Host population density as the major determinant of endoparasite species richness in floodplain fishes of the upper Paraná River, Brazil

R.M. Takemoto[1], G.C. Pavanelli[1], M.A.P. Lizama[1], J.L. Luque[2]* and R. Poulin[3]

[1]Nupélia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura), Universidade Estadual de Maringá, Bloco G-90, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil: [2]Departamento de Parasitologia Animal, Universidade Federal Rural do Rio de Janeiro, Caixa Postal 74.508, CEP 23851-970, Seropédica, RJ, Brazil: [3]Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

Abstract

A comparative analysis of parasite species richness was performed across 53 species of fish from the floodplain of the upper Paraná River, Brazil. Values of catch per unit effort, CPUE (number of individuals of a given fish species captured per $1000\,m^2$ of net during 24 h) were used as a rough measure of population density for each fish species in order to test its influence on endoparasite species richness. The effects of several other host traits (body size, social behaviour, reproductive behaviour, spawning type, trophic category, feeding habits, relative position in the food web, preference for certain habitats and whether the fish species are native or exotic) on metazoan endoparasite species richness were also evaluated. The CPUE was the sole significant predictor of parasite species richness, whether controlling for the confounding influences of host phylogeny and sampling effort or not. The results suggest that in the floodplain of the upper Paraná River (with homogeneous physical characteristics and occurrence of many flood pulses), population density of different host species might be the major determinant of their parasite species richness.

Introduction

Parasite assemblages are playing an increasingly important role as models for the study of biodiversity and biogeography (Poulin & Morand, 2000). Different events can lead to new species joining parasite assemblages, but identifying key factors that have caused certain parasite assemblages to diversify more than others over evolutionary time remains a challenge (Poulin, 1998). Yet, the results currently available are inconsistent (Poulin, 1997; Morand, 2000). One reason for this inconsistency may be that most data sets used in previous analyses have been compiled from many different sources. Differences in the methods used to detect and identify parasites from a variety of sources can generate too much error and statistical noise for any existing signal to emerge. In addition, different host species included in the same data set often come from different geographical areas and the availability of, and exposure to, different parasite species varies across regions, adding another element of variability to such data sets. Whereas these caveats are unavoidable for investigations on geographical scales, they pose problems for studies focusing on host traits. For the

*Author for correspondence
Fax: 55 21 2682 1617
E-mail: jlluque@ufrrj.br

latter, one would ideally examine interspecific variation in parasite species richness among a group of host species from the same area, all examined in a standard way by the same researcher(s).

Predictions about which host features may promote the diversification of parasite assemblages have come from two theoretical frameworks. Firstly, following from the island biogeographical theory (MacArthur & Wilson, 1967; Kuris *et al.*, 1980), host features that promote high rates of parasite speciation or colonization by new parasite species should be associated with high parasite species richness. These features may include host body size, geographical range size, diet breadth, etc. Empirical support exists for most of these variables, but with the inconsistencies alluded to above (see Poulin, 1997; Morand, 2000). The second theoretical source of predictions regarding parasite species richness has been epidemiological modelling (Roberts *et al.*, 2002). These models indicate that host population density, which regulates the contact rate between parasite infective stages and hosts, is the key factor determining whether a parasite species can invade and persist in a host population. Host species occurring at higher population density should harbour more species of parasites, because they exceed the persistence threshold of more parasite species than hosts with a low population density. A comparative study on fishes (Morand *et al.*, 2000) found support for this prediction, as did studies on parasite richness of terrestrial mammals (Morand & Poulin, 1998; Arneberg, 2002). However, this prediction has not been tested across the majority of host species recorded in a given ecosystem.

In the present study, the relationship between different features of host species and the parasite species richness of metazoan endoparasite assemblages are examined across species of fish hosts from the floodplain of the upper Paraná River. This study represents the first serious attempt to investigate patterns and causes of variation in parasite species richness across most of the host species in a given ecosystem.

