significantly between host species (Figure 2). When comparing α TD, α FD, and α PPD of each host species, all hosts showed similar values, and no significant differences were found (Table 2 and Supplementary Material: Figure 1), that is, taxonomic, functional, and phylogenetic values of the parasitic fauna are similar within each host species.

Table 1. Results of Type I ANOVAs of α taxonomic (TD), functional (FD) and proxy for the phylogenetic (PPD) diversity. P values are given (significance level *P* < 0.05).

	F	***P***
TD	2.88	**0.02**
FD	1.47	0.17
PPD	2.36	**0.04**

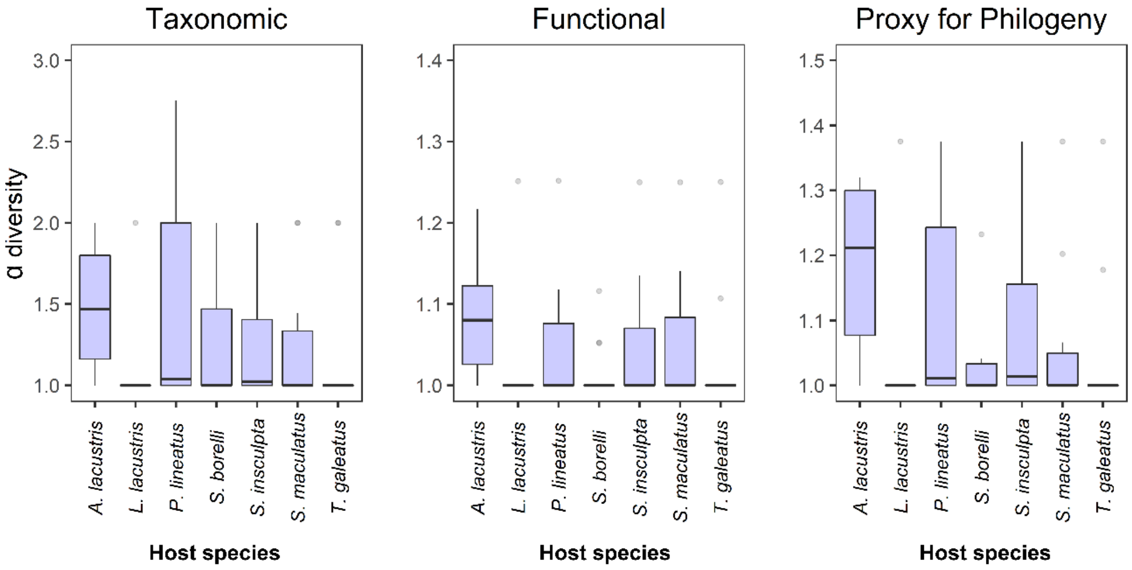

Figure 2. Parasite α diversity in terms of taxonomic (TD), functional (FD) and proxy for the phylogenetic (PPD) diversity for each host individual of each fish species.

Table 2. Kruskal-Wallis test for differences between taxonomic α (TD), functional α (FD) and proxy for the phylogenetic α (PPD) of each fish host species. P values are given at the $p<0.05$ significance level. (df = degrees of freedom; X^2 = chi-squared).

Kruskal-Wallis test	**Df**	**$\chi 2$**	***P***
Acestrorhynchus lacustris	2	4.4	0.11
Leporinus lacustris	2	0.01	0.99
Prochilodus lineatus	2	4.94	0.08
Schizodon Borelli	2	0.34	0.84
Serrasalmus maculatus	2	0.91	0.63
Steindachnerina insculpta	2	0.23	0.88
Trachelyopterus galeatus	2	0.01	0.99

At the β1 level, the parasitic communities of fish of the same species (within the host species) tended to be more similar, as the observed values (Obs) were lower than the simulated values (Std. Obs) (Table 3). Positive β1 values indicate that the community structure is clustered in the host species (Table 3; Figure 3 a-c). At the β2 level (between host species), the parasitic communities differed significantly from randomness, indicating that the similarity of the infracommunities was lower than the simulated values (Table 3; Figure 3 d-f). The positive standardized β2 values reflected that TD, FD, and PPD were clustered at this level of the organizational scale.

Table 3. Statistical results of partitioning taxonomic (TD), functional (FD), and proxy for the phylogenetic (PPD) diversity at two organizational levels: β1 (among host individuals within host species) and β2 (between host species). Obs.: Observed β values; p-value: significance level $p<0.05$; and Std. Obs.: Simulated β values.

