The influence of host ecology and biogeography on the helminth species richness of freshwater fishes in Mexico

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SUMMARY

Freshwater fish helminths, the most well known Mexican vertebrate parasites, include approximately 260 species (platyhelminthes, acanthocephalans, nematodes, and hirudineans). The distribution patterns of adult helminth diversity (throughout parasite and host groups and hydrological regions) are described and the effects of host traits and environmental and geographical factors on diversity are evaluated. Adult helminths include 160 species, parasitizing 149 fish species of 23 families distributed in 21 regions. Nematoda was the most species-rich (> 50 species). Cichlidae harboured rich helminth assemblages, with widespread parasites. By contrast, Atherinopsidae and Goodeidae showed relatively poor helminth assemblages, including specific parasites with narrow distribution. Helminth richness in southeastern Mexico was higher than northern or central regions. Non-parametric richness estimators were used to avoid confusion in comparisons with unequal sampling efforts. Bootstrap values, the method with the best performance, indicated that estimated richness shows the same distribution pattern that observed richness. Non-phylogenetic and phylogenetic analyses were used to determine the role of different factors in the parasite diversification. The distribution range was the most important richness predictor (widespread fishes harbour richer parasite assemblages), although interactions between this variable and others such as trophic level, latitude, habitat temperature and precipitation are also important. Likewise, biogeographical factors can also affect parasite diversity.

Key words: geographical range, parasites, diversity, independent contrasts, Nearctic region, Neotropical region, hydrological regions, Osteichthyes.

INTRODUCTION

The evolutionary events determining the structure of a parasite assemblage are relatively well understood. A parasite species may have been inherited by the host species from its ancestor, may be the result of an intra-host speciation event, and/or may have colonized the host species from another sympatric host species (host switching) (Paterson and Gray, 1997). Therefore, it is possible to search for the key factors that have caused certain parasite assemblages to diversify more than others over evolutionary time (Poulin, 1998*a*; Page, 2003). The studies attempting to determine which host features may promote the diversification of parasite assemblages are based on 2 theoretical frameworks. First, following island biogeography theory (MacArthur and Wilson, 1967; Kuris *et al*. 1980), host features that promote high rates of parasite speciation or colonization, and low probabilities of extinction, by parasite species should be associated with high parasite diversity (e.g. large body size, broad geographical range, breadth of habitats). Epidemiological modelling represents the second theoretical source of predictions regarding parasite diversity (Dobson and Roberts, 1994; Roberts *et al*. 2002). These models suggest 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. Comparing different host species, those occurring at higher population density (e.g. schooling fish species) should harbour more species of parasites, because they exceed the persistence threshold of more parasite species than hosts with low population density.

Several studies have investigated the factors potentially controlling the number of parasite species in freshwater and marine fishes (Bell and Burt, 1991; Guégan and Kennedy, 1993; Poulin, 1995; Poulin and Rohde, 1997; Sasal *et al*. 1997; Morand *et al*. 2000; Luque and Poulin, 2004, 2008). However, the

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results available to date show very little consistency, since some studies claim that a certain variable is a predictor of parasite species richness, either host body size, host geographical range, host diet, etc., but no consensus on a particular variable as the main determinant has been reached.

Freshwater fish helminths are undoubtedly the most well known group of vertebrate parasites in Mexico, because fishes have been studied more than any other group (Pérez-Ponce de León and Choudhury, 2010; Pérez-Ponce de León *et al*. 2011). The helminth fauna of these hosts includes approximately 260 species (Oceguera-Figueroa *et al*. 2010; Pérez-Ponce de León and Choudhury, 2010). The first descriptions of distributional patterns of fish-parasite and drainage associations indicated that the parasite fauna is largely circumscribed by higher levels of monophyletic host taxa, especially at the level of fish family. Likewise, areas within a certain biogeographical region and consequently with similar fish composition possess more similar parasite faunas compared to areas with less similar fish faunal composition (Pérez-Ponce de León and Choudhury, 2005). Recently, Pérez-Ponce de León and Choudhury (2010) evaluated the progress made on the inventory of freshwater fish helminths of Mexico and suggested that following a traditional approach, the inventory is nearing completion for most helminth groups (except monogeneans). These authors suggested that host species and geographical areas that would be targeted in the future could be expected, with very few exceptions, to have helminth faunas that are consistent with the fish composition in those areas. However, they argued that in the future DNA-based taxonomic methods have the potential to alter drastically the estimates of helminth diversity in freshwater fishes, because of the existence of cryptic species (morphologically indistinguishable but genetically distinct, see Poulin, 2011; Nadler and Pérez-Ponce de León, 2011) in several lineages of helminths in Mexico. Despite this fact, they described species richness patterns and pointed out that the diversity is distributed heterogeneously. These patterns were described by considering all freshwater helminth parasites irrespective of their developmental stage i.e. larval and adult forms, under a strict definition of what constitutes a freshwater species and by including both native and introduced fish species. However, Pérez-Ponce de León and Choudhury (2010) did not use the proper methods to analyse data with unequal sampling effort that might act as a confounding factor. In addition, potential factors that cause the heterogeneous distribution of helminth species richness were not explored. For these reasons, our aims in this paper are to describe the distribution patterns of adult helminth diversity throughout parasite and host groups as well as across hydrological regions, and to investigate the host traits and/or environmental and geographical factors that determine the uneven diversification of assemblages of freshwater fish helminths.

MATERIALS AND METHODS

A database updated to November, 2011, with distribution records for Mexican freshwater fish helminths (trematodes, monogeneans, cestodes, acanthocephalans, nematodes, and hirudineans) was constructed. Our study was restricted to adult helminths of the native freshwater fishes, which are unable to disperse across brackish and marine waters (i.e., presumably non-diadromous). Larval helminths were excluded because of the confounding effects of dispersal caused by their definitive hosts in any distribution pattern. Also, if we consider larval stages, the parasite species count could be underestimated because they often cannot be identified to the species level and one putative taxon might actually consist of more than one species.

The data set was mostly obtained from monographs (e.g. Pérez-Ponce de León *et al*. 1996, 2007; Garrido-Olvera *et al*. 2006; Kohn *et al*. 2006; Salgado-Maldonado, 2006; García-Prieto *et al*. 2010; Oceguera-Figueroa *et al*. 2010) and specimens deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. Nomenclature was updated using specialized literature (e.g. Scholz *et al*. 1997; Moravec, 1998; Scholz *et al*. 2001; Vidal-Martínez *et al*. 2001; Aguirre-Macedo and Scholz, 2005; Caspeta-Mandujano, 2005; Pérez-Ponce de León *et al*. 2007). To avoid cases of synonymies among fish species, valid species names were adopted according to FishBase (Froese and Pauly, 2011).

