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Filling the knowledge gap of Middle American freshwater fish parasite biodiversity: metazoan parasite fauna of Nicaragua

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Abstract

The heterogeneous landscape of Nicaragua harbours a large diversity of freshwater fishes. The great Nicaraguan lakes, Managua and Nicaragua, and several adjacent crater lakes harbour numerous endemic fish species. However, information about their parasite fauna is still fragmentary. Here, we surveyed the great Nicaraguan lakes and four crater lakes and provide data for 17 metazoan parasite taxa infecting seven fish host species. We also gathered all the published records from the literature on the parasites reported from Nicaraguan freshwater fishes, as well as those for Costa Rica and Panama to discuss the region of Lower Central America as a whole. With this information we built a parasite–host and a host–parasite checklist. With data from near 50% of the native and endemic freshwater fishes in Nicaragua, the parasite fauna comprises 101 taxa in 51 fish species allocated in 11 families. Cichlids are the most diverse group of fishes in this region and have been the most extensively surveyed for their metazoan parasites. Helminths are the best-represented groups of metazoan parasites, with 42 trematodes, five cestodes, 24 monogeneans, two acanthocephalans, 20 nematodes and one hirudinean. Additionally, freshwater fishes are parasitized by copepods, branchiurans and oribatid mites. Even though the inventory is not yet complete, the patterns of diversity uncovered revealed promising information about the origin, biogeography and evolutionary history of the Nicaraguan freshwater fish parasite fauna. More studies are necessary to complete our knowledge about the diversity, host association and distribution of metazoan parasites in Nicaragua and other Central American countries.

Introduction

The geographical position of Nicaragua in Lower Central America, along with Costa Rica and Panama, places the region in a pivotal biogeographical position bridging North and South America. The uplift of the Isthmus of Panama created a land bridge, which allowed the dispersal of freshwater fauna through the biogeographical event known as the Great American Biotic Interchange (GABI) (see Bacon *et al.*, 2016 and references therein). Irrespective of the date of the closure of the seaway, freshwater fishes dispersed northwards throughout different routes, and experienced diversification events (Perdices *et al.*, 2002; Hulsey *et al.*, 2004; Ornelas-García *et al.*, 2008; Říčan *et al.*, 2016). Nicaragua lies on one of the most active volcanic areas on the planet, the Central American volcanic arc. Over this arch, on the Pacific coast, lie the great Nicaraguan lakes, Managua and Nicaragua. These lakes were formed in the early Pleistocene, and were originally connected, separating later when the lakes opened towards the Atlantic Ocean via the San Juan River (Villa, 1976). In the surrounding of the great lakes lies a chain of active volcanoes dating back to the Holocene (Kutterolf *et al.*, 2007). The calderas of the volcanoes collapsed and filled with water from precipitation and/or underground seeps, creating lakes of different ages and isolated environments without interconnections with other waterbodies. Each lake has a different origin and time of formation – Lake Apoyo is the oldest and Lake Masaya was formed 1800 years ago (Kutterolf *et al.*, 2007). Besides the lakes, Nicaragua has dozens of rivers, several draining from the Central Highlands towards the Atlantic Lowlands.

The heterogenous landscape of this region has shaped the evolution of its biodiversity, with 114 species of fish, of which 104 are native, belonging to 28 families (Froese & Pauly, 2021). The most diverse freshwater fish group is the family Cichlidae (28 species), followed by Poeciliidae (ten species) and Characidae (seven species) (Froese & Pauly, 2021). Within cichlids, the Midas cichlid, *Amphilophus* spp., forms the largest biomass in the lakes, and experienced adaptive radiations in several crater lakes (Barluenga *et al.*, 2006; Kautt *et al.*, 2020). These three fish families have South American origin, and expanded northwards in their dispersal routes (Ornelas-García *et al.*, 2008; Říčan *et al.*, 2008, 2013, 2016; Reznick *et al.*, 2017; García-Andrade *et al.*, 2021).

Knowledge on the parasite diversity of freshwater fishes in this region is still scarce, representing a gap in the parasitological knowledge of the parasite fauna between South and North America, where a larger number of studies have been conducted. In addition, some fragmentary information has also been published regarding the parasite fauna of Costa Rica and Panama (e.g. Sandlund *et al.*, 2010; Choudhury *et al.*, 2017). These three countries comprise the geographic region known as Lower Central America, where eight biogeographic provinces are recognized – namely, the Nicaraguan depression, the Sandino fore arc, the Nicaraguan volcanic front, the Chorotega volcanic front, the Chorotega fore arc, the Chorotega back arc, the Panama Canal Zone lowlands and the Darién isthmus (Bagley & Johnson, 2014). Furthermore, Bagley & Johnson (2014) pointed out that Lower Central America represents a geologically complex area and a richly biodiverse model for studying the current composition and the diversification history of the Neotropical biota. A more detailed inventory of the parasite fauna of the region will be fundamental in explaining the history diversification of the biota across the Panama isthmus, providing further data to explain the biotic exchange between North and South America as discussed by Choudhury *et al.* (2017)