	β1			**β2**		
	TD	**FD**	**PPD**	**TD**	**FD**	**PPD**
Obs.	0.32	0.17	0.23	0.53	0.08	0.12
p-value	0.56	0.61	0.64	0.001	0.001	0.001
Std. Obs.	0.57	0.45	0.31	10.34	9.72	11.4

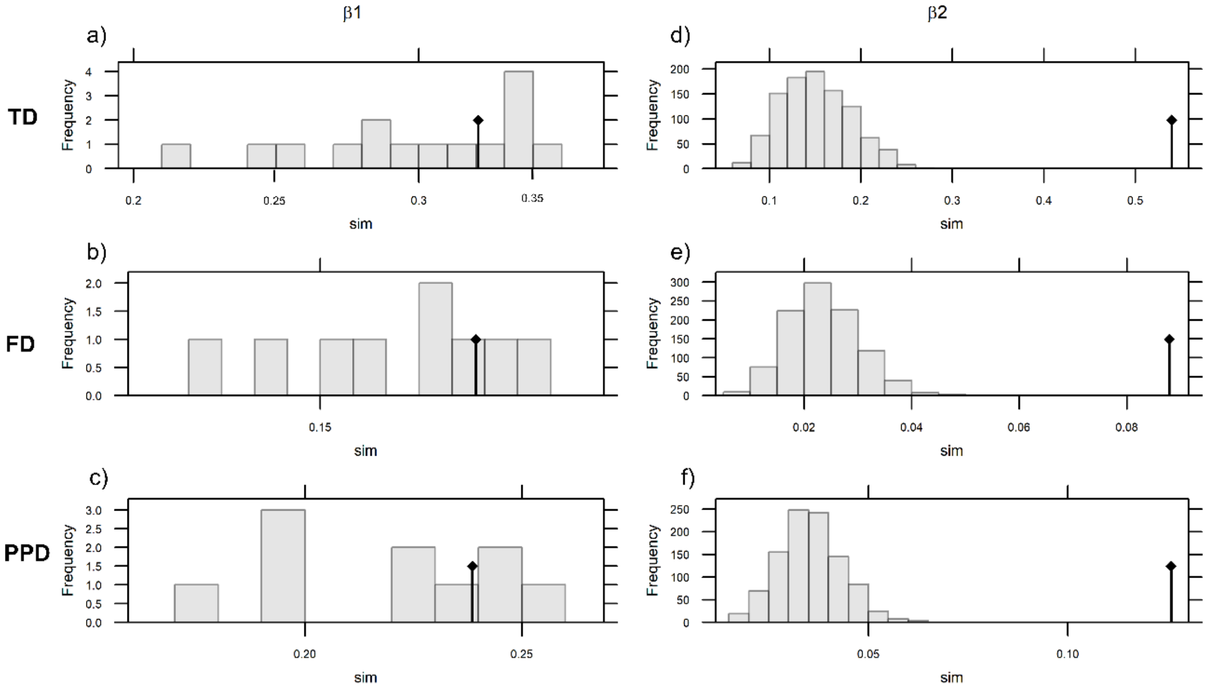

Figure 3. Observed and simulated β diversity values. (a, b, c) β1 diversity or extent of dissimilarity in the diversity of parasite communities between host individuals within each host species. (d, e, f) β2 diversity or extent of dissimilarity in the diversity of parasite communities between host species. Diversity was measured in terms of taxonomic (TD), functional (FD), and proxy for the phylogenetic (PPD) diversity. Observed β values (black diamond on top of the black vertical line) and distribution of simulated β values (x-axis: gray bars).

3.4 Discussion

The α-diversity of endoparasite species differed mainly in terms of TD and PPD. As for β-diversity, the parasitic communities showed clustered patterns at different levels (β1 and β2, respectively). These results suggest that the composition of endoparasite infracommunities, in terms of species and phylogeny, is strongly affected by the characteristics of the host species, which are determining factors for the acquisition of these parasites, mainly because they depend on trophic interactions to reach their hosts.

Host assemblages that share many parasites are more likely to include species with similar activity patterns (Moreno-García & Baiser, 2021). Parasites can contribute differently to TD, FD, and PPD as in other biological communities. For example, two parasites from different taxonomic groups that coexist, may have similar functional traits and, therefore, may contribute less at a functional level, but may contribute more at a taxonomic and phylogenetic level (Webb et al., 2002; Wong et al., 2018). We verified that α FD probably did not differ because some parasite species can be functionally redundant. However, these species share roles in all ecological functions and play multiple roles in an ecosystem through their biotic and abiotic interactions. More generally, the idea that functionally similar species cannot coexist has rarely been supported when considering the entire community (Kingston et al., 2000; Stubbs & Wilson, 2004; Mouillot et al., 2005) and at the infracommunity level, it can be highlighted that species that are closely related, show differences in morphological characteristics, which influence the use of resources (Schluter, 2000).