The geographical distribution patterns were recognized through distribution maps for each taxon, which were prepared using ArcView GIS 3.2 (ESRI, 1999). Sample-based rarefaction curves considering the number of localities studied as a measure of sampling effort were used to compare the helminth species richness (the number of parasite species in an assemblage) between host families and hydrological regions at comparable sampling effort (Colwell *et al*. 2004). Non-parametric species richness estimators are also used to analyse data with unequal sampling effort. Therefore, total helminth species richness for each data set was calculated using 5 estimation methods: ICE, Chao2, Jackknife1, Jacknife2, and Bootstrap (Poulin, 1998*b*; Walther and Morand, 1998). In addition, an evaluation of the performance of these estimators with the unscaled measures of bias, precision, and accuracy was conducted (Walther and Moore, 2005). EstimateS version 8.2 was used to obtain rarefaction curves and total species richness (Colwell, 2006).

In order to examine the possible factors determining the helminth species richness in an assemblage, we gathered detailed information on the fish species and geographical areas. The host traits were obtained from Miller *et al.* (2005) and Froese and Pauly (2011) (Table 1). The environmental and geographical data for each hydrological region were obtained from the Comisión Nacional del Agua (2008) and Fernandez-Eguiarte *et al.* (2010) (Table 2).

The helminths include various taxonomic groups, with different biological characteristics related with life-cycle dynamics and transmission modes. Therefore, these parasite taxa may be subjected to different factors potentially influencing their species richness. For this reason, helminth species richness for each assemblage was estimated in 3 ways: for all parasites, for endoparasites only (trematodes, cestodes, acanthocephalans, and nematodes), and for ectoparasites only (monogeneans and hirudineans).

To analyse factors influencing differences in species richness among assemblages, the information on the fish species and their distribution regions was combined. In the initial analyses, fish species were treated as independent observations. The relationships between helminth species richness and continuous variables were tested through correlations, while the influence of categorical variables was assessed by inspecting mean values. Next, we determined which factors played a role in the diversification of parasite assemblages, i.e., we tested whether any of those associations were significant and whether there were interactions between the explanatory variables by performing generalized linear models, where species richness (total parasites, ectoparasites, and endoparasites, independently) was the response variable and host traits were explanatory variables. The models were fitted with a log link (to ensure that the fitted values are bounded below) and Poisson errors (to account for the non-normality) (Crawley, 2007).

Parasite assemblages of closely related host species are not truly independent statistical observations. Therefore, we used Felsenstein's (1985) comparative method to control for the effects of phylogenetic association between host species. The PDAP: PDTREE software (Midford *et al.* 2011), implemented in Mesquite Modular System for Evolutionary Analysis, Mesquite version 1.12 (Maddison and Maddison, 2011) was used to compute independent contrasts. Host phylogeny was constructed from mainly molecular studies and the phylogenetic relationships of the orders were based on Nelson (2006), as follows: (((((*Ophisternon aenigmaticum*, (*Eugerres mexicanus*, *Etheostoma* sp., ((*Lepomis megalotis*, *L. macrochirus*), *Micropterus salmoides*), *Aplodinotus grunniens*, (*Awaous banana*, *Sicydium multipunctatum*), (*Cichlasoma geddesi*, *C. mayorum*, (((*C. beani*, *C. istlanum*), ((*Parachromis friedrichsthalii*, *C. trimaculatum*), (*Petenia splendida*, *C. urophthalmus*))), ((*Rocio octofasciata*, *Amphilophus robertsoni*), ((*C. salvini*, ((*Thorichthys helleri*, *T. pasionis*), (*T. meeki*, (*T. ellioti*, *T. callolepis*)))), ((*Herichthys labridens*, (*H. minckleyi*, *H. cyanoguttatus*)), ((*C. pearsei*, (*Theraps lentiginosus*, *Vieja intermedia*)), ((*V. fenestrata*, (*V. bifasciata*, *V. hartwegi*)), (*V. synspila*, *V. argentea*)))))))))), (((((*Cyprinodon meeki*, *C. nazas*), ((((*Poecilia butleri*, *P. mexicana*), (*P. sphenops*, *P. catemaconis*)), (*P. velifera*, (*P. petenensis*, *P. latipunctata*))), (((*Poeciliopsis catemaco*, *P. gracilis*), (*P. infans*, *P. baenschi*), *P. balsas*), ((*Xiphophorus hellerii*, *X. variatus*), (*Heterandria bimaculata*, (*Belonesox belizanus*, ((*Gambusia vittata*, *G. marshi*), *G. senilis*, *G. yucatana*))))))), ((*Profundulus hildebrandi*, *P. punctatus*, *P. labialis*), ((*Characodon audax*, *C. lateralis*), (((*Ilyodon cortesae*, *I. whitei*, *I. furcidens*), (*Xenotaenia resolanae*, ((*Allodontichthys tamazulae*, *A. hubbsi*), *A. zonistius*))), (((((((*Chapalichthys encaustus*, *C. pardalis*), *Ameca splendens*), *Xenotoca variata*), *Alloophorus robustus*), *Zoogoneticus quitzeoensis*), (*X. eiseni*, *X. melanosoma*)), ((*Ataeniobius toweri*, (*Goodea atripinnis* , *G. gracilis*)), (((*Girardinichthys multiradiatus*, *G. viviparus*), (*Hubbsina turneri*, (*Skiffia bilineata*, *S. multipunctata*, *S. lermae*))), (((((*Allotoca catarinae*, (*A. diazi*, *A. meeki*)), *A. zacapuensis*), *A. dugesii*), *A. maculata*), *A. regalis*)))))))), (*Strongylura* sp., *Hyporhamphus mexicanus*)), ((*Atherinella crystallina*, *A. balsana*), (((((*Poblana letholepis*, *P. squamata*), *P. alchichica*), *Chirostoma riojai*), *Ch. arge*), (*Ch. attenuatum*, ((*Ch. jordani*, *Ch. labarcae*), (*Ch. lucius*, (*Ch. humboldtianum*, (*Ch. grandocule*, *Ch. estor*)))))))))), *Typhliasina pearsei*), (((*Rhamdia guatemalensis*, (*Potamarius nelsoni*, (*Ameiurus melas*, (*Pylodictis olivaris*, ((*Ictalurus furcatus*, *I. punctatus*), *I. balsanus*, *I. mexicanus*, *I. pricei*, *I. dugesii*))))), ((*Ictiobus meridionalis*, *Catostomus nebuliferus*), ((((*Algansea lacustris*, *A. tincella*), *A. monticola*), *Gila conspersa*), (*Campostoma ornatum*, (*Dionda ipni*, (*Pimephales promelas*, (((((*Notropis calientis*, *Aztecula sallaei*), *Yuriria alta*), *Hybopsis boucardi*), *N. nazas*, *N. chihuahua*), (*Codoma ornata*, ((*Cyprinella garmani*, *C. lutrensis*), *C. xanthicara*)))))))), ((((*Astyanax aeneus*, *A. mexicanus*), *A. fasciatus*), *Bramocharax caballeroi*), *Brycon guatemalensis*)), ((*Dorosoma cepedianum*, *D. petenense*), *D. anale*))), *Atractosteus tropicus*); (Ptacek and Breden, 1998; Breden *et al.* 1999; Harris and Mayden, 2001; Reznick *et al.* 2002 ; Miya *et al.* 2003; Schönhuth and Doadrio 2003; Simons *et al.* 2003; Cunha *et al.* 2002; Doadrio and Dominguez, 2004; Wilcox *et al.* 2004; Near *et al.* 2005; Hulsey *et al.* 2006; Chakrabarty, 2007; Concheiro Pérez *et al.* 2007; Hrbek *et al.* 2007; Hardman and Hardman, 2008; Hertwig, 2008; Lavoué *et al.* 2008; Rícan *et al.* 2008; Bloom *et al.* 2009, 2012; Mirande 2009; Pérez-Rodríguez *et al.* 2009; McMahan *et al.* 2010; Schönhuth and Mayden, 2010).