Particularly in Nicaragua, the first study was performed by Watson (1976), where several species of digeneans from Lake Nicaragua were reported. After that, a few studies were conducted across Nicaragua, representing isolated records of parasites in some fish species in scattered sampling areas in Nicaragua (Aguirre-Macedo *et al.*, 2001a, b; Vidal-Martínez *et al.*, 2001b; Mendoza-Franco *et al.*, 2003; González-Solís & Moravec, 2004; Scholz *et al.*, 2004; Andrade-Gómez *et al.*, 2017; López-Jiménez *et al.*, 2018; González-García *et al.*, 2021). Particularly for the crater lakes, McCrary *et al.* (2001) referred to an outbreak of blindness among native cichlids in crater Lake Apoyo caused by a trematode infection. Also, some nematodes were reported from crater lakes Xiloá and Apoyo (González-Solís & Jiménez-García, 2006). Recently, intensive survey work aimed at describing the metazoan parasite fauna of cichlids, with an emphasis on the Midas cichlid species complex, yielded the description of an additional set of species (Santacruz *et al.*, 2020, 2021, 2022).

The main objective of this study was, first, to characterize the parasites infecting non-cichlid fishes in the two great Nicaraguan lakes and four crater lakes based on field surveys; second, to provide an overview of all the records published of parasites infecting fishes dwelling in the Nicaraguan freshwater systems; and, third, to briefly discuss their historical biogeography in a wider context related with the information we provide in two supplementary files regarding the checklists of parasites of freshwater fishes of Costa Rica and Panama to consider Lower Central America as a whole.

Materials and methods

Sampling and fish dissection

Fish were sampled in three consecutive years (2017–2019), at the end of the rainy season (November and December), in the two great lakes Nicaragua and Managua and in four crater lakes (Asososca León, Xiloá, Masaya and Apoyo). The procedures to sample, maintain and euthanize the fish specimens followed those described in Santacruz *et al.* (2022), and followed procedures approved by the American Veterinary Medical Association Guidelines for Euthanasia of Animals, 2020 edition (available at https://www.avma.org/sites/default/files/2020-02/Guidelines-on-Euthanasia-2020.pdf). All parasites recovered were counted, and representative samples of each morphotype were fixed for morphological or molecular study in hot formalin or molecular-grade ethanol, respectively.

Parasite processing and identification

All parasites collected were analysed morphologically to achieve the highest taxonomic resolution following Santacruz *et al.* (2022). Morphological vouchers of some species, and in some cases hologenophores (*sensu* Pleijel *et al.*, 2008), were deposited at the Colección Nacional de Helmintos (CNHE), Universidad Nacional Autónoma de México, Mexico City, with the accession numbers 11,482, 11,491, 11,492, 11,497, 11,499, 11,500 and 11,503. In some cases, parasite specimens representing a particular morphotype were sequenced for identification, particularly those whose morphological characteristics or developmental stage impeded reaching an identification to the lowest taxonomic level. The molecular markers used were the mitochondrial *cox*1, *cox*2 and the nuclear 28S genes, depending on the genetic library available for each parasite group. The description of the methods for sequencing and primers used can be seen in Santacruz *et al.* (2020, 2021, 2022). Sequence data were deposited in GenBank under the following accession numbers: *Genarchella astyanactis*, 28S (OM502567); *Saccocoelioides* cf. *lamothei*, *cox*1 (OM509699–700); *Saccocoelioides orosiensis*, *cox*1 (OM509696–98); Dactylogyridae gen. sp., 28S (OM502566) and *cox*1 (OM509707–08); *Characithecium costaricensis*, *cox*1 (OM509703–06); and *Contracaecum* sp., *cox*2 (OM524389).

All existing records of parasites from freshwater fishes were retrieved from the literature, considering all published accounts for the period 1976–2021. Host names follow those currently recognized in FishBase (Froese & Pauly, 2021). The checklist of the freshwater fishes of Nicaragua, Costa Rica and Panama was retrieved from the same source. The checklists of the parasite fauna of freshwater fishes of Costa Rica and Panamá were built from the existent records of specimens deposited in the CNHE, Biology Institute, National Autonomous University of México, and by gathering the data from various bibliographical sources. To conduct a comprehensive bibliographic search, we retrieved all of the records from the ISI Web of Knowledge database using the following terms: and 'freshwater fish' and parasit*, or helminth, or monogen*, or digen* or acanthoceph*, or nematod*, or hirudinea*, or copepod*. We used those terms in combination with the name of the country, as Panama or 'Costa Rica'.

Results

We analysed 136 fishes from seven species (see table 1) during the three sampling seasons. The analysis yielded 17 parasite taxa, including trematodes, cestodes, monogeneans, nematodes, copepods and oribatid mites (table 1). Specimens of *Poecilia* spp. were collected in all lakes. Overall, poeciliids were infected by six parasite taxa, including trematodes, cestodes, copepods and oribatid mites. In the crater lakes Asososca León and Xiloá, two congeneric species of trematodes – namely, *Saccocoelioides*. cf. *lamothei* Aguirre-Macedo & Violante-Gonzalez, 2008 and *S. orosiensis* Curran, Pulis, Andres & Overstreet, 2018 – were

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Table 1. Fish species analysed for metazoan parasites in the two great lakes and four crater lakes of Nicaragua, and parasite records within lakes presented in alphabetical order per host species, with some ecological parameter data on the infection.