The effect of host species on endoparasites is mainly related to the functional proximity between feeding guilds, as many endoparasites are transmitted trophically (Lafferty, 1999; Lagrue et al., 2011; Lima et al., 2016; Lehun et al., 2023). Species that share food sources often use similar habitat types, consequently, ecological convergence may play a key role in the taxonomic diversification of parasite assemblages (Benesh et al., 2014; Marcogliese, 2002; Poulin, 2004; Carrassón et al., 2019). Thus, hosts provide resources and this environment is represented by abiotic and biotic variables, and in this case, the host can act as an environmental filter in parasite communities (Krasnov et al., 2014).

The taxonomic dissimilarity of the parasite species, mainly at the TD and PPD levels, can also be explained by the phylogenetic difference of the hosts. Some parasite species exhibit specificity for certain host species, and indeed, specific parasites may decrease the similarity between infracommunities within different host species (Luque et al., 2004; Muñoz et al., 2006). Changes in host species distributions can have different effects on parasite dispersal depending on the evolutionary history of the host, thus, host phylogeny can act as an important environmental barrier in the formation of parasite turnover (Clark et al., 2018). However, phylogenetically distant hosts can provide the same resource for parasites if they share the same habitat, as is the case in the floodplain. In these cases, the parasitic communities may show some similarity (which may explain the similarity in FD), where we see the same species of generalist parasites in different host species (Locke et al., 2013; D'Bastiani & Campião, 2021). Thus, the composition of species in infracommunities may be the result of simultaneous actions of these factors related to the host species (Combes, 2001), which are shown to be a determining force.

The positive standardized observations at the β1 and β2 levels are similar to those found by Krasnov et al. (2021) and Llopis-Belenguer et al. (2020) and indicate that TD, FD, and PPD were grouped, that is, the species, characteristics and phylogenetic compositions of parasite communities depend on the host species. Llopis-Belenguer et al. (2020) report that the host species is the more determining factor of the parasite community than the locality, at least for

TD, since the parasite communities of different host species can overlap in the FD and PPD spaces.

We expected that at level β2 the parasite species would present a superdispersed and different pattern of TD, FD, and PPD among the host species, indicating that each host presented a particular parasite fauna. However, these study, some parasites seem to co-occur more or less frequently than expected by chance, in addition, the positive standardized value of β1 and β2 TD indicates that parasite species that share the same resources are coexisting. If an environment presents high heterogeneity, it can weaken or prevent competitive exclusion, even among species with identical responses to the environment (Kohler, 1992; Litchman et al., 2004; Adler et al., 2013; Segre et al., 2014). More generally, all the mechanisms that improve the coexistence of species, such as the floodplain that undergoes drought and flood events, increasing the variability between environments, are capable of predicting the occurrence of similar patterns (Chesson et al., 2004; Thomaz et al., 2007).

Parasite alpha and beta diversity are expected to follow host diversity due to the obvious reasons that (1) a parasite's main habitat is its host and (2) even though generalist parasites infect multiple hosts, these can exploit only a limited set of host species (Combes, 2001; Poulin et al., 2011). We conclude that assembly patterns in endoparasite infracommunities of different floodplain host species mirror those characteristics of their component and composite communities. These results contribute to the understanding of how different facets can vary in the parasitic community, as these studies are rarely reported for parasitic communities. Thus, to prevent conclusions from studies with parasite communities from being biased and neglected (Jarzyna and Jetz, 2016; Timi & Poulin, 2020), all facets must be included.

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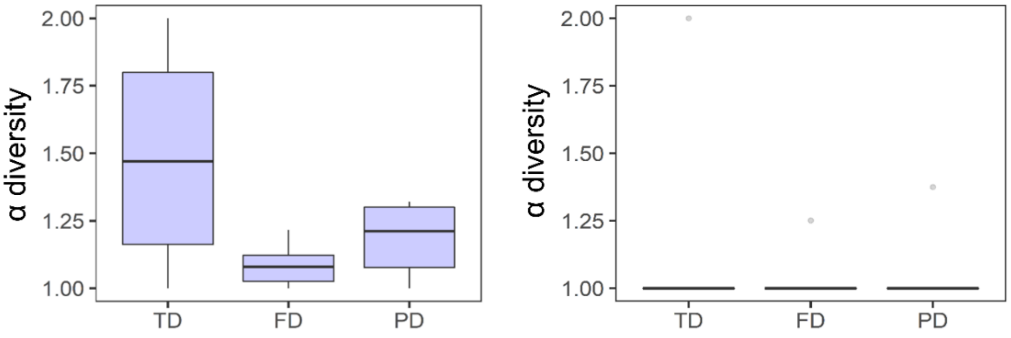
Supplementary Material