Materials and methods

Study area

The floodplain of the Upper Paraná River, Brazil (22°43′, 53°10′W) (fig. 1) has the shape of a large braided
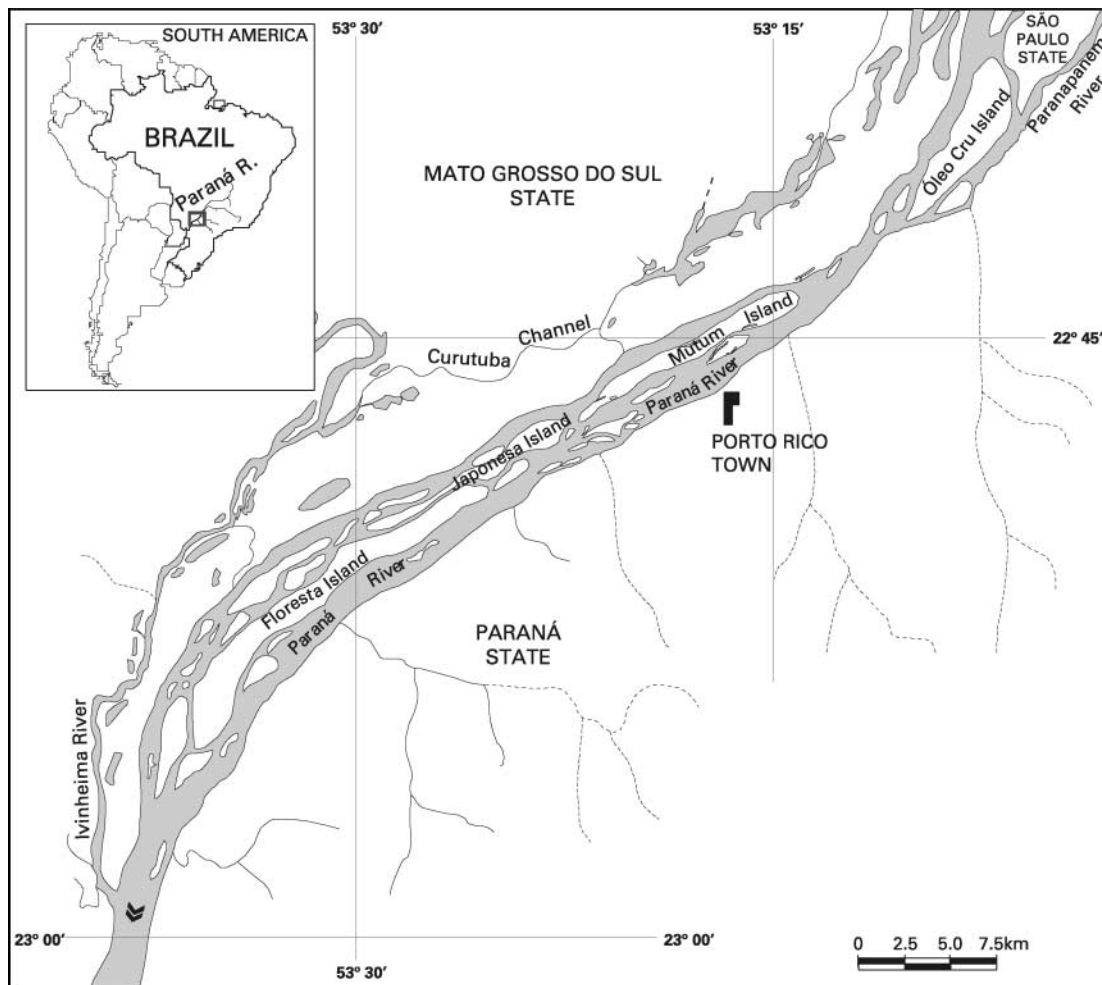

Fig. 1. Floodplain of the upper Paraná River, Brazil.

channel, and includes several lagoons, channels and small rivers. The floodplain has a weak gradient (0.09 m km^{-1}), and its area (in Brazil) is approximately 800,000 km^2, constituting the last stretch not dammed (until 1998 when the construction of the Dam of Porto Primavera was finished) of the Paraná River in Brazilian territory (Souza Filho & Stevaux, 1997). The Paraná River floodplain has a period of high water levels from October to January that can extend to April and July (the months with higher temperatures). Oscillations in the water level can reach up to 3 m and are coupled with the occurrence of many flood pulses (see Junk et al., 1989) in the same hydrological cycle (Thomaz et al., 1992, 1997). The ichthyofauna comprises approximately 103 known species, dominated by characiform and siluriform fishes. The majority of fish species are native, and only six exotic species have been recorded in this region (Agostinho et al., 1997a). Pavanelli et al. (1997) published a preliminary list of the helminth parasites of fishes from the floodplain of the Upper Paraná River with data collected from 81 host species. More detailed information about the biota of this region can be found in Vazzoler et al. (1997a).