Lake and host	*N*	Parasite taxa	Si	S	Prevalence %	Mean intensity ± SD
Nicaragua						
Astyanax sp.	31	*Centrocestus formosanus* (Nishigori, 1924) (T)	Gills	L	3.2	1
		Characithecium costaricensis (Price & Bussing, 1967) (M)	Gills	A	50	18.4 ± 14.8
		Contracaecum sp. 1 (N)	Body cavity	L	23.3	1.8 ± 1.4
		Lernaea cyprinacea Linnaeus, 1758 (Cr)	Skin	A	3.2	1
Bramocharax sp.	7	*Characithecium costaricensis* (Price & Bussing, 1967) (M)	Gills	A	1.5	5.5 ± 4.9
		Dactylogyridae gen. sp. (M)	Gills	A	14.3	1
		Ergasilidae gen. sp.(Cr)	Gills	A	60	1
		Lernaea cyprinacea Linnaeus, 1758 (Cr)	Skin	A	14.2	1
Gobiomorus sp.	1	—	—	A	—	—
Poecilia sp.	7	Cyclophyllidea gen. sp. (C)	Liver/body cavity	L	28.5	1
		Ergasilidae gen. sp. (Cr)	Gills	A	16.6	1
		Oribatide gen. sp. (Ac)	Body cavity	A	14.2	5
		Posthodiplostomum sp. 1	Muscle	L	71.4	5.8 ± 7.6
		Saccocoelioides orosiensis Curran, Pulis, Andres & Overstreet, 2018 (T)	Gut	A	71.4	5.4 ± 6.9
Roeboides sp.	1	—	—		—	—
Pomadasys croco	1	*Neocasmus ackerti* (Watson, 1976) (=*Siphoderina ackerti*) (T)	Gut	A	100	33
Rhamdia sp.	2	*Clinostomum* sp. (T)	Body cavity	L	50	1
		Proteocephalidae gen. sp. (C)	Gut	A	50	1
Managua						
Astyanax sp.	53	*Austrodiplostomum compactum* (Lutz, 1928) (T)	Eye	L	13.2	1.5 ± 1.5
		Centrocestus formosanus (Nishigori, 1924) (T)	Gills	L	5.4	1
		Characithecium costaricensis (Price & Bussing, 1967) (M)	Gills	A	55.6	27.6 ± 17.3
		Contracaecum sp. 1 (N)	Body cavity	L	56.9	4.1 ± 4.5
		Ergasilidae gen. sp. (Cr)	Gills	A	11.1	1
		Genarchella astyanactis (Watson, 1976) (T)	Gut	A	5.7	2 ± 1
		Lernaea cyprinacea Linnaeus, 1758	Skin	A	11.3	1
Bramocharax sp.	1	*Characithecium costaricensis* (Price & Bussing, 1967) (M)	Gills	A	100.0	31
Poecilia sp.	6	*Posthodiplostomum* sp. 1 (T)	Muscle	L	100.0	62.6 ± 48.1
		Saccocoleioides spp. (T)	Gut	A	50.0	0.8 ± 1.1
Asososca León						
Poecilia sp.	4	*Acusicola margulisae* Santacruz, Morales-Serna, Leal-Cardín, Barluenga & Péresz-Ponce de León, 2020 (Cr)	Gills	A	100	26 ± 22.6
		Saccocoelioides cf. *lamothei* Aguirre-Macedo & Violante-Gonzalez, 2008 (T)	Gut	A	100	13 ± 4.5
		Saccocoelioides orosiensis Curran, Pulis, Andres & Overstreet, 2018 (T)	Gut	A		
		Saccocoleioides spp. (T)	Gut	A		

(*Continued*)

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Table 1. (*Continued.*)

Lake and host	*N*	Parasite taxa	Si	S	Prevalence %	Mean intensity ± SD
Xiloá						
Gobiomorus sp.	4	—	—	—	—	—
Poecilia sp.	12	Ergasilidae gen. sp. (Cr)	Gills	A	100	1
		Saccocoelioides cf. *lamothei* Aguirre-Macedo & Violante-Gonzalez, 2008 (T)	Gut	A	58.3	2.1 ± 1.7
		Saccocoelioides orosiensis Curran, Pulis, Andres & Overstreet, 2018 (T)	Gut	A		
		Saccocoleioides spp. (T)	Gut	A		
Masaya						
Gobiomorus sp.	1	*Contracaecum* sp. 1 (T)	Body cavity	L	100	5
Apoyo						
Gobiomorus sp.	3	—	—	—	—	—
Poecilia sp.	2	—	—	—	—	—

S, stage; A, adult; L, larvae; Si, site of infection; SD, standard deviation; Ac, acari; C, cestode; Cr, crustacean; M, monogenean; N, nematode; T, trematode.

found in mixed infections in individual poeciliids. The eleotrid *Gobiomorus* sp. was collected from Lake Nicaragua and three crater lakes. No *Gobiomorus* sp. was infected by parasites, but sample size was very low. *Astyanax* spp. were sampled from the great Nicaraguan lakes (they are absent in the crater lakes) and harboured seven parasite taxa. The sister characiform *Bramocharax* sp. was parasitized by four parasite taxa, all of them shared parasite species with *Astyanax* spp. Individuals of *Bramocharax* sp. harboured mixed infections of the monogeneans *C. costaricensis* (Price & Bussing, 1967) and an unidentified species of Dactylogyridae. One individual of the haemulid *Pomadasys croco* (Cuvier) was sampled in Lake Nicaragua and was infected with the cryptogonomid trematode *Neochasmus ackerti* (Watson, 1976), now considered a synonym of *Siphoderina* Manter, 1934.