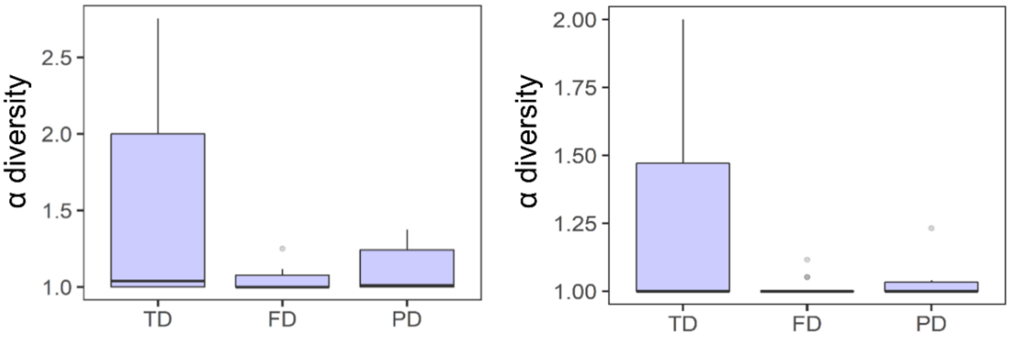
Table S1: Prevalence (P), Mean Intensity (MI) and Mean Abundance (MA) of fish parasites in the upper River Paraná floodplain.

Host	Parasite	P(%)	MI	MA
Acestrorhynchus lacustris	*Contracaecum* sp.	50	2	1
	Eustrongylides sp.	10	1	0.1
	Quadrigyrus brasiliensis	50	3.4	1.7
	Rhipidocotyle gibsoni	20	2.5	0.5
Leporinus lacustris	*Contracaecum* sp.	17.85	1.4	0.25
	Echinorhynchus salobrensis	3.57	1	0.03
	Hysterothylacium sp.	7.14	4	0.32
	Proteocephalus vazzolerae	7.14	1	0.07
Prochilodus lineatus	*Colocladorchis ventrastomis*	31.7	1.84	0.58
	Contracaecum sp.	2.46	1	0.02
	Neoechinorhynchus curemai	60.79	2.24	1.36
	Neoechinorhynchus prochilodorum	17.07	2.14	0.36
	Saccocoelioides sp.	4.87	1.5	0.73
	Saccocoelioides magnorchis	2.46	5	0.12
	Saccocoelioides nanii	12.19	6.4	0.78
	Saccocoelioides saccodontis	12.19	2.2	0.27
Schizodon borelli	*Contracaecum* sp.	2.7	3	0.08
	Cucullanus pinnai pinnai	8.1	3.6	0.29
	Megacoelium plecostomi	2.7	1	0.05
	Octospiniferoides incognita	5.55	4	0.22
	Paralecithobothrys brasiliensis	8.1	23.3	1.89
	Procamallanus (Spirocamallanus) inopinatus	2.7	1	0.05
	Saccocoelioides magniovatus	16.21	15.6	2.51
Serrasalmus maculatus	*Contracaecum* sp.	23.8	2.2	0.35
	Echinorhynchus salobrensis	12.9	6.5	0.83
	Eustrongylides sp.	9.6	1	0.09
	Procamallanus (Spirocamallanus) inopinatus	3.22	1	0.03
Steindachnerina insculpta	*Cosmoxynema vianai*	50	2	1
	Quadrigyrus brasiliensis	8.33	1	0.08
	Sphincterodiplostomum musculosum	63.6	17.81	17.81
	Travnema travnema	25	2.33	2.33
Trachelyopterus galeatus	*Cangatiella arandasi*	3.33	1	0.03
	Eustrongylides sp.	3.33	1	0.03
	Microrchis oligovitellum	76.66	1.7	1.3
	Quadrigyrus brasiliensis	3.33	1	0.03

