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Randomness of component communities of parasites of fish in a neotropical floodplain

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Abstract. The distribution of organisms within communities is one of the most studied topics in Ecology, including the Ecology of Parasites. The present study tested the hypothesis that major groups of enteric parasites of fish (Digenea, Cestoda, Nematoda and Acanthocephala) show random distribution in the environment, indicating the possible absence of interactions between these groups structuring the community. In total, 1588 examined fish from 96 different species were collected in seven sampling stations in the floodplain of the upper Paraná River (including open lagoons, closed lagoons and rivers), quarterly, from March 2004 to December 2007. Matrices of presence-absence, where groups of parasites were arranged in rows and hosts in columns, were analyzed by the *C*-score index (a null model) using the FF (fixed-fixed) algorithm, revealing the random distribution to nearly all levels and sampling stations considered, except for one closed lagoon. For this location, there was positive association between the groups Digenea and Nematoda, evidenced by the statistical chi-square. The null distribution of the groups was confirmed, but additional studies focusing on other aspects of the community are suggested.

Keywords: co-ocurrence, distribution patterns, endoparasites, null model, upper Paraná River

Resumo. Aleatoriedade de comunidades componentes de parasitos de peixes em uma planície de inundação neotropical. Como os organismos estão distribuídos dentro das comunidades é um dos tópicos mais estudados na Ecologia, inclusive na Ecologia de Parasitos. O presente estudo testou a hipótese de que os principais grupos de parasitos entéricos de peixes (Digenea, Cestoda, Nematoda e Acanthocephala) mostram distribuição aleatória no ambiente, indicando a provável ausência de interações estruturando a comunidade. No total, 1.588 peixes de 96 espécies foram examinados, provenientes de sete estações de amostragem na planície de inundação do alto rio Paraná (incluindo lagoas abertas, lagoas fechadas e rios), coletados trimestralmente de março de 2004 a dezembro de 2007. Matrizes de presença-ausência, onde grupos de parasitos foram dispostos em linhas e colunas em hospedeiros, foram analisados pelo índice C-score (um modelo nulo), utilizando o algoritmo FF (fixo-fixo), revelando a distribuição aleatória de quase todos os níveis e estações de amostragem consideradas, exceto por uma lagoa fechada. Para este local, houve associação positiva entre os grupos Digenea e Nematoda, evidenciado pela estatística qui-quadrado. A distribuição nula dos grupos foi confirmada, mas estudos com maior precisão taxonômica e focando em outros aspectos da comunidade são sugeridos.

Palavras chave: co-ocorrência, padrões de distribuição, endoparasitos, modelos nulos, alto rio Paraná

Introduction

A major issue addressed by ecologists is to understand how species are distributed within communities. In an attempt to answer this question, in the last 30 years ecologists became interested by null models and started to apply them to the mechanisms studied by community ecology (Gotelli and Graves 1996). A null model consists of a technique to generate patterns based on randomization of data and is defined considering the ecological processes of interest. In the model, certain elements can be fixed or vary stochastically in order to create new patterns. Such models confront a matrix of real data with randomly generated matrices, measuring how much the organization of real communities is similar to randomized distributions (Gotelli and Graves 1996).

In the null models applied to biological communities, there are two possibilities: the real data can be statistically similar to the data generated randomly or it may be different, in this case presenting less or more associations of species pairs than expected at a random matrix. The first case is interpreted as an indicator of the absence of interspecific interactions structuring the distribution of organisms. On the other hand, if biological interactions within communities are significant, there should be less or more combinations of species than expected within a suitable null model (Connor and Simberloff 1986; Gotelli and Graves 1996). When combinations of species occur less in real communities than expected at random, competition is considered the factor responsible for the distribution patterns (Diamond 1975). If the opposite is observed and the species pairs occur more in real matrices than would be expected by chance, aggregation mechanisms (*e.g.* facilitation) may be structuring the community (Krasnov *et al.* 2006).