We sequenced the 28S gene for two species of monogeneans: *C. costaricensis* and Dactylogyridae gen. sp., both from characids. The *cox*1 gene was also sequenced for the Dactylogyridae gen. sp. Additionally, sequences of the *cox*1 gene allowed the identification of two species of *Saccocoeiliodes* Szidat, 1954, which caused mixed infections in poecilids. A fragment of the 28S gene of *G. astyanactis* (Watson, 1976) from the type locality matched with available sequences of the species sampled in *Astyanax aeneus* from Mexico (GenBank number MK648277), and their sister species, *Genarchella isabellae* (Lamothe-Argumedo, 1977) from a cichlid also from Mexico. Sequences of the 18S rRNA gene were obtained for crustaceans. Finally, sequences of *cox*2 recovered from larval stages of *Contracaecum* (Railliet & Henry, 1912) did not allow species identification, as they did not match with available sequences in the GenBank database.

Our literature revision yielded records of 96 parasite taxa in Nicaraguan freshwaters. With the records generated in the present study, there are a total of 101 parasite taxa described in Nicaraguan fish (supplementary table S1). Parasite diversity includes species of trematodes, cestodes, monogeneans, acanthocephalans, nematodes, hirudineans, copepods, branchiurans and oribatid mites. Most species correspond to trematodes, with 42 taxa included in 16 families. Sixteen of them are reported as metacercaria. Monogeneans and nematodes are represented by 24 and 20 taxa, respectively. The oribatid mites, hirudineans and branchiurans are considered as rare records since they exhibit low prevalence values in their respective hosts. They are represented by a single taxon and reported only from one or two host species. In addition, three of the 101 parasite taxa are invasive species – namely, the anchor worm *Lernaea cyprinacea* Linnaeus, 1758 in the characids *Astyanax* sp. and *Bramocharax* sp., the Asian fish tapeworm *Schizochotyle acheilognathi* (Yamaguti, 1934) in the cichlids *Amphilophus citrinellus* and *Parachromis* sp., and the larval trematode *Centrocestus formosanus* (Nishigori, 1924) in *Astyanax* sp.

The area with the greatest diversity was Lake Nicaragua with 37 parasite taxa, followed by the Black Water River (in the Atlantic slope of Nicaragua) with 36 parasite taxa. Sampling was asymmetrical among localities for both fish host species and number of individuals analysed, resulting in asymmetric patterns of distribution of parasite diversity among waterbodies (fig. 1). Most studies have focused thus far on the lowlands of either the Pacific or the Atlantic slopes, but there is, to date, no study in the Cordillera Central. Considering the Nicaraguan crater lakes, Lake Xiloá exhibited the greatest diversity, with 20 parasite taxa.

The 101 parasite taxa reported for Nicaragua were found in 51 fish species belonging to 11 families (figs 2, 3 and supplementary table S2). Therefore, parasite records are still lacking for 55.2% of the freshwater fish species diversity of Nicaragua. Cichlids are the best studied fish group in terms of their parasite fauna, with records from 30 fish species (fig. 2). Three parasite groups are only reported from cichlid hosts: acanthocephalans, hirudineans and branchiurans. Among cichlids, the Midas cichlid harbours the most species-rich fauna of all studied hosts, with 21 parasite taxa. Four species of poeciliids have been studied and 17 parasite taxa were recorded. For characids, including the genera *Astyanax* Baird & Girard, 1854, *Bramocharax* Gill, 1877 and *Roeboides* Günther, 1864 sampled in the great lakes and streams of the Atlantic slope, the parasite fauna includes 26 parasite taxa. In four species of catfishes (Heptapteridae), ten parasite taxa have been reported. The remaining fish families exhibited a poor parasite diversity, although we acknowledge that the sampling size for

