

Influence of host diet and phylogeny on parasite sharing by fish in a diverse tropical floodplain

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(Received 15 July 2015; revised 19 October 2015; accepted 1 November 2015; first published online 9 December 2015)

SUMMARY

The patterns of parasite sharing among hosts have important implications for ecosystem structure and functioning, and are influenced by several ecological and evolutionary factors associated with both hosts and parasites. Here we evaluated the influence of fish diet and phylogenetic relatedness on the pattern of infection by parasites with contrasting life history strategies in a freshwater ecosystem of key ecological importance in South America. The studied network of interactions included 52 fish species, which consumed 58 food types and were infected with 303 parasite taxa. Our results show that both diet and evolutionary history of hosts significantly explained parasite sharing; phylogenetically close fish species and/or species sharing food types tend to share more parasites. However, the effect of diet was observed only for endoparasites in contrast to ectoparasites. These results are consistent with the different life history strategies and selective pressures imposed on these groups: endoparasites are in general acquired via ingestion by their intermediate hosts, whereas ectoparasites actively seek and attach to the gills, body surface or nostrils of its sole host, thus not depending directly on its feeding habits.

Key words: Ecological networks, phylogenetic signal, host–parasite interactions.

INTRODUCTION

Parasites are widely distributed and play a key role in ecological communities (Dobson *et al.* 2008). About 30–40% of energy flows in food webs occurs via parasitism (Lafferty *et al.* 2006; Thielges *et al.* 2013), and parasites are responsible for the emergence of diseases affecting host species abundance patterns of the entire communities (Kelly *et al.* 2009a). The host–parasite interactions are distributed in a continuum with some parasite species having many hosts (i.e. a generalist species) while other species have one or few hosts (i.e. a specialist species). In addition, the manner in which specialized *vs* generalized parasite species are distributed among host species can have profound consequences for the structure and functioning of ecosystems (Lafferty and Kuris, 2009; Bellay *et al.* 2015a). It is then important to understand the patterns of parasite infection among hosts and how they are influenced by ecological and evolutionary factors, which include

both host's and parasite's traits (Poulin, 1997; Bellay *et al.* 2011; Poulin *et al.* 2011; Kamiya *et al.* 2014).

Host body size, abundance, geographic distribution and phylogenetic closeness are some examples of host traits with known or expected influence on parasite infection (Poulin, 2010; Poulin and Forbes, 2011; Lima-Junior *et al.* 2012; Dallas and Presley, 2014). In general, hosts that are ecologically or evolutionarily more similar tend to share more parasite species than more distantly related hosts (Poulin, 2010; Lima-Junior *et al.* 2012; Bellay *et al.* 2013, 2015b) which can be explained by phylogenetic niche conservatism (Wiens and Graham, 2005; Mouillot *et al.* 2006) as well as a number of ecological factors such as microhabitat use and life history strategies (Poulin, 2010).

Host diet can be another factor influencing host–parasite interactions. Many parasite species are only transmitted via ingestion (trophic links), so host species that share food types are also more likely to share parasites (Poulin and Leung, 2011; Benesh *et al.* 2014). The influence of diet can be magnified by the fact that species with similar diets also tend to share habitats, increasing the probability of infection by similar parasites. One of the predicted

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consequences of such diet-mediated parasite sharing is a positive relation between the number of food types eaten by a host species (i.e. diet breadth) and the number of its parasite species (i.e. parasite diversity), which has been previously demonstrated (Chen *et al.* 2008; Thieltges *et al.* 2013; Locke *et al.* 2014).