Parasites are considered excellent material for investigations on the structure of communities using null models, because hosts are habitats with well-defined borders, and various communities, replicates of the same host species, can be collected with relative facility (Gotelli and Rohde 2002; Tello *et al.* 2008). Despite the consensus that parasites of the same species tend to aggregate distribution (Kennedy 2009), *i.e.*, few hosts harbor large numbers of parasites, while many hosts harbor few parasites or are not parasitized, the distribution patterns of infracommunities and component communities are still obscure (parasitological terminology follows Bush *et al.* (1997). Considering the supracommunity level, some studies using null models showed random patterns (Gotelli and Rohde 2002; Mouillot *et al.* 2005; Kennedy 2009), suggesting that parasites are randomly distributed, independent of interspecific relationships (Poulin 1996). Others reveal a tendency for aggregation (Lotz and Font 1991; Leung 1998; Krasnov *et al.* 2006; Tello *et al.* 2008), or even segregation, pointing competition as the key factor (Friggens and Brown 2005). There are also studies using comparison of indices with contradictory results (Haukisalmi and Henttonen 1998, Krasnov *et al.* 2010a). Thus, the patterns structuring parasite communities do not present much definition yet, and the common classification of individual hosts in natural populations as infected or uninfected considering only one parasite alone fails to recognize that much more may be implied by the categorization “infected” (Telfer *et al.* 2010).

In this study we use large groups of parasites (Digenea, Cestoda, Nematoda and Acanthocephala), taking off the focus on interspecific interactions and emphasizing taxonomic groups that are part of the same guild (Root 1967). The group approach was used because the priority was to analyze long term data, which was only available at low taxonomic resolution. These four different groups of endoparasites use fishes as intermediate and/or final hosts, have autogenic and allogenic life cycles and have the viscera as common site of infection, allowing some degree of comparison. These groups can therefore be considered as an enteric guild (Bush *et al.* 1997) by exploiting the same class of environmental resources in a similar and comparable way. Moreover, the need for studies considering larger taxa instead of species of parasites and using a variety of host species has already been pointed out by Krasnov *et al.* (2010b). It is important to consider that, in this context of using major taxonomic groups and different species of hosts, aggregation/segregation could mean convergence/divergence of factors favoring/disfavoring pairs of groups within an environment, instead of the facilitation/competition proposed to justify nonnull patterns at specific levels. The objective was to determine if parasite groups are randomly distributed or if they exhibit patterns of distribution in a wide area, considering different environments and different host species. The null hypothesis is that the distribution of parasites is random considering different types of environment (lagoons, channels and rivers) and different host species (94), using the null model index C-score and the algorithm FF (fixed-fixed). The prediction is that if local factors have similar effects over the parasite community, the groups will be randomly distributed within the environments. Since our results are based on major groups of the regional component community, the analyses of other guilds (ectoparasites, different infection sites) should lead to different results.

Material and Methods

Study area

The study area is part of the floodplain of the upper Paraná River, between the states of Parana and Mato Grosso do Sul (22°43'S and 53°10'W), Brazil. The region is composed of heterogeneous environments such as open and closed lagoons, channels and rivers, where the following points were sampled: Ivinheima River, Ventura Lagoon, Patos Lagoon, Fechada Lagoon, Guaraná Lagoon, Baía River and Paraná River (Figure1).

