Biota Neotropica 24(1): e20231481, 2024
www.scielo.br/bn

biotaneotropica
ISSN 1676-0611 (online edition)
Article

Fish fauna of the Río San Pedro and Río La Pasión, Usumacinta River Basin, Guatemala

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QUINTANA, Y. **Fish fauna of the Río San Pedro and Río La Pasión, Usumacinta River Basin, Guatemala.** Biota Neotropica 24(1): e20231481. https://doi.org/10.1590/1676-0611-BN-2023-1481

Abstract: The Río San Pedro and Río La Pasión lie within the Usumacinta River Basin, a globally significant center of freshwater fish diversity. Both rivers are listed among Central America's top 50 regions for conserving freshwater biodiversity. This study presents an updated checklist of 70 fish species, of which six are non-native to the Usumacinta River Basin. From these species, 69 are reported from the Río La Pasión and 56 reported from the Río San Pedro, representing higher species richness than previously reported. The checklist derives from a systematic survey of fishes conducted in 2019 and records available in public databases and published literature. Seventy-eight percent of the species were reported in both rivers, and Cichlidae and Poeciliidae had the most species. Secondary species represent 59% of the species reported, followed by peripheral species with 22% of the species. The species with highest fidelity in Río La Pasión were the armored catfish *Pterygopichthys* spp. and the livebearer *Gambusia sexradiata*; and the cichlids *Thorichthys meeki* and *Oscura heterospila* had highest fidelity in the Río San Pedro. *Thorichthys helleri* was widely distributed in both rivers. According to the IUCN Red List of Threatened Species, there are four species classified as Vulnerable in Río La Pasión. However, 62% of the species are of Least Concern, 25% of the species are Data Deficient, and 6% are listed as Not Evaluated. More research is needed to document the status of the fish fauna, and improved habitat protection is required to conserve stocks.
Keywords: *Usumacinta River Basin; ichthyofauna; endemic fishes; freshwater conservation.*

Ictiofauna del Río San Pedro y Río La Pasión, Usumacinta River Basin, Guatemala

Resumen: El río San Pedro y el río La Pasión se encuentran dentro de la cuenca del río Usumacinta, un centro de diversidad de peces de agua dulce de importancia mundial. Ambos ríos figuran entre las 50 regiones principales de América Central para conservar la biodiversidad de agua dulce. Este estudio presenta un listado actualizado de 70 especies de peces, de las cuales 6 son especies no nativas para la cuenca del Río Usumacinta. De estas especies, 69 se reportan para el Río La Pasión y 56 para el río San Pedro, lo que representa una riqueza de especies más alta que la reportada previamente. La lista de verificación se deriva de un muestreo sistemático de peces realizado en 2019 y registros disponibles en bases de datos públicas y literatura publicada. El 78% de las especies se reportan en ambos ríos, siendo Cichlidae y Poeciliidae las familias con mayor riqueza. Las especies con mayor fidelidad en Río La Pasión fueron el bagre acorazado *Pterygopichthys* spp. y el pez vivíparo *Gambusia sexradiata*; y los cíclidos *Thorichthys meeki* y *Oscura heterospila* tuvieron mayor fidelidad en el Río San Pedro. *Thorichthys helleri* se distribuyó ampliamente en ambos ríos. Según la Lista Roja de Especies Amenazadas de la UICN, existen cuatro especies clasificadas como Vulnerable en el Río La Pasión. Sin embargo, el 62 % de las especies son de Preocupación Menor, el 25 % de las especies tienen Datos Insuficientes y el 6 % se enumeran como No Evaluadas. Se necesita más investigación para documentar el estado de la fauna de peces, y se requiere una mejor protección del hábitat para conservar las poblaciones.
Palabras clave: *Cuenca del Río Usumacinta; ictiofauna; peces endémicos; conservación de agua dulce.*

Introduction

The Usumacinta River Basin is the largest in Mesoamerica, and its tributaries (i.e., Lacantún, La Pasión, Chixoy, and San Pedro; Figure 1) rank among the largest within this region (Yañez-Arancibia et al. 2009). The Usumacinta and Grijalva River Basins are considered a center of global significance for freshwater fish diversity (Miller 1966). The Usumacinta alone harbors approximately 200 fish species from 9 families (Miller 1966), with 172 species reported for the lower reaches of the Usumacinta in southern México (Soria-Barreto et al. 2018).

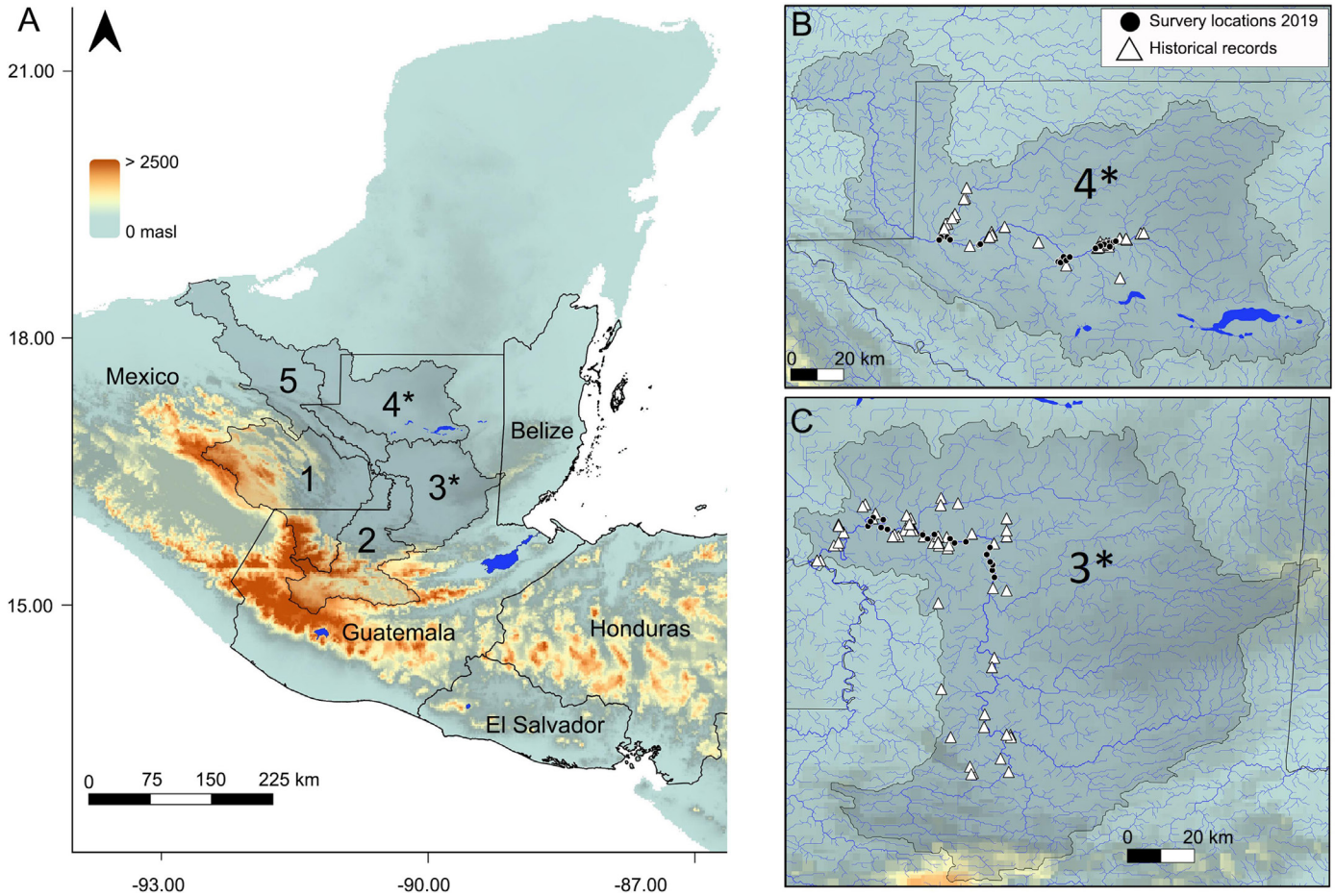

Figure 1. Map of the **A.** Usumacinta River Basin (dark grey) showing the extension of the sub-basins in the Upper Usumacinta: 1. Río Lacantún, 2. Río Chixoy, 3*. Río La Pasión, and Lower Usumacinta: 4*. Río San Pedro, and 5. Río Usumacinta., **B.** Río San Pedro sub-basin, **C.** Río La Pasión sub-basin. B and C indicate surveyed sites with a black doth and historical records with a white triangle. The main canal of the Río San Pedro and Río La Pasión is represented by a thick blue line. Source: Diego J. Elías.