Data collection

All fish were collected from the floodplain of the Upper Paraná River, Brazil, during the period 1986 to 2003. Fish collections were carried out at the same time of year (during the period of high water levels), and at the same site in the floodplain (Porto Rico Town, see fig. 1). The taxonomy of the fishes follows that of Reis et al. (2003). Each individual fish was measured (standard length) and examined for internal metazoan parasites using parasitological methods described in Eiras et al. (2000). Washings from the lumen of the gut were passed through a sieve (154 μm mesh size) to recover even the smallest parasites. The metazoan parasites recovered consisted of platyhelminths (trematodes and cestodes), acanthocephalans and nematodes. All fish collections and dissections, and recovery of parasites were made using the same methods, in the same laboratory, and all parasite identifications were carried out or confirmed by the same persons (GCP, MAPL and RMT). Thus the data represent a single data set, and do not suffer from the problems associated with data sets compiled from different sources and based on different methods. Quantitative information on the prevalence and intensity of infection by different parasites and on parasite community descriptors have been published previously for some of the fish species in the data sets (Machado et al., 1994, 1995, 1996, 2000; Takemoto & Pavanelli, 1994, 2000; Pavanelli et al., 1997; Pavanelli & Takemoto, 2000; Guidelli et al., 2003; Lizama, 2003). The present analysis is the first to combine all these data; and the entire data set of host species included in the analyses is shown in table 1. For each host species, the total number of fish examined for parasites and the total number of endoparasite species (i.e. parasite species richness) found were recorded. The number of hosts examined, or sampling effort, is included as a potential confounding variable.

Values of catch per unit effort, CPUE (number of individuals of a given fish species captured per 1000 m^2 of net during 24 h) were obtained from Agostinho et al.

(1997a,b) and used as an approximate measure of population density for each fish species (King, 1996). These values were obtained monthly throughout 1986–1988 and 1992–1994, using a range of specific nets installed to catch fish, with various mesh sizes (3–16 cm) covering the size range of the different fish species.

In addition to data on average host body length obtained from the individual fish examined, data were also obtained from Vazzoler, 1996; Agostinho et al., 1997a; Hahn et al. 1997, 1998; Vazzoler et al., 1997b; Luiz et al., 1998; Agostinho & Júlio, 1999 and from personal communications with other researchers (see Acknowledgements), on the following variables for each fish species: (i) whether the fish species forms schools or not, with species forming schools during only certain parts of the year being classified as schooling; (ii) the trophic category, where the fish species were distributed into eight categories (according to Agostinho et al., 1997b): herbivorous, planktivorous, insectivorous, iliophagous (ingesting the top layer of bottom sediments with the associated micro- and meiofauna), detritivorous, benthophagous, piscivorous and omnivorous; (iii) the relative position in the local food web (basal, intermediate or top level); (iv) reproductive behaviour: species with external fertilization, migratory; external fertilization, sedentary, guarders; external fertilization, sedentary, non-guarders; and internal fertilization; (v) spawning type, whether having repeated bouts of spawning (iteroparous), or with a single spawning effort (semelparous); (vi) preference of certain habitat in the floodplain: lentic, lotic, semilotic; (vii) whether the fish's habitat is benthic, benthopelagic or pelagic; and (viii) whether the fish species are native (majority) or exotic. When local data were not available, information from Froese & Pauly (2003) were included.

Statistical analyses

Data were analysed, on endoparasites only, in two ways, i.e. one that highlighted any existing pattern in the distribution of parasite richness among host species, and one that emphasized those factors which may have played a role in the evolutionary diversification of parasite assemblages. In the first series of analyses, fish species were treated as independent observations, using standard parametric tests on log-transformed continuous variables. In analyses using categorical variables (e.g. schooling behaviour or feeding habits), it was not possible to use multifactorial ANOVAs because there were too few species in some categories and thus too many empty cells in the factorial matrix. Nevertheless, the analyses allowed us to determine which features of host species are associated with richer parasite assemblages. In the second round of analyses, host phylogeny was taken into account. Closely related host species are likely to harbour similar numbers of parasite species because these were inherited from a recent common ancestor; and this means that they do not represent truly independent statistical observations. We must therefore control for phylogenetic influences when evaluating the potential effects of host features (body size, schooling, feeding habits, etc.) on the evolution of parasite assemblages. To achieve this, we used the phylogenetically independent contrasts method (Felsenstein, 1985;

Table 1. Summary of data on the 53 fish species from the floodplain of the upper Paraná river included in the analyses.