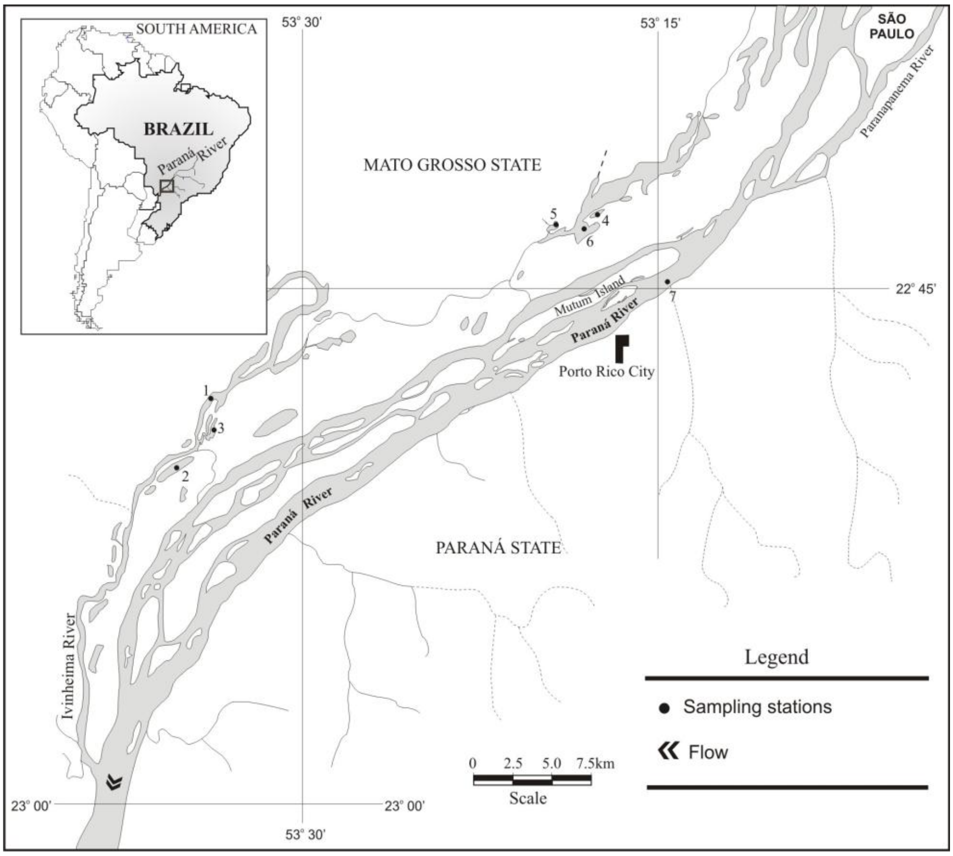

Figure 1. Upper Paraná River floodplain. Sampling stations: 1-Ivinheima River; 2-Ventura Lagoon; 3-Patos Lagoon; 4-Fechada Lagoon; 5-Guaraná Lagoon; 6-Baía River; 7-Paraná River.

Sampling of hosts and parasites

Fish were collected using gill nets of different mesh sizes, located in different parts of the floodplain, exposed for 24 hours. The collections were part of the research project LTER (Long Term Ecological Research - site 6/National Council for Research and Development) and were performed quarterly, from March 2004 to November 2007. Within each set of fish caught by the nets, some were randomly selected for necropsy. At least one specimen of each species of fish was selected in each sampling station.Hosts were sacrificed and their guts were examined under stereomicroscope according to the methodology described by Eiras *et al.* (2002). The presence or absence of the metazoan groups Digenea, Cestoda, Nematoda and Acanthocephala were recorded, at any stage of development, for each specimen of fish. The present work considered only enteric parasites, because it was the only site of infection examined in absolutely all the fish in the analysis.

Null model analysis of co-occurrence

To test the null hypothesis of random structure of communities of parasites, we used a null model of co-occurrence based on presence-absence matrices. Eleven presence-absence matrices were analyzed, where each column represented one host and each line represented one group of parasites. Number "1" meant the presence of the parasite, while "0" demonstrated its absence. Co-occurrence patterns were analyzed at three levels: considering the floodplain of the Paraná River as a whole, the types of environments (open lagoons, closed lagoons and rivers) and each of the seven sampling stations separately. Originally there were 11 sampling stations, but the environments kept for analysis were those in which all groups of parasites were present, thereby maximizing the probability of each host to be colonized by parasites of all the groups.

The index of co-ocurrence C-score (Checkerboard score) proposed by Stone and Roberts (1990) was used. This index calculates the number of checkerboard units (units of pairs that do not co-occur) per pair of groups within the matrix, and also the empirical average of the numbers of these units found for the matrices generated randomly. When the observed C-score (empirical matrix) did not differ significantly from the expected (random matrix), the null hypothesis was accepted, indicating the absence of interactions structuring the community. On the other hand, when the observed C-score differed significantly from the expected, the null hypothesis was rejected and there was evidence of aggregation (obs.<exp.) or segregation (obs.>exp.) of species (Krasnov *et al.* 2006), in our case groups. This index, used with the algorithm FF (fixed rows-fixed columns), was considered by Gotelli (2000) the less vulnerable to type I errors and less prone to sampling problems.