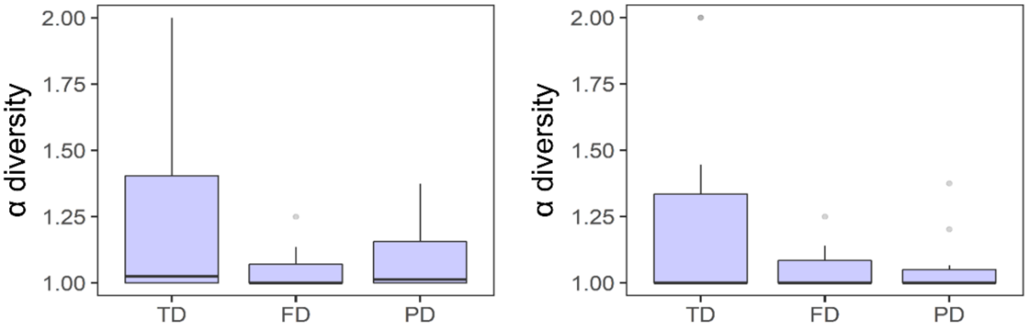
Figure S1: Parasite α diversity in terms of taxonomic, functional and a proxy for the phylogenetic diversity among each host fish species.



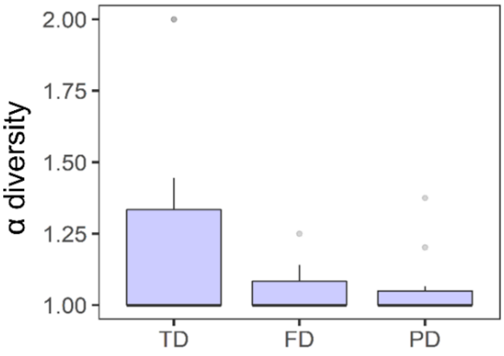
A. lacustris *L. lacustris*



P. lineatus *S. borelli*



S. insculpta *S. maculatus*



T. galeatus

4 FINAL CONSIDERATIONS

The host-determining parasitic fauna results from variations in host characteristics, phylogenetic relationships, and environmental characteristics. These can be examined at different levels of diversity: alpha (local diversity) and beta (variation in community composition between locations), including multiple facets, such as taxonomic (TD), functional (FD), and phylogenetic (PD).

The results indicated that the host's diet was the factor that had the greatest influence on the composition and similarity of endoparasites in floodplain fish, but that together with the functional characteristics and phylogeny of the host, they can act as drivers of the structure of the parasite community.

In the α diversity of endoparasite species, we found differences mainly in terms of TD and PPD, indicating that parasites may contribute differently to TD, FD, and PPD as in other biological communities and host assemblages that share many parasites are more likely to include species with similar activity patterns. As for β diversity, the parasite communities presented patterns grouped at different levels (β1 and β2, respectively), indicating that some parasites seem to co-occur with greater or lesser frequency than expected by chance, in addition, the positive standardized value of β1 and β2 TD indicates that parasite species that share the same resources are coexisting.

Expected assembly patterns in endoparasite infracommunities of different floodplain host species are expected to reflect the characteristics of their component and composite communities, and parasite alpha and beta diversity follow host diversity and diet, the functional traits and phylogeny can be predictors of the parasite community.

COMPLEMENTARY INFORMATIONAL NOTE – List of activities performed and published papers during the thesis

EDUCATION

1. Experiências do doutorado no exterior. Palestra proferida ao Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais – Universidade Estadual de Maringá, Maringá, PR. 2022.

2. Participação como membro titular da banca examinadora de defesa de Trabalho de Conclusão de Curso da aluna Fabricia da Silva Lima. Título: Helmintos parasitas de *Hoplias malabaricus* (Bloch, 1794) em áreas da Amazônia Brasileira com diferentes graus de desmatamento. Graduação em Ciências Biológicas - Universidade Federal do Acre. 2022.

3. Membro da Comissão de Avaliação dos Projetos de Mestrado do XXV EPGPEA - Encontro de Pós-Graduandos do Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, realizado no dia 31 de outubro de 2022.

4. Tutora-orientadora de projetos de Mestrado apresentados pelos pós-graduandos durante o XXIV EPGPEA - Encontro de Pós-Graduandos do Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, realizado nos dias 25 e 26 de janeiro de 2022.

5. Membro da Comissão de Avaliação dos Projetos de Mestrado do XXIII EPGPEA - Encontro de Pós-Graduandos do Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, realizado entre os dias 26 e 28 de outubro de 2020.

6. Participação como membro titular da banca examinadora de defesa de Trabalho de Conclusão de Curso da aluna Larissa Lechinovski. Efeitos ecotoxicológicos do herbicida atrazina e herbicida natural no modelo biológico *Danio rerio*. Graduação em Ciências Biológicas - Universidade Estadual do Paraná. 2020.

