



Are host phylogeny and ecology two major determinants in parasitic structuring in fish?

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ABSTRACT

The present study evaluates the metazoan parasite fauna of two fish species with similar feeding habits, but which are phylogenetically distant, to understand the degree of similarity in the parasites fauna between these host species. In all, 30 specimens of *Chalceus epakros* and 30 of *Tetragonopterus chalceus* were analyzed. A total of 1572 parasites were collected, 1414 in *C. epakros* and 158 in *T. chalceus*. The PERMANOVA showed that the ectoparasite community of *C. epakros* and *T. chalceus* has a high difference ($R^2 = 0.813$; $F = 235.41$; $p = 0.001$); while for endoparasites, this difference reduced drastically ($R^2 = 0.156$; $F = 9.262$, $p = 0.001$). When combining the two groups (ectoparasites + endoparasites), the difference between the groups increased again ($R^2 = 0.730$; $F = 146.49$, $p = 0.001$). High differences observed between *C. epakros* and *T. chalceus* when considering only ectoparasites were due to the fact that both host species were not phylogenetically related; in this case, these differences were caused by Monopisthocotyla, parasites known for their host specificity. On the other hand, the high similarity in endoparasite composition occurred because these two host species occupy the same position in the food chain and consume the same food items.

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Introduction

Fish are vertebrates that occupy different positions in the trophic chain, feed on a wide variety of foods and exploit diverse habitats in aquatic ecosystems, and can therefore be definitive, intermediate and/or paratenic hosts for a great diversity of endoparasites (Alarcos and Timi 2012; Lima et al. 2015; Hoshino et al. 2016; Oliveira et al. 2016). As such, the levels of parasitism and the diversity of parasites between hosts of the same species and/or between different species have great variations, which makes them difficult to predict (Alarcos and Timi 2012; Lima et al. 2015; Hoshino et al. 2016; Oliveira et al. 2016).

For the fish community, host phylogeny has an effect on parasite abundance and composition, since many parasite species are restricted to one host lineage, as is the case with Monopisthocotyla (Bakke et al. 2002; Šimková et al. 2006; Braga et al. 2014). On the other hand, it has been shown that the diversity of endoparasites is mainly influenced by the ecology of the host (Bush et al. 1990). As a result, host fish species that have in their diet items containing

infective forms for endoparasites, and overlap their ecological niches (e.g. similar diet), increase the probability of these hosts presenting a high similarity of endoparasite species, even if they are phylogenetically distant host species (Marcogliese 2002, 2003; Lima et al. 2015).

Recent studies have reported a high similarity in the parasitic composition and abundance of phylogenetically related fish species, as occurred between two species of Acestrorhynchidae (Hoshino et al. 2016), Triportheidae (Oliveira et al. 2016) and Erythrinidae (Alcántara and Tavares-Dias 2015). However, these studies evaluated the general parasite fauna of the host fish, and did not consider functional groups (e.g. parasites with the same life cycle, lifestyle, type of infection by endo- or ectoparasites), which leads us to think that both the ecology and the phylogeny of the host act simultaneously in the structuring of the parasite communities of fish species, which has not been taken into account in the studies.

Thus, two questions direct this study: (i) how does the simultaneous action of phylogeny and ecology of

the hosts structure the fish metazoan parasite fauna? (ii) does host fish phylogeny have an effect on parasite species composition? Our hypotheses are: (I) host ecology is determinant in the structuring of endoparasite fauna, while phylogeny is determinant mainly in ectoparasite fauna; (II) phylogenetically distant fish species have low similarity in ectoparasite composition and high similarity in endoparasite composition, while there will be more similarity for endoparasite composition when the hosts overlap diet.