The taxonomy of fishes has been studied extensively in the Usumacinta. New species have been described in recent years, and extensions of geographic distributions have been reported, particularly within the lower basin (e.g., *Potamarius usucamcintae, Lacantunia enigmatica, Heterophallus echeagarayi*) (Rodiles-Hernández et al. 2005, Betancur-R & Willink 2007, Álvarez-Pliego et al. 2016, Quintana et al. 2019).

A recent review of the Central America freshwater fish fauna identified the Grijalva-Usumacinta as an area of high endemism (Matamoros et al. 2015). Elías et al. (2020) suggested that the basin can be subdivided into five endemic areas, with the upper Usumacinta harboring the highest proportion of endemic species. A portion of the upper Usumacinta River and the lower Usumacinta lie within Guatemala's boundaries, comprising 58% of the basin. The basin contains a variety of habitats, including streams, lagoons, floodplains, waterfalls, rapids, and large tributaries. Two tributaries, the Río La Pasión (upper Usumacinta) and Río San Pedro (lower Usumacinta), are among Guatemala's ten largest rivers and have been listed among Central America's top 50 regions for conserving freshwater biodiversity (Calderón et al. 2004).

Ichthyological surveys in Río San Pedro and Río La Pasión have increased since 1999. Although ecological and fisheries studies are lacking in this region, efforts to characterize the ichthyofauna in these rivers were made by Barrientos (1999), who identified 27 fish species in the upper Río San Pedro and Río Sacluc, 11 of them being important in subsistence fisheries. Willink et al. (2000) surveyed Río San Pedro within the Parque Nacional and Biotope Laguna del Tigre and reported 44 species. A fish checklist at the departments El Petén and Alta Verapaz reported 43 species for Río San Pedro and 51 species in Río La Pasión (Valdez-Moreno et al. 2005). Castillo-Domínguez et al. (2011) surveyed the wetlands of Río San Pedro in Balancán, México, and recorded 25 species. Ixquiac (2016) reported 22 species of commercial importance in the Río La Pasión. Barrientos et al. (2018) surveyed the Usumacinta in Guatemala, reporting 18 for Río San Pedro and 29 for Río La Pasión.

The Usumacinta River Basin is experiencing environmental impacts, including land-cover changes for agriculture, African palm plantations, logging, wildfires, as well as overfishing, pollution, and hydropower development (Cotler Ávalos et al. 2010, Gandin 2012, Tapia-Silva et al. 2015, Dürr 2017, Camacho-Valdez et al. 2022) putting at risk numerous endemic species. Also, invasive species have proliferated in the Usumacinta basin, but their contribution to the fish assemblage in Río La Pasión and Río San Pedro is still unknown. A comprehensive checklist of fish species would support conservation efforts and management to protect regional fish stocks. The aim of this study was: 1) to provide an updated inventory of the fish fauna in Río La Pasión and Río San Pedro, 2) to describe the diversity and

composition of these fish assemblages, 3) to assess the conservation status of fishes in both rivers based on the most updated IUCN Red List of Threatened Species assessment of freshwater fish (IUCN 2022). This study highlights information on the fish assemblages and fish conservation status useful for evaluating current conservation efforts such as the Endangered Species List, LEA (CONAP 2021), and provides information to monitor fish assemblage in the long term, assessing threats such as biodiversity loss and increase of invasive species.

Material and Methods

1. Study area

The Usumacinta River Basin is a tri-national watershed shared by Guatemala, México, and Belize (Figure 1A). Along the basin, there are complex and heterogeneous habitats such as wetlands, lakes, streams, rapids, waterfalls, tributaries, and floodplains, as well as a tropical moist broadleaf forest, with primary forest occupying less than 25% of the natural vegetation cover (Cotler Ávalos at al. 2010, Corrales et al. 2015, Soria-Barreto et al. 2018). The Guatemalan portion of the Usumacinta River Basin comprises 58% of the entire basin and harbors the Río La Pasión, Río San Pedro, Río Lacantún, and Río Chixoy sub-basins (Figure 1A; for higher resolution see Elías et al. 2020), which contain tributaries with seasonal hydrology that are connected to numerous aquatic environments (i.e., streams, lagunes, and floodplains) along their course.

The Río San Pedro lies in the lower Usumacinta Basin (Figure 1A, 1B) (17°8'5.2908" N-89°54'9.6048"W; ~50 meters above sea level), originates near the southern border of Laguna del Tigre National Park (Juárez-Sánchez et al. 2019) within the lowlands of the Maya Biosphere Reserve in the department El Petén, and not within the highlands of north Guatemala like some authors have suggested (e.g., Castillo-Domínguez et al. 2010). This river flows 186 km in Guatemala and has a watershed of ~14,335 km^2. The upper Río San Pedro originates at the juncture of the Río Sacluc and Laguneta Yalá. Downstream tributaries include the Río San Juan, Laguna Perdida, Laguna Larga, Río Lagarto, Río Chocop, and Río Escondido. A wetland complex (Laguna del Tigre) occurs alongside the river's lower reaches. The Río San Pedro sub-basin contains multiple protected areas, such as the Parque Nacional and Biotopo Laguna del Tigre, San Miguel La Palotada, Finca San José, Katherine, Laguna Perdida, Cerro Cahuí, and Tikal Nacional Park (Figure S1, CONAP 2009).

The Río La Pasión rises in the upper Usumacinta basin in the Department of Alta Verapaz (Figure 1A, Figure 1C) (16°28'51.1716" °N-90°32'35.142"; ~150 meters above sea level). The river begins near Río Santa Isabel and Río Sebol, with influence from Río Chajmaic (~271 masl) at the limit of the highlands and runs along the department El Petén, finally draining into the Usumacinta River. Río La Pasión has a length of 354 km with an extension of ~12,083 km^2. The river is connected to Río Machaquilaito, Río Machaquila, Río San Juan, Río Santa Amelia, the streams San Martín and Pucté, Los Chorros waterfalls, Río El Subin, Laguna Petexbatún, and Laguna las Pozas. Multiple protected areas are observed within La Pasión sub-basin, including El Pucté, El Manantial, El Rosario, Ceibal, Dos Pilas, Petexbatún, Aguateca, Los Lagartos, Machaquilá, La Cumbre Flor de la Pasión, and Xutilha and private lands used for cattle ranching and