The real data matrix was randomized to produce random patterns, which theoretically would be found in nature in the absence of physical or biological interactions (Gotelli & Graves 1996). To perform the randomizations, the sums of rows and columns of the empirical matrix (real data) was maintained in the randomized matrices using the algorithm FF (fixed rows-fixed columns). This way the differences between the wealth of the hosts (columns total) and the occurrence of the groups (lines total) were retained, while the occurrences were randomized, making the model suitable for detecting patterns caused by biological interactions (Gotelli 2000). Moreover, by using the FF algorithm the non parasitized hosts were interpreted as hosts inappropriate for colonization, and not as hosts that are not parasitized at random (Gotelli & Rohde 2002). This interpretation was used because the analysis includes different host species, with probable interspecific variation in the susceptibility to parasitism. The number of iterations performed for each matrix was 30,000, as suggested by Lehsten and Darbar (2006), using the software Ecosim 7 (Gotelli & Entsminger 2009). When the null hypothesis was rejected, an association test was performed using the statistical chi-square (χ^2), with the objective of detecting which groups were associated within the same sampling station. The test followed the model of Ludwig and Reynolds (1988). In total, six pairs of groups were formed with the real data, and then compared to the expected values for each pair as if their occurrences were independent, generating the observed χ^2. When the observed χ^2 was higher than the theoretical χ^2=3,84 (df=1, $p \leq 0.05$), the null hypothesis that the pair of groups have independent occurrences was rejected.

Results

A total, 1,588 specimens of fish belonging to 94 species, 20 families and six orders were examined (Supplementary data). The most frequent species were: *Serrasalmus marginatus* (N=93), *Astyanax altiparanae* (N=81) *Parauchenipterus galeatus* (N=69), *Acestrorhynchus lacustris* (N=66), *Hoplosternum littorale* (N=62) and *Schizodon borelli* (N=62). The prevalence of parasites considering all the sampling stations was led by the group Nematoda (14.61%), followed by Cestoda (8.63%), Digenea (8.19%) and Acantocephala (2.33%), varying according to the considered level (Figure 2).

Co-occurrence patterns calculated for the empirical (observed) matrix did not differ significantly from those expected for random matrices in most analyzed levels, confirming the null hypothesis of the community structure. The only sample that differed from the random pattern was a closed lagoon, Lagoa Fechada, where the observed C-score was lower than expected, indicating aggregation of the groups (Table I).

The association test applied to the data matrix of the sampling station Fechada Lagoon revealed positive interaction between the groups Digenea and Nematoda (Table II).

Discussion

The investigation of the patterns of distribution of helminthes parasites in large scale is important to aquatic ecosystems because of the effect of these organisms in the different levels of the food webs. Parasites can represent a significant portion of the biomass of individual hosts, often increase their mortality and reduce their birth rates, affect their nutritional status and its growth, alter the outcome of intra-and interspecific competition, increase host susceptibility to predation, influence the choice of the partner and increase the sex ratio in the population, the abundance and the diversity of organisms in the environment (Minchella & Scott 1991).