To answer these questions, we used two species of Characiformes: *Chalceus epakros* Zanata & Toledo-Piza, 2004 (Chalceidae) and *Tetragonopterus chalceus* Spix & Agassiz, 1829 (Characidae), which are phylogenetically distant (Melo et al. 2016), and have an omnivorous feeding habit, but both species consume some similar food items, such as small crustaceans, aquatic and terrestrial insects (Ferreira and Santos 2006; Maldonado-Ocampo and Ramirez-Gil 2006; Dary et al. 2017). These are also intermediate hosts for endoparasite species. Three characteristics were determinant in the choice of these species: (i) phylogenetic distance of the species, (ii) similar diet and (iii) occurrence in the same collection region.

Materials and methods

Area of collection of the fish

The fish were collected in January and February 2018, in the lower Jari River, near the district of Jarilândia, municipality of Vitória do Jari, state of Amapá, Brazil (Figure 1). In all, 30 specimens of *C. epakros* and 30 of *T. chalceus* were collected to study the metazoan parasite fauna. These fish were caught using hooks and gillnets with different mesh sizes. The total length (cm) and body weight (g) of the fish were also measured. Each fish was then euthanized using the spinal cord transection method for necropsy and collection of metazoan parasites. The gastrointestinal tract and viscera were examined using a stereomicroscope. For the morphological identification of the metazoan parasites, an optical microscope was used.

This study was conducted according to the principles of the Brazilian College of Animal Experimentation and approved by the Ethics Committee on the Use of Animals at Embrapa Amapá (No. 014/2018). All fish were collected with ICMBio approval (No. 27,447-1/2011). The collection, fixation, conservation and preparation of the parasites for identification followed the previous recommendations (Amato and Amato 2010).

Data analysis procedures

Prevalence, mean intensity, mean abundance (Bush et al. 1990) and relative dominance (Rohde et al. 1995) were calculated for the parasites that were found. Permutational Analysis of Variance (PERMANOVA) was applied to evaluate the effect of parasite functional groups on parasite community structuring using the vegan package with the Bray-Curtis distance method (Oksanen et al. 2020). For this, the abundance matrix was transformed ($\sqrt{x+1}$). For this, three groups of parasites were created; group 1 = ectoparasites; group 2 = endoparasites; and group 3 = endoparasites + ectoparasites. Using non-metric multidimensional scaling (NMDS), three graphs were created to show the similarity of the parasites between the host species, considering each group of parasites. For this, ordering of the parasite abundance data was performed from the similarity matrix generated by the quantitative Bray-Curtis distance method, using the vegan package (Oksanen et al. 2020). These analyses were carried out using the R Software (R Core Team 2022) and the figures were generated using the ggplot2 package (Wickham 2016).

Results

The 30 specimens of *C. epakros* measured 15.9 ± 1.7 cm and weighed 51.1 ± 26.0 g, while the 30 specimens of *T. chalceus* measured 10.1 ± 1.6 cm and weighed 33.9 ± 2.5 g. A total of 1572 parasites were collected from both host populations. For *C. epakros* 1414 parasites were collected, while for *T. chalceus* 158 parasites were collected. *Chalceus epakros* was parasitized by *Anacanthorus* sp. 1 and *Jainus jainus* Mizelle, Kritsky & Crane, 1968 (Monopisthocotyla), *Procamallanus inopinatus* (Travassos, Artigas & Pereira 1928), larvae of *Pseudoproleptus* sp. and *Rhabdochona acuminata* (Molin 1860) (Nematoda). *Tetragonopterus chalceus* was parasitized by *Anacanthorus dipelecinus* Kritsky, Boeger & Van Every, 1992, *Ancistrohaptor* sp. 1 and *Ancistrohaptor* sp. 2 (Monopisthocotyla), *P. inopinatus*, larvae of *Contracaecum* sp., larvae of *Pseudoproleptus* sp., *R. acuminata* and larvae of *Hysterothylacium* sp. (Nematoda), and *Hysterothylacium* sp. was the dominant parasite (Table 1). *Chalceus epakros* and *T. chalceus* did not share the ectoparasite species, characterizing it as a totally dissimilar fauna. These two host species shared only three endoparasite species: *P. inopinatus*, *Pseudoproleptus* sp. and *R. acuminata*.