True branch lengths are not available in this tree, so all branch lengths were set to unity, which adequately standardized contrasts of all variables.

Table 1. Summary information to family level of freshwater fish species recorded as hosts of adult helminths in Mexico

(The number of fish species was obtained from Miller *et al.* (2005) and Froese and Pauly (2011).)

Family	Fishes	Helminths	Size ± S.D.	Regions	Environment	Geographical range	Trophic level ± S.D.	Climate
Ariidae*	3/1	4/-, 1, 3	39	1	D	M	3·58	Tr
Atherinopsidae	39/14	10/12, 2, 8	13·91 ± 9·53	4	B, P	M	3·06 ± 0·15	Tr
Belonidae*	4/1	4/-, -, 4	49·8	1	P	MCA	4·13	Tr
Bythitidae*	1/1	1/-, -, 1	9·7	1	D	M	3·3	Tr
Catostomidae	18/2	8/10, -, 8	39·95 ± 34·72	4	P, D	M, MCA	2·94 ± 0·24	Tr
Centrarchidae	10/3	16/21, 8, 8	37·67	5	B	MNA	3·55	S, Tm
Characidae	10/5	28/34, 9, 19	17·26 ± 13·46	11	B	M, MSA, MCA, MNA	2·81 ± 0·34	S, Tr
Cichlidae	55/27	58/69, 12, 44	18·56 ± 7·07	12	B, D	M, MCA, MNA	3·12 ± 0·73	S, Tr
Clupeidae	11/3	9/11, 2, 7	26·13 ± 8·52	3	P, PN	MCA, MNA, NAMCA	2·96 ± 0·51	Tr, S
Cyprinidae	69/23	14/17, 4, 10	10·02 ± 6·26	7	B, D	M, MNA	2·815 ± 0·27	S, Tm, Tr
Cyprinodontidae	28/2	5/6, 1, 4	4·75 ± 0·21	2	B	M	2·94 ± 0	Tr
Gerreidae*	11/1	3/-, 2, 1	20·8	2	D	MCA	3·35	Tr
Gobiidae*	4/2	3/-, -, 3	21·5	3	B, D	NAMCASA	2·025	Tr
Goodeidae	41/33	24/28, 5, 19	7·72 ± 3·01	7	B, D, P	M	2·09 ± 0·17	S, Tm, Tr
Hemiramphidae*	4/1	1/-, -, 1	16·1	1	P	MCA	3·02	Tr
Heptapteridae	4/1	24/28, 6, 18	30 ± NA	4	B	MSA	3·16 ± NA	Tr
Ictaluridae	14/8	35/40, 7, 28	67·23 ± 26·99	13	B, D	M, MNA, NAMCA	3·63 ± 0·15	S, Tm, Tr
Lepisosteidae	4/1	6/7, 1, 5	85·9 ± NA	2	D	MCA	4·23 ± NA	Tr
Percidae*	6/1	1/-, 1, -	5	1	B	M	3·17	Tr
Poeciliidae	82/20	22/26, 5, 17	7·55 ± 3·28	12	B, D	M, MCA, MSA, MNA	2·72 ± 0·48	S, Tr
Profundulidae*	5/3	4/-, -, 4	10·4	2	B	MCA	3·073	Tr
Sciaenidae*	1/1	5/-, 3, 2	50	3	D	NAMCA	3·36	S
Synbranchidae*	3/1	7/-, -, 7	20·8	1	D	MCA	3·25	Tr

* Data were insufficient for estimating total parasite species richness. Fishes, total/known host fish species; Helminths, observed/estimated total species richness, ectoparasites, endoparasites; Size ± S.D., mean body size (standard length in cm) ± standard deviation; Regions, number of regions where fish family is distributed; Environment: B, Benthopelagic, D, Demersal, P, Pelagic, PN, Pelagic-neritic; Trophic level ± S.D. = mean trophic level ± standard deviation; Climate: S, subtropical, Tr, tropical, Tm, temperate; Geographical range: M, Mexico, MCA, Mexico and Central America, MNA, Mexico and North America, MSA, Mexico and South America, NAMCA, North America, Mexico and Central America, NAMCASA, North America, Mexico, Central America, and South America.

Table 2. Summary information on Mexican hydrological regions, where adult helminth species have been recorded as parasites of freshwater fishes

(The number of fish species is result of a review of databases of fish collections and fish lists of Miller *et al.* (2005) and Froese and Pauly (2011).)

