

Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects

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Abstract The enemy release hypothesis is frequently used to explain the success of invaders, postulating that introduced species have escaped from their native enemies, including parasites. Here, we tested this hypothesis for the tucunaré (*Cichla piquiti*), a predatory cichlid, and its endoparasites. First, the parasites and their influence on the condition of the hosts in the native environment, the Tocantins River (TO), were compared to an environment where the fish was introduced, the Paraná River (PR). Then, comparisons of the abundances of Diplostomidae eye flukes and *Contracaecum* sp. larval nematodes were made between the introduced tucunaré and two predators native to the PR, *Hoplias malabaricus* and *Raphiodon vulpinus*. Nine species of endoparasites were recorded in total, five of which occurring in both localities. Total species richness did not differ between localities, and fish condition was negatively affected by the cestodes *Sciaidocephalus megalodiscus* only in the TO. In the PR, abundance of *Contracaecum* sp. did not differ between natives and invaders; however, eye flukes were more abundant in the native fish *H. malabaricus*, which may represent an advantage to the invader if they were competing for prey. These results did not support the idea that the escape from parasites favoured the establishment of *C.*

piquiti in the PR. Instead, the escape from the parasites' effects seems a better explanation, and further studies examining effects on host physiology and/or fitness in the native and introduced ranges are needed.

Introduction

The introduction of species in new environments by anthropogenic action, on purpose or accidentally, has received great attention since Charles Elton's (1958) classic monograph. One of the reasons for this attention is the capacity of introduced species to become invasive, causing extensive loss of biodiversity through biotic homogenization (Rahel 2002), as well as adverse economic impacts (Born et al. 2005). Just as the role of parasites has had late recognition in community ecology (Minchella and Scott 1991), it also took some time to be considered in invasion ecology. Although the idea of the enemy release as a hypothesis for the success of introduced species goes back much farther (Darwin 1859; Elton 1958), scientists have paid more attention to the role of parasites in invasions after the application of the hypothesis to invasive plants by Keane and Crawley (2002). The 'enemy release hypothesis' (ERH) explains the success of introduced species using three predictions: (1) specialist enemies (parasites, pathogens or predators) will be absent from the new region; (2) specialist enemies of native hosts will rarely switch to exotic invasive species and (3) generalist enemies will have a smaller impact on exotic species than on natives (Keane and Crawley 2002).

A general test of the ERH focused on parasite release in animal invasions was performed by Torchin et al. (2003), who studied 26 species of hosts including mammals, birds, reptiles, amphibians, fishes, crustaceans, molluscs and their parasites. They concluded that the number of parasites

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found in native populations is twice that found in introduced populations and that introduced populations are less parasitized (with regard to prevalence of infection) than native populations. Other authors have tested the ERH with different species of hosts and parasites, in other types of environments. Some studies support the hypothesis (Kvach and Skóra 2007; Maar et al. 2008; Vignon et al. 2009; Roche et al. 2010; Ross et al. 2010), while others show that not all the proposed arguments work for all situations (Poulin and Mouillot 2003; Krakau et al. 2006; Dang et al. 2009; Ondračková et al. 2009, 2010).

Here, we tested the ERH for the tucunaré, *Cichla piquiti* (Cichlidae), in two Brazilian basins. This fish species is native to the Amazonas River basin, specifically the Tocantins-Araguaia sub-basin (Kullander and Ferreira 2006). It was introduced to the Paraná River basin in the early 1990s (Vieira et al. 2009) because of its value to sport fishing and its marketable meat (Kullander 2003). Species of *Cichla* are known to be very invasive visual predators, reaching great abundances in several reservoirs throughout Brazil (Agostinho et al. 2007) and showing high competitive ability and significant potential to reduce populations of native fish species in the Paraná River (Pelicice and Agostinho 2009).

Earlier tests of the ERH with animals focused on parasite species richness and infection level, without quantifying potential differences in the actual effect of parasitism on host condition factor between the invaded and native areas. Here, in addition to differences in parasite numbers, we examined the relationships between parasite infection and the condition factor of the host, which in fish is considered a convenient measure of an individual's energetic state (Le Cren 1951; Neff and Cargnelli 2004). We also tested the ERH using two scales of analyses (Colautti et al. 2006). At the biogeographical scale, we compared the endoparasite fauna and the condition of *C. piquiti* between its native environment (Tocantins River) and an environment where the fish was introduced (Paraná River). At the community scale, we compared the endoparasite fauna and condition of *C. piquiti* to the endoparasite fauna of two fish species native to the Paraná River that are also piscivorous (Hahn et al. 2008), *Hoplias malabaricus* (Erythrinidae) and *Raphiodon vulpinus* (Cynodontidae). Our predictions are that *C. piquiti* hosts from the Paraná River have fewer parasites and/or incur lower reductions in body condition from parasitism than either *C. piquiti* hosts from the Tocantins River or the natives *H. malabaricus* and *R. vulpinus* from the Paraná River. If our predictions are correct and the ERH is confirmed, the release from parasites can be considered an important factor favouring the invasion success of *C. piquiti*.