PERMANOVA showed that the ectoparasite community of *C. epakros* and *T. chalceus* has a high

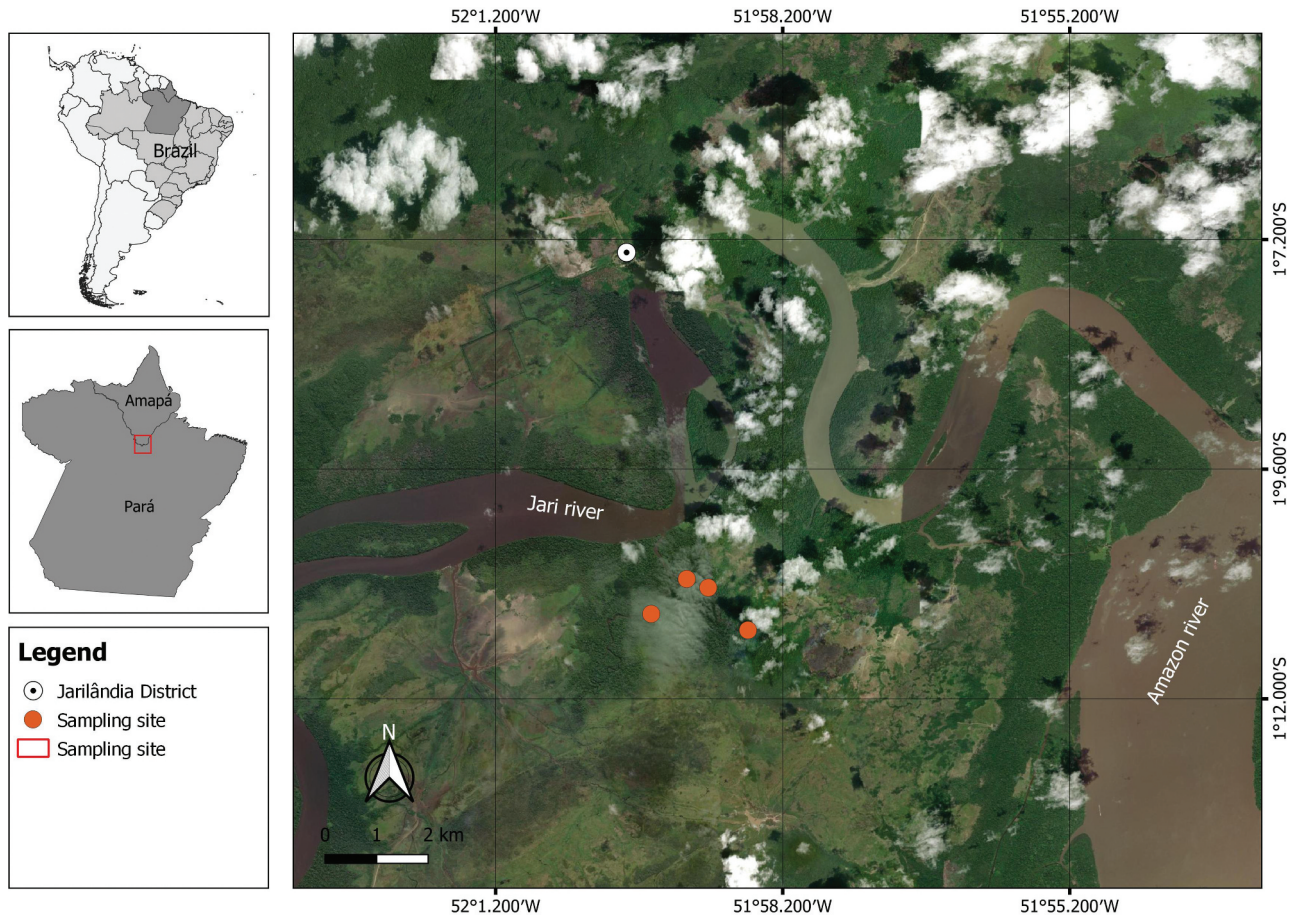


Figure 1. Map of the collection site of the species of *Chalceus epakros* and *Tetragonopterus chalceus* from the lower Jari River, eastern Brazilian Amazon.