Species	n^1	Parasite richness	Standard size (cm)	CPUE²	Habitat³	Trophic category⁴	FWL⁵	Benthic?⁶	School⁷	Reproductive behaviour⁸	Spawning⁹	Native?¹⁰
Acestrorhynchus lacustris	307	7	26.4	7.5	1	7	3	3	1	2	1	1
Ageneiosus inermis	15	2	44.8	20.39	2	7	3	2	2	4	1	1
Ageneiosus ucayalensis	28	1	32.5	1.25	3	7	3	2	1	4	1	1
Apareiodon affinis	11	1	13.6	5.11	3	8	3	3	2	2	1	1
Astronotus ocellatus	21	1	24.7	1.21	3	7	3	3	2	3	2	2
Astyanax altiparanae	203	15	21	37.84	2	8	2	3	1	2	1	1
Auchenipterus osteomystax	225	2	27	12.51	1	3	2	2	1	4	1	1
Brycon orbignyanus	56	1	29.1	0.06	2	3	2	3	1	1	2	1
Cichla monoculus	183	8	37.8	2.54	4	7	3	3	2	3	1	2
Cichlasoma paranaense	20	1	13.5	0.75	4	3	3	3	2	3	1	1
Crenicichla britskii	50	2	19.8	3.36	1	7	2	3	2	3	1	1
Crenicichla sp.	15	2	18.4	–	2	7	2	3	2	3	1	1
Cyphocharax modestus	18	1	15.5	1.57	1	4	1	3	2	2	1	1
Cyphocharax nagelii	68	2	16.5	1.96	3	4	1	3	1	2	1	1
Eigenmannia trilineata	11	0	23.2	2.16	2	6	2	3	1	2	1	1
Galeocharax knerii	44	1	21.5	0.13	2	7	3	3	1	2	1	1
Gymnotus carapo	231	17	32	2.87	1	3	2	3	2	4	1	1
Hemisorubim platyrhynchos	365	15	51.4	2.59	4	7	3	1	2	1	1	1
Hoplerythrinus unitaeniatus	49	3	27.5	4.38	3	7	3	2	2	3	2	1
Hoplias malabaricus	542	19	38.4	23.98	4	7	3	3	2	3	1	1
Hoplosternum littorale	60	1	19.4	10.67	1	6	2	1	1	3	1	1
Hypophthalmus edentatus	35	1	43	1.14	3	2	1	2	2	2	1	1
Iheringichthys labrosus	222	2	27.6	6.3	4	6	2	1	2	2	2	1
Leporinus friderici	223	7	30.8	5.82	2	8	2	3	2	1	2	1
Leporinus sp.	177	6	40	2.95	3	8	2	3	1	2	2	1
Leporinus lacustris	273	10	22	15.4	1	8	2	3	2	2	1	1
Leporinus obtusidens	42	8	20.7	1.66	2	8	2	3	1	1	2	1
Loricariichthys platymetopon	203	2	38.8	92.78	3	5	1	1	2	3	1	1
Metynnis cf. *maculatus*	15	2	15	0.88	3	1	2	2	1	2	2	1
Moenkhausia intermedia	88	1	9	31.53	1	3	2	3	2	2	1	1
Parauchenipterus galeatus	515	5	22	37.85	3	8	2	1	2	4	2	1
Piaractus mesopotamicus	68	4	41.6	0.11	1	1	1	1	1	1	2	1
Pimelodus maculatus	690	20	31.5	6.56	3	8	2	3	1	1	?	1
Pimelodus ornatus	12	2	28.9	0.32	4	8	2	3	1	1	2	1
Pinirampus pirinampu	73	3	57	0.28	3	7	3	1	1	1	2	1
Plagioscion squamosissimus	145	2	44	4.65	4	7	3	3	1	2	1	2
Potamotrygon motoro	18	1	32.5	0.045	2	6	2	3	2	4	2	1
Prochilodus lineatus	491	19	54.2	10.09	4	4	1	3	2	2	2	1
Pseudoplatystoma corruscans	362	12	136	2.72	4	7	3	1	2	1	2	1
Pterodoras granulosus	92	4	54.3	0.94	2	8	2	1	2	1	1	1
Rhamphichthys hahni	23	1	98	0.78	4	7	3	3	2	3	1	1
Rhaphiodon vulpinus	115	2	65.7	8.19	4	7	3	2	2	1	2	1
Roeboides paranensis	81	3	10.5	17.94	4	3	2	3	1	2	2	1
Salminus brasiliensis	173	5	75.5	0.32	2	7	3	3	1	3	2	1
Satanoperca pappaterra	204	2	18	4.53	4	6	2	3	2	3	1	2
Schizodon borellii	861	11	29.5	16.02	1	1	1	3	2	2	2	1
Schizodon altoparanae	104	5	31.7	0.99	3	1	1	3	1	2	1	1
Serrasalmus marginatus	799	8	22.1	62.54	4	7	3	3	2	3	1	1