Material and methods

Sampling

Fish collections were carried out in two areas: (1) the Tocantins River, in the Lajeado reservoir (10°66'55" S 48°42'36" W), where *C. piquiti* is native, and (2) the Paraná River, in the Itaipu reservoir (25°24'29" S 54°35'20" W), where the species was introduced (Fig. 1). Fish were captured by fishing rods, in October 2009 in Tocantins River and March 2010 in Paraná River (State University of Maringá, Ethics Committee on the Use of Animals in Experiments—protocol no. 051/2010). In total, 51 *C. piquiti* were collected, 24 in the Tocantins River and 27 in the Paraná River. The standard length ranged from 20.4 to 42.7 (31.9±5.3) considering both localities, from 20.4 to 42.7 (32.6±6.4) in the Tocantins River and from 23.4 to 32.2 (31.2±4.2) in the Paraná River. Finding sufficient number of specimens of the right species of *Cichla* was difficult, because new species were described in the revision of the genus by Kullander and Ferreira (2006), and their identification throughout the basins is still little documented, justifying why we could not include more times or localities of sampling. Although large seasonal differences were not observed by other authors studying the same species in a different locality (Martins et al. 2009), we recognise that ideally all fish should have been collected approximately at the same time, though this was logistically impossible. All fish were measured (standard length) and weighed, and their condition was estimated by the relative condition factor, which is the ratio between a fish's observed weight and that predicted by the weight-versus-length regression across all fish in the sample (Le Cren 1951). The necropsy of hosts and the collection, fixation and preservation of endoparasites followed the methods detailed by Eiras et al. (2002); ectoparasites were not considered in this study. Data regarding *H. malabaricus* and *R. vulpinus* were derived from a random subset of 27 fish taken from the samples obtained by Almeida (1998) and another random subset of 27 fish taken from Alvarenga (2008). The parasitological variables considered were infracommunity richness (number of different parasite species per individual fish), prevalence (percentage of fish infected by a given parasite species), mean intensity (mean number of individuals of a particular parasite species among the parasitized fish), abundance (number of individual parasites per fish) and mean abundance (arithmetic mean of the number of individuals of a particular parasite species per host) of given parasite species, in accordance with Bush et al. (1997). Representation of quantitative data followed the recommendations by Rozsa et al. (2000) regarding the report of the confidence limits for the prevalence and the bootstrap confidence intervals (BCa) for the mean intensity and mean abundance.