Table 1. Metazoan parasites of *Chalceus epakros* and *Tetragonopterus chalceus* from the lower Jari River, eastern Brazilian Amazon.

Parasite species	Host											
	<i>Chalceus epakros</i>						<i>Tetragonopterus chalceus</i>					
	P (%)	MI	MA	RD	TNP	IS	P (%)	MI	MA	RD	TNP	IS
Monopisthocotyla												
<i>Anacanthorus</i> sp.	13.3	5.0	0.7	0.014	20	Gills	–	–	–	–	–	–
<i>Jainus jainus</i>	100	45.6	45.6	0.967	1367	Gills	–	–	–	–	–	–
<i>Anacanthorus dipelecimus</i>	–	–	–	–	–	–	20.0	1.2	0.2	0.044	7	Gills
<i>Ancistrohaptor</i> sp. 1	–	–	–	–	–	–	36.7	1.7	0.6	0.12	19	Gills
<i>Anacanthorus</i> sp. 2	–	–	–	–	–	–	46.7	2.8	1.2	0.247	39	Gills
Nematoda												
<i>Contracaecum</i> sp. (larvae)	–	–	–	–	–	–	16.7	3.0	0.5	0.095	15	Mesentery
<i>Procamallanus inopinatus</i>	6.7	1.0	0.1	0.001	2	Intestine	3.3	1.0	0.03	0.006	1	Intestine
<i>Pseudopropleptus</i> sp. (larvae)	3.3	1.0	0.03	0.001	1	Intestine	3.3	1.0	0.03	0.006	1	Intestine
<i>Rhabodochoa acuminata</i>	46.7	1.7	0.8	0.017	24	Intestine	33.3	3.1	1.0	0.196	31	Intestine
<i>Hysterothylacium</i> sp. (larvae)	–	–	–	–	–	–	60.0	2.5	1.5	0.285	45	Mesentery

P (%): Prevalence; MI: Mean intensity; MA: Mean abundance; TNP: Total number of parasites; IS: Infection site, RD: Relative dominance.

difference ($R^2 = 0.813$; $F = 235.41$; $p = 0.001$); while, for endoparasites, this difference reduced drastically ($R^2 = 0.156$; $F = 9.262$, $p = 0.001$). When analyzing the two groups together (ectoparasites + endoparasites), the difference between the groups increased again ($R^2 = 0.730$; $F = 146.49$, $p = 0.001$). The NMDS showed that the spatial distribution of parasite abundance, in which

there were spatial differences for ectoparasites between *C. epakros* and *T. chalceus*, formed two distinct groups ($R^2 = 0.999$; stress = 0.00004) (Figure 2). For endoparasites, high similarity was observed and groups were distinguished ($R^2 = 0.999$; stress = 0.03) (Figure 3). For ectoparasites + endoparasites, there were spatial differences, and two distinct