7. Participação no curso de Extensão: Modelos Regressivos e Análises Multivariadas. 2020.

8. Participação projeto PELD - A Planície de Inundação do Alto Rio Paraná (PELD)/CNPq.

PUBLISHED PAPERS

1. **LEHUN, A. L.**; MUNIZ, C. M.; SILVA, J. O. S.; CAVALCANTI, L. D.; TAKEMOTO, R. M. The functional traits of host fish can act as good predictors for parasite composition in a Neotropical floodplain. **Journal of Fish Biology**, v. 79, p. 466-485, 2023.

2. **LEHUN, A. L.**; SILVA, J. O. S.; MICHELAN, G.; LANSAC'TÔHA, F. M.; CAVALCANTI, L. D.; TAKEMOTO, R. M. The occurrence of trophically transmitted parasites is influenced by the trophic level and body size of the fish host. **Ecology of Freshwater Fish**, v. 32, p. 1-8, 2023.

3. **LEHUN, A. L.**; DUARTE, G. S.; TAKEMOTO, R. M. Nematodes as indicators of environmental changes in a river with different levels of anthropogenic impact. **Anais da Academia Brasileira de Ciências**, v. 95, p. e20200307, 2023.

4. CASALI, G. P.; SANTOS SILVA, J. O.; **LEHUN, A. L.**; CAVALCANTI, L. D.; MICHELAN, G.; CAPPARROS, E. M.; TAKEMOTO, R. M. Infection pattern of *Echinorhynchus salobrensis* (Acanthocephala) in congeneric piranha species from a Neotropical floodplain region. **Folia Parasitologica**, v. 70, p. 022, 2023.

5. CAVALCANTI, L. D.; GOUVEIA, É. J.; MICHELAN, G.; **LEHUN, A. L.**; SILVA, J. O. S.; HASUIKE, W. T.; RUSSO, M. R.; TAKEMOTO, R. M. Components influencing parasitism by *Dadaytrema oxycephala* (Digenea: Cladorchiidae) in Neotropical fish. **Parasitology Research**, v. 122, p. 1221-1228, 2023.

6. MICHELAN, G.; HASUIKE, W. T.; CAVALCANTI, L. D.; **LEHUN, A. L.**; SILVA, J. O. S.; TAKEMOTO, R. M. First record of two Copepoda species parasitizing *Colomesus tocantinensis* (Tetraodontiformes: Tetraodontidae) in the Tocantins-Araguaia basin, Brazil. **Revista Brasileira de Parasitologia Veterinária**, v. 32, p. e006523, 2023.

7. MICHELAN, G.; **LEHUN, A. L.**; MUNIZ, C. M.; TAKEMOTO, R. M. Absence of parasites in non-native fish from a Neotropical floodplain: evidence for the enemy release hypothesis. **Environmental Biology of Fishes**, v. 106, p. 1879-1888, 2023.

8. **LEHUN, A. L.**; CAVALCANTI, L. D.; LIZAMA, M. D. L. A. P.; SILVA, J. O. S.; CASALI, G. P.; TAKEMOTO, R. M. Temporal effects and changes in the parasitic community of *Prochilodus lineatus* (Valenciennes, 1837)(Characiformes: Prochilodontidae) in a floodplain. **Journal of Helminthology**, v. 96, p. e4, 2022.

9. DE FÁTIMA CRACCO, A.; **LEHUN, A. L.**; TAKEMOTO, R. M. Composition and structure of the parasitic fauna of *Hypostomus* spp. (Loricariidae: Hypostominae) from a Neotropical river in Brazil. **Parasitology Research**, v. 121, p. 2253-2262, 2022.

10. **LEHUN, A. L.**; MENDES, A. B.; TAKEMOTO, R. M.; BUENO KRAWCZYK, A. C. D. D. Genotoxic effects of urban pollution in the Iguaçu River on two fish populations. **Journal of Environmental Science and Health, Part A**, v. 56, p. 984-991, 2021.

11. SILVA, J. O. S.; **LEHUN, A. L.**; RODRIGUES, A. D. F. C.; CAVALCANTI, L. D.; NICOLA, D. N.; HASUIKE, W. T.; TAKEMOTO, R. M. Investigating the diversity of fish parasites in the floodplain of the upper Paraná River: a long-term ecological monitoring. **Acta Limnologica Brasiliensia**, v. 33, 2021.

12. **LEHUN, A. L.**; NOLETO, R. B.; MODA, D. B.; KRAWCZYK, A. C. D. D. B. Effects of phenol on *Astyanax bifasciatus* and *Daphnia magna*. **Oecologia Australis**, v. 24, p. 590-600, 2020.