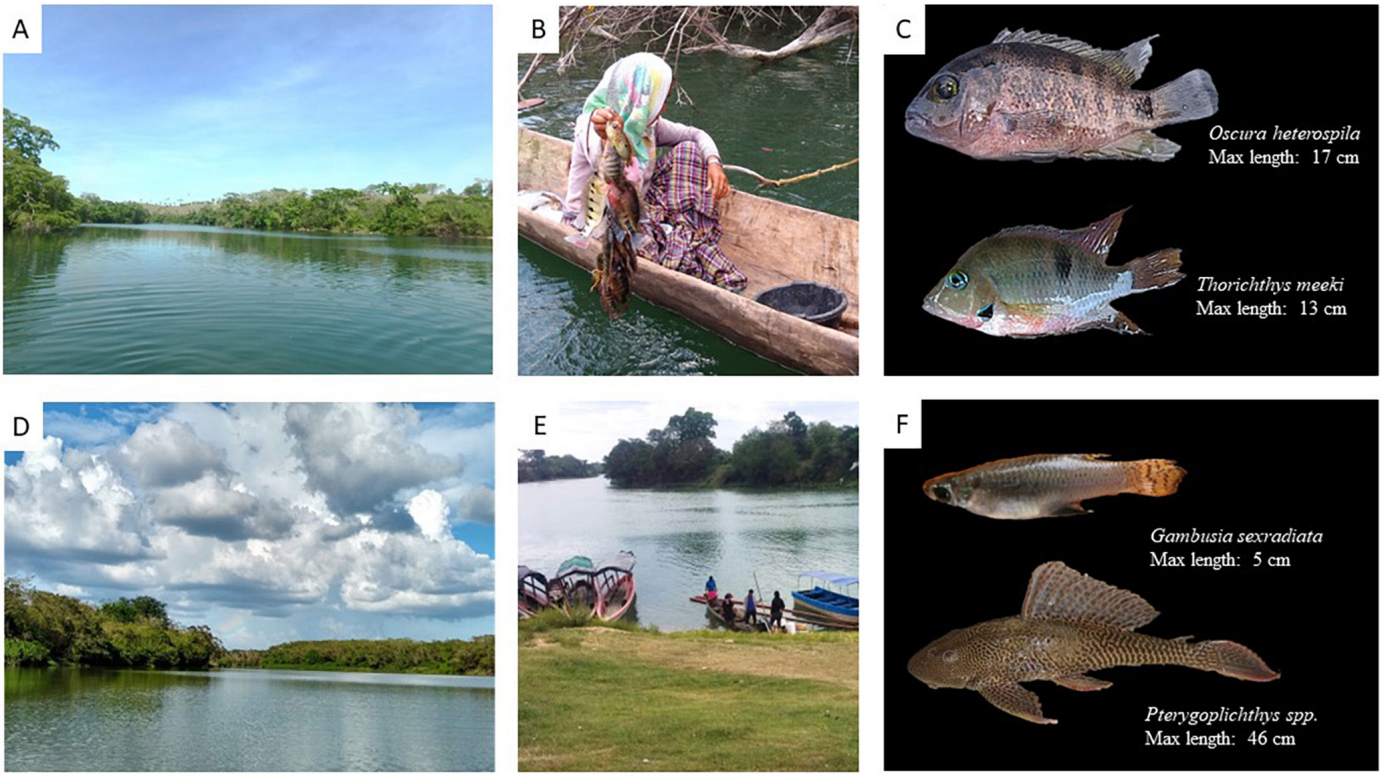

Figure 2. A. Río San Pedro main canal, **B.** Subsistence fishing in Río San Pedro, **C.** Indicator species for Río San Pedro. **D.** Río La Pasión main canal, **E.** Landing site in Río La Pasión, Sayaxché, **F.** Indicator species for La Pasión River. Credits: Yasmín Quintana.

Table 1. Georeferenced locations surveyed in 2019.

River	Site	Latitude (N)	Longitude (W)	Altitude (mamsl)
San Pedro	SP01	17°14'37.98"	90°17'48.54"	62
	SP02	17°14'48.66"	90°16'53.46"	54
	SP03	17°14'20.28"	90°18'51.42"	52
	SP05	17°13'59.58"	90°19'40.74"	50
	SP06	17°13'29.04"	90°20'41.82"	54
	SP07	17°15'0.23"	90°16'23.04"	51
	SP08	17°11'9.36"	90°27'51.96"	43
	SP09	17°10'31.38"	90°28'41.82"	47
	SP10	17°10'5.78"	90°27'5.22"	53
	SP11	17°11'40.86"	90°27'28.68"	50
	SP12	17°10'55.2"	90°26'55.08"	49
	SP13	17°11'38.53"	90°26'10.04"	53
	SP14	17°15'53.76"	90°52'13.44"	48
	SP15	17°14'12.72"	90°45'25.98"	41
	SP16	17°15'52.5"	90°53'30.72"	54
	SP17	17°14'22.92"	90°45'10.44"	49
	SP18	17°15'19.74"	90°51'35.7"	41
	SP19	17°15'17.34"	90°53'55.14"	41
La Pasión	LP01	16°31'54.84"	90°8'40.98"	115
	LP02	16°32'37.32"	90°9'24.78"	114
	LP03	16°33'19.32"	90°12'2.34"	114
	LP04	16°32'34.8"	90°13'009"	114
	LP05	16°32'6.36"	90°6'46.92"	115
	LP06	16°33'16.03"	90°13'59.6"	116
	LP07	16°34'43.32"	90°23'5.94"	115
	LP08	16°36'8.16"	90°22'13.62"	117
	LP09	16°34'29.94"	90°20'54.78"	118
	LP10	16°35'28.26"	90°22'40.2"	118
	LP11	16°34'10.2"	90°20'51"	119
	LP12	16°35'46.56"	90°20'32.94"	116
	LP13	16°27'21.24"	90°2'22.86"	115
	LP14	16°29'59.28"	90°3'18.72"	135
	LP15	16°26'11.22"	90°2'1.8"	112
	LP16	16°28'16.92"	90°2'20.16"	108
	LP17	16°28'45"	90°2'44.52"	125
	LP18	16°31'9.54"	90°2'46.52"	162

African palm plantations (Figure S1, CONAP 2009, Juárez-Sánchez et al. 2019).

2. *Literature review and public databases*

The literature review included studies by Willink et al. (2000), Valdez-Moreno et al. (2005), Barrientos et al. (2018), and Elías et al. (2020). These studies report results from surveys of the Río La Pasión and Río San Pedro mainstems and adjacent aquatic habitats. The checklist was complemented with data associated with preserved specimens archived in the Global Biodiversity Information Facility (GBIF.org, 2022) and Fishnet2.net. These records include specimens reported from Río La Pasión, Río San Pedro, and neighboring localities (Figure 1C, 1D). Voucher specimens are archived in the American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Cornell University Museum of Vertebrates (CUMV), El Colegio de la Frontera Sur (ECOSUR), FishBase, Florida Museum of Natural History (UF), Field Museum of Natural History (FMNH), Louisiana State University Museum of Natural Science (LSUMZ), Stuttgart State Museum of Natural History (SMNS), Senckenberg Naturhistorische Sammlungen (SNSD), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM), and Universidad del Valle de Guatemala (UVG) (See Data Availability; Acronyms follow Sabaj 2020). The final database for this study was curated to remove duplicates and species with probable errors (i.e., different distribution reported, misidentification). Some records are reported only at the generic level. Locations of records reported on GBIF.org and FishNet2.net were plotted using ArcMap 10.7.1. The final checklist follows the most updated valid taxonomy (Frike et al. 2022). Fishes from the checklist were classified as primary, secondary, or peripheral freshwater fish following Myers (1938). Details of the conservation status for each species were obtained from the IUCN Red List of Threatened Species (IUCN 2022).

3. *Fish survey*

A systematic survey of fishes was conducted at 36 locations (Table 1) along the littoral zone in the main channel of Río San Pedro (Figure 1C, 2A, 2B) and Río La Pasión (Figure 1D, 2D, 2E). At each location, surveys were done using complimentary fishing gears and consistent effort: 15 beach seine drags (8 × 2 m, 0.5 cm bar mesh), 100 castnet throws (2.7 m radius, 0.95 cm bar mesh), and two experimental gillnets deployed for 8 hours (100 × 2 m divided in 4 panels of 25 m with 6.4, 8.8, 10.2, 11.4 cm bar mesh). A sample of voucher specimens was preserved in 10% formalin and transferred to 70% ethanol. The collection was deposited at the Sistema de Colecciones Biológicas, Escuela de Biología, Universidad de San Carlos de Guatemala (USAC) and the Biodiversity Research and Teaching Collections (BRTC Ichthyology), Texas A&M University. Collection and preservation procedures followed the Guidelines for the Use of Fishes in Research (Use of Fishes in Research Committee, joint committee of the American Fisheries Society, the American Institute of Fishery Research Biologists 2014). Research was conducted under IACUC 2018-0454, CONAP research permit No.00375-B and collecting permit No. 3927.