Parasite life history is another fundamental aspect of host–parasite interactions (Lima-Junior *et al.* 2012; Joannes *et al.* 2014). Some parasite species require two or more hosts for development (i.e. multiple-host life cycle parasites) (Thatcher, 2006; Woo, 2006). In general, these parasites are also endoparasites, which infect the internal organs or musculature of hosts by active penetration during the larval stages or passively via ingestion of larvae and/or adult forms (Lafferty *et al.* 2006; Poulin *et al.* 2013; Thieltges *et al.* 2013). Endoparasites also tend to be generalists (low host specificity), especially larval stages, which has an adaptive value as it enables them to infect a broad range of host species and enhances the probability of completing the life cycle (Poulin, 2010; Bellay *et al.* 2013). In contrast, ectoparasites infect their hosts preferentially in an active way (Pariselle *et al.* 2011), and usually require only one host to complete its life cycle (i.e. single-host life cycle parasites) and tend to show high host specificity. Given such differences, particularly regarding mechanisms of infection, we expect that the influence of host's diet on parasite species composition should be stronger for endoparasites than for ectoparasites.

In the Upper Paraná River Floodplain, a system of key ecological importance in South America, this diversity of parasite life histories has been related to a continuum of host specificities within one of the largest fish–parasite interaction network studied to date (Takemoto *et al.* 2009; Lima-Junior *et al.* 2012; Bellay *et al.* 2013). This gradient in parasite specificity is strongly related to taxonomic distances among hosts and, in turn, determines the relative importance of distinct patterns of interactions in the network (i.e. nestedness *vs* modularity, Lima-Junior *et al.* 2012), with potential implications for community stability and species' responses to distinct perturbations (Thébault and Fontaine, 2010; Stouffer and Bascompte, 2011; Bellay *et al.* 2015a). Despite these recent advances, the mechanisms linking host and parasite traits to patterns and processes at the community level are still not fully understood. One particular mechanism still not evaluated in the study system is diet choice by the host, which is important as it potentially determines both the ecological performance of hosts and their relative chance of infection by parasites with different life history strategies. Understanding the influence of host diet on parasite composition is also an important step towards the integration host–parasite and food web ecology.

In this paper, we analyse fish–parasite interactions of the Upper Paraná River Floodplain to determine

how host diet influences parasite composition, controlling for the effect of phylogeny. We tested the following predictions: (i) diet sharing has a positive influence on parasite sharing, and (ii) this influence is stronger for endoparasites than for ectoparasites. Given that host phylogeny is a strong predictor of both diet (Cattin *et al.* 2004; Bersier and Kehrli, 2008; Rezende *et al.* 2009; Naisbit *et al.* 2012; Stouffer *et al.* 2012) and parasite composition (Thieltges *et al.* 2009; Bellay *et al.* 2011; Krasnov *et al.* 2012, 2014; Lima-Junior *et al.* 2012; Poulin *et al.* 2013; Braga *et al.* 2015), controlling for phylogenetic relationships between hosts is important to properly assess the effect of diet sharing.

MATERIAL AND METHODS

Study area

The Paraná River has a catchment area of about 880 000 km², which represents approximately 10% of the Brazilian territory and includes the stretch of the Paraná River upstream of the Itaipu Reservoir (Agostinho *et al.* 2008). The upper sections of the Upper Paraná River basin are characterized by intensive human activities (Agostinho *et al.* 2007a). The Upper Paraná River floodplain is a 230 km stretch between the Porto Primavera Dam and Itaipu Reservoir, and is the only remaining dam-free stretch of the Paraná River (Hoeinghaus *et al.* 2009, Fig. 1). Maintaining this floodplain is fundamental to the conservation of local biodiversity, which has more than 4500 known species of terrestrial plants, aquatic macrophytes, zooplankton, benthic invertebrates, fish parasites, fish, amphibians, reptiles, birds and mammals (Agostinho *et al.* 2007a; Hoeinghaus *et al.* 2009; Pendleton *et al.* 2014).

The fish assemblage in the Upper Paraná River floodplain is represented by approximately 182 species in 35 families and 9 orders (Graça and Pavanelli, 2007). The orders Characiformes and Siluriformes have the highest species richness and abundance, corresponding to 80% of all fish species in this area (Agostinho *et al.* 2007b). The wide range of habitats and the high biodiversity in the Upper Paraná River floodplain favour the high diversity of parasites that use fish as intermediate or definitive hosts. In a survey of the parasite fauna in the Upper Paraná River floodplain, Takemoto *et al.* (2009) analysed 72 fish species and recorded 337 parasite taxa, consisting largely of helminth parasites (nematodes, monogeneans, digeneans, and cestodes).