Region	Fishes	Helminths	MxL	MnL	ML	Length	Area	Flow	Basins	MAP	PDM	PWM	MTWM	MTCM	Slope
9*	34/4	3/-, -, 3	31·33	26·6	28·97	39 635	139 370	4935	48	507·2	0·11	22·8	34·55	7·21	P
11	33/13	16/19·73, 2, 14	25·18	21·69	23·44	19 704	51 717	7956	9	815·2	7·36	215·91	32·88	5·88	P
12	74/41	36/44·03, 12, 24	23·42	19·06	21·24	51 096	132 916	13 637	8	723·2	0·37	81·02	34·33	9·51	P
14*	25/6	4/-, -, 4	21·28	20·07	20·68	6132	12 255	2236	1	122·7	4·34	92·2	32·49	3·21	P
15*	17/1	3/-, -, 3	20·45	18·88	19·67	6307	12 967	3684	45	1185·5	16·3	153·35	34·47	8·83	P
16	29/11	14/18·05, -, 14	20·45	18·59	19·52	7393	17 628	3882	8	911·3	7·28	71·58	30·69	4·16	P
18	54/27	33/40·01, 3, 30	19·99	17·02	18·51	45 372	118 268	1757	3	949·7	15·22	184·34	30·82	7·72	P
19*	16/1	1/-, -, 1	18·14	16·7	17·42	4992	12 132	691	41	1232	5·27	182·06	29·94	4·83	P
20*	24/3	4/-, 1, 3	17·62	15·98	16·8	12 907	39 936	18 714	21	1393·1	42·26	288·22	30·45	11·11	P
23*	17/1	1/-, -, 1	16·54	14·53	15·54	3908	12 293	12 554	25	2352·7	5·46	261·16	31·43	8·25	P
24	101/14	27/33·81, 7, 20	31·77	24·85	28·31	77 898	229 740	5156	2	448·5	2·82	318·3	33·27	13·73	A
25*	41/4	9/-, 4, 5	25·76	22·28	24·02	16 729	54 961	4328	27	758·5	4·27	224·06	31·37	10·11	A
26	77/21	24/28·74, 4, 20	23·95	19·04	21·5	34 263	96 989	20 329	2	889·2	34·07	200·23	33·66	16·87	A
27*	38/3	10/-, 1, 9	22·2	19·48	20·84	10 139	26 592	14 306	38	1423·2	4·08	216·68	32·42	10·13	A
28	67/23	49/58·6, 11, 38	19·74	16·93	18·34	19 382	57 355	49 951	31	1447·1	22·85	220·73	35·28	15·79	A
29*	52/19	28/-, 11, 17	18·44	16·63	17·54	8866	30 217	39 482	10	1953·8	28·39	344·94	30·99	12·36	A
30	86/37	61/71·03, 19, 42	18·9	15·3	17·1	23 249	102 465	117 546	4	1708·9	38·47	326·82	32·86	15·17	A
31*	32/7	12/-, 3, 9	19·97	17·81	18·89	1704	25 443	591	6	1227·4	2·78	272·12	31·39	12·94	A
32	42/15	40/45·98, 17, 23	21·61	19·63	20·62	523	58 135	0	1	192·4	45·93	424·76	33·66	16·71	A
33	37/10	19/22·31, 6, 13	20·1	17·81	18·96	2926	38 308	1989	2	1239·8	2·8	323·08	33·58	17·24	A
36	33/14	9/11·24, -, 9	26·6	22·67	24·64	31 046	9332	1912	1	422·1	7·3	457·02	34·1	16·7	I

* Data were insufficient for estimating total species richness. Region, 9, Sonora Sur; 11, Presidio-San Pedro; 12, Lerma-Santiago; 14, Río Ameca; 15, Costa de Jalisco; 16, Armería-Coahuayana; 18, Balsas; 19, Costa Grande de Guerrero; 20, Costa Chica de Guerrero; 23, Costa de Chiapas; 24, Bravo-Conchos; 25, San Fernando-Soto La Marina; 26, Pánuco; 27, Norte de Veracruz; 28, Papaloapan; 29, Coatzacoalcos; 30, Grijalva-Usumacinta; 31, Yucatán Oeste; 32, Yucatán Norte; 33, Yucatán Este; 36, Nazas-Aguanaval; Fishes, total/ known host fish species; Helminths, observed/estimated total species richness, ectoparasites, endoparasites; MxL, maximum latitude; MnL, minimum latitude; ML, mean latitude; Length, total length of rivers (in km); Area, area (in km^2); Flow, mean current flow (in hm3/year); Basins, basin number in the region; MAP, mean annual precipitation (mm); PDM, precipitation of driest month (mm); PWM, precipitation of wettest month (mm); MTWM, maximum temperature of warmest month (°C); MTCM, minimum temperature of coldest month (°C); Slope, A, Atlantic, I, Interior, P, Pacific.

The program can only compute independent contrasts in continuous variables. In order to obtain independent contrasts of categorical variables, we treated these variables as continuous with states of 1, 2, 3 or more as recommended by Midford *et al.* (2011) in the PDAP:PDTREE manual.

The relationships among independent contrasts were assessed using least-squares regressions forced through the origin (Garland *et al.* 1992). The possibility that multiple host traits influence parasite diversity was also addressed and then contrasts in independent variables (host traits) were entered into multiple regression methods (computed through the origin) to predict contrasts in species richness (total parasites, ectoparasites, and endoparasites, independently) (Crawley, 2007).

In both generalized linear models and multiple regression analyses, the minimal adequate models were obtained with categorical and continuous explanatory variables, separately (i.e., models without redundant parameters or factor levels). We achieved this by fitting a maximal model and then simplifying it by stepwise deletion: non-significant terms were left out, and significant terms were added back (Crawley, 2007). All statistical analyses were conducted in the software R version 2.11.0 for Windows (http://www.r-project.org/).

RESULTS

The adult helminth fauna parasitizing freshwater fishes in Mexico is composed by 160 species belonging to 6 groups. The most numerous group was Nematoda with more than 50 species, followed by Trematoda and Monogenea, with 39 species each. The remaining groups were composed by no more than 10 species each (4 Hirudinea, 6 Acanthocephala, and 9 Cestoda). No parasite species occurred in all hydrological regions, but the cestode *Bothriocephalus acheilognathi* and the acanthocephalan *Neoechinorhynchus golvani* were distributed in 14 and 11 regions, respectively. In contrast, more than 100 species (approximately 60% of total parasite species) were recorded from only 1 region. The most generalist helminth species were the cestode *B. acheilognathi* and the nematode *Rhabdochona kidderi* parasitizing 11 and 10 host families, respectively. However, approximately 120 species (75% of total parasite species) infected only 1 fish family each.

In total, 149 fish species belonging to 23 families have been recorded as hosts of adult helminths. This means that approximately 40% of Mexican freshwater fishes have been recorded as hosts of these parasites. Helminths were found infecting 8% to 100% of the species included in each host family, though the highest percentages correspond to monotypical families. With the exception of the Cyprinodontidae and Catostomidae, the more species-rich host groups (i.e., Poeciliidae, Cyprinidae, Cichlidae, Goodeidae, Atherinopsidae, and Ictaluridae, which account for more than 80% of the Mexican ichthyofauna) have been sampled with relatively high intensity, since at least 24%, 33%, 49%, 81%, 36%, and 57%, of their species, respectively, have been recorded as hosts of helminths (Table 1).