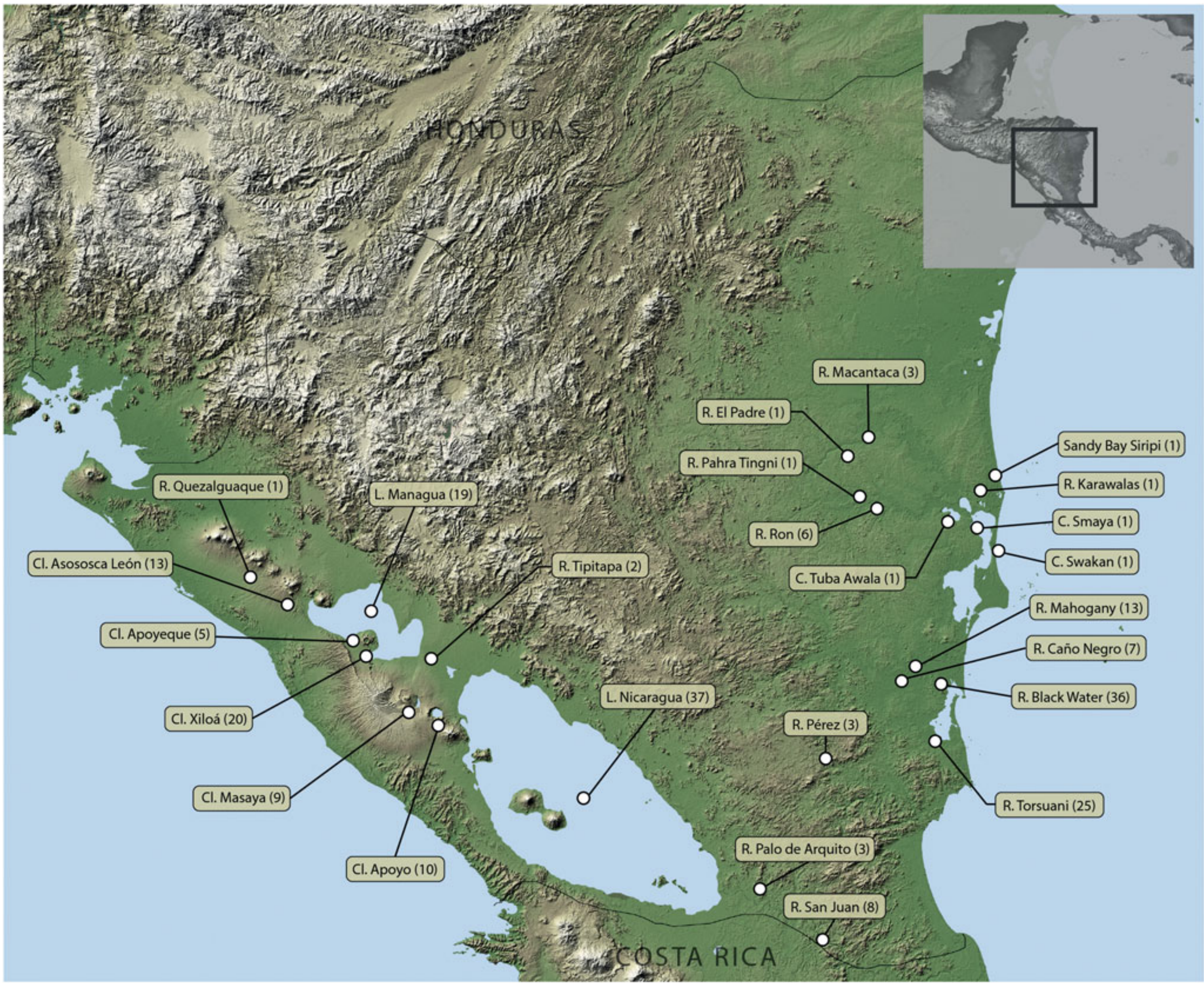

Fig. 1. Map of Nicaragua showing the sites where parasites have been from freshwater systems in Nicaragua. Parenthetical values next to site names indicate the number of parasite taxa reported for each site. Abbreviations: Cl, crater lake; L, lake; C, creek; R, river.

these fish is small: Bryconidae (one taxa), Carcharhinidae (three taxa), Eleotridae (three taxa), Haemulidae (one taxa), Lepisosteidae (two taxa), Megalopidae (one taxa) and Pristidae (two taxa) (supplementary table S2).

Complementarily, the parasite fauna of freshwater fishes of Costa Rica and Panama were compiled in two checklists. The parasite–host list of freshwater fish parasites of Costa Rica comprises around 21 bibliographical references accounting for 59 parasite taxa reported from 44 fish species (supplementary table S3); cichlids have been the most studied hosts, with 26% of the species analysed. In contrast, the parasite–host list of freshwater fishes of Panama is based on solely eight references, on which 63 parasite taxa were reported from 25 fish species (supplementary tables S4). In this case, characiforms are the most intensively studied hosts, with 32% of the total number of species analysed.

Discussion

Nicaragua has a natural setting that favours diversification, with large freshwater bodies combined with smaller isolated crater lakes, which collectively are sources of biological endemism. In the last few years, we increased our sampling effort in the great Nicaraguan lakes and several crater lakes occurring on the Pacific coast of Nicaragua, where cichlids experienced evolutionary success and recent adaptive radiations, similar, albeit to a smaller extent, to the well-known adaptive radiations of cichlids in the East African Great Lakes (Barluenga *et al.*, 2006; Salzburger *et al.*, 2014; Kautt *et al.*, 2020). The freshwater fish fauna of Nicaragua comprises around 104 native species (Froese & Pauly, 2021), of which four siluriforms and nine characiforms are primary fish restricted to freshwater environments, but the rest are secondary freshwater fishes tolerant to different degrees of salinity. The most abundant fish in the Nicaraguan freshwaters are cichlids and poeciliids, which together account for almost 50% of the fish fauna.