Data

Diet information for fish species was gathered from previous studies in the Upper Paraná River floodplain (online Supplementary material S1). Most of these studies involved primary data collection (long

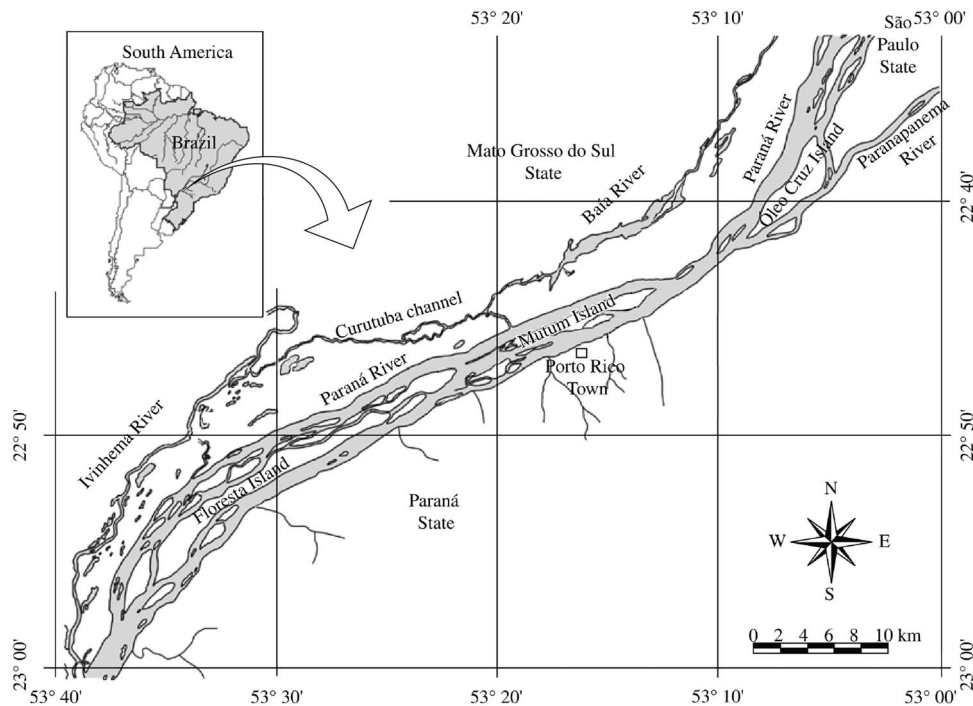


Fig. 1. Study area in the Upper Paraná River floodplain.

term ecological research (LTER/CNPq/UEM-SITE 06) (Isaac *et al.* 2014). We constructed a binary network of diet data made up of 52 fish species with available data and 58 food types (online Supplementary material S2).

The network containing host–parasite interactions was compiled from Takemoto *et al.* (2009) and Lima-Junior *et al.* (2012). All species were identified by morphological features. We limited our study to hosts for which diet information was available, creating an interaction network of 52 host and 303 parasite species (online Supplementary material S3). We also analysed two different sub-networks based on parasite life history (endo- *vs* ecto-parasites).

Statistical analysis

To test whether host diet influenced parasite composition, we firstly calculated two 52×52 dissimilarity matrices: one for diet and another for parasite dissimilarity between pairs of host species, using the Jaccard dissimilarity index $1 - J$ (Magurran, 2004; Legendre and Legendre, 2012). We controlled for the effect of evolutionary history by calculating a matrix of phylogenetic distances between fish hosts. We compiled available phylogenies (online Supplementary material S4) to build a supertree with all the species analysed (Fig 2) using the Mesquite Program (Maddison and Maddison, 2015). This topology was expressed as a 52×52 distance matrix in which the distance unit between species was the number of nodes in the phylogeny, thus expressing numerically the evolutionary proximity between species (Beaulieu *et al.* 2012).