In terms of geographical distribution, freshwater fish adult helminths were found in 198 localities pertaining to 21 of the 37 Mexican hydrological regions. The number of records was reduced in most of the regions located in the Nearctic biogeographical region and in coastal areas. In contrast, Lerma-Santiago, Balsas, Grijalva-Usumacinta, Nazas-Aguanaval, and Presidio-San Pedro were the best known hydrological regions, considering the number of fish species recorded as hosts and the actual number of fish species occurring in each region as well as the number of localities studied (Fig. 1, Table 2).

Although the sample-based rarefaction curves did not reach the asymptote, the majority showed a certain stability indicating that the sample size in each data set was large enough to consider that their adult helminth fauna was properly known. The comparisons of rarefaction curves at comparable sampling effort indicated that the difference in helminth species richness was significant among both host families and hydrological regions. The cichlids and ictalurids harboured the highest helminth species richness, whereas an intermediate number of species parasitized characids, goodeids, heptapterids, and poeciliids. The remaining host families did not harbour helminth faunas with more than 10 species (rarefaction curves not shown). At the species level, most fish species (60%) harboured poor helminth faunas (i.e., fewer than 5 species per host species). In contrast, only 6% of the fish species were parasitized by helminth faunas comprising more than 10 parasite species. The parasite species richness among hydrological regions also varied significantly. In southeastern Mexico, particularly in the Grijalva-Usumacinta and Papaloapan river basins, the highest helminth species richness was found. In contrast, with the exception of the regions situated in the Yucatán Peninsula, the hydrological regions with intermediate or low helminth species richness were always located in northern and central areas of the country (e.g. the Balsas, Lerma-Santiago, Nazas-Aguanaval and Pánuco systems) (rarefaction curves not shown).

We only considered the estimations of species richness produced by the bootstrap method, which achieved the best performance measures in all data sets. Based on these values, the minimum number of missing species remaining to be found varies from 1 to 11 and from 2 to 10 in the 13 host families and 11 hydrological regions analysed, respectively. Interestingly, the estimated species richness was distributed in the same way as the observed species

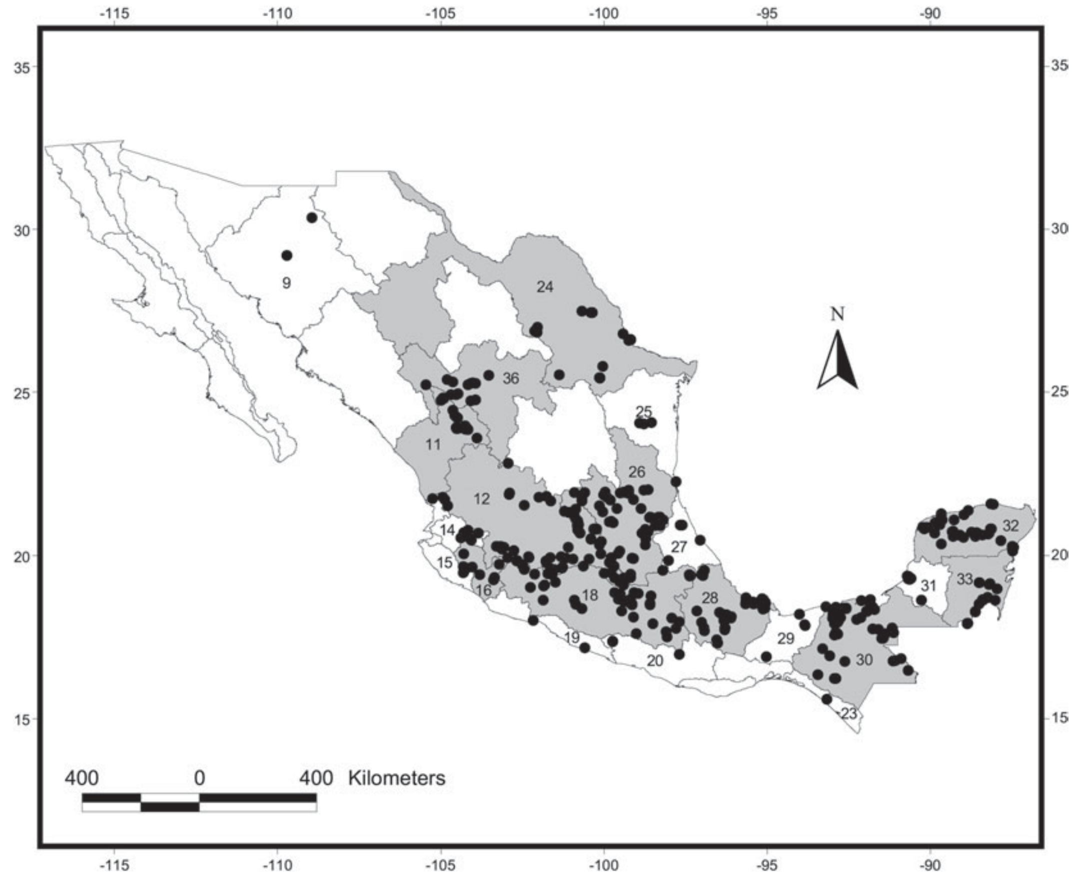

Fig. 1. Distribution of adult helminth parasites of freshwater fishes in Mexico. The country is divided in 37 hydrological regions and numbers indicate the regions where data are available: 9, Sonora Sur; 11, Presidio-San Pedro; 12, Lerma-Santiago; 14, Río Ameca; 15, Costa de Jalisco; 16, Armería-Coahuayana; 18, Balsas; 19, Costa Grande de Guerrero; 20, Costa Chica de Guerrero; 23, Costa de Chiapas; 24, Bravo-Conchos; 25, San Fernando-Soto La Marina; 26, Pánuco; 27, Norte de Veracruz; 28, Papaloapan; 29, Coatzacoalcos; 30, Grijalva-Usumacinta; 31, Yucatán Oeste; 32, Yucatán Norte; 33, Yucatán Este; 36, Nazas-Aguanaval. Shaded regions are those for which the data were sufficient for comparative analysis.

richness in both host families and hydrological regions (Tables 1 and 2).