4. *Analysis*

Species richness, diversity, and assemblage composition were estimated for each river using all data from the systematic survey. Species richness and diversity were estimated through rarefaction and extrapolation curves using the R package "iNEXT" 3.0 (Hsieh et al. 2022, R Core Team 2022). Richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2) indexes were estimated as the mean of 200 bootstrap replications with 95% confidence intervals based on individual-based abundance data. Sample-size-based curves show rarefied and extrapolated diversity estimates regarding sample size and coverage-based curves (Hsieh et al. 2016). Relative abundance percentage (No. of individuals of a species/Density of species * 100) for each species and location is presented in a bubble plot generated with the R package "ggplot2" (Wickham et al. 2007, R Core Team 2022). Indicator species and species fidelity to each river (i.e., probability of finding the species at each location of the study area) were identified using the function multipatt from the R package "indicspecies" (De Cáceres & Legendre 2009, R Core Team 2022) with 999 random permutations.

https://doi.org/10.1590/1676-0611-BN-2023-1481

Table 2. List of species from Río La Pasión (LP) and Río San Pedro (SP) recorded by different studies, including their classification by salinity tolerance and the most updated IUCN Red List Status. The list indicates the endemic species to the country (‡) and non-native species (*). Data from Valdez-Moreno includes only data collected in their study, including connected tributaries (i.e., Río La Pasión includes data from Río El Subin).

No.	Taxon	Classification	IUCN red list category	This study 2019	Willink et al. 2000	Valdez-Moreno et al. 2005	Barrientos et al. 2018	Elías et al. 2020	GBIF, FishNet2	Collection code
	Order Lepisosteiformes									
	Family Lepisosteidae									
1	*Atractosteus tropicus*	Sec	LC	LP, SP	SP		LP, SP	LP, SP	LP, SP	FMNH, LSUMZ, UMMZ
	Order Clupeiformes									
	Family Clupeidae									
2	*Dorosoma anale*	Per	LC	LP, SP	SP				LP	UMMZ
3	*Dorosoma petenense*	Per	LC	LP, SP	SP	LP, SP	LP	LP	LP, SP	ECOSUR, FMNH, LSUMZ, UF, UMMZ
	Order Cypriniformes									
	Family Cyprinidae									
4	*Cyprinus carpio**	Pri					LP		LP	LSUMZ
	Family Xenocyprinidae									
5	*Ctenopharyngodon idella**	Pri		SP	SP		LP		SP	FMNH
	Family Catostomidae									
6	*Ictiobus meridionalis*	Pri	DD					LP, SP	LP	UMMZ
	Order Characiformes									
	Family Characidae									
7	*Astyanax aeneus*	Pri	LC	LP, SP	SP	LP, SP		LP, SP	LP, SP	ECOSUR, FMNH, LSUMZ, SNSD
8	*Astyanax baileyi* ‡	Pri	DD					LP		
9	*Astyanax dorioni* ‡	Pri	DD			LP		LP		
10	*Hyphessobrycon compressus*	Pri	LC	SP	SP	LP, SP		LP, SP	LP, SP	FMNH, SNSD, UMMZ
	Family Bryconidae									
11	*Brycon guatemalensis*	Pri	LC	LP, SP	SP	LP, SP	LP	LP, SP	LP, SP	FMNH, UMMZ
	Order Siluriformes									
	Family Lacantuniidae									
12	*Lacantunia enigmatica*	Pri	VU				LP	LP		ECOSUR
	Family Loricariidae*									
13	*Pterygoplichthys pardalis**	Pri					LP, SP			
14	*Pteygoplichthys disjunctivus**	Pri					LP, SP			
	Family Ariidae									
15	*Cathorops aguadulce*	Per	NE		SP		LP		LP, SP	FMNH, UMMZ
16	*Potamarius nelsoni*	Per	LC	LP, SP	SP		LP		LP, SP	FMNH, UF, UMMZ
17	*Potamarius usumacintae*	Per	DD	LP, SP					LP, SP	UMMZ
	Family Ictaluridae									
18	*Ictalurus furcatus*	Sec	LC		SP				LP, SP	FMNH, LSUMZ, UMMZ

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No.	Taxon	Classification	IUCN red list category	This study 2019	Willink et al. 2000	Valdez-Moreno et al. 2005	Barrientos et al. 2018	Elías et al. 2020	GBIF, FishNet2	Collection code
19	*Ictalurus meridionalis*	Sec	NE	LP, SP			LP	LP, SP	LP	UF, UMMZ
	Family Heptapteridae									
20	*Rhamdia guatemalensis*	Pri	LC	SP	SP	LP, SP	SP	LP, SP	LP, SP	ECOSUR, FMNH, LSUMZ, UMMZ
21	*Rhamdia laticauda*	Pri	LC					LP, SP	LP, SP	UMMZ
	Order Synbranchiformes									
	Family Synbranchidae									
22	*Ophisternon aenigmaticum*	Sec	LC	LP, SP		LP, SP		LP, SP	LP, SP	UMMZ
	Order Batrachoidiformes									
	Family Batrachoididae									
23	*Batrachoides goldmani*	Per	LC	LP, SP	SP	LP, SP			LP, SP	CUMV, FMNH, UF, UMMZ
	Order Gobiiformes									
	Family Eleotridae									
24	*Leptophilypnus guatemalensis*	Per	DD						LP	UMMZ
	Order Mugiliformes									
	Family Mugilidae									
25	*Mugil curema*	Per	LC		SP				SP	FMNH
	Order Cichliformes									
	Family Cichlidae									
26	*Chuco intermedium*	Sec	LC			LP		LP, SP	LP	ECOSUR, UMMZ
27	*Cincelichthys pearsei*	Sec	LC	LP, SP	SP	LP, SP	LP, SP	LP, SP	LP, SP	FMNH, LSUMZ, UMMZ
28	*Cribroheros robertsoni*	Sec	LC	LP, SP	SP		LP, SP	LP, SP	SP	FMNH
29	*Kihnichthys ufermanni*	Sec	DD	LP				LP	LP	FMNH
30	*Maskaheros argenteus*	Sec	LC	LP, SP			LP, SP	LP, SP	LP	UF, UMMZ
31	*Mayaheros urophthalmus*	Sec	LC	LP, SP		LP, SP	LP, SP	SP	SP	FMNH, UMMZ
32	*Oreochromis aureus**	Sec							LP	ECOSUR
	*Oreochromis spp.**	Sec		SP	SP	SP				
33	*Oscura heterospila*	Sec	DD	LP, SP	SP		LP, SP	LP, SP	LP, SP	FMNH, LSUMZ, UMMZ
34	*Parachromis managuensis**	Sec		LP			LP		LP	UF
35	*Parachromis multifasciatus*	Sec	NE	LP, SP			LP, SP	LP, SP	LP, SP	ECOSUR, FMNH, UMMZ
36	*Petenia splendida*	Sec	LC	LP, SP	SP	LP, SP	LP, SP	LP, SP	LP, SP	CAS, ECOSUR, FMNH, LSUMZ, UF, UMMZ
37	*Rheoheros lentiginosus*	Sec	LC	LP, SP	SP	LP, SP	LP, SP	LP, SP	LP, SP	FMNH, UMMZ

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No.	Taxon	Classification	IUCN red list category	This study 2019	Willink et al. 2000	Valdez-Moreno et al. 2005	Barrientos et al. 2018	Elías et al. 2020	GBIF, FishNet2	Collection code
38	*Rocio octofasciata*	Sec	LC	SP			LP, SP	LP, SP	LP, SP	FMNH, UMMZ
39	*Theraps irregularis*	Sec	LC			LP		LP	LP	SMNS, UMMZ
40	*Thorichthys helleri*	Sec	DD	LP, SP	SP	LP, SP	LP	LP, SP	LP, SP	FMNH, LSUMZ, UF, UMMZ
41	*Thorichthys meeki*	Sec	LC	LP, SP	SP	LP, SP	LP	LP, SP	LP, SP	ECOSUR, FMNH, UF, UMMZ
42	*Thorichthys pasionis*	Sec	LC	LP, SP	SP		LP	LP, SP	LP, SP	FMNH, LSUMZ, UMMZ
43	*Trichromis salvini*	Sec	LC	LP, SP		SP	LP, SP	LP, SP	LP, SP	FMNH, UF, UMMZ
44	*Vieja bifasciata*	Sec	DD	SP	SP		SP	LP, SP	LP, SP	FMNH, UMMZ
45	*Vieja melanurus*	Sec	NE	LP, SP	SP		LP	LP, SP	LP, SP	ECOSUR, FMNH, LSUMZ, UF, UMMZ
46	*Wajpamheros nourissati*	Sec	LC					LP	LP	UMMZ
	Order Atheriniformes									
	Family Atherinopsidae									
47	*Atherinella alvarezi*	Per	LC		SP	SP		LP, SP	LP, SP	FMNH, LSUMZ
48	*Atherinella cf. schultzi*	Per	DD		SP				LP, SP	
	Order Beloniformes									
	Family Hemiramphidae									
49	*Hyporhamphus mexicanus*	Per	DD	LP, SP				LP	LP	CUMV, UMMZ
	Family Belonidae									
50	*Strongylura hubbssi*	Per	LC	LP, SP	SP				LP, SP	AMNH, CUMV, FMNH, UMMZ
	Order Cyprinodontiformes									
	Family Rivulidae									
51	*Cynodonichthys tenuis*	Sec	DD					LP, SP	LP	UMMZ
	Family Poeciliidae									
52	*Belonesox belizanus*	Sec	LC	LP, SP	SP	LP, SP		LP, SP	LP, SP	ECOSUR, FMNH, UMMZ
53	*Carlhubbsia kidderi*	Sec	DD	LP, SP	SP			LP, SP	LP, SP	FMNH, LSUMZ, UMMZ

Continue...