13. **LEHUN, A. L.**; HASUIKE, W. T.; SILVA, J. O. S.; CICCHETO, J. R. M.; MICHELAN, G.; RODRIGUES, A. D. F. C.; NICOLA, D. N.; DUARTE DE LIMA, L.; CORREIA, A. N.; TAKEMOTO, R. M. Checklist of parasites in fish from the upper Paraná River floodplain: an update. **Revista Brasileira de Parasitologia Veterinária**, v. 29, p. e008720, 2020.

14. DUARTE, G. S. C.; **LEHUN, A. L.**; LEITE, L. A. R.; CONSOLIN-FILHO, N.; BELLAY, S.; TAKEMOTO, R. M. Acanthocephalans parasites of two Characiformes fishes as

bioindicators of cadmium contamination in two neotropical rivers in Brazil. **Science of the Total Environment**, v. 738, p. 140339, 2020.

Book chapter

CAVALCANTI, L. D.; LEHUN, A. L.; MICHELAN, G.; HASUIKE, W. T.; SILVA, J. O. S.; LIMA, L. D.; BALABUCH, E.; CORREIA, A. N.; GROU, C. E. V.; SCORSIM, I. A.; BOLLER, L. L. A.; NICOLA, D. N.; LIZAMA, M. L. A. P.; TAKEMOTO, R. M. Parasitas de *Piaractus mesopotamicus*, *P. brachypomus* e *Colossoma macropomum* (Serrasalmidae) e seus híbridos em ambiente de cultivo. In: PILARSKI, F.; TAVARES, G. C.; VALLADÃO, G. M. R.; DOTTA, G.; LIZAMA, M. L. A. P.; TAKEMOTO, R. M. (Org.). Sanidade de Organismos Aquáticos: Avanços no diagnóstico, controle e monitoramento de doenças. 1 ed. Maringá: ABRAPOA, 2023, p. 165-176.

EXTENSION

1. “ Conversa com o cientista e um dia na universidade” – Semana Nacional de Ciências e Tecnologia, Nupelia, Maringá, 2023.

2. UEM na Expoingá – mostra científica de diferentes grupos biológicos durante a Expoingá, Pró-Reitoria de Extensão e Cultura da UEM, Maringá, PR. 2023.

3. Participação da divulgação em mídias sociais do projeto SOS Riachos. 2022 e 2023.

4. Mostra científica promovida pelo PELD/CNPq – UEM – Nupélia – PEA na sede do Parque Estadual das Várzeas do Rio Ivinhema e na Base Avançada do Nupélia, Porto Rico. 2019 e 2022.

EVENTS AND ABSTRACTS

1. IV Congreso Iberoamericano de Limnología y X Congreso Argentino de Limnología. Resumo: Variação da diversidade taxonômica, funcional e filogenética de endoparasitas de peixes de uma planície neotropical. 2023. (Congresso).

2. XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos. Resumo: Fatores que influenciam na abundância de parasitas encontrados em *Hypostomus* spp. (loricariidae: hypostominae) na América do Sul, brasil. 2023. (Encontro).

3. XXIV Encontro Brasileiro de Ictiologia. Resumo: Determinantes da estrutura da comunidade de endoparasitas de peixes em uma planície neotropical. 2022. (Congresso).

4. XVI Congresso Brasileiro de Ecotoxicologia. 2021. (Congresso Online).

5. SILVA, J. O. S.; CASALI, G. P.; **LEHUN, A. L.;** MICHELAN, G.; CAVALCANTI, L. D.; LIMA, L. D.; GROU, C. E. V.; CAPPARROS, E. M.; BALABUCH, E.; TAKEMOTO, R. M. Índices parasitários de *Echinorhynchus salobrensis* machado filho, 1948 (acanthocephala) em espécies de piranhas congenéricas de uma planície neotropical. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

6. LIMA, L. D.; CAVALCANTI, L. D.; SILVA, J. O. S.; MICHELAN, G.; **LEHUN, A. L.;** HASUIKE, W. T.; BALABUCH, E.; GROU, C. E. V.; NICOLA, D. N. TAKEMOTO, R. M. Primero Registro de *Haementeria* sp. (Glossiphoniidae) ectoparasitas de peixes redondos no Rio Ivinhema bacia do Rio Paraná, Mato Grosso do Sul, Brasil. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

7. CAVALCANTI, L. D.; MICHELAN, G.; **LEHUN, A. L.;** BALABUCH, E.; LIMA, L. D.; SILVA, J. O. S.; HASUIKE, W. T.; PASSERE, M. D.; RUSSO, M. R.; TAKEMOTO, R. M. Fauna endoparasitária de pacu (*Piaractus mesopotamicus*), pirapitinga (*Piaractus brachypomus*) e híbridos pirapicu (*P. brachypomus* ♀ x *P. mesopotamicus* ♂) e tambacu (*Colossoma macropomum* x *Piaractus mesopotamicus*) no alto rio paraná. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