The analyses across fish species values, not corrected for possible phylogenetic effects, revealed that the extent of their geographical distribution correlated positively with species richness of ectoparasites, endoparasites, and total parasites. The r values obtained by considering the number of sites as well as the regions in which a host species occurs (within its regional distribution range) were 0·73 and 0·77, 0·78 and 0·70, and 0·83 and 0·78, N=149, P=<2·2e-16, respectively. In addition, the total area of hydrological regions where fishes are distributed correlated positively with ectoparasite species richness (r=0·70, N=149, P=<2·2e-16). Based on main effect means of categorical variables, we also found that the distribution range of the host is an important variable and it seems that neotropical fishes have higher parasite species richness than those occurring in nearctic ones (Table 3).

In the generalized linear models performed on fish species values, only the following variables, geographical distribution, trophic level, temperature, precipitation and latitude were retained, with the distribution range being the most important explanatory variable. The aforementioned trend is significant and there is compelling evidence that fish species with a broad distribution range tend to harbour more parasite species. In addition, these models showed significant interactions between distribution range and temperature and between latitude and precipitation in determining the number of endoparasites (Table 4).

After controlling for phylogenetic influences by using the independent contrasts method (Felsenstein, 1985), the same factors (the number of sites and regions in which a host species occurs) were correlated with the helminth species richness (ectoparasites r=0·66 and 0·74, endoparasites r=0·74 and 0·65, and total parasites 0·79 and 0·74, respectively, N=148, P=<2·2e-16).

The results of the regression analyses corroborated that the geographical range was a key determinant of the variability in parasite species richness among host species (Figs 2–4). These findings suggest that, on average, widespread fish species harbour more species

Table 3. Main effect means of categorical variables on helminth richness

(See Tables 1 and 2 for details of variables.)

Variable	Level	Ectoparasites	Endoparasites	Total parasites
Environment	B	2·10	4·67	6·77
	D	1·65	4·46	6·10
	P	1·38	3·25	4·63
	PN	2	3·5	5·5
Geographical range	M	1·51	3·72	5·23
	MCA	2·5	5·62	8·12
	MNA	2·07	4·47	6·53
	MSA	6	12·67	18·67
	NAMCA	3·33	9·33	12·67
Climate	S	2·65	5·96	8·61
	Tm	1·43	2·71	4·14
	Tr	1·80	4·34	6·13
Slope	A	2·14	4·93	7·07
	AI	3	8	11
	AP	3·56	6·94	10·50
	I	1	2·4	3·4
	IP	1	4·2	5·2
	P	1·33	3·52	4·85
	PIA	2	4	6

of helminth parasites and that this pattern is explained mainly by recent processes. Although, some results were similar when phylogenetic relationships were considered, there were some changes in the relationships between helminth species richness and their explanatory variables. For example, trophic level and latitude were not important in determining the number of endoparasites. In addition, a difference in parasite species richness between fish species with larger *vs* smaller body size was detected when data were corrected for host phylogeny (Table 4).

DISCUSSION

In this paper, we only considered adult helminth species found in native Mexican freshwater fishes unable to disperse across the sea (i.e., presumably non-diadromous), because of the fact that the parasite fauna of exotic fishes is not necessarily one they have acquired over evolutionary time in their area of origin. The species count provided in this study for adult helminths parasitizing freshwater fishes in Mexico (160) is not in agreement with species counts presented in previous studies. Part of the problem is the challenge in defining what is a freshwater fish (Miller *et al.* 2005). Salgado-Maldonado (2006) quantified approximately 180 adult parasite species of freshwater fishes, but this author listed some helminth species found in marine or brackish water fishes that regularly enter freshwater at some life-history stage. In a recent publication, after a detailed consideration of the status of the freshwater fish fauna where objective criteria were followed, Pérez-Ponce de León and Choudhury (2010) considered that the adult helminth fauna of freshwater fish in Mexico consists of 177 species (37 trematodes, 62 monogeneans, 15 cestodes, 6 acanthocephalans, and 54 nematodes); however, they considered both native and exotic species of fishes. In this context, the inclusion of either marine and brackish water fish species or exotic species could obscure not only any biodiversity pattern, but also biogeographical patterns, since the processes that determine the distribution of parasites are different in the sea than in freshwater.

An obvious pattern uncovered in this study after the analysis of the information is the asymmetrical distribution of the species richness per parasite group. The group with the highest species richness is the nematodes, and even though we cannot establish at this point the reason for this, we argue that it is due to some of the nematode genera occurring in Mexican freshwater fishes (e.g. *Rhabdochona*, with 12 species, see Aguilar-Aguilar *et al.* 2010) not conforming to monophyletic assemblages (Mejía-Madrid *et al.* 2007). This means that their diversification is not associated strictly with vicariance/dispersal events from the same ancestor. Instead, they seem to derive from different lineages from fishes whose affinities are found in both the Nearctic and Neotropical biogeographical regions.

Recent papers have discussed the appropriateness of taxonomic distinctness of parasite assemblages as an alternative measure of parasite diversity in comparative analyses (Luque *et al.* 2004; Luque and Poulin, 2008; Ponlet *et al.* 2011). However, we decided to use species richness since we were only looking for factors that influence species number in an assemblage and not the causes of a narrow or broad

Table 4. Coefficients obtained from generalized linear models performed on fish species values and results of multiple regressions of standardized independent contrasts (estimated through the origin) predicting species richness

(See Tables 1 and 2 for details of variables.)