...Continuation

No.	Taxon	Classification	IUCN red list category	This study 2019	Willink et al. 2000	Valdez-Moreno et al. 2005	Barrientos et al. 2018	Elías et al. 2020	GBIF, FishNet2	Collection code
54	*Gambusia sexradiata*	Sec	LC	LP, SP	SP	LP, SP		LP, SP	LP, SP	FMNH, LSUMZ, UMMZ, USNM
55	*Gambusia yucatana*	Sec	LC					LP, SP	LP	LSUMZ
56	*Phallichthys fairweatheri*	Sec	DD	LP, SP	SP			LP, SP	LP, SP	FMNH, UMMZ
57	*Poecilia mexicana*	Sec	LC	LP, SP	SP	LP, SP		LP, SP	LP, SP	FMNH, ECOSUR, UF, UMMZ, UVG
58	*Poecilia petenensis*	Sec	DD	SP	SP	SP		SP	LP, SP	FMNH, UMMZ
	Pseudoxiphophorus sp.	Sec								
59	*Pseudoxiphophorus bimaculatus*	Sec	LC		SP	LP, SP		LP, SP	LP	UMMZ
60	*Pseudoxiphophorus diremptus* ‡	Sec	VU					LP		
61	*Scolichthys iota* ‡	Sec	VU					LP		
62	*Xiphophorus alvarezi*	Sec	LC					LP		
63	*Xiphophorus helleri*	Sec	LC		SP	LP		LP, SP	LP	UMMZ
64	*Xiphophorus maculatus*	Sec	DD					LP, SP	LP	UMMZ
65	*Xiphophorus signum* ‡	Sec	VU					LP		
	Order Perciformes									
	Family Centropomidae									
66	*Centropomus undecimalis*	Per	LC	LP, SP			LP, SP			
	Family Gerreidae									
67	*Diapterus spp.*	Per							LP, SP	UMMZ
68	*Eugerres mexicanus*	Per	LC	LP, SP			LP, SP		LP, SP	FMNH, UMMZ
69	*Eugerres plumieri*	Per	LC						LP	LSUMZ
	Order Acanthuriformes									
	Family Sciaenidae									
70	*Aplodinotus grunniens*	Sec	LC	LP, SP	SP		LP, SP		LP, SP	FMNH, LSUMZ, UMMZ

Nonmetric multidimensional scaling (NMDS) ordination was used to identify community dissimilarities between the littoral zone in two rivers. The input data for this analysis included 18 locations from each river and abundance data from species collected with seine and castnet at each location. Gillnet data were excluded from this analysis because of its lower efficiency than seine and castnet. Both beach seine and castnet are active techniques that collected similar species. The NMDS was performed after "Hellinger" data transformation using the function decostand from the R package "vegan" (Oksanen et al. 2022), with "Bray-Curtis" dissimilarity distances, using two axes. Statistical testing of community dissimilarities was done with a multivariate analysis of permutational variance (PERMANOVA) using the "adonis2" test (permutations = 999, method = bray) from the R package vegan (Anderson 2001, Oksanen et al. 2022) after verifying homogeneity of dispersion in both rivers.

Maps were created using shapefiles for protected areas and basins from UNEP-WCMC, UICN (2022), and Lehner & Grill (2003).

Results

A total of 70 species from 25 families and 15 orders was identified in this study (Table 2). Five of these species are endemic to Guatemala, *Astyanax baileyi, A. dorioni, Pseudoxiphophorus diremptus, Scolichthys iota*, and *Xiphophorus signum.* Six species are non-native to the Usumacinta River, *Cyprinus carpio, Ctenopharyngodon idella, Pterygoplichthys pardalis, P. disjunctivus, Parachromis managuensis*, and *Oreochromis aureus*. Public databases yielded 1,013 records from 64 species and 22 families (See Data Availability). Sixty-percent of these records belong to Río La Pasión, and 32% belong to Río San Pedro. At least 10 species not reported in public databases were reported in

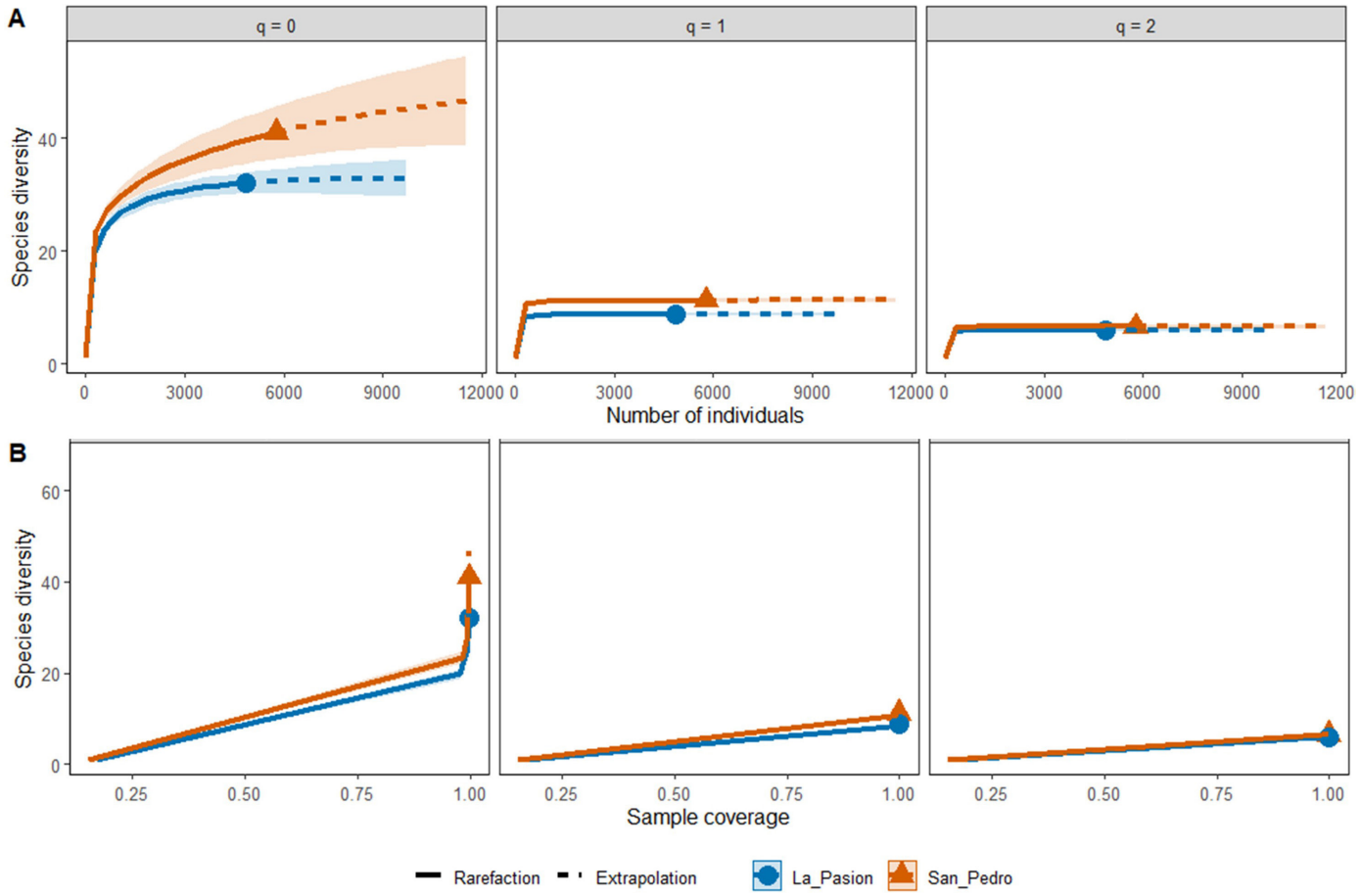

Figure 3. A. Sample-size-based diversity and **B.** coverage-based rarefaction and extrapolation curves for richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2) estimated for Río La Pasión and Río San Pedro. Shaded areas indicate 95 % confidence intervals.