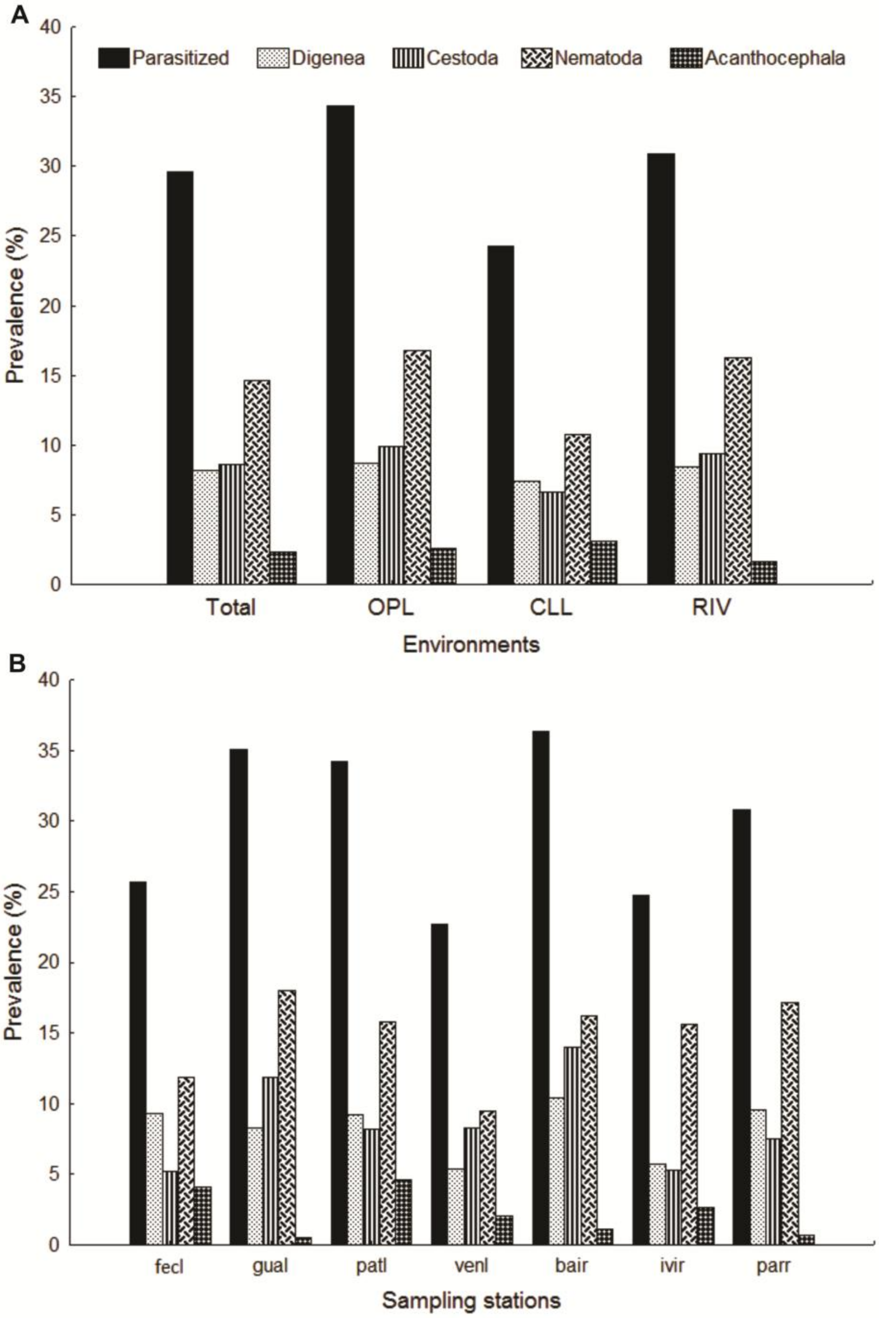

Figure 2. Percentage of parasitized fish (prevalence) by the helminthes of the groups Digenea, Cestoda, Nematoda and Acanthocephala in the floodplain of the upper Paraná River, from March 2004 to November 2007: **A** All sampling stations (Total), open lagoons (OPL), closed lagoons (CLL) and rivers (RIV); **B** Sampling stations analyzed separately: Fechada Lagoon (fecl), Guaraná Lagoon (gual), Patos Lagoons (patl), Ventura Lagoon (venl), Baía River (bair), Ivinheima River (ivir) and Paraná River (parr).

Nematoda was the most prevalent group and, it is also one of the groups of parasites with the highest species richness in the study region (Takemoto *et al.* 2009) and throughout the world. Its high prevalence and richness may be due to the variety of sites occupied within the host, which is related to the fact that they have a complete digestive system (absent in the other groups), facilitating the occupation of sites that digenean, cestodes and acanthocephalans could not occupy (Pavanelli *et al.* 2004).

The community of endoparasites showed random distribution pattern considering all the entire floodplain, all types of environments and almost all the sampling stations analyzed separately (except for Fechada Lagoon). This random pattern indicates that the interactions between groups are not strong enough to structure their distributions within the community.

Table I. Values of the C-score index applied to the community of endoparasites of fish collected from March 2004 to November 2007 in the floodplain of the upper Paraná River (N=number of hosts, SD=standard deviation, *=significant value).

Level	N	C-Score			
		Obs.	Exp.	SD	p(obs.≤exp.)
Total	1588	12474.50	12548.01	65.14	0.12
Open Lagoons	393	1043.00	1041.14	9.67	0.62
Guaraná Lagoon	194	243.33	244.87	2.89	0.41
Patos Lagoon	196	271.50	268.78	3.21	0.81
Closed Lagoons	511	953.33	964.56	7.84	0.06
Fechada Lagoon	269	298.16	303.95	3.65	0.04*
Ventura Lagoon	242	175.66	177.60	2.26	0.21
Rivers	684	2328.83	2335.50	21.66	0.39
Baía River	278	539.83	540.13	5.11	0.54
Ivinheima River	263	207.50	205.76	5.41	0.67
Paraná River	146	101.16	101.23	2.01	0.57