	Total parasites				Ectoparasites				Endoparasites			
	Species		Contrasts		Species		Contrasts		Species		Contrasts	
Variable	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value
(Intercept)	0·83	7·25***			2·002e-02	0·20			2·84	1·93		
Size							2·47e-02	4·55***				
Regions	0·23	6·26***	0·92	4·12***	2·14e-01	4·56***	−1·14e-01	−0·77	−5·28–02	−0·77	0·29	1·42
Localities	0·05	6·43***	0·33	9·48***			5·41e-02	4·68***	7·50e-02	7·24***	0·28	9·02***
Trophic level									1·74e-01	2·64**		
MxL							−1·48e-01	−3·25**				
MnL							1·79e-01	2·80**	−8·03e-02	−2·26*		
ML							na	NA				
Length							1·59e-06	0·28				
Area							6·74e-06	3·38***				
Flow					2·74e-06	2·45*	9·58e-06	4·34***	5·47e-06	3·58***		
Basins							−2·68e-04	−0·04	5·96e-03	2·22*		
MAP	0·001	4·22***	0·002	2·76**			−5·10e-05	−0·14			0·002	2·65**
PDM	−0·01	−2·59**	−0·05	−2·36*			4·78e-04	0·06	−1·24e-01	−2·70**	−0·05	−2·47*
MTWM							9·23e-02	1·31	−2·08e-02	−0·51		
MTCM			0·01	0·07			−1·36e-02	−0·44			0·01	0·10
Flow:Basins							1·36e-06	9·61***				
Basins:MAP							−1·33e-04	−7·20***				
Size:MTCM							−2·10e-02	−6·91***				
Localities:MTCM			0·05	5·09***			3·14e-02	4·32***			0·04	4·73***
MnL:PDM									6·09e-03	2·40*		
Localities:PDM							−7·18e-03	−4·29***				
Regions:Localities	−0·01	−3·82***							3·32e-01	4·23***		
Regions:Basins							−2·37e-02	−7·09 ***				
Size:MTWM							−1·40e-02	−2·20*				
Localities:MTWM							−3·55e-02	−2·55*				
Area:PDM							−4·38e-07	−2·40*				
Length:PDM							9·36e-07	1·99*				
Localities:Flow							−6·25e-07	−2·70**				
Localities:MnL							−2·49e-02	−2·60*				
Regions:PDM			−0·05	−2·26*							−0·03	−1·60
Regions:MAP			−0·002	−2·88**							−0·002	−2·85**
Size:Localities:Area							−3·18e-08	−3·21**				
Size:Regions:Basins							2·11e-03	5·43***				
Basins:MAP:MTCM							−1·77e-05	−3·15**				
Area:Basins:MTWM							1·92e-07	4·57***				

Table 4. (*Cont.*)

Variable	Total parasites				Ectoparasites				Endoparasites			
	Species		Contrasts		Species		Contrasts		Species		Contrasts	
	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value	Estimate	z value	Estimate	t value
Length:Flow:MTWM							−1·25e-10	−4·002***				
Regions:Localities:Flow							2·26e-07	2·68**				
Regions:Localities:PDM			−0·006	−2·24*							−0·01	−2·24*
Regions:Localities:MTCM			0·02	2·79**							0·02	2·99**
Regions:Localities:MTCM									−1·04e-02	−4·31***		
p-value			<2·2e-16				<2·2e-16				<2·2e-16	
Adjusted R-squared			0·76				0·85				0·68	
Degrees of freedom			138				117				138	

Species, results of non-phylogenetic analyses; Contrasts, results of phylogenetic analyses; the sign indicates the direction of the effect; significance codes = 0 '***' 0·001 '**' 0·01 '*' 0·05 '.' 0·1 ' ' 1.

taxonomic range of parasite species in a host species, or we were not attempting to distinguish between the different origins of parasite species, an approach that necessarily requires detailed and robust phylogenetic hypotheses. Likewise, measurements of diversity that incorporate information on the relationships among parasite species would be necessary (i.e., taxonomic distinctness).

Patterns of species richness among hydrological regions show that southeastern areas of Mexico possess higher adult helminth species richness, whereas northern and central areas have lower richness. Previous studies have also pointed out that the geographical regions in which goodeids occur, i.e. central regions, are characterized by depauperate helminth communities in freshwater fishes (Espinosa-Huerta *et al*. 1996; Rojas *et al*. 1997, Pérez-Ponce de León *et al*. 2000; Sánchez-Nava *et al*. 2004), while the parasite communities of fishes occurring in southern regions are more diverse, i.e., Cichlidae (see Vidal-Martínez, 1995; Salgado-Maldonado and Kennedy, 1997). It has been argued that the basin's geological age, magnitude, and ichthyofaunal composition could explain those differences in helminth species richness among hydrological regions (Pérez-Ponce de León and Choudhury, 2005; Salgado-Maldonado *et al*. 2005). In addition, the biogeographical position of Mexico could be another explanation, since fish species occurring in the Nearctic or Neotropical region are not exposed to the same pool of parasite species. The size of the pool of available parasite species must differ from one geographical region 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.

Several studies have searched for correlations between parasite diversity (in terms of species richness) and various fish host features such as body size, feeding habits, schooling behaviour and population density (for freshwater fishes: Poulin, 2001; Simková *et al*. 2001; Takemoto *et al*. 2005; Luque and Poulin, 2008; for marine fishes: Sasal *et al*. 1997; Morand *et al*. 2000; Luque *et al*. 2004; Luque and Poulin, 2004, 2008). However, there is no consensus regarding the role, if any, of these host traits in the evolutionary diversification of parasite faunas. Here, we found that adult helminth richness was not distributed randomly among freshwater fish species with respect to host traits and environmental and geographical factors. In addition to that, in the search for the factors that determine the parasite species richness, our study supports the need to take into account the transmission mode of the parasites, either direct or indirect (i.e., ectoparasites versus endoparasites), as has been shown in earlier studies (e.g., Luque and Poulin, 2004).

The results correspond in general with the patterns recognized previously by other authors at a comparable study scale. For instance, the distribution range,

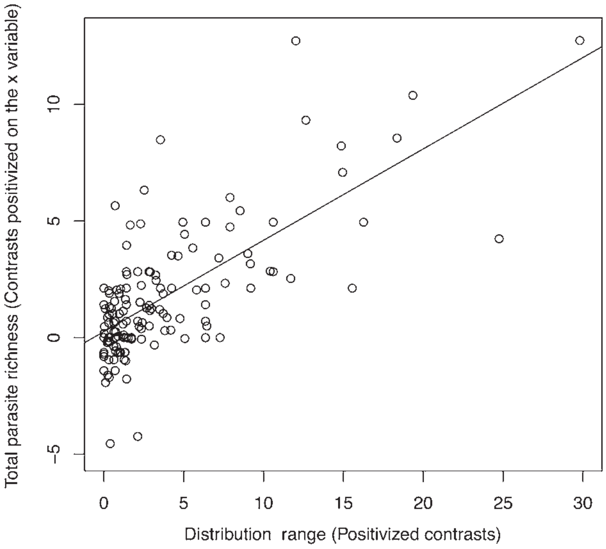

Fig. 2. Relationship between the total parasite species richness and the geographical range of the Mexican freshwater fish species ($r = 0{\cdot}62{\cdot}85$, $p < 2{\cdot}2\text{e-}16$). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al*. (1992).