Table 3. Richness and diversity index estimated through rarefaction and extrapolation curves using the R package "iNEXT" 3.0 (Hsieh et al. 2022, R Core Team 2022). Diversity analysis were done using individual-based abundance data, with 200 bootstrap replications and 95% confidence intervals.

	Río La Pasión			Río San Pedro		
	Observed	**Estimate**	**C.I**	**Observed**	**Estimate**	**C.I**
Richness	32	33	32–38.9	41	52	41–77.59
Shannon Diversity	8.78	8.8	8.54–9.07	11.22	11.27	10.95–11.59
Simpson Diversity	5.89	5.9	5.67–6.12	6.56	6.57	6.31–6.83

other studies (Barrientos et al. 2018, Elías et al. 2020). The 2019 survey yielded 10,937 fish specimens belonging to 42 species and 19 families. Including all records from previous studies and this study, the Río La Pasión had 69 fish species and the Río San Pedro had 56 fish species. The most species-rich families were Cichlidae and Poeciliidae, with 30% and 20% of the species, respectively. The two rivers share 78% of the species. Fourteen species (20%) are reported exclusively to Río La Pasión, including *Cyprinus carpio, Ictiobus meridionalis, Astyanax baileyi, A. dorioni, Lacantunia enigmatica, Leptophilypnus guatemalensis, Kihnichthys ufermanni, Parachromis managuensis, Theraps irregularis, Wajpamheros nourissati, Pseydoxiphophorus diremptus, Scholicththys iota, Xiphophorus alvarezi,* and *X. signum. Mugil curema* was reported exclusively from the Río San Pedro. Secondary freshwater species are widely distributed in the area, including 59% of reported species. Peripheral species comprise 22% of the species reported, and primary freshwater species comprised only 19% of the ichthyofauna. According to the most updated assessment of the IUCN Red List of Threatened Species, four species are classified as threatened under the category Vulnerable (Vu), including the Chiapas catfish *Lacantunia enigmatica* and the poeciliids *Pseudoxiphophorus diremptus, Scolichthys iota,* and *Xiphophorus signum.* Thirty-nine species are currently listed as Least Concern (LC), 16 species are Data Deficient (DD), and four species are Not evaluated (NE).

During the 2019 survey, eight species were captured only with the gillnet (Table S1); these included *Atractosteus tropicus*, *Brycon guatemalensis*, *Centropomus undecimalis*, *Ctenopharyngodon idella*, *Aplodinotus grunniens*, *Ictalurus meridionalis*, *Oreochromis* spp., and *Potamarius usumacintae*. The iNEXT sample-size-based diversity

Table 4. Indicator species and fidelity identified from fish surveys. Fidelity = 1 indicates that the species was present in all surveyed locations.

		Fidelity	Indicator value	p-value
	Río La Pasión			
1	*Pterygoplichthys* spp.	1	0.997	0.001
2	*Gambusia sexradiata*	1	0.89	0.001
3	*Maskheros argenteus*	0.61	0.78	0.001
4	*Ictalurus meridionalis*	0.61	0.73	0.015
5	*Potamarius usumacintae*	0.5	0.68	0.006
6	*Eugerres spp.*	0.5	0.65	0.016
	Río San Pedro			
1	*Thorichthys meeki*	1	0.96	0.001
2	*Oscura heterospila*	1	0.93	0.001
3	*Vieja melanura*	0.88	0.89	0.001
4	*Trichromis salvini*	0.88	0.84	0.003
5	*Atractosteus tropicus*	0.72	0.84	0.001
6	*Hyphessobricon compressus*	0.61	0.78	0.001
7	*Dorosoma anale*	0.61	0.76	0.002
8	*Brycon guatemalensis*	0.61	0.73	0.008
9	*Mayaheros urophthalmus*	0.44	0.62	0.017

curve indicates that species richness based on the multi-gear sampling was higher in the Río San Pedro (Figure 3A, Table 3). The estimated richness for Río La Pasión was 33 species, and the observed richness was 32 species. The expected richness estimated for Río San Pedro was 52 species, and the observed richness was 41 species. The Shannon Diversity index was slightly higher in Río San Pedro, and the Simpson diversity was similar in both rivers (Table 3). A high degree of completeness was observed in both rivers (Figure 3B). Indicator species varied between rivers. The armored catfish *Pterygopichthys* spp. and *Gambusia sexradiata* showed the highest indicator value for the Río La Pasión (Figure 2C, Table 4). The strongest indicator species for the Río San Pedro were *Thorichthys meeki* and *Oscura heterospila* (Figure 2F, Table 4). These indicator species were also the only ones present at all survey locations in their respective rivers (Table 4). Nine indicator species were found in the Río San Pedro and six in the Río La Pasión.

The relative abundance of most species differed significantly between the two rivers (Figure 4). The three most common species in the Río La Pasión were *Atherinella* spp., *Carlhubssia kidderi*, and *G. sexradiata*. In the Río San Pedro, the most common species were *Hyphessobrycon compressus, Thorichthys helleri,* and *Carlhubbsia kidderi. Hyphessobrycon compressus* was not recorded in the Río La