Table 1. *continued.*

Species	n[1]	Parasite richness	Standard size (cm)	CPUE[2]	Habitat[3]	Trophic category[4]	FWL[5]	Benthic?[6]	School[7]	Reproductive behaviour[8]	Spawning[9]	Native?[10]
Serrasalmus spilopleura	353	8	26.1	3.84	3	7	3	3	2	3	1	1
Sorubim lima	122	5	48.2	0.5	4	7	3	1	1	1	2	1
Steindachnerina insculpta	115	1	16	20.14	4	4	1	3	1	2	1	1
Trachydoras paraguayensis	183	3	13.5	13.54	2	6	2	1	1	2	1	1
Zungaro zungaro	10	7	140	–	4	7	3	1	2	1	2	1

[1] Number of fish examined.
[2] Catch per unit effort (number of individuals of a given fish species captured using 1000 m² of net during 24 h).
[3] Lentic = 1; lotic = 2; semilotic = 3; all habitats = 4.
[4] Herbivorous = 1; planktivorous = 2; insectivorous = 3; iliophagous = 4; detritivorous = 5; benthophagous = 6; piscivorous = 7; omnivorous = 8.
[5] Food web level: basal = 1; intermediate = 2; top = 3.
[6] Benthic = 1; pelagic = 2; benthopelagic = 3.
[7] Schooling behaviour = 1; solitary = 2.
[8] Migratory with external fertilization = 1; sedentary, guarders, with external fertilization = 2; sedentary, non-guarders, with external fertilization = 3; internal fertilization = 4.
[9] Repeated spawning effort (iteroparous) = 1; single spawning effort (semelparous) = 2.
[10] Native species = 1; exotic species = 2.

Harvey & Pagel, 1991), implemented with the CAIC version 2.0 program (Purvis & Rambaut, 1994). Contrasts were derived from a host tree constructed from published studies on the phylogenetic relationships of fish (Alves-Gomes *et al.*, 1993; Nelson, 1994; Ortí *et al.*, 1996; Ortí & Meyer, 1997; Kullander, 1998; Pinna, 1998; Farias *et al.*, 2000). Contrasts were computed on log-transformed data and all regression analyses were forced through the origin (Garland *et al.*, 1992). We obtained contrasts corrected for the influence of sampling effort as a confounding variable by taking the residuals of regressions of a selected variable (e.g. parasite species richness) against the host sample size. For categorical variables (schooling behaviour, feeding habit, reproductive behaviour, etc.), contrasts were computed following Burt (1989). As many of the categorical variables studied were not dichotomous, the original data was reorganized to perform this analysis: Trophic category, (1) Herbivorous + Planktophagous + Insectivorous + Iliophagous + Detritivorous + Benthophagous, (2) Piscivorous + Omnivorous; Food web level, (1) Basal + Intermediate, (2) Top; Reproductive behaviour, (1) Migratory, (2) Sedentary; Preference of certain habitat, (1) Lentic, (2) Lotic + Semilotic; Benthic/pelagic, (1) Benthic + Benthopelagic, (2) Pelagic. The values of parasite species richness for sister taxa in different categories were compared using paired *t*-tests.