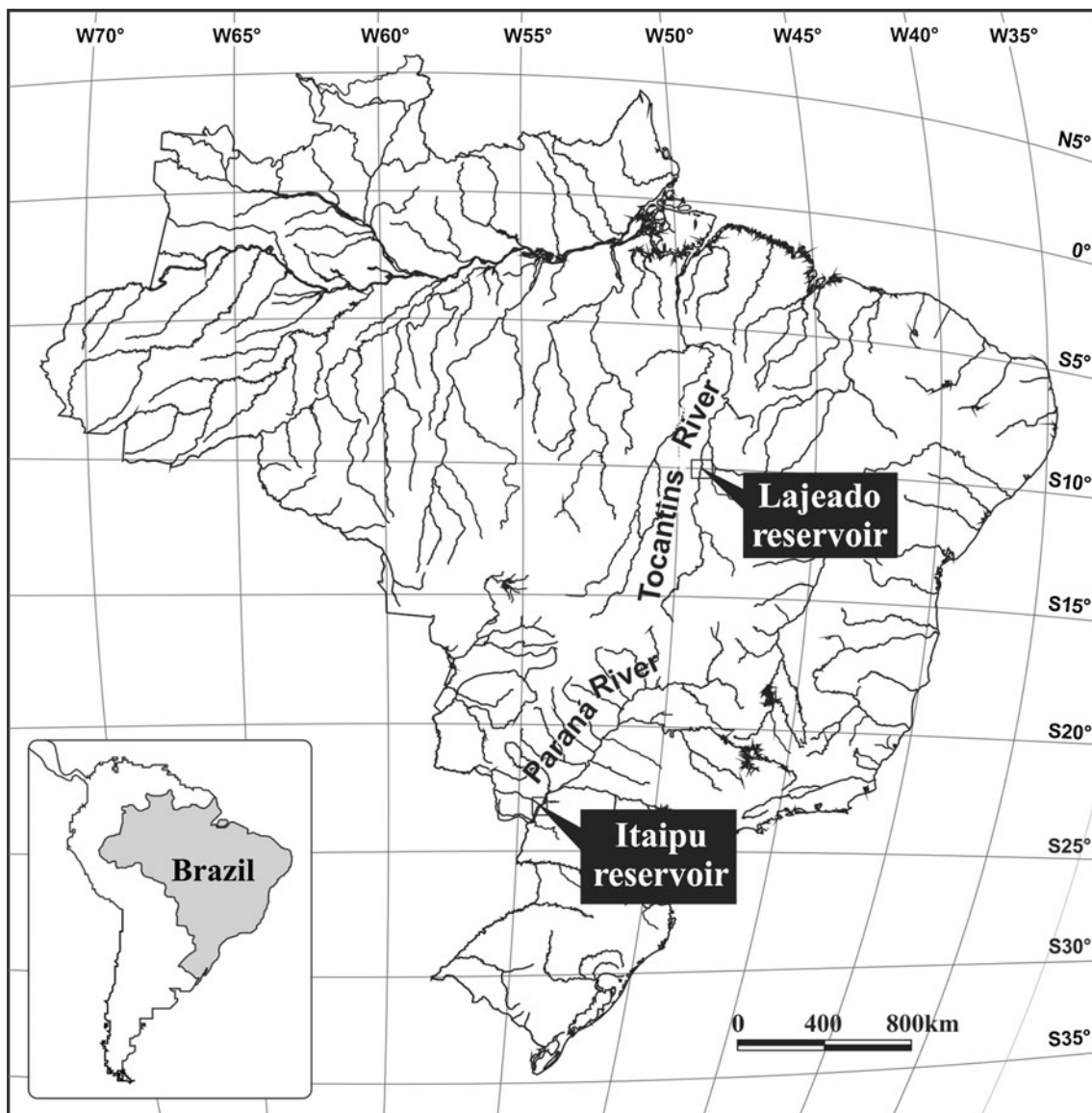


Fig. 1 Map of Brazilian basins with indication of the sampling sites in the Tocantins-Araguaia and Paraná Basins

Data analyses

The first series of analyses included only *C. piquiti* from their native and introduced areas combined. In order to determine which factors were responsible for the condition of individual hosts, we used a general linear model (GLM) with condition as response variable and the following variables as possible predictors: locality, infracommunity richness, abundance of each of the five parasite species that were found in both localities (*Austrodiplostomum* sp., *Proteocephalus macrophallus*, *Proteocephalus microscopicus*, *Sciadocephalus megalodiscus* and *Contracaecum* sp.), interactions between locality and parasite abundance and pairwise interactions between abundance of each species of parasite. To evaluate what factors determine how many

parasite species are harboured by individual fish, we then performed a generalized linear model (GLZ) with infracommunity richness as the response variable, assuming Poisson distribution, and length, condition and locality as possible predictors.

Finally, to determine which factors affect the abundance of given parasite species in individual fish, we performed GLZs with the abundance of each species of parasite that were recorded in both localities as response variables, assuming quasi-Poisson distribution, and using length and condition of host and abundance of all other species of parasite as possible predictors. For the first two analyses, selection of the best models was based on Akaike's Information Criterion (AIC). For the models that assumed quasi-Poisson distribution, quasi-AIC was used to select the

most parsimonious model (Burnham and Anderson 2002). The models only included parasite species that were found in both localities, and predictors were considered significant to the model using $\alpha=0.05$.

Additional analyses were conducted to compare *C. piquiti* to other predatory fish native to the Paraná River. The Mann–Whitney test was used to assess differences in the abundances of eye flukes of the family Diplostomidae between the introduced host *C. piquiti* and the native host *H. malabaricus*. We also used the Kruskal–Wallis test to compare the abundances of the nematode larva *Contracaecum* sp. among the introduced host *C. piquiti* and the two native hosts *H. malabaricus* and *R. vulpinus*. We finally performed another GLM with fish condition as response variable and two possible predictors: host species (*C. piquiti* and *R. vulpinus*; *H. malabaricus* was not included as no condition data are available for this species) and abundance of *Contracaecum* sp., to determine if the body condition of the introduced species was more affected than that of the native species by the abundance of the parasite. All analyses were conducted in R, version 2.7.2 (R Development Core Team 2010).