As the diet dissimilarity matrix may be related to the phylogenetic distance matrix, we examined the influence of each separately on the fish–parasite interaction matrix, while controlling for the influence of the other. In order to do so, we used partial Mantel tests (Legendre and Legendre, 2012). We performed these analyses for the entire fish–parasite interaction network and for the sub-networks based on life history (endoparasites or ectoparasites) totalling six partial Mantel tests. Significances of all tests were assessed using 1000 permutations of the predictor variable matrix (diet or phylogenetic dissimilarity). Partial Mantel tests and the calculation of Jaccard dissimilarity index were performed using the *vegan* package (Oksanen *et al.* 2013) by *partial.mantel* and *vegdist* functions, respectively. All analyses were performed using R version. 3.1.2 (R Core Team, 2014).

RESULTS

The 52 fish species analysed belong to five orders and 18 families. On average each fish species was infected by 9 parasite taxa (s.d. = 8.88; range: 1–33 species) and consumed 16 food types (s.d. = 11.42; range: 1–40 types). *Hoplosternum littorale*, *Astyanax altiparanae* and *Iheringichthys labrosus* had the most diverse diets, consuming 40, 40, and 35 food types, respectively. The most prevalent food types were: particulate organic matter, Ostracoda, and Chironomidae, found in 37, 33, and 32 fish species, respectively. Fish species with the most diverse parasite composition were *Prochilodus lineatus*, *Pimelodus maculatus*, and *Leporinus friderici*,

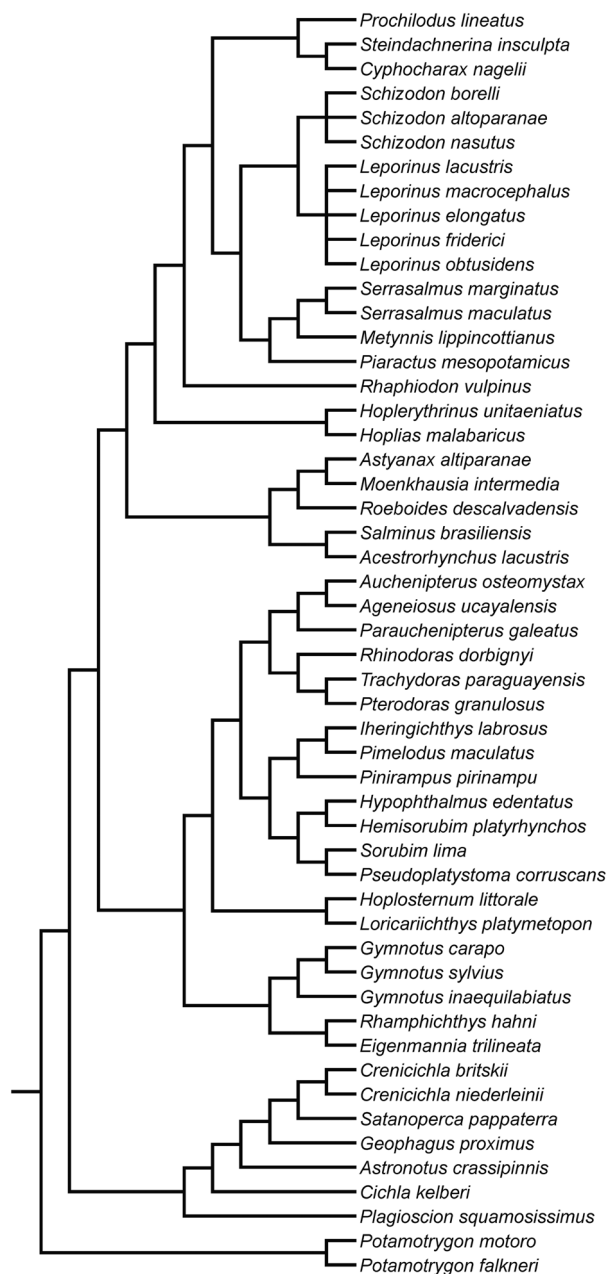


Fig. 2. Supertree topology including all 52 host species analysed in this study. Phylogenetic studies used to compile the topology are provided in the online Supplemental material.

infected with 33, 29, and 29 parasite taxa, respectively. These and more details on hosts and parasites analysed in this paper can be found in the online Supplementary material.