Kennedy *et al.* (1986) and Kennedy (1990) studied the parasite fauna of fishes and concluded that the presence of certain species of helminthes in a particular habitat depends primarily on the events of colonization, so that the assemblages of parasites were organizations more randomized than structured. Gotelli and Rohde (2002) also found evidence of randomness in the community structure of ectoparasites of 45 species of marine fish. The authors suggested an ecological continuum, where animals with little vagility and/or small individuals or populations have broad niches and are less vulnerable to regulatory mechanisms (competition, facilitation) than big animals with high vagility that live in large populations closer to saturation. In this context, parasites would be on the basis of this continuum, with broad niches and low population densities, tending to randomness. Thus, competition would not be sufficient to structure the community.

Price (1980) defended the idea that there are numerous broad niches for parasites, and they represent a fundamental factor in the evolution of the infracommunities. Since the niches are broad, composition and distribution of species within communities of parasites tend to vary unpredictably and stochastically (Kennedy 1985). According to Rohde (1991), the availability of niches and the weak effect of potentially competing species in the same microhabitat do not support the idea that the interspecific competition has ecological or evolutionary importance; the biggest problem for most parasites is not to prevent competition, but to find suitable sites for feeding and reproduction (Rohde 1991). In addition, the limited number of species within infracommunties may be consequence of differential transmission rates and lifespans and, in the case of species occurring in very small densities, the Allee effect reducing the survival chance of individuals (Rohde 1998).

Table II. Values of the chi-square (χ2) and associations between pairs of groups of endohelminthes (Digenea, Cestoda, Acanthocephala and Nematoda), parasites of fishes from Fechada Lagoon, in the floodplain of the upper Paraná River, collected from March 2004 to November 2007 (significance level p ≤ 0.05).

Pairs of Groups	χ^2	Association
Digenea x Cestoda	0.08	Absent
Digena x Acanthocephala	1.17	Absent
Digenea x Nematoda	15.28	Positive
Cestoda x Acanthocephala	0.63	Absent
Cestoda x Nematoda	1.99	Absent
Acanthocephala x Nematoda	2.59	Absent

The only sampling stations that did not present the random trend was Fechada Lagoon, a relatively small environment (area of 7.5 ha, average depth of 2.46 m) and highly productive, characterized by high phosphorus and nitrogen rates (Roberto *et al.* 2009). These nutrients can lead to high rates of primary production, which theoretically would support the development of a rich trophic web, including free-living larval stages, intermediate and definitive hosts of parasites in a small area, favoring the process of infection. Furthermore, it was one of the sampling stations with the highest number of examined fish (N=269). However, even in this rich environment, negative association between the groups was not observed, *i.e.*, there was no evidence of competition within the component communities of the Fechada Lagoon. In contrast, positive association was found between the parasites of the groups Digenea and Nematoda.

How to explain the co-ocurrence of individuals of the groups Digenea and Nematoda? The two groups have in common the active transmission in the infection process, a characteristic that may have supported their co-ocurrence. Moreover, they exhibit higher degree of development of the digestive system in relation to other groups and can therefore occupy similar microhabitats. The occupation of similar sites without competition is a possible situation when the resource used in common is abundant.

Another explanation for the positive association between the groups Digenea and Nematoda is that this may be a consequence of the heterogeneity of the community of hosts. Within a fish population, individuals may exhibit different levels of susceptibility to infection, and some individuals are genetically predisposed to acquire large numbers of parasites (Poulin 1998) and certainly such variation also occurs between different host species studied. The co-ocurrence of the groups can also be a reflection of the longevity of parasites, correlated exposure of the host and/or broader effects of the host immune responses through phenotypic features (Behnke 2008).

It is important to highlight that the co-ocurrence of groups does not mean that one group facilitates or inhibits the other's presence. In this study, the co-occurrence of the groups Digenea and Nematoda appears to be more a result of the convergence of common ecological processes that unite or separate species (way of transmission or nutritional requirements) than properly a co-occurrence based on direct interactions between the groups (Howard *et al.* 2002; Behnke 2008).

Despite the divergent results of recent studies on the distribution of communities of parasites, we concluded that the structure of the communities of visceral parasites of fish is not determined by the strength of interactions between groups, accepting the null hypothesis. However, we suggest other aspects of the community of parasites that need to be considered in future studies so that there is confirmation of these patterns for smaller scales: separate component communities, other taxa of hosts (molluscs, birds), ectoparasites, differentiation of larvae and adults and inclusion of the values of abundance and species richness in the analysis.