Results

Ten species of endoparasites were identified, and five species were present in hosts from both localities (Table 1). One specimen of *Sphincterodiplostomum* (metacercariae) was found in the lumen and considered accidental; therefore, it was not included in the analyses. Seven species were found in fish from the Tocantins River and seven in fish from the Parana River. As the taxonomy and identification to the species level of metacercariae of Diplostomidae and *Contracaecum* are very difficult and not previously studied in these regions, we cannot confirm that the same species is parasitizing fish in both rivers. However, we considered that even if they were different species of eye flukes and nematodes, they would still have similar biology and should affect the host in similar ways. Voucher specimens of *Austrodiplostomum* sp. and *Contracaecum* sp. from both localities, fixed in 5 % formalin and conserved in 70 % ethanol, were deposited in the Coleção Helminologica do Instituto Oswaldo Cruz—CHIOC, Rio de Janeiro, Brazil (numbers 37809, 35836 and 35837—*Austrodiplostomum* sp.; 37805 and 35835—*Contracaecum* sp.).

According to the GLM with host condition as a response variable (see ‘Electronic supplementary material’), there was a significant interaction between the abundances of the parasites *Austrodiplostomum* sp. and *S. megalodiscus* ($t=3.47, P=0.001$) and those of *P. macrophallus* and *S. megalodiscus* ($t=2.60, P=0.013$), indicating that the effect of one parasite on host

condition was dependent on the other's presence. For instance, abundance of *Austrodiplostomum* sp. correlated negatively with host condition in the absence of *S. megalodiscus*, but almost positively in its presence. On the other hand, abundance of the larval nematode *Contracaecum* sp. showed a significant negative correlation with the condition of hosts in both localities and independently of the presence of other parasites ($t=-2.34, P=0.025$). The abundances of the parasites *Austrodiplostomum* sp. ($t=-2.19, P=0.035$) and *S. megalodiscus* ($t=-3.06, P=0.004$) also correlated negatively with host condition, but only in fish from the native environment. Regarding the infracommunity richness, none of the considered predictors were significantly correlated with the response variable. Almost all the models built with the abundances of parasites as response variables revealed no significant predictor. In the condition model, only *Contracaecum* sp. abundance was negatively correlated with fish condition ($t=-4.00, P<0.001$) and generally higher in the native environment ($t=3.96, P<0.001$) (Fig. 2). In the length model, *Contracaecum* sp. abundance was also positively correlated with fish length in the native environment ($t=3.86, P<0.001$), and *P. microscopicus* abundance was positively correlated with length ($t=3.96, P<0.001$). No predictors were retained in the GLZs performed with *Austrodiplostomum* sp., *P. macrophallus* and *S. megalodiscus* abundances as response variables.

According to the Mann–Whitney test, the abundances of the nematode larvae *Contracaecum* sp. did not differ between native and introduced hosts, only between native hosts (Table 2, Fig. 3a). Regarding the abundance of eye flukes, abundance values were significantly higher in the native host *H. malabaricus* ($U=1656.5, P=0.007$; Fig. 3b).

The GLZ performed using the condition of the introduced host *C. piquiti* and that of the native host *R. vulpinus* as response variable showed that the species of host and the abundance of *Contracaecum* sp. are not strong predictors of the condition of these fishes in the Paraná River, since none of the variables were retained in the model.

Discussion

The ERH is widely invoked to explain the success of invading species (Torchin et al. 2003). The findings of the present study, however, suggest that a variant of the ERH might provide a better explanation for the success of the fish *C. piquiti* in the Paraná River. Indeed, our results at both the biogeographical and the local community scales indicate that introduced fish are not released from their parasites, but may be released from the negative effects of those parasites. However, the ideal design for a test of the ERH would involve sampling several localities in both the

Table 1 Endoparasites of *C. piquiti* in the native environment, Tocantins River, and in the invaded environment, the Paraná River, and the parasite's effect on the relative condition factor of the hosts