The present study represents an additional step to an ongoing effort to characterize the metazoan parasites of Nicaraguan fish (see Santacruz *et al.*, 2020, 2021, 2022). Here, we report new data on the parasite fauna of non-cichlid fish hosts. We recorded 17 parasite taxa from seven fish species. The poecilids, widely distributed across all lakes (Astorqui, 1971; Waid *et al.*, 1999), harboured the most parasite species-rich fauna, with six taxa,

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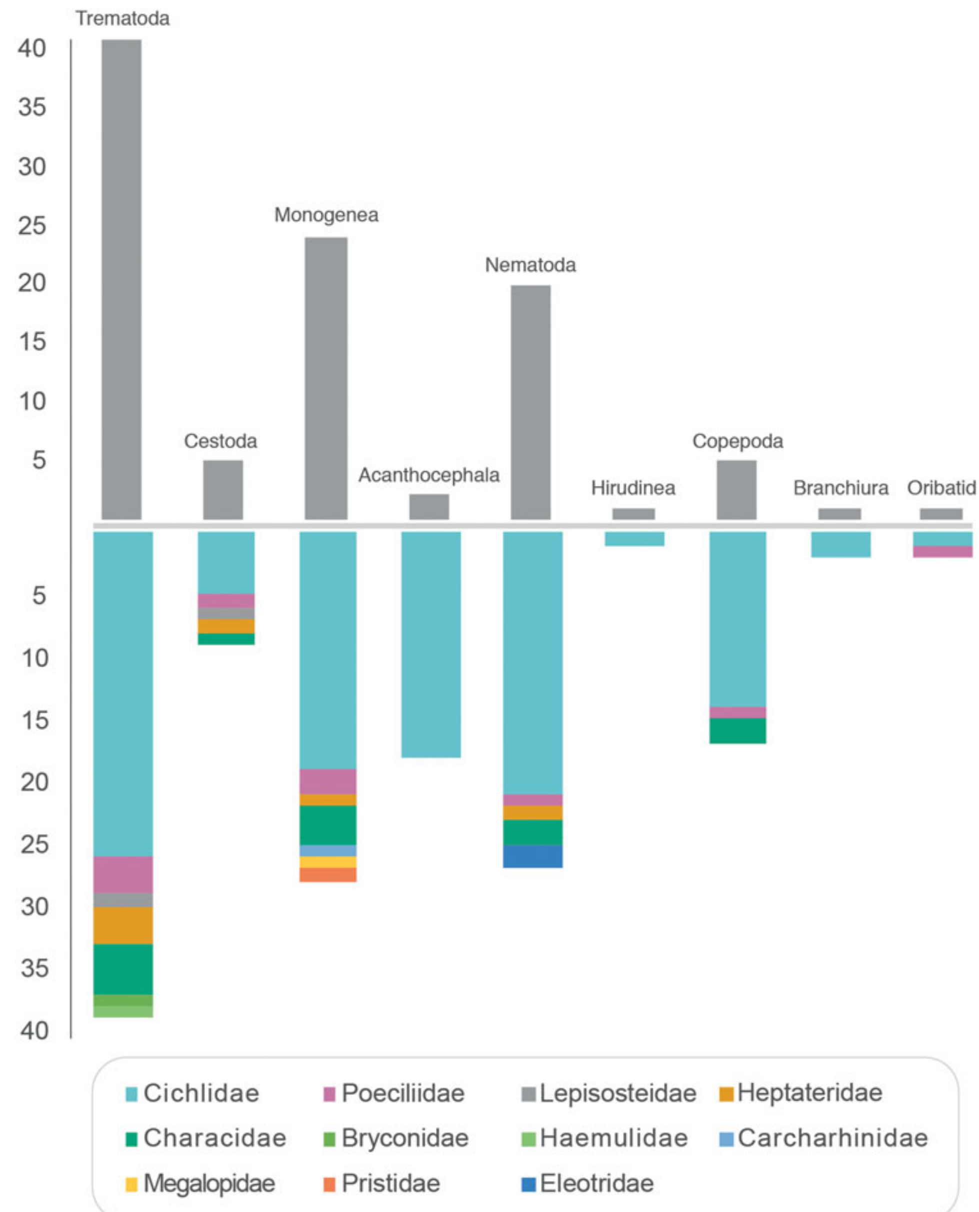

Fig. 2. Parasites in freshwater fishes of Nicaragua. Total number of parasite taxa per parasitic group (top graph) and number of fish host species per host family in colour (bottom graph) reported.

whereas, in characids, we found adult stages typical of their biogeographical core parasite fauna (*sensu* Pérez-Ponce de León & Choudhury, 2005), including the trematode *G. astyanactis* and the monogenean *C. costaricensis*. Interestingly, the eleotrid *Gobiomorus* sp. (introduced in crater Lake Apoyo; Waid *et al.*, 1999) harboured a poor parasite fauna; host invasive species usually loss parasites when they colonize a new environment (Roche *et al.*, 2010).

In Nicaragua, considering all existing parasite records, the Midas cichlid species complex *Amphilophus* spp. possess the highest parasite species richness, with 26 taxa. The large parasite species diversity of these cichlids agrees with the observed diversity in Middle American cichlids of the tribe Heroini (Razo-Mendivil *et al.*, 2009, 2010, 2015). This high parasite species richness in cichlids may be a response to their remarkable dominance in Middle American freshwaters, and the great number of endemisms in the lacustrine systems. However, the differences may also account for a sampling bias given the large interest these fishes raise. Overall, Middle American cichlids are parasitized by a large diversity of taxa, particularly helminth parasites (see Vidal-Martínez *et al.*, 2001a).