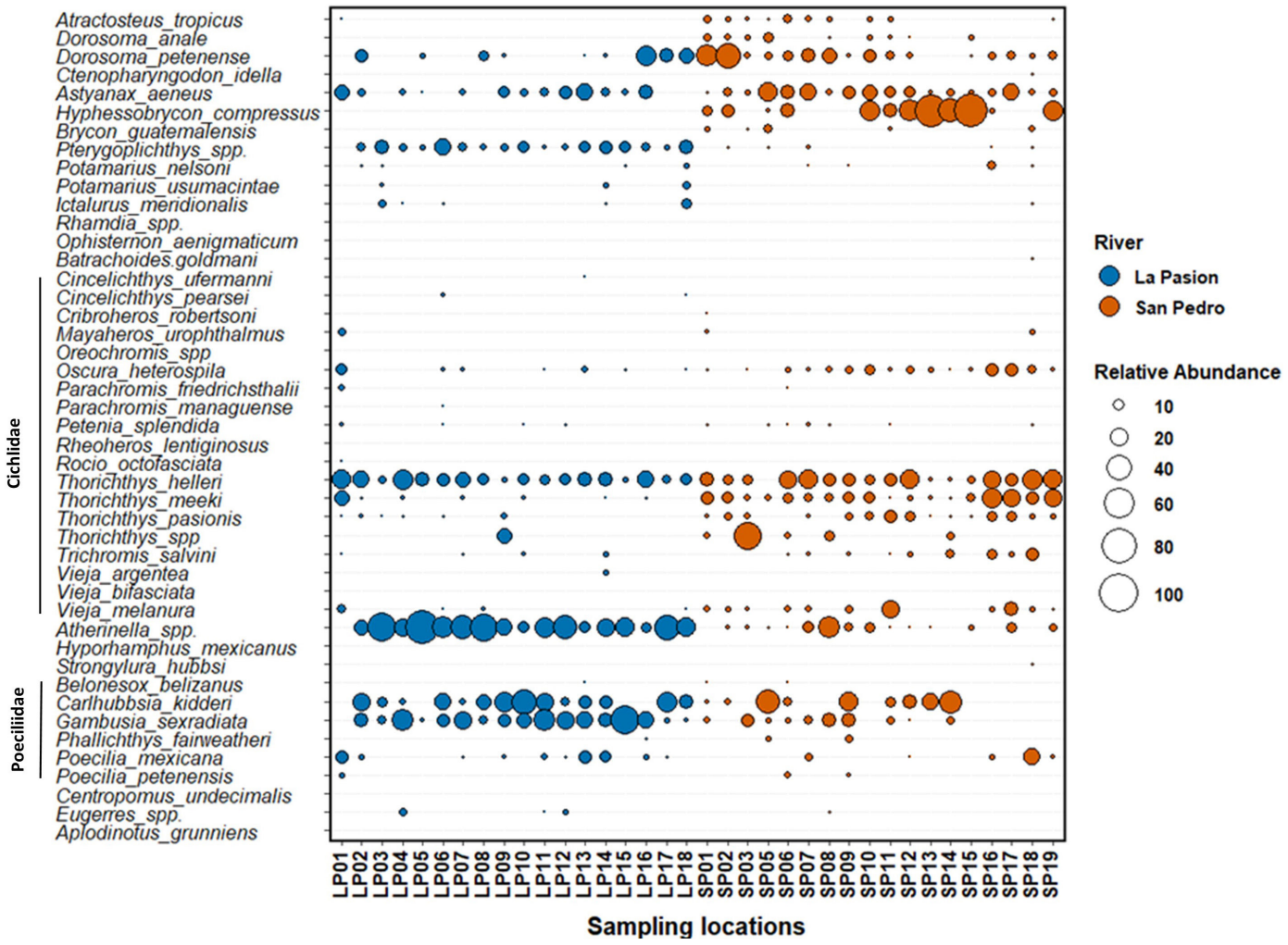

Figure 4. Relative abundance (%) of species recorded at each survey location.

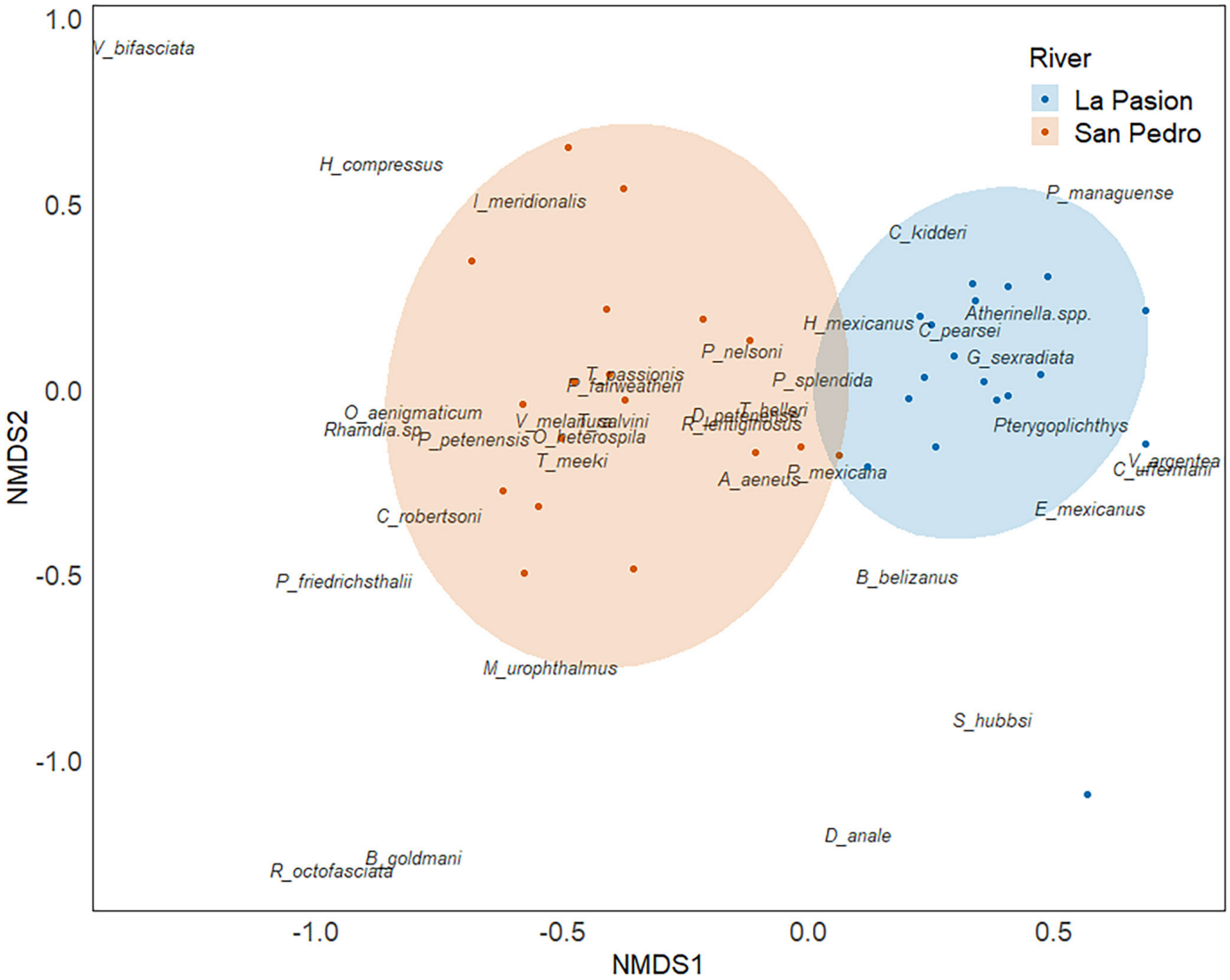

Figure 5. NMDS plot visualization for community abundance data collected in 18 locations in Río La Pasión, and 18 locations in Río San Pedro (Stress = 0.13).

Pasión during the surveys. Visual examination of the NMDS analysis and PERMANOVA showed that species composition in littoral areas significantly differs between rivers (stress = 0.13; $R^2 = 0.33$, $p = 0.001$) (Figure 5).

Discussion

This study provides an updated checklist with 69 species reported from the Río La Pasión and 56 species from the Río San Pedro, with a high percentage of shared species between rivers. This checklist surpasses the richness previously reported of 43 and 51 species, respectively, for each river (Valdez-Moreno et al. 2005). The fish assemblage in La Pasión and San Pedro rivers is mainly composed of secondary freshwater fishes (59%) from the families Cichlidae and Poecilidae, which are the most species-rich families with numerous endemic species for the Usumacinta region (Miller 1966, Matamoros et al. 2015). Peripheral and primary fishes comprise a lower portion of the checklist, as previously reported in the Usumacinta River basin (Valdez-Moreno et al. 2005, Barrientos et al. 2018), following the ichthyofauna composition expected for Central America. It has been hypothesized that primary freshwater fishes dispersed into the region more recently and have less diversification and dispersion compared to secondary freshwater fishes that arrived in the early Cenozoic (Myers 1966). However, a more recent proposed hypothesis based on the discovery of the relictually endemic catfish *Lacantunia* (Rodiles-Hernandez et al. 2005) suggests that primary fishes in this region were more diverse that currently known, but these species went extinct before the closure of the Panamian Isthmus (Elías et al. 2022). The increase in richness reported in this checklist is likely associated with three main factors. First, several species added are considered rare, based on the number of historical records and data collected in this study and increased research efforts and diversification of fishing methods in recent years (e.g., Barrientos et al. 2018) have improved the detection of rare species. Second, historically, surveys were more sporadic and biased to a few locations. In the last ten years, research along the basin has increased, and reporting on public databases (Heberling et al. 2021) and

scientific publications has improved. Lastly, more non-native species have been reported in both river basins (Elías et al. 2022).

