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Freshwater Fishes of Central America: Distribution, Assessment, and Major Threats

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Abstract: Central America contains a rich diversity of freshwater habitats that support more than 600 species of freshwater fishes. However, despite several perceived threats to the integrity of the freshwater habitats throughout the region, a formal analysis of extinction risk for the region's ichthyofauna is lacking. In this manuscript, we report an updated checklist of species and a novel comprehensive assessment of the conservation status of Central American freshwater fishes by applying the IUCN Red List Categories and Criteria to species at the global level. We also analyze the distribution of freshwater fishes across Central America and generate baseline geospatial data that can be used in multi-species conservation planning processes, which is available through the Red List Website. Our results indicate that between 15 and 28% of freshwater fishes in the region are threatened with extinction, with considerable uncertainty resulting from elevated data deficiency. We identify major and widespread threats in the region, including pollution, agriculture, aquaculture, biological resource use, natural system modifications, invasive species, and land development. This analysis represents an important first step in formulating effective conservation planning and action initiatives for a taxonomic group that historically has received few protections and can be used to inform conservation priorities of freshwater ecosystems at both national and regional scales.

Keywords: freshwater fishes; Central America; threats; red list; conservation

1. Introduction

The political boundaries of Central America lie within the geographic space between Mexico in North America and Colombia in South America (Figure 1). The land surface area of the Central American region is 522,402 km^2 and is shared among seven countries: Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. The Central American region possesses more than 6000 km of coastline, with a relatively even distribution of coastline on the eastern and western margins [1,2]. Additionally, it is worth noting that there is a stark difference in the proportion of surface area covered by river basins that drain into the Caribbean (61%) and Pacific (39%) versants [1,3].

The Central American region has a long-shared and complex geological history with the Caribbean and the Greater Antilles through land movements during the Paleocene, Eocene, and Miocene [4,5]. The final closure of the Panamanian isthmus in southern Central America created a land bridge that connected North and South America [4]. This complex geographic area (i.e., Central America) has played an important role in the evolution of the American continent's biodiversity.

Several physiographic and geologic characteristics within the region have contributed to patterns of diversification and the creation of different habitats throughout Central America [6]. The region contains 15 physiographic provinces from the Yucatan platform in the north, southward to the Darien isthmus. All of these areas are influenced by the presence of complex mountain and plains systems, the most notable of which include the Volcanic Cordillera in Guatemala and El Salvador, the Chortis Highlands of Honduras, the Nicaraguan Depression in Nicaragua, the Talamanca Cordillera of Costa Rica and Panama, and the Central Cordillera and Panama Canal Zone in Panama [4,7].

Central America is characterized by a mixture of climatic regions, including tropical savannah, tropical monsoon, tropical rainforest, tropical highland dry, and tropical highland wet [4]. The climate is largely defined by ocean currents and complex orography, along with altitude and other physiographic constraints. Precipitation is a major factor in the region's climate and varies widely across the region, with dry areas that receive less than 500 mm of annual rainfall, located north of the Volcanic Cordillera, and the very humid areas in western Guatemala, southeast Nicaragua, and central Costa Rica, which receive over 6000 mm of annual rainfall [8,9]. Despite this, a major classification indicates that tropical dry forests are found mostly over the Pacific versant, while tropical moist forests are more frequent over the Caribbean versant [4,8]. The average temperature in Central America ranges from 5 °C to 27 °C.

Central America has several important lotic freshwater systems, and many of them are shared among two or more countries (Figure 1). Among the main river systems draining to the Pacific Coast are the María Linda River in Guatemala, the Lempa River shared among Guatemala, El Salvador, and Honduras, and the Tempisque and Térraba Rivers in Costa Rica. Major Caribbean coast drainages include the Hondo River shared among Guatemala, Belize, and Mexico; the Mopan River shared between Guatemala and Belize; the Cahabón and Polochic Rivers in Guatemala; the Motagua River shared between Guatemala and Honduras; the Aguán, Patuca, and Ulúa rivers in Honduras; the Coco, shared among Nicaragua and Honduras; the Escondido and Grande de Matagalpa rivers in Nicaragua; the San Juan River shared between Nicaragua and Costa Rica; and the Sixaola River shared among Costa Rica and Panama. Two rivers drain into the Gulf of Mexico: the Grijalva River, which shares its headwaters with Guatemala and Mexico, and the Usumacinta River, the largest river basin in the region, which is shared among Belize, Guatemala, and Mexico. The region also possesses several lentic ecosystems, the largest of which are lakes Nicaragua (Cocibolca) and Managua in Nicaragua, Atitlán, Izabal, and Petén Itzá in Guatemala, Coatepeque, and Ilopango in El Salvador, Yojoa, in Honduras, Arenal in Costa Rica, and Bayano and Gatún in Panamá [7,8]. Moreover, there are several smaller lakes, ponds, and lagoons across the region.