Locality	Taxonomic group	Parasite	Infection site	P	MI	MA	Parasite effect on host condition ^a
Tocantins River (n=24)	Digenea	<i>Austrodiplostomum</i> sp.	Aqueous humour	0.12 (0.03–0.31)	1.00	0.13 (0–0.25)	Negative
		Cyst	Fin	0.04 (0.00–0.20)	1.00	0.04 (0.00–0.13)	None
	Cestoda	<i>Proteocephalus macrophallus</i> (Diesing 1850)	Intestine	0.42 (0.23–0.63)	3.60 (2.10–6.30)	1.50 (0.67–2.88)	None
		<i>Proteocephalus microscopicus</i> (Woodland, 1935)	Intestine	0.83 (0.63–0.94)	211.20 (62.25–760.25)	176.00 (45.08–586.29)	None
		<i>Sciadocephalus megalodiscus</i> (Diesing, 1850)	Intestine	0.58 (0.37–0.77)	11.00 (6.21–19.37)	6.42 (3.38–12.25)	Negative
	Nematoda	<i>Contracaecum</i> sp. (larvae)	Mesentery and intestine	0.92 (0.73–0.98)	28.00 (17.41–42.14)	25.67 (15.88–40.92)	Negative
Paraná River (n=27)	Digenea	<i>Cucullanus</i> sp.	Intestine	0.29 (0.14–0.50)	2.00 (1.29–2.71)	0.58 (0.21–1.08)	None
		<i>Austrodiplostomum</i> sp.	Aqueous humour	0.26 (0.12–0.46)	13.43 (3.57–41.29)	3.48 (0.70–11.56)	None
	Cestoda	<i>Proteocephalus macrophallus</i>	Intestine and stomach	0.70 (0.50–0.85)	13.11 (6.16–35.53)	9.22 (4.15–26.26)	None
		<i>Proteocephalus microscopicus</i>	Intestine and stomach	0.78 (0.58–0.90)	80.48 (45.62–151.57)	62.59 (32.85–123.33)	None
		<i>Sciadocephalus megalodiscus</i>	Intestine	0.11 (0.03–0.29)	81.00 (1.00–160.67)	9.00 (0.04–44.48)	None
	Nematoda	Cysts	Mesentery	0.04 (0.00–0.18)	1.00	0.04 (0.00–0.11)	None
	<i>Contracaecum</i> sp. (larvae)	Mesentery, stomach and intestine	0.59 (0.40–0.76)	4.38 (2.69–8.25)	2.59 (1.48–5.22)	Negative	
	<i>Procammallanus</i> (<i>Spirocammallanus</i>) <i>rarus</i> Travassos, Artigas and Pereira, 1928	Intestine	0.04 (0.00–0.18)	4.00	0.15 (0.00–0.44)	None	

95 % confidence limits between parentheses

P prevalence, MI mean intensity of parasitism, MA mean abundance of parasitism

^a Considering significant correlation ($P < 0.05$) according to the generalized linear models using the relative condition factor of the hosts as response variable and abundance of parasites and locality as possible predictors