The parasite fauna of Nicaraguan freshwater fishes is mainly of Neotropical origin, and only a few records have been reported for Nearctic fish hosts, such as gars, which extend their southernmost distribution range to the San Juan River, which joins Lake Nicaragua with the Atlantic slope. Trematodes represent the dominant component of the parasite fauna, with the list including taxa from 16 families, reported in 39 fish species, both as adults and as metacercariae. Most of the trematode fauna of Nicaragua is shared with that of Mexican freshwaters, where Neotropical fishes reach their northernmost distributional range (see Pérez-Ponce de León & Choudhury, 2005).

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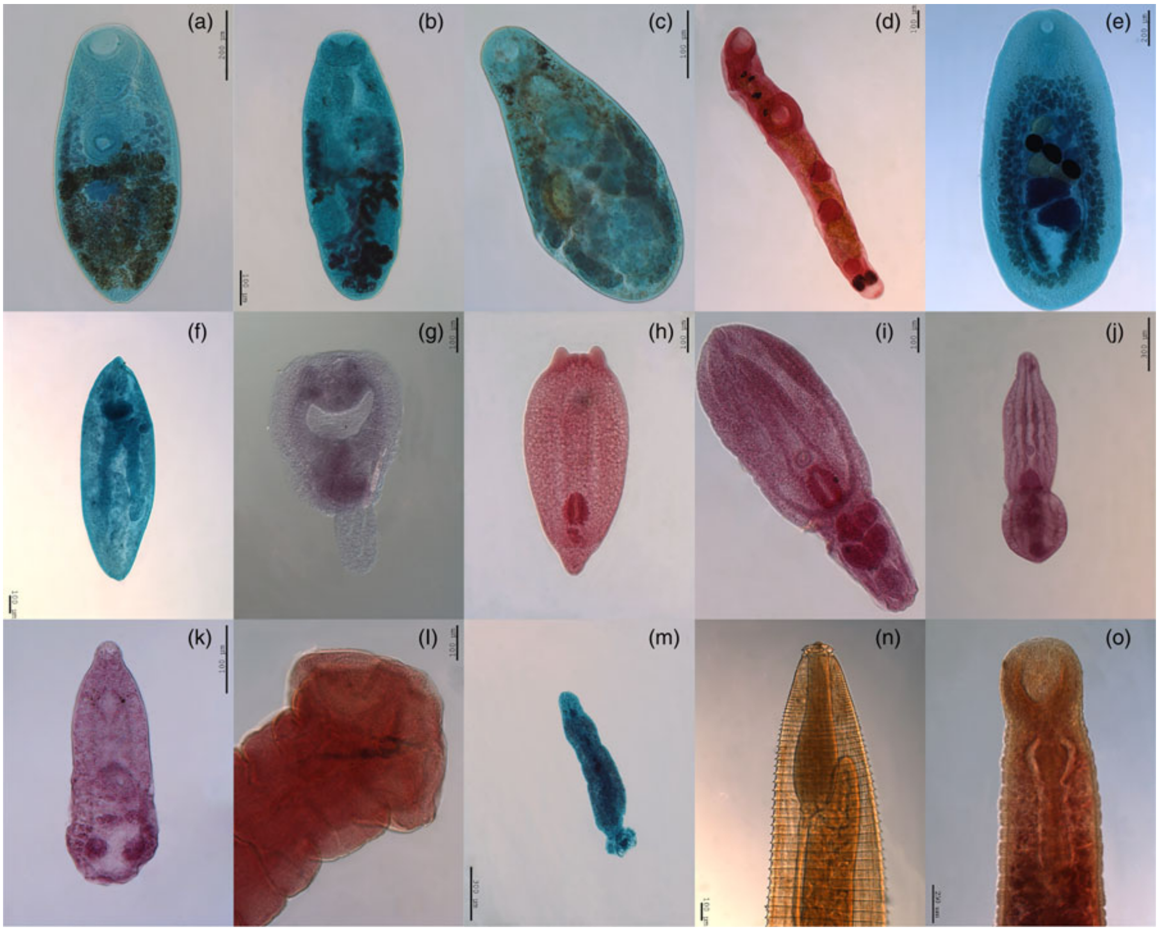

Fig. 3. Photomicrographs of representative parasites in freshwater fishes from the Nicaraguan lakes. Trematodes (a) Criptogonomidae gen. sp., (b) *Oligogonotylus manteri*, (c) *Saccocoeilioides* sp., (d) *Genarchella astynactys*, (e) *Crassicutis cichlasomae*, (f) Trematoda gen. sp., (g) Strigeidae gen. sp., (h) *Austrodiplostomum* sp., (i) *Posthodiplostomum* sp. 2, (j) *Posthodiplostomum* sp. 1, (k) Heterophyidae gen. sp., (l) cestode *Cichlidocestus janikae*, (m) monogenan *Sciadicleithrum mexicanum*, (n) nematode *Goezia* sp., (o) hirudinean *Myzobdella*.