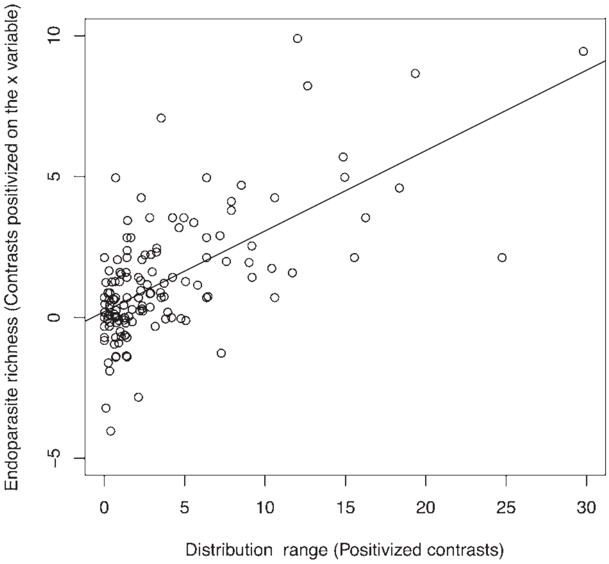

Fig. 4. Relationship between the endoparasite species richness and the geographical range of the Mexican freshwater fish species ($r = 0{\cdot}5497$, $p < 2{\cdot}2\text{e-}16$). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al*. (1992).

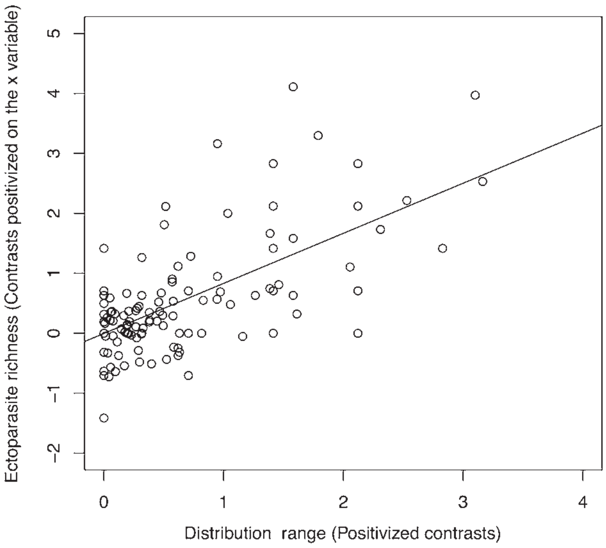

Fig. 3. Relationship between the ectoparasite species richness and the geographical range of the Mexican freshwater fish species ($r = 0{\cdot}5507$, $p < 2{\cdot}2\text{e-}16$). Points are phylogenetically independent contrasts positivized as suggested by Garland *et al*. (1992).

host size, precipitation, temperature and latitude, appear to influence the number of parasite species exploiting a freshwater fish species. The host geographical range (the number of sites in which a host species occurs) was the main predictor of the species richness in our study. This characteristic correlated positively with parasite richness, i.e., fishes with broad geographical distributions have richer assemblages than those with limited distribution. This relationship suggests that new parasite species can be acquired in various geographical regions because fishes living across many localities feed on a wider array of prey species and therefore are exposed to colonization by more parasite species than fishes restricted to a narrow distribution. Under this scenario, fishes are also exposed to colonization by more ectoparasite species with the consequent increase in species richness.

A positive correlation between host body size and ectoparasite species richness was also found. This finding can be explained in the light of island biogeography theory (Kuris *et al*. 1980), where larger hosts offer a larger number of habitats for parasite colonization than smaller ones.

Another pattern detected in the present study was the correlation between the parasite species richness and latitude as well as precipitation and temperature of the distribution area of the fish species. This relation has been addressed in several earlier papers dealing with species richness and latitudinal gradients. Rohde (1992) and Rohde *et al*. (1995) observed that marine fish from tropical latitudes typically harbour richer ectoparasite communities than fish from temperate latitudes. Later, Poulin and Rohde (1997) suggested that the relationship between temperature and the marine-fish ectoparasite community richness was an indicator of the importance of temperature in the diversification of fish parasites in the tropics. Rohde and Heap (1998) confirmed that pattern, but they did not find a correlation between temperature and endoparasite species richness in marine fishes, suggesting that biological differences between ecto- and endoparasites may explain this difference. In accordance with Rohde (1992) the increase in parasite species diversity towards tropical areas is the result of higher diversification rates or effective evolutionary time, which are correlated with temperature. In the case of freshwater fishes a negative relationship between parasite species richness and temperature has been observed (Choudhury and Dick, 2000; Poulin, 2001). However, in a more recent study Luque and Poulin (2008) found a positive correlation between the parasite taxonomic distinctness of freshwater fishes from the Neotropical Region and temperature for all parasites and for ectoparasites and endoparasites treated separately. Apparently, in marine and freshwater environments, temperature is a major force driving not only the increase in the number of parasite species but also the increase of their taxonomic complexity over evolutionary time, mediated by greater rates of speciation and host colonization (Poulin and Morand, 2004).

Trophic level (host feeding habits, host diet or trophic category) influenced endoparasite species richness, but only when the analyses were conducted with fish species values, i.e., fish species at higher trophic levels may not only acquire more parasites through their diet, but also they may be exposed to a broader range of different parasite taxa. This pattern was only evident when endoparasite assemblages were analysed separately, because helminth endoparasites are usually acquired by ingestion due to their indirect life cycle. For instance, predatory fish (fishes with higher trophic levels) should be exposed to more infective helminth larvae in their diet than planktivores. Over evolutionary time, this should translate in higher parasite colonization rates in predatory fish than in planktivorous fish, pushing up the equilibrium of parasite species richness.

Another host trait that was evaluated in this paper was the position of the host in the water column and its relation with parasite species richness. In particular, no correlation was found between these two variables even though previous studies have shown that benthic fish may harbour more directly transmitted parasite species than pelagic fish. The reason for that pattern has not been identified for freshwater fish parasites, although it has been argued that the benthic boundary layer is a focal point for parasite exchange among faunas inhabiting different vertical zones in marine habitats (Marcogliese, 2002).

Finally, on a larger scale, several other important factors can influence the parasite species distribution and the diversification of parasite assemblages in Mexican fish (e.g. high levels of endemism in certain river basins (Domínguez-Domínguez *et al.* 2006; Huidobro *et al.* 2006) and a significant number of exotic species introduced in the region). Therefore, the patterns uncovered in this study support the contention that parasite diversity, in this case parasite species richness, is largely affected by both host ecology and biogeography.

Although our approach uses the best available data for the helminth parasites of freshwater fishes, our attempts to identify the factors that determine parasite species richness are preliminary and provide but a glimpse of the patterns and processes that determine the species distribution of the helminth fauna of freshwater fish. Further sampling needs to be conducted in certain host families and particular river basins along the country, even though, as stated by Pérez-Ponce de León and Choudhury (2010), the inventory of the helminth parasite fauna in freshwater fishes in Mexico may be nearing completion (with the exception of the monogeneans).

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