8. MICHELAN, G.; CAVALCANTI, L. D.; **LEHUN, A. L.;** HASUIKE, W. T.; LIMA, L. D.; SILVA, J. O. S.; BALABUCH, E.; PASSERE, M. D.; GROU, C. E. V.; TAKEMOTO, R. M. Levantamento da fauna endopasitária do híbrido pirapicu (*Piaractus brachypomus* x *Piaractus mesopotamicus*) do Rio Ivinhema, Brasil. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

9. **LEHUN, A. L.;** RODRIGUES, A. F. C.; BALABUCH, E.; MICHELAN, G.; SILVA, J. O. S.; LIMA, L. D.; CAVALCANTI, L. D.; HASUIKE, W. T.; NICOLA, D. N.; TAKEMOTO, R. M. Fatores que influenciam na abundância de parasitas encontrados em *Hypostomus* spp.

(Loricariidae: Hypostominae) na América Do Sul, Brasil. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

10. HASUIKE, W. T.; SCORSIM, B.; SCORSIM, I. A.; AMARAL, R. B.; SILVA, L. D.; MICHELAN, G.; CAVALCANTI, L. D.; **LEHUN, A. L.;** OLIVEIRA, A. V.; TAKEMOTO, R. M. Nova espécie de *Tereancistrum* Kritsky, Thatcher & Kayton, 1980 (Monogenea: Dactylogyridae) parasita de brânquias de *Brycon nattereri* (Characiformes, Bryconidae) do Cerrado Brasileiro. In: XVII Encontro Brasileiro de Patologistas de Organismos Aquáticos, Belo Horizonte, 2023.

11. **LEHUN, A. L.;** SILVA, J. V. F.; SILVA, J. O. S.; BREDARIOL, J. V.; TAKEMOTO, R. M. Variação da diversidade taxonômica, funcional e filogenética de endoparasitas de peixes de uma planície neotropical. In: IV Congreso Iberoamericano de Limnología y X Congreso Argentino de Limnología, Buenos Aires, 2023.

12. **LEHUN, A. L.;** MUNIZ, C. M.; SILVA, J. O. S.; CAVALCANTI, L. D.; MICHELAN, G.; HASUIKE, W. T.; NICOLA, D. N.; BOLLER, L. L. A.; TAKEMOTO, R. M. Determinantes da estrutura da comunidade de endoparasitas de peixes em uma planície neotropical. In: XXVI Encontro Brasileiro de Ictiologia, Gramado, 2022.

13. MICHELAN, G.; CAVALCANTI, L. D.; HASUIKE, W. T.; **LEHUN, A. L.;** NICOLA, D. N.; TAKEMOTO, R. M. Parasitofauna do bagre invasor *Trachelyopterus galeatus* (Linnaeus, 1766) de uma planície Neotropical é alterada após 27 anos. In: XXVI Encontro Brasileiro de Ictiologia, Gramado, 2022.

14. CAVALCANTI, L. D.; LIMA, L. D.; HASUIKE, W. T.; **LEHUN, A. L.;** MICHELAN, G.; BOLLER, L. L. A.; TAKEMOTO, R. M. Marcadores genéticos evidenciam a presença de híbridos de *Piaractus* no rio Ivinhema: uma ameaça a biodiversidade. In: XXVI Encontro Brasileiro de Ictiologia, Gramado, 2022.

15. BOLLER, L. L. A.; NICOLA, D. N.; SILVA, J. O. S.; MICHELAN, G.; RODRIGUES, A. F. C.; **LEHUN, A. L.;** LIMA, L. D.; TAKEMOTO, R. M. Primeiro registro de *Procamallanus (Spirocamallanus) inopinatus* Travassos, Artigas & Pereira, 1929 em *Brycon falcatus* Müller

& Troschel, 1844 da Bacia Amazônica. In: XXVI Encontro Brasileiro de Ictiologia, Gramado, 2022.

16. HASUIKE, W. T.; MICHELAN, G.; **LEHUN, A. L.;** CAVALCANTI, L. D.; RODRIGUES, A. F. C.; TAKEMOTO, R. M. Fauna endoparasitária do peixe invasor *Trachelyopterus galeatus* (Linnaeus, 1766) no rio Paraná. In: Encontro Brasileiro de Patologistas de Organismos Aquáticos, Online, 2021.