Because the aim was to reveal associations between host features and measures of parasite species richness, a Bonferroni correction was not applied to the present results. Applying the correction could possibly mask interesting trends worthy of further investigation (Moran, 2003).

Results

In total, data from 87 fish host species were obtained, which represent 84.5% of 103 species recorded in this ecosystem by Agostinho *et al.* (1997a). These data were derived from an examination of 9501 fish, for an average of 158.5 hosts per species (range 1–861). For comparative analyses only fish species with ten or more individuals examined (53 species) were used (table 1). Data from the other 34 species are included in appendix 1.

Using data on metazoan endoparasites across all fish species, the number of hosts examined per species correlated positively with parasite species richness ($r = 0.961$, $n = 53$, $P < 0.0001$). Thus, in all comparative analyses, parasite species richness is corrected for sampling effort (using residuals from a regression).

Using species values as independent statistical observations, CPUE was found to be correlated positively with parasite species richness ($r = 0.539$, $n = 51$, $P < 0.0001$). This pattern is independent of sampling effort, and is repeated when using phylogenetically independent contrasts ($r = 0.674$, $n = 37$, $P = 0.0001$) (fig. 2). No significant relationships were found between parasite species richness and any of the other variables studied either using species values as independent statistical observations or phylogenetically independent contrasts (table 2).
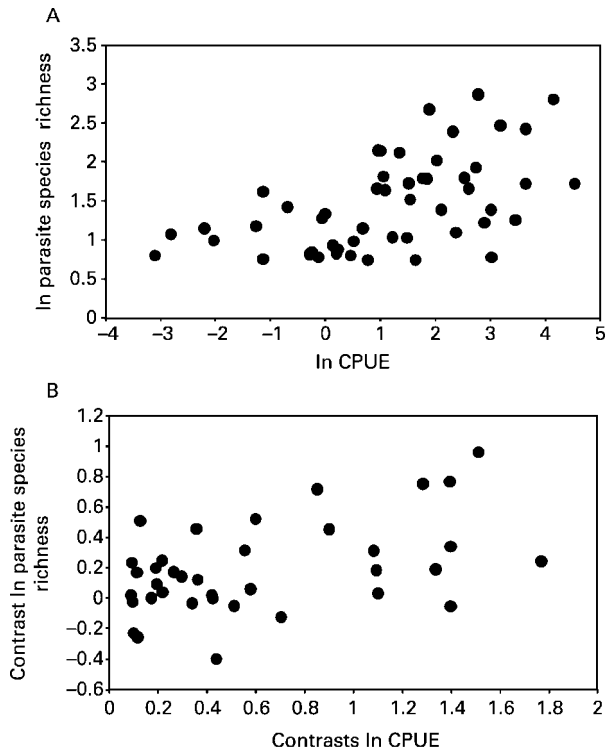
A

B

Fig. 2. Relationships between metazoan endoparasite species richness and catch per unit effort (CPUE) (number of individuals of a given fish species captured per $1000\,m^2$ of net during 24 h). Measures of species richness are corrected for host sampling effort using residuals of a regression of species richness against number of fish examined. A. Relationships between logarithmic (ln) values of corrected parasite species richness and ln values of CPUE. B. Relationships between metazoan endoparasite species richness and CPUE using independent contrasts of ln-transformed values.

Discussion

The search for key determinants of parasite species richness has blossomed in recent years (see reviews in Poulin, 1997; Morand, 2000; Poulin & Morand, 2000). Yet, there is no consensus view regarding the role, if any, of various host traits in the evolutionary diversification of parasite faunas. This may in part be due to the nature of previous studies, which have often suffered from important limitations. Here, we found that parasite species richness in freshwater fish species shows no association with several host characteristics, with the exception of host population density. We have examined some features long thought to be associated with parasite acquisition in ecological time by individual fish, and over evolutionary time by fish species (see Dogiel *et al.*, 1961).

The floodplain of the Upper Paraná River is a region extensively studied with respect to its physical and biological aspects (see Vazzoler *et al.*, 1997a). It was therefore possible to collect information about local hosts that allowed us to test new ecological variables, e.g. reproductive behaviour and spawning type, as possible determinants of parasite species richness. For instance, differences among fish species in reproductive and social behaviour could affect the transmission of parasites (Bartoli *et al.*, 2000). Yet, none of these host features showed any association with parasite species richness.