The richest groups of parasites were monogenean, digenean, and nematodes with 79, 60, and 60 species, respectively (51.3% of all recorded parasites species). Regarding parasite life history, 181 (59.7%) species are endoparasites and 122 (40.2%) species are ectoparasites. *Contracaecum* sp. (larvae), *Procamallanus* (*Spirocamallanus*) *inopinatus*, and *Clinostomum complanatum* (larvae) were the most prevalent, found in 15, 9, and 8 fish species, respectively.

Parasite composition was related to both host diet and phylogeny (Table 1). Phylogeny was significantly associated with parasite composition in all sub-networks representing parasite life history (Table 1). In contrast, host diet influenced the composition of endoparasites only, having no significant effect on ectoparasites (Table 1).

DISCUSSION

Our results confirmed the expected influence of both host phylogeny and diet on fish parasite composition. The influence of phylogeny was relatively stronger and corroborates previous studies (Bellay *et al.* 2011; Poulin *et al.* 2013; Krasnov *et al.* 2014; Braga *et al.* 2015). In addition, we showed that the influence of host diet was dependent on parasite life history, being detected only within endoparasites but not in ectoparasites.

The prominence of host phylogeny in determining parasite composition can be explained by the phylogenetic niche conservatism associated with parasitism (Mouillot *et al.* 2006; Poulin, 2010; Poulin *et al.* 2013). This conservatism emerges in part from purely historical factors: host species belonging to same lineage tend to share parasites due to a common close ancestor, which was itself a host of these same parasites. In addition, phylogenetically close hosts tend to have similar physiological and immunological features, which make them susceptible to the same groups of parasites and which evolve relatively slowly when compared with changes in diet (Bersier and Kehrlri 2008; Krasnov *et al.* 2014; Locke *et al.* 2014).

The host diet had a significant influence on parasite infection pattern, although weaker than phylogeny. In part, this can be explained by the relatively high plasticity of diet, in contrast to the aforementioned physiological and immunological factors that are more strongly conserved and whose pattern of evolutionary change is collectively represented in the phylogeny. Another reason is the occurrence of ectoparasites and larval stages of parasites in the assemblage. Ectoparasites (such as monogenean) and larval stages of some endoparasites (such as digenetic) infect their hosts actively (Pariselle *et al.* 2011), so they are not expected to be affected as much by the hosts' feeding habits (Strona, 2015).

The differences between ecto- and endo-parasites can be explained by two related aspects: (i) low to high specificity continuum; and (ii) differences in selection pressure to maximize cross-fertilization of parasites occurring in the definitive host (Brown *et al.* 2001). Most endoparasites belong to groups known for their low specificity in larval stages (see Bellay *et al.* 2013), and infect definitive hosts (or some intermediate hosts) mainly by food ingestion. Given their lower specificity, such groups can infect a large

Table 1. Results from partial Mantel tests relating dissimilarity matrices (parasite-host dissimilarity as dependent matrix, diet dissimilarity and phylogenetic distance as predictor matrices), for the complete network and sub-networks (ectoparasites or endoparasites)

Partial mantel	R_{Mantel}	R_{null}	P
Complete network			
Parasite \times diet, controlled by the effect of phylogeny	0.09602	0.0209	$P = 0.0239^*$
Parasite \times phylogeny, controlled by the effect of diet	0.208	0.0009	$P = 0.0009^*$
Sub-networks			
<i>Parasitism mode</i>			
Endoparasites \times diet, controlled by the effect of phylogeny	0.1091	0.0139	$P = 0.0169^*$
Endoparasites \times phylogeny, controlled by the effect of diet	0.2154	0.0009	$P = 0.0009^*$
Ectoparasites \times diet, controlled by the effect of phylogeny	0.0667	0.1498	$P = 0.2907$
Ectoparasites \times phylogeny, controlled by the effect of diet	0.317	0.0009	$P = 0.0009^*$