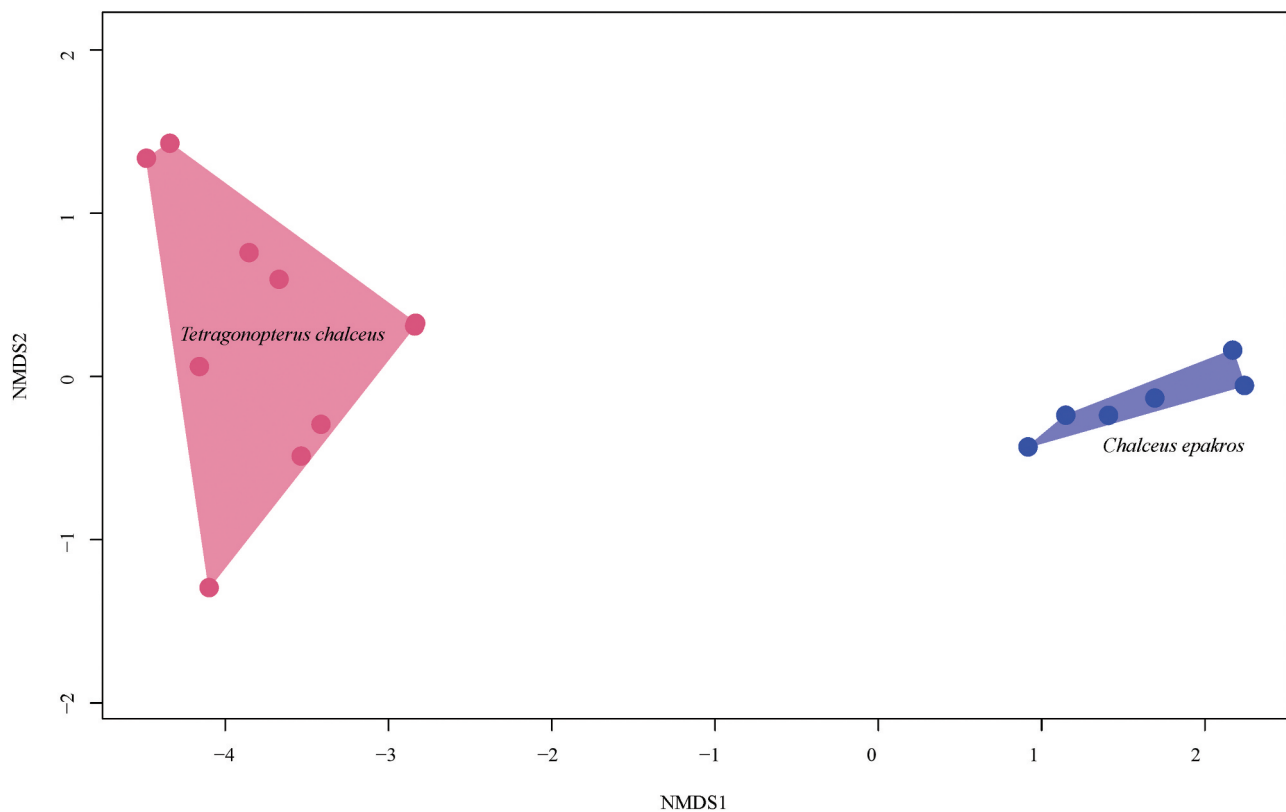


Figure 2. NMDS for ectoparasite fauna of *Chalceus epakros* and *Tetragonopterus chalcus* from the eastern Brazilian Amazon.

groups were formed, which were closer ($R^2 = 0.996$; stress = 0.06) (Figure 4).

Discussion

Fish are important hosts in the biological cycle of several species of parasites, whether they have a direct or indirect life cycle (Marcogliese 2002, 2003; Alarcos and Timi 2012; Lima et al. 2015; Hoshino et al. 2016; Oliveira et al. 2016). In the present study, metazoan parasites were collected from *C. epakros* and *T. chalcus* from the Jari River, Amapá state, Brazil (eastern Amazon), whose fauna was composed of Monopisthocotyla and Nematoda species. The parasite fauna of *C. epakros* was composed of *Anacanthorus* sp., *J. jainus*, *Procamallanus inopinatus*, larvae of *Pseudopropleptus* sp. and *R. acuminata*; however, *J. jainus* was the dominant parasite. For *T. chalcus*, *A. dipelecinus*, *Ancistrohaptor* sp. 1, *P. inopinatus*, *R. acuminata* and larvae of *Hysterothylacium* sp. were found, the latter being the dominant parasite. The present study recorded lower species richness of metazoan parasites (8 taxa) for *T. chalcus*, when compared with this same species from the Tres Marias reservoir, São Francisco River, state of Minas Gerais

(Brazil), which presented 10 taxa belonging to Digenea, Cestoda and Nematoda, even though the authors analyzed only endoparasites (Albuquerque et al. 2016). Despite this, there are no data to compare the diversity of parasites of *C. epakros*, since this is the first study on the parasite fauna of this host species.