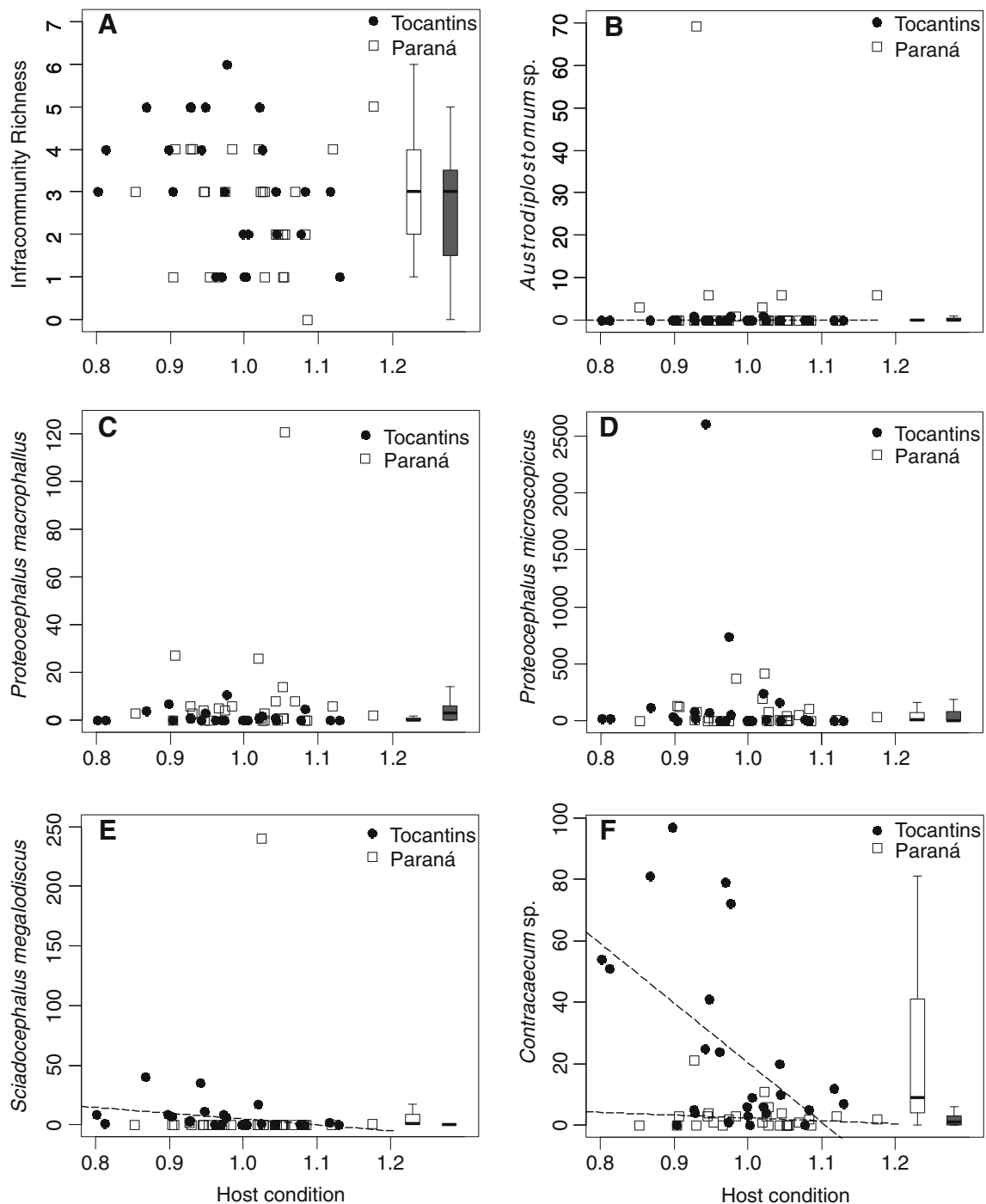


Fig. 2 Correlation between the infracommunity richness (a) and abundance of endoparasites (b–f), and the condition of the host *C. piquiti*, in the rivers Tocantins (black circles) and Paraná (white squares). Dashed

lines show significant correlation for Tocantins and Paraná, respectively, and boxplots represent medians, interquartile ranges and minimum–maximum ranges without outliers

original and invaded areas, and because this was not possible, our conclusions must be interpreted with caution. In addition, we are also aware that parasitism in different host species from the invaded area may be affected by factors other than the original distribution of the fish, such as their biology and behaviour.

Biogeographical scale

In contrast to what was expected, total parasite species richness of *C. piquiti* did not differ between the invaded environment and the area where the fish is native, as well as infracommunity richness, if we consider *Sphinctrodiplostomum* sp. an

Table 2 Results of Kruskal–Wallis test and Mann–Whitney test between the abundances of *Contracaecum* sp. in the hosts *C. piquiti*, *H. malabaricus* and *R. vulpinus* from the Paraná River

Hosts of <i>Contracaecum</i> sp. in the Paraná River (n=81)	Kruskal–Wallis		Mann–Whitney	
	<i>H</i>	<i>P</i>	<i>U</i>	<i>P</i>
<i>C. piquiti</i> × <i>H. malabaricus</i> × <i>R. vulpinus</i>	6.728	0.035 ^a	–	–
<i>C. piquiti</i> × <i>H. malabaricus</i>	–	–	296.5	0.229
<i>C. piquiti</i> × <i>R. vulpinus</i>	–	–	454.0	0.088
<i>H. malabaricus</i> × <i>R. vulpinus</i>	–	–	495.5	0.015 ^a

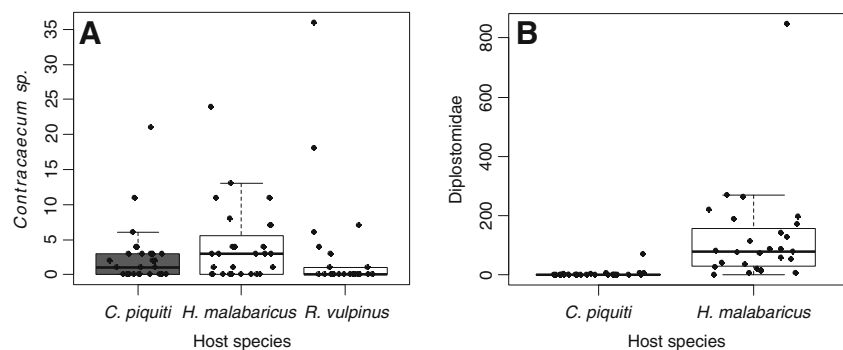
^aSignificant values

accidental parasite. The introduced hosts were not released from the number of species of parasites they harbour or even from particular parasite species. The communities of parasites were very similar, because the species that were found in only one locality presented low values of prevalence and abundance. However, species richness is not a good indicator of ‘enemy release’, because a reduction in the number of parasite species could theoretically decrease inter-specific competition between parasites within infracommunities, potentially resulting in increased abundance of the remaining parasite species (Roche et al. 2010).