Among the rare species added to this checklist are *Astyanax bailey, Lacantunia enigmatica, Leptophylypnus guatemalensis, Wajpamheros nourissati, Parachromis multifasciatum, Xiphophorus alvarezi, Gambusia yucatana, Diatperus* spp., and *Eugerres plumieri.* These species are only represented by a few specimens in museum records, particularly in the Río La Pasión, where the highest proportion of endemic species occur (Kihn-Pineda et al. 2006, Elías et al. 2020). This river has complex hydrology (Marshall 2007, Demarest et al. 2014) that needs more exploration, and increased research efforts in the area have enhanced our understating of species distribution. For example, the eleotrid *L. guatemalensis* restricted to the upper La Pasión, was previously documented in Río San Ramon and Río Ixcán and was recently reported to Río Lacantún (Espinosa-Pérez et al. 2014). Species with low reporting, like the pelagic *Potamarius usumacintae*, *Ictalurus meridionalis,* and the benthopelagic *Oreochromis aureus* are common in fish markets (personal observation) but are rarely collected with fishing methods commonly used in fish surveys. Some species still need taxonomic verification to confirm their distribution in the area. For example, *Atherinella schultzi* is common in coastal zones of the lower Grijalva-Usumacinta and Río Coatzacoalcos in México (Miller et al. 2005, GBIF.org 2022), although a few reports exist in upper Usumacinta. The non-native *Cyprinus carpio, Parachromis managuensis, Pterygoplichthys pardalis,* and *P. disjunctivus,* although reported in the Mexican portion of the Usumacinta more than 20 years ago (Armador-del-Ángel and Wakida-Kusonoki 2014) were only documented in La Pasión and San Pedro River recently (Elías et al. 2022).

The survey from 2019, which includes 60% of the species in the checklist, indicates differences in fish assemblage composition with unique dominant species for each river. A higher richness was expected in the Río San Pedro, with a slight difference in the Simpson index between rivers. Similar to other community studies (e.g., Magurran & Henderson 2003), only a few species were abundant and broadly distributed (i.e., *Astyanax aeneus* and *Thorichthys helleri*). This pattern could be associated with spatial and local environmental variation not considered here. Two cichlids, *Thorichthys meeki* and *Oscura heterospila* had the highest indicator and fidelity values for the Río San Pedro. The mosquito fish *G. sexradiata* and the invasive loricariid *Pterygoplichthys* spp. are the indicator species for the Río La Pasión. The armored catfish *Pterygoplichthys* spp. have become widely distributed in the Usumacinta Basin (Wakida-Kusunoki et al. 2007, Wakida Kusunoki et al. 2008, Escalera-Vázquez et al. 2019, Gaitán et al. 2020, Elías et al. 2022); however, it is noteworthy that during this survey they were rarely found in the Río San Pedro (Quintana et al. 2023) and its relevance in Río La Pasión is cause of concern. This study shows diversity patterns of common littoral species from the main canals, with a low representation of seasonal-migratory or rare species. Most migratory species reported to the Usumacinta River (see Soria-Barreto et al. 2019) were not collected in this study (*Mugil curema, Megalops atlanticus, Centropomus poeyi,* and *Joturus pichardi*) and their addition to the checklist would increase total richness to 73 species. Fish assemblage composition in fast-flow deep canal rivers like the Río San Pedro and Río La Pasión is strongly affected by seasonal environmental changes (e.g., Winemiller 1990, 1996, Galacatos et al. 2004, Freitas et al. 2018), therefore, surveys along the year would be necessary better to document the fish assemblage in the area (Winemiller 1983).

All species classified as Vulnerable are considered rare and were not collected during the 2019 survey. Among the Vulnerable species, *P. diremptus, S. iota,* and *X. signum* are endemic to Guatemala and are classified under Category Two (In Danger) by the National Endangered Species List (CONAP 2021). These species have restricted distribution in Río La Pasión, Alta Verapaz, where the abstraction of surface water, expansion of palm oil plantations, urban development, and expansion of agriculture represent the main threats to aquatic ecosystems (IUCN 2023). *Lacantunia enigmatica* is also classified as Vulnerable but is not included in the National Endangered Species List. *Lacantunia* is distributed in Río La Pasión and Río Lacantún in México (Rodiles-Hernández et al. 2005, Quintana et al. 2019), where the main threats are habitat fragmentation due to dam constructions and unregulated fishing (IUCN 2023). Other endemic species restricted to a few locations along the Río La Pasión in Alta Verapaz (see *A. baileyi* and *A. dorioni*, *L. guatemalensis*, and *C. tenui*) are potentially at high risk of extinction due to rapid environmental degradation in the area (e.g., see Camacho-Valdez et al. 2022). Most species in this checklist are classified under the Least Concern category, following the pattern found for Central America (Contreras-MacBeath et al. 2022); however, some species could be at risk on a local scale. The current population trend is unknown for most species, and monitoring is lacking in the region. Among the Data Deficient species, several cichlids and catfishes are commonly targeted by artisanal and subsistence fisheries (Barrientos et al., 2018). The fisheries in Río La Pasión and Río San Pedro have significant socioeconomic importance; however, fishing regulations are rarely enforced (Gandin 2012, Barrientos et al. 2018). An international snook (*Centropomus* spp.) angling tournament has been held in the La Pasión River since 2017, creating temporary jobs for local communities. Snook are among the most valuable fishes in the Usumacinta Basin, and intense fishing has impacted stocks in most regions (Perera-García et al. 2011). Periodic-like species such as snook (i.e., long-lived species with relatively low demographic resilience; Winemiller 2005) can be severely impacted by unregulated fishing at the local scale. Simmilar to snook, *Atractosteus tropicus* and ariid catfishes are particularly vulnerable to overfishing.

This updated checklist advances our understanding of the ichthyofauna of the Usumacinta Basin in Guatemala. The Río San Pedro and Río La Pasión are highly threatened by intense anthropogenic activities, including the rapid increase of African palm monoculture and unregulated fisheries (Mifsut & Castro 2010, Gandin 2012, Vaca et al. 2019, Camacho-Valdez et al. 2020, 2022, Ferat et al. 2020). A massive fish kill documented in 2015 in the Río La Pasión caused an estimated loss of 40-70 MT of the fish biomass. Although the primary source of the fish kill was not specified, it likely was due to agrochemicals and/or aquatic hypoxia (Ixquiac 2016). Moreover, the rapid increase of non-native species introductions in both rivers is cause for concern (Gaitán et al. 2020, Elías et al. 2022). The proliferation of *Pterygoplichthys* spp. in the La Pasión River is of particular concern since it can alter river ecosystem processes and displace native species (Capps et al. 2015, Quintana et al. 2023).

Given the relatively high incidences of species endemism, the Río San Pedro and Río La Pasión are critical for fish conservation. These rivers are among Central America's 50 priority regions for biodiversity conservation (Calderón et al. 2004). Despite the coverage of Protected Areas within these two sub-basins, most of the management focus has been on terrestrial biota and largely neglects the need for aquatic

ecosystem conservation. Conservation efforts focused on aquatic ecosystems and biodiversity are urgently needed to protect these unique rivers that harbor some of the richest fish fauna in Guatemala and several endemic species in the Mesoamerican region.

Supplementary Material

The following online material is available for this article:

Table S1 - Gear selectivity for species found during the 2019 survey.

Figure S1 - Map of Protected Areas coverage across Río San Pedro sub-basin and Río La Pasión sub-basin.

Acknowledgments

The author thanks the Russell E. Train Education for Nature Fellowship (award # RH31)-World Wildlife Fund, the Faculty For the Future Fellowship-Schlumberger Foundation, the American Association of University Women-International Fellowship (award # 2020-21), The Rufford Foundation (award # 26506-1), and the Tom Slick Fellowship – Texas A&M, for the financial support, and for the logistical support to the Estación Biológica las Guacamayas, Autoridad para el Manejo y Desarrollo Sostenible de la Cuenca del Lago Petén Itzá, Consejo Nacional de Áreas Protegidas-Sayaxché, Centro Universitario de Zacapa-USAC, and Escuela de Biología and Centro de Estudios del Mar y Acuicultura from the Universidad de San Carlos de Guatemala. Special thanks to K.O. Winemiller, Diego Elías, Josh Perkin, William Rogers, and Jacquelyn Grace for comments to improve the manuscript. Thanks to Diego J. Elías for designing the maps for this study. Thanks to Ben Fry for suggested edits. Thanks to Marlon Córdoba, Diego Juárez, César Fuentes, Francis Santos, and local fishers for assistance during field and laboratory work.

Associate Editor

Rosana Mazzoni

Conflicts of Interest

The author declares that there is no conflict of interest related to the publication of this manuscript.

Data Availability

The datasets analyzed during the current study are available at https://doi.org/10.18738/T8/SSVWQC.

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Received: 22/03/2023
Accepted: 19/03/2024
Published online: 07/06/2024