The parasite fauna of fish is strongly influenced by two large factors. One is phylogeny (Šimková et al. 2006; Poulin 2007; Alarcos and Timi 2012; Braga et al. 2014; Hoshino et al. 2016; Oliveira et al. 2016) and the other the ecology, more specifically the diet of the host fish (Marcogliese 2002, 2003; Chen et al. 2008). Studies show that phylogenetically related hosts tend to show greater similarity between their communities of ectoparasite species, whereas the opposite occurs for phylogenetically unrelated host species (Šimková et al. 2006; Poulin 2007; Alarcos and Timi 2012; Braga et al. 2014; Hoshino et al. 2016; Oliveira et al. 2016). These are associated with historical events of coevolutionary processes, as well as host specificity (Poulin 1992, 2007; Bakke et al. 2002). On the other hand, the diet of the host is of great importance in the structuring of the endoparasite fauna of fish, since most endoparasites are transmitted trophically, with low host specificity (Marcogliese 2002, 2003; Chen

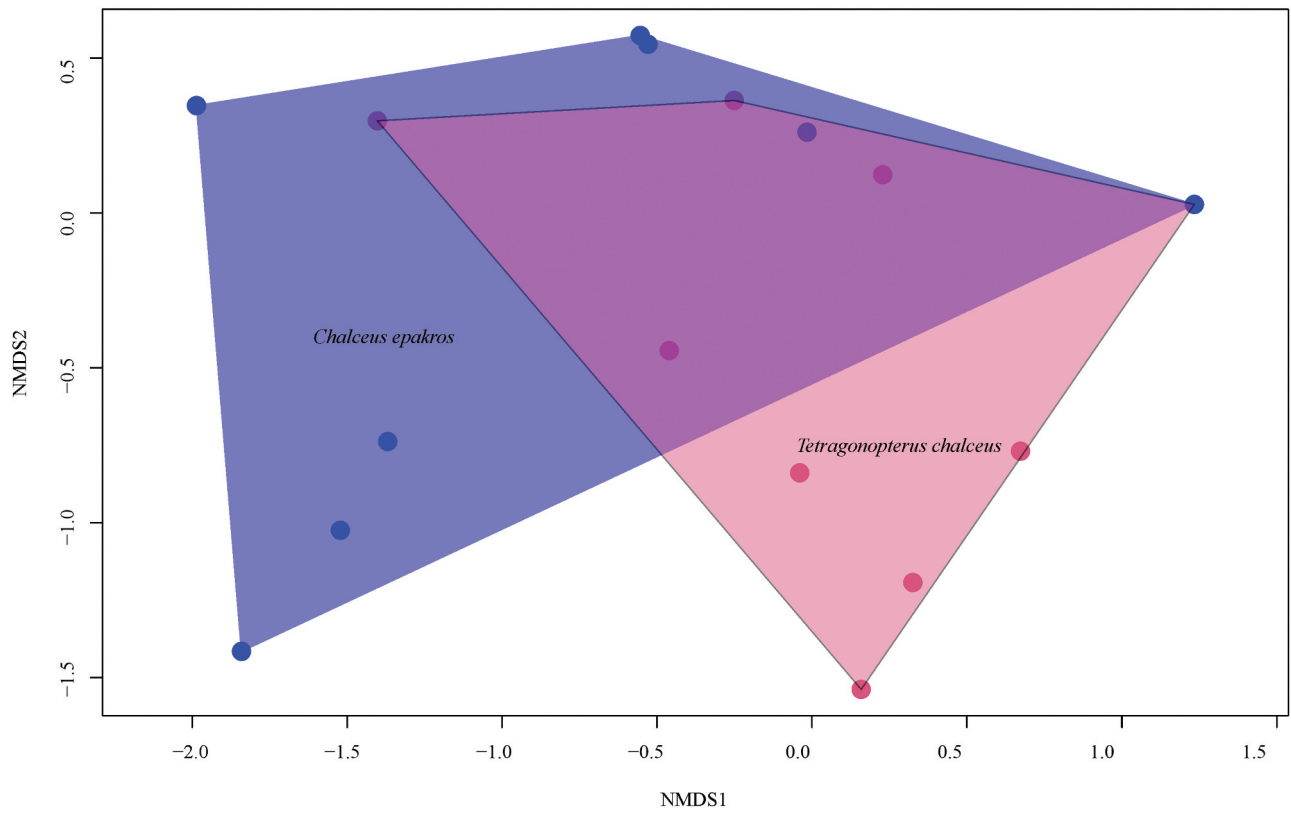


Figure 3. NMDS for endoparasite fauna of *Chalceus epakros* and *Tetragonopterus chalcus* from the eastern Brazilian Amazon.

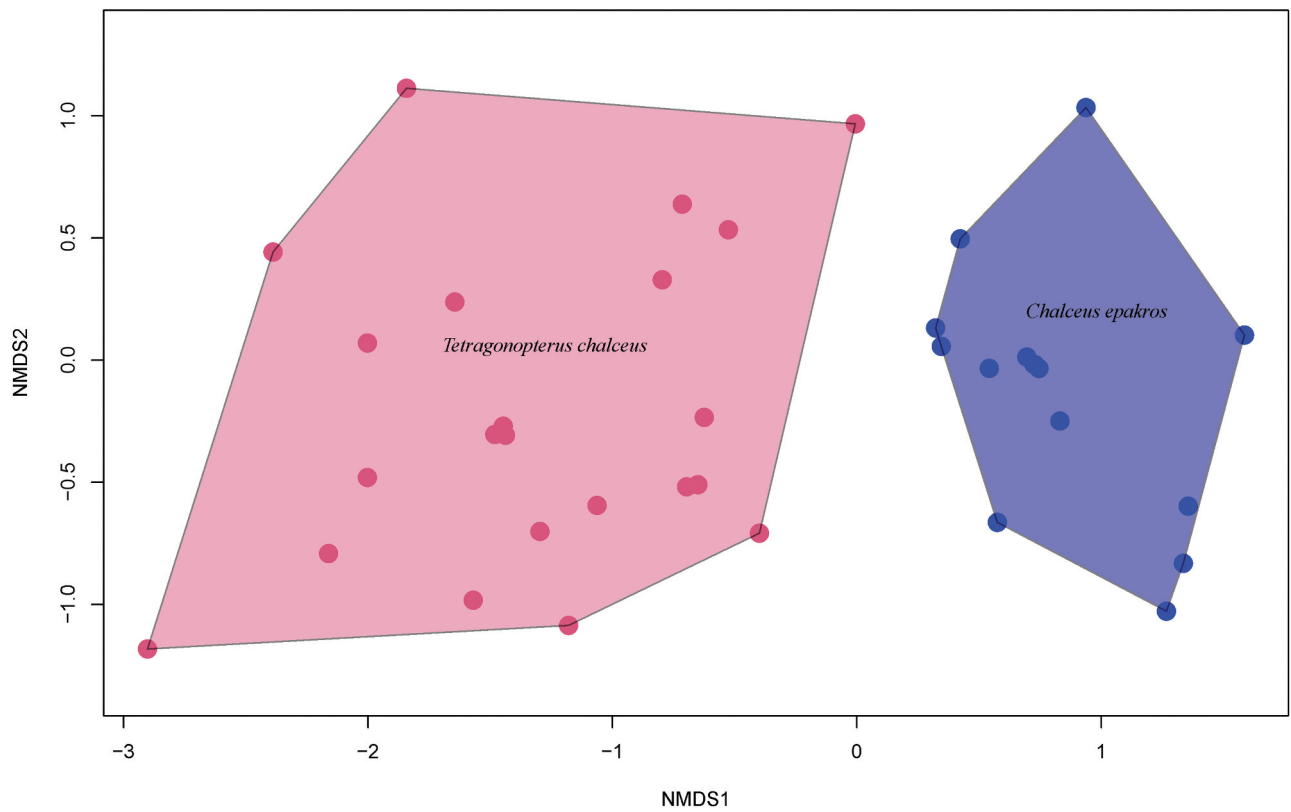


Figure 4. NMDS for ectoparasite + endoparasite fauna of *Chalceus epakros* and *Tetragonopterus chalcus* from the eastern Brazilian Amazon.