Each test comprised 1000 random permutations. R_{Mantel} represents the Mantel statistic r (i.e. the partial correlation between dissimilarity matrices); R_{null} represents the mean statistic from the null distribution; *statistically significant result, $P \leq 0.05$).

number of hosts and thus increase the probability of reaching the definitive host (e.g. a piscivorous bird or a fish at the top of the food chain) and continuing the life cycle of the species. Any strategy that maximizes the chance of the parasite reaching the definitive host should be favoured by natural selection (Choisy *et al.* 2003; Seppälä and Jokela, 2008). In particular, concerning the transmission of parasites via food ingestion, Choisy *et al.* (2003) demonstrates that endoparasites are favoured in situations where the intermediate hosts are more abundant than the definitive hosts. Interestingly, fish with the greatest number of shared parasites in our study system, i.e. *P. lineatus*, *P. maculatus* and *L. friderici* are low trophic level species (i.e. they are preyed upon by other species of fish or birds), are abundant in the studied system (Takemoto *et al.* 2005; Lima-Junior *et al.* 2012), and have omnivorous diets (except for *P. lineatus*, which is a detritivorous species that feeds on the bottom of rivers and lakes). Species with broad diet tend to be more susceptible to parasitism and have a greater diversity of parasites (Poulin and Forbes, 2011; Locke *et al.* 2013, 2014). Still, *P. lineatus* is a species whose detritivorous feeding habit probably exposes it to infection by free-living parasites, eggs or cysts present in the detritus.

It is worth emphasizing that ectoparasites found in the Paraná River Floodplain consist mainly of monogeneans, a group of parasites recognized by their high host specificity (Poulin, 1992; Dobson *et al.* 2008). In ectoparasites, transmission via food ingestion is not the common form (Strona, 2015). Normally, the groups of parasites that infect hosts through active search present traits enhancing the ability of detecting and infecting hosts, besides are expected to be under stronger selective pressure (Pariselle *et al.* 2011). The evolutionary arms race between parasites and hosts (Foitzik *et al.* 2003) can lead to higher host specificity, limiting the chance of interacting with other hosts (Agosta *et al.* 2010; Poisot *et al.* 2011, 2013).

Our results have some interesting implications. The first is related to biological invasions. Previous studies have shown that non-native species tend to have more flexible diet, consuming a greater number of food items than their native congeners (Tillberg *et al.* 2007; Harms and Turingan, 2012; Hayden *et al.* 2014) or feed on lower trophic levels (e.g. omnivores and detritivorous) than native species (Gido and Franssen, 2007). Thus, we expect that non-native fish species that share many food items with native species will have a greater chance of being infected with native parasites (spill-back setting; Kelly *et al.* 2009b), mainly parasites that infect their hosts via food ingestion as adult endoparasites. This problem is particularly relevant for the study region, which has been impacted by many fish species invasions in the last three decades (Júlio-Júnior *et al.* 2009). A similar problem occurs with habitat modification, such as in artificial reservoirs and rivers impacted by dams, in which fish species with higher plasticity tend to be favoured (Abelha *et al.* 2001; Agostinho *et al.* 2007a). Dietary plasticity can increase diet overlap and make these species susceptible to the same groups of parasites, and ultimately favouring generalist endoparasites. These scenarios are not mutually exclusive, and exploring their potential synergisms in determining the patterns of parasite infection within the ecosystem is an important venue for future research.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S003118201500164X>

ACKNOWLEDGEMENTS

We thank Tad Dallas, Eddie Lenza, Vanessa Abril and two anonymous referees for their suggestions to improve the manuscript.

FINANCIAL SUPPORT

We thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for the Social Demand scholarship to Luciano Benedito de Lima and FAPEMAT for his Doctor Degree scholarship. Sybelle Bellay thanks CNPq for a Post-doctoral Fellowship.

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