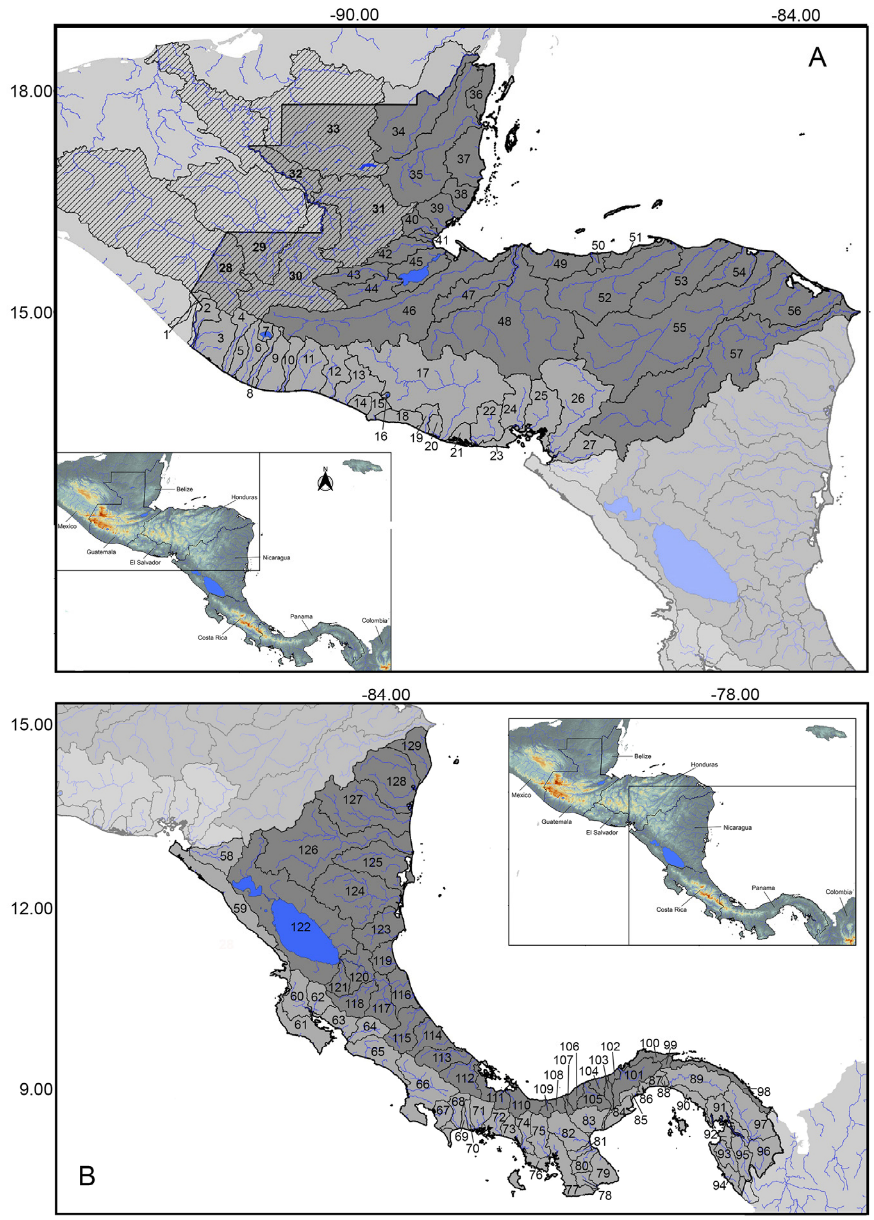

Figure 1. Major River basins across Central America. (**A**) River basins in northern Central America. Pacific Coast (light-gray-shaded basins): (1) Coatán (GT, MX), (2) Suchiate (GT, MX), (3) Ocosito-Naranjo (GT), (4) Samalá (GT), (5) Sis-Icán (GT