et al. 2008). We observed that, although *C. epakros* and *T. chaldeus* have no phylogenetic relationship, both have low difference in the composition of endoparasites, since they share most of the species of Nematoda. Possibly, this was because these two species of fish occupy the same position in the food chain and consume the same food items (Ferreira and Santos 2006; Maldonado-Ocampo and Ramirez-Gil 2006; Dary et al. 2017), containing nematode infective stages, such as the shrimp *Macrobrachium amazonicum*, an intermediate host for *Pseudoproleptus* spp. (Moravec and Santos 2009), insects of the genus *Hexagenia* and the crustacean *Hyalella knickerbockeri* which are intermediate hosts of *Rhabdochona* spp. (Poinar Jr and Kannangara 1972), as well as chironomids, which are intermediate hosts of nematodes of the genus *Procamallanus* (Moreira et al. 2009).

Unlike endoparasites, fish ectoparasites have higher levels of specificity for their hosts, mainly monopisthocotylans, and such characteristics help us to understand and predict how the ectoparasite fauna in fish may be structured (Poulin 1992; Braga et al. 2014). Therefore, *C. epakros* and *T. chaldeus* are not phylogenetically related species (Melo et al. 2016), and both host species do not share the same ectoparasite species, such as monopisthocotylans, corroborating hypothesis I. This occurred because monopisthocotylan species have close relationships with their hosts, and these relationships cause monopisthocotylan species to be restricted to a certain host lineage (Poulin 1992; Bakke et al. 2002; Braga et al. 2014).

Our results allowed us to understand that both the phylogeny and ecology of hosts are two factors acting simultaneously in a single direction (e.g. in hosts that are close phylogenetically and overlap their ecological niches, the acting force tends to be greater for similarity; in hosts that are close phylogenetically, but do not overlap their ecological niches, the force tends to be lower for similarity) or in opposite directions (e.g. in hosts that are phylogenetically distant and do not overlap their ecological niches, strength tends to be greater for dissimilarity; in hosts that are phylogenetically distant and overlap their ecological niches, strength tends to be less for dissimilarity). Therefore, higher similarity values will occur when two forces (ecology and phylogeny) follow in the same direction, and higher dissimilarity values will occur when the two forces (ecology and phylogeny) go in opposite directions. The similarity of endoparasites and dissimilarity of ectoparasites that we observed between *C. epakros* and *T. chaldeus* clearly show that the ecology and phylogeny of the hosts acted in opposite directions, and these observations need to be considered in studies of parasite ecology, since species of

ectoparasites and endoparasites have distinct cycles and lifestyles, and it is these factors that go unnoticed, leading to a misinterpretation of the structuring of the fish parasite.

In conclusion, the hypotheses raised were answered and accepted; in other words, although *C. epakros* and *T. chaldeus* are phylogenetically distant, they have high similarity in the composition of metazoan endoparasites, and low similarity in the composition of metazoan ectoparasites. Addressing endoparasites and ectoparasites separately in the analyses, allowed us to obtain a pattern that could have been masked if we had considered them as a single group. Thus, this study shows that both phylogeny and ecology of the hosts are two forces that act simultaneously in the structuring of the parasite community, and these need to be considered in parasite ecology studies. Finally, this study was the first record of *Anacanthorus* sp., *J. jainus*, *P. inopinatus*, *Pseudoproleptus* sp. and *R. acuminata* for *C. epakros*, as well as *A. dipelecimus*, *Ancistrohaptor* sp., *R. acuminata* and *P. inopinatus* for *T. chaldeus*.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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