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SUPPLEMENTARY DATA

List of fish species collected and analyzed for enteric parasites in the upper Paraná River floodplain between March 2004 and December 2007.

Order	Family	Species
Myliobatiformes	Potamotrygonidae	*Potamotrygon* cf. *falkneri*
		Potamotrygon cf. *motoro*
Characiformes	Parodontidae	*Apareiodon affinis*
		Pareiodon nasus
	Curimatidae	*Cyphocharax modestus*
		Steindachnerina brevipinna
		Steindachnerina insculpta
	Prochilodontidae	*Prochilodus lineatus*
	Anostomidae	*Leporellus vittatus*
		Leporinus elongatus
		Leporinus friderici
		Leporinus lacustris
		Leporinus macrocephalus
		Leporinus obtusidens
		Leporinus striatus
		Schizodon altoparanae
		Schizodon borellii
		Schizodon nasutus
	Crenuchidae	*Characidium* aff. *zebra*
	Characidae	*Astyanax altiparanae*
		Acestrorhynchus lacustris
		Astyanax aff. *fasciatus*
		Astyanax aff. *paranae*
		Astyanax schubarti
		Brycon orbignyanus
		Bryconamericus stramineus
		Colossoma macropomum
		Galeocharax knerii
		Hemigrammus marginatus
		Hoplerythrinus unitaeniatus
		Hoplias sp. (grupo *lacerdae*)
		Hoplias sp. 1 (grupo *malabaricus*)
		Hoplias sp. 2 (grupo *malabaricus*)
		Hyphessobrycon eques
		Metynnis lippincottianus
		Moenkhausia aff. *intermedia*
		Moenkhausia aff. *sanctaefilomenae*
		Piaractus mesopotamicus
		Raphiodon vulpinus
		Roeboides descalvadensis
		Salminus brasiliensis
		Salminus hilarii

Continued. List of fish species collected and analyzed for enteric parasites in the upper Paraná River floodplain between March 2004 and December 2007.

Order	Family	Species
		Serrasalmus maculatus
		Serrasalmus marginatus
Siluriformes	Callicthydae	*Callichthys callichthys*
		Hoplosternum littorale
		Lepthoplosternum pectorale
	Loricariidae	*Hypostomus ancistroides*
		Hypostomus cf. *strigaticepis*
		Hypostomus cochliodon
		Hypostomus regani
		Hypostomus sp.
		Loricaria sp.
		Loricariichthys platymetopon
		Loricariichthys rostratus
		Pterigoplichthys anisitsi
		Rhinelepis aspera
	Heptapteridae	*Pimelodella avanhandavae*
		Pimelodella gracilis
		Rhamdia quelen
	Pimelodidae	*Hemisorubim edentatus*
		Hemisorubim platyrhynchus
		Iheringichthys labrosus
		Pimelodus cf. *argenteus*
		Pimelodus maculatus
		Pimelodus ornatus
		Pinirampus pirinampu
		Pseudoplatystoma corruscans
		Sorubim lima
		Zungaro zungaro
	Doradidae	*Pterodoras granulosus*
		Trachydoras paraguayensis
	Auchenipteridae	*Ageneiosus inermis*
		Ageneiosus militaris
		Auchenipterus osteomystax
		Parauchenipterus galeatus
Gymnotiformes	Gymnotidae	*Gymnotus inaequilabiatus*
		Gymnotus sylvius
	Sternopygidae	*Eigenmannia trilineata*
		Eigenmannia virescens
		Sternopygus macrurus
	Rhamphichthydae	*Rhamphichthys hahni*
	Apteronotidae	*Apteronotus caudimaculosus*
Perciformes	Sciaenidae	*Plagioscion squamosissimus*
	Cichlidae	*Astronotus crassipinnis*
		Cichla kelberi

Continued. List of fish species collected and analyzed for enteric parasites in the upper Paraná River floodplain between March 2004 and December 2007.

Order	Family	Species
		Cichla piquiti *Cichlasoma paranaense* *Crenicichla britskii*
		Crenicichla haroldoi
		Crenicichla niederleinii
		Geophagus cf. *proximus*
		Satanoperca papaterra
Pleuronectiformes	Achiridae	*Catathyridium jenynsii*