Considering both the approach and the results, the present study includes both key improvements on earlier studies of this kind and novel findings, making its contribution particularly relevant. The majority of earlier studies on the richness of freshwater fish parasites have used data from fish species that do not occur in the same geographical areas (e.g. Bell & Burt, 1991; Aho & Bush, 1993; Poulin, 1995). While relationships between parasite species richness and host features may still be detected in such studies, they are confounded by the fact that the different fish species come from different areas and are therefore not exposed to the same pool of parasite species. The size of the pool of available parasite species must differ from one geographical area to the next, and thus it can limit how many parasite species a host can acquire over time, regardless of the characteristics of this host species. The present study focused on a set of fish species from the same general area (the floodplain of the upper Paraná River, Brazil), thus minimizing any differences in parasite availability. In addition, the study was the first investigation of parasite species richness based on a representative data set of freshwater fishes from the Neotropical Region, and focused on a single type of environment (a river floodplain) for the first time in this type of analysis.

The key result in the present study was the clear positive relationship between the host species density and

Table 2. Values obtained from analyses of the different ecological variables versus the corrected values of parasite species richness.

Variables	Using species values as independent statistical observations	Using phylogenetically independent contrasts
Fish standard length	$r = 0.129$, $n = 53$, $P = 0.357$	$r = 0.213$, $n = 38$, $P = 0.193$
Habitat preference	$F_{(3,49)} = 1.379$, $P = 0.260$	$t = -0.035$, $n = 13$, $P = 0.735$
Trophic category	$F_{(7,45)} = 0.274$, $P = 0.961$	$t = -0.950$, $n = 10$, $P = 0.389$
Food web level	$F_{(2,50)} = 0.176$, $P = 0.839$	$t = -0.767$, $n = 10$, $P = 0.463$
Benthic?	$F_{(2,50)} = 1.618$, $P = 0.208$	$t = 1.135$, $n = 4$, $P = 0.379$
Schooling?	$F_{(1,51)} = 0.059$, $P = 0.809$	$t = -1.772$, $n = 9$, $P = 0.114$
Reproductive behaviour	$F_{(3,49)} = 0.158$, $P = 0.924$	$t = 0.508$, $n = 6$, $P = 0.633$
Spawning type	$F_{(1,51)} = 0.289$, $P = 0.593$	$t = -1.018$, $n = 7$, $P = 0.348$
Native/exotic species	$F_{(1,51)} = 0.002$, $P = 0.963$	$t = -4.138$, $n = 2$, $P = 0.151$

parasite species richness. This pattern is in concordance with epidemiological theory (see introduction) predicting that hosts with larger or denser populations will more readily sustain several parasite populations. Because parasites in our study use fish as either intermediate or definitive hosts, depending on species, this situation might reflect a combination of large intermediate and definitive host populations facilitating parasite transmission and reproduction, respectively (Morand *et al.*, 2000). The present results, combined with those on mammalian hosts (Morand & Poulin, 1998; Arneberg, 2002), suggest that host density may play a general role in maintaining parasite species richness.

Other ecological variables tested did not show any influence on parasite species richness and this might reflect the ecological homogeneity of the floodplain of the upper Paraná River. Spatial and temporal variations of abiotic and limnological variables are frequently recorded in floodplain systems and are strongly correlated with variation in the hydrological level; in addition, the occurrence of different pulses during the same hydrological cycle could influence the biology of the host species (Junk *et al.*, 1989), and consequently the parasite fauna. Some relationships expected between parasite species richness and host ecological variables may not become established because the interconnection between the various microhabitats during the period of high water levels minimizes the heterogeneity of the ecosystem and its biota. This result could be viewed in the light of habitat modifications resulting from human activities. Recently, reservoirs created by dams in the floodplain of the upper Paraná River have altered the ecosystem, and the trophic behaviour of some fish (Lizama, 2003). A potential consequence of human-induced modifications to the river could be changes in the density of key fish species and based on the present results, this could influence the richness of their parasite faunas. The impact of human activities on the parasite fauna of fishes from the floodplain is unknown, but this is a question that should be addressed in future studies.

Acknowledgements

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Appendix 1. Summary of data on 34 fish species from the floodplain of the upper Paraná river not included in the analyses.