The freshwater fish parasite fauna of Lower Central America

The data gathered on the metazoan parasites of freshwater fishes of Nicaragua reveal a species-rich fauna, with a total of 101 parasite taxa belonging to eight parasitic groups, and these parasites infect 51 host species (less than 50% of the fish fauna). This makes Nicaragua the most thoroughly studied region of Central America. In contrast, for other areas in Lower Central America with higher fish richness – for example, Costa Rica and Panama – parasite surveys reported lower parasite species richness (see supplementary tables S3 and S4). To the best of our knowledge, in Costa Rica at least 44 of the 178 freshwater fish species (Froese & Pauly, 2021) have been studied for parasites to a certain extent, and 59 parasite taxa have been reported (Chandler *et al.*, 1995; Choudhury *et al.*, 2002, 2006; López-Caballero *et al.*, 2009; Arguedas Cortés *et al.*, 2010; Sandlund *et al.*, 2010; Pinacho-Pinacho *et al.*, 2015, 2020, 2021; Tkach & Curran, 2015; Andrade-Gómez *et al.*, 2017, 2019; De Chambrier *et al.*, 2017; Curran *et al.*, 2018; López-Jiménez *et al.*, 2018; Briosio-Aguilar *et al.*, 2019; Sereno-Uribe *et al.*, 2019; González-García *et al.*, 2021; supplementary table S3). In Panama, 25 of the 213 freshwater fish species (Froese & Pauly, 2021) have been studied for parasites, and 63 parasite taxa have been reported (Sogandares-Bernal, 1955; Mendoza-Franco *et al.*, 2007, 2008, 2009a, b; Mendoza-Franco & Reina, 2008; Kritsky *et al.*, 2009; Roche *et al.*, 2010; Choudhury *et al.*, 2013, 2017; supplementary table S4). Nicaragua, along with Costa Rica and Panama, comprise a geographical region known as Lower Central America. Overall, the freshwater fish fauna of Lower Central America is composed of at least 176 parasite taxa, although the proportion of fish species analysed thus far is still relatively low. This clearly indicates that the inventory of the freshwater fish parasite fauna is far from complete. However, some interesting biogeographical patterns emerged, particularly when adult stages are considered, since larval forms might obscure patterns as they can be dispersed with their definitive hosts – usually fish-eating birds. An initial interesting pattern refers to the fact that the parasite fauna of Lower Central America is mainly composed of adult parasites, with 127 taxa out of the 173 reported (73%). Ecologically, this may indicate that the analysed host species play a minor role in the transmission dynamic of some parasites in the freshwaters of Lower Central America. Still, 46 larval stages of parasites complete their life cycle in another vertebrate. Most of the larval forms are found in fish-eating birds (32 of the 42 taxa), while the other use either larger fish, mammals or reptiles as definitive hosts. Current data show that only five adult taxa – that is, the trematodes *Acanthostomum minimum* Stunkard, 1938, *Oligogonotylus*

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manteri Watson, 1976, *Prosthenhystera obesa* (Diesing, 1850), *Saccocoelioides cichlidorum* (Aguirre-Macedo & Scholz, 2005) and the nematode *Rhabdochona* sp. – are shared across all of Lower Central America. However, this might be a sampling artifact, and the result of incomplete sampling of hosts or inaccurate species identifications. The parasite fauna shared across Lower Central America is the result of the influence of the regional fauna, as well as the biogeographical patterns of their hosts. All the species are also distributed in Middle America; they have been reported in freshwater fishes of Mexico, particularly in the Neotropical part of the country, where the same groups of hosts are distributed (Pérez-Ponce de León & Choudhury, 2005). Interestingly, at least 29 parasite taxa are endemic in freshwater fishes in river basins across Nicaragua, Costa Rica and Panama, accounting for 16.7% of endemism.

In summary, the results of our study highlight the diversity of parasites in freshwater systems of Nicaragua, and show the spatial distribution of the sampling effort, mainly in the lowlands of the west and east of the Cordillera Central. Our data add information to the inventory of the parasite fauna of freshwater fishes in this important region. The biogeographical event referred to as the GABI requires the use of different taxa to better explain the major patterns of distribution derived from the formation of the land bridge. We acknowledge that the inventory of the freshwater fish parasite fauna of Nicaragua is still far from complete, but the current information is very useful for better understanding the role of GABI in the diversification of both hosts and parasites. In addition, we concur with Poulin *et al.* (2020) in that the research programs on fish parasite discovery require an improvement in their efficiency to achieve a better understanding of parasite diversity patterns, which is central to comprehending the evolutionary-based classification of living forms on the planet. In our study, we targeted a geographical hotspot of fish biodiversity, and we used molecular tools to study parasite genetic diversity in cases where morphology was not enough to establish proper species identifications. For the descriptions of new taxa, we followed an integrative taxonomy approach that considered traits such as morphology, DNA, host association and geographical distribution; this sets a standard quality criterion for new species descriptions. Poulin *et al.* (2020) clearly stated that since taxonomy and systematics underpin all other research in ecology and evolution, and applied science related, for example, with fisheries and aquaculture, it is necessary first to discover parasite species and then to characterize host–parasite associations. In addition, our study on the parasite fauna of Nicaraguan freshwater fishes is part of a larger project aimed at understanding the potential role of parasites in the diversification of the Midas cichlid species complex, which mirrors the case of adaptive radiations of cichlids in African lakes. Information on the parasite fauna of these fish sheds light on the factors that determine cases of sympatric speciation.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0022149X2200013X

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Conflicts of interest. None.

Ethical standards. The authors assert that hosts were studied following all applicable international, national and/or institutional guidelines for the care and use of animals. Fish were euthanized and killed following procedures of the American Veterinary Medical Association. Hosts were collected under a collection permit (number 001-012015) issued by MARENA.

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