Most parasite species were found in both localities (*Austrodiplostomum* sp., *P. macrophallus*, *P. microscopicus*, *S. megalodiscus* and *Contracaecum* sp.). For the three species of cestodes (*P. macrophallus*, *P. microscopicus* and *S. megalodiscus*), this means they were introduced to the new environment, since the only record of these species in the Paraná River is for *Cichla kelberi*, another introduced fish native to the Amazonas basin (Takemoto and Pavanelli 1996; Takemoto et al. 2009) and the only other possible source of the introduction of these parasites. The presence of the cestodes in the new environment do not support the statement made by Kennedy and Bush (1994), which argued that specialist parasites (see Bush and Homes 1986) are more likely to be lost in invaded environments because they depend on a narrow range of host taxa. Unfortunately, little is known about the life cycles of species of the Order Proteocephalidea in South America, although they generally need three hosts, one invertebrate (a copepod) and two vertebrates (fish) (Dick et al. 2006). Somehow, these cestodes are able to complete their life cycles in the new

environment, using intermediate hosts native to the invaded area or that were introduced with the invasive host as associate fauna, maintaining populations with considerable levels of prevalence and abundance. The co-generic introduced fish *C. kelberi* may play an important role in their population dynamics. Cases of introduction and establishment of parasites with their hosts have been reported by Jiménez-García et al. (2001) and Ramalho et al. (2009) and seem to depend more on parasite transmission efficiency than on propagule pressure (MacLeod et al. 2010). The set of individuals released in the non-native environment is called propagule, and the combination of the propagule's population size, the number of release events and the health of individuals released is described as the propagule pressure (Lockwood et al. 2007).

The larval parasites *Austrodiplostomum* sp. (Diplostomidae) and *Contracaecum* sp. were observed parasitizing *C. piquiti* in both localities, but we cannot determine if they were introduced because it is not possible to ascertain whether they are the same species without performing genetic studies. The taxonomy of larval forms of *Austrodiplostomum* is still obscure, especially in South America (Niewiadomska 2005). A recent study by Locke et al. (2010) on the diversity of metacercariae of *Diplostomum* spp. separated 12 very similar species by their genotypes, within Canada alone. A similar cryptic diversity might characterise *Austrodiplostomum* in South America. Identifying larvae of *Contracaecum* at the species level is also complicated (Moravec 1998) and involves much uncertainty. In addition, *Austrodiplostomum* and *Contracaecum* use piscivorous birds as definitive hosts (Niewiadomska 2005; Molnár et al. 2006), and these hosts could have a strong influence on the

Fig. 3 Abundances of the nematodes *Contracaecum* sp. (a) and eye flukes from the family Diplostomidae (b) in the introduced fish *C. piquiti* (solid circle) and in the native hosts *H. malabaricus* and *R. vulpinus* (in open square), in the Paraná River

parasite fauna of fish from both environments. The differences between basins of these unspecific larvae can largely rely in the distribution and migratory behaviour of their definitive hosts rather than in the context of the ERH. The two species of parasites found in the Tocantins River that were not recorded in the Paraná River, one digenean cyst and the nematode *Cucullanus* sp., also presented low prevalence in the native environment, indicating that they were perhaps not introduced to the new environment as a consequence of the sub-sampling nature of host introduction (Torchin et al. 2003; Colautti et al. 2004).

Although acquisition of native parasites by introduced hosts has been reported frequently (Criscione and Font 2001; Jiménez-García et al. 2001; Poulin and Mouillot 2003; Krakau et al. 2006; Kvach and Skóra 2007; Kelly et al. 2009; Ondračková et al. 2009; Roche et al. 2010), only two species, one larval digenean, *Sphincterodiplostomum* sp. (larvae), and one adult nematode, *Procamallanus* (*Spirocamallanus*) *rarus*, were found in hosts introduced to the Paraná River. *Sphincterodiplostomum* sp. (larvae) was recorded parasitizing other piscivorous fishes in the region, i.e. *H. malabaricus* (Erythrinidae) and *Hemisorubim platyrhynchos* (Pimelodidae) (Takemoto et al. 2009). Since only one specimen was found in *C. piquiti*, it was considered accidental. The parasites of the subgenus *Procamallanus* (*Spirocamallanus*) can be found in several hosts in the region (Takemoto et al. 2009), and only one specimen was observed in *C. piquiti*. It is possible that new fish are resistant to native parasite species, as reported by Fromme and Dybdahl (2006) for freshwater snails. The abundance of the most prevalent and abundant species of cestode, *P. microscopicus*, was not correlated with the condition of the hosts in both localities. Probably these two characteristics, high parasitism levels and absence of significant influence on the host condition, were responsible for the successful establishment of the cestode in the invaded environment, in addition to the presence of another host species, *C. kelberi*.