Species	n[1]	Parasite richness	Standard size (cm)	CPUE[2]	Habitat[3]	Trophic category[4]	FWL[5]	Benthic?[6]	School?[7]	Reproductive behaviour[8]	Spawning[9]	Native?[10]
Ageneiosus militaris	5	1	33.2	0.19	2	7	3	P	1	4	1	1
Aphyocharax anisitsi	7	1	4.5	–	2	8	2	3	1	3	1	1
Apteronotus albifrons	1	0	50	–	2	3	2	3	2	?	–	1
Astyanax schubarti	1	0	9.1	0.39	2	8	2	3	1	3	1	1
Bryconamericus straminaeus	2	1	5.4	0.06	4	3	2	3	2	3	1	1
Catathyridium jenynsii	4	0	21.4	0.21	4	7	3	1	2	3	1	1
Cichlasoma sp.	1	0	34.1	–	4	6	2	3	2	2	1	1
Colossoma macropomum	5	0	80	–	2	1	1	3	1	1	2	2
Crenicichla haroldoi	3	0	18.4	0.39	2	3	2	3	2	2	2	1
Crenicichla lacustris	3	1	29	–	1	3	2	3	2	2	1	1
Cyprinus carpio	1	0	120	–	2	1	1	3	1	3	1	2
Eigenmannia virescens	1	0	29.3	0.43	3	3	2	3	2	2	1	1
Hoplerythrinus sp.	1	0	–	–	3	7	3	2	2	2	1	1
Hypostomus sp.	1	0	31.5	0.82	2	5	1	1	2	2	1	1
Laetacara sp.	3	1	5.2	0.02	2	8	–	3	1	2	1	1
Leporellus vittatus	1	1	16.6	0.06	2	3	2	3	2	1	2	1
Leporinus macrocephalus	1	1	48.5	0.06	2	8	2	3	3	2	2	1
Leporinus octofasciatus	1	1	19	0.04	2	8	2	3	1	3	1	1
Megalonema platanum	5	0	140	0.06	2	7	3	1	3	3	1	1
Moenkhausia sanctaefilomenae	5	1	7.0	–	3	3	2	3	3	3	1	1
Myleus cf. *tiete*	7	1	20.2	0.11	2	1	1	3	1	3	1	1
Oxidoras eigenmanni	1	0	10.1	0.19	2	6	2	1	1	3	1	1
Pimelodella gracilis	1	0	13.7	0.11	3	3	2	1	2	3	–	1
Pimelodella sp.	2	0	15.7	0.41	4	3	2	1	2	3	1	1
Potamotrygon falkneri	4	1	47	–	2	6	2	3	2	4	1	1
Pseudopimelodus mangurus	3	1	140	–	4	7	3	1	2	2	–	1
Rhamdia quelen	2	1	22.1	0.06	3	3	2	3	2	3	1	1
Rhamdia sp.	3	1	20.9	–		3	2	3	2	3	1	1
Rhinelepis aspera	3	0	49	0.32	3	5	1	1	2	1	2	1
Rhinodoras dorbignyi	4	1	14	0.02	2	6	2	1	1	3	1	1
Salminus hillari	2	0	24.3	0.21	2	7	3	3	1	1	1	1
Serrapinnus notomelas	6	1	3.7	–	3	1	1	3	1	3	1	1
Sternopygus macrurus	1	1	42.1	0.31	1	3	2	3	2	3	1	1
Synbranchus marmoratus	1	1	140	0.02	2	3	2	1	2	2	1	1

[1] Number of fish examined.
[2] Catch per unit effort (number of individuals of a given fish species captured using $1000\,m^2$ of net during 24h).
[3] Lentic = 1; lotic = 2; semilotic = 3; all habitats = 4.
[4] Herbivorous = 1; planktivorous = 2; insectivorous = 3; iliophagous = 4; detritivorous = 5; benthophagous = 6; piscivorous = 7; omnivorous = 8.
[5] Food web level: basal = 1; intermediate = 2; top = 3.
[6] Benthic = 1; pelagic = 2; benthopelagic = 3.
[7] Schooling behaviour = 1; solitary = 2.
[8] Migratory with external fertilization = 1; sedentary, guarders, with external fertilization = 2; sedentary, non-guarders, with external fertilization = 3; internal fertilization = 4.
[9] Repeated spawning effort (iteroparous) = 1; single spawning effort (semelparous) = 2.
[10] Native species = 1; exotic species = 2.