The opposite was observed for other parasite species. *Austrodiplostomum* sp. and *S. megalodiscus* presented significant negative correlation with the condition factor of fish within the native range, implying they did not affect the same fish species in the introduced region in the same way. In the case of the eye fluke *Austrodiplostomum*, we believe the result is derived from too few data, since only three fish were parasitized by only one metacercariae each (Table 1). Thus, it is not expected that these results have a real biological sense. On the other hand, the negative effects of *S. megalodiscus* on the condition of hosts only within the native range may indicate not an ‘enemy release’, but a ‘release from the effect of the enemy’ for introduced fish, since the abundance of parasites did not differ between localities. Although we know the condition is affected by periods of starvation, reproduction and maturation (Neff and

Cargnelli 2004), the outcome of these factors on the condition of the hosts was considered similar for both environments, since there was no significant difference between the condition values of the two populations. According to Colautti et al. (2004), in a situation where the success of introduction and establishment depends upon the health of the host, parasites with strong effects will be more readily excluded from the introduced population. In the case of *C. piquiti*, two possible and not mutually exclusive bottlenecks could have happened: (1) the population of hosts in the Paraná River could be the result of a selection for fish with greater resistance to the effects of the parasites, in comparison to fish from the native range, and (2) the parasites *S. megalodiscus* may have undergone selection for reduced pathogenicity. Non-native populations may undergo micro-evolutionary shifts in their morphology or physiology in response to strong selection pressures, and this genetic reshuffling can be quite extreme (Lockwood et al. 2007). Torchin et al. (2002) say that, if a species does not bring its natural enemies with it, it should experience a release in its new geographic range, and this release will be of a magnitude proportional to the ecological importance of the natural enemies left behind (although nothing is said about how to measure the ecological importance). In this case, *C. piquiti* was released from the negative influence of its parasite species on its condition factor.

Contracaecum sp. showed significant negative correlations with the condition of the hosts in both localities. This may be a causal relationship, since larval anisakids are known to be very pathogenic to their fish hosts (Moravec 1998). And although this negative correlation occurred in both localities, *Contracaecum* sp. was more abundant and more prevalent in the Tocantins River; therefore, the parasite load was higher in the native environment, and more hosts in the population were parasitized. In addition, abundance of the cestode *P. microscopicus* was positively correlated with length in both localities, which could be the result of a simple age-related process occurring in both localities, where the host accumulates parasites along its lifespan (Dogiel et al. 1958), as reported by Machado et al. (2000) for the same parasite species parasitizing *C. kelberi* in the Paraná River.

Community scale

Results for the abundance of *Contracaecum* sp. in the Paraná River indicate that it does not have a weaker effect on the introduced host species than it does for natives, considering the abundance of the parasite and also its correlation with host condition. Thus, if there is some advantage related to parasitism in the new environment for the invader, it does not involve generalist parasites (Bush and Homes 1986) that exhibit very low host specificity like

Contracaecum sp. On the other hand, the native hosts were more heavily parasitized by Diplostomidae eye flukes, another generalist group. However, in this case, there may be a significant advantage for the invader, because eye flukes have direct effects on both feeding efficiency and risk of predation, manipulating the behaviour of the fish host by reducing its ability to capture prey and making it more susceptible to predation by the definitive host, a piscivorous bird (Voutilainen et al. 2008; Fig. 3). Roche et al. (2010) found that the abundance of several parasite species of *Oreochromis niloticus*, a cichlid introduced to the Panama Channel watershed, was lower in the introduced fish than in the native fish *Vieja maculicauda*. Similarly, Krakau et al. (2006) and Dang et al. (2009) found that prevalence and intensity of native parasites were lower in introduced bivalves, compared to native ones. Lower levels of parasitism in introduced hosts may indicate that native parasites do not demonstrate the ability required to infect the new hosts or instead a differential investment in immune defences between introduced and native hosts (Cornet et al. 2010). When considering parasite–host coevolution, local parasites should be more effective at exploiting native hosts than invaders (Fromme and Dybdahl 2006; Genner et al. 2008; Cornet et al. 2010).

In conclusion, the present results do not support the ERH as a possible explanation for the success of *C. piquiti* in the new environment. Effective host switching by native parasites to invaders did not occur, even if specialist enemies of the genus *Cichla* had also been introduced to the invaded region (cestodes). In addition, the abundance of generalist enemies (*Austrodiplostomum* sp. and *Contracaecum* sp.) in native and introduced hosts in the invaded environment showed trends opposite to those predicted by the ERH. In the case of *C. piquiti*, the low abundance of *Austrodiplostomum* sp. compared to what is seen in the native host *H. malabaricus* could be considered an advantage if the two fish species compete for prey. Finally, the fact that *S. megalodicus* only have significant negative effects on host condition in their native environment showed that perhaps the explanation for the invasion success is not the release from certain enemies *per se*, but the release from the effect of those enemies. Clearly, it is not sufficient to look merely at the number of parasites infecting exotic hosts in their original and new areas; it is also important to look at the parasites' effects on host physiology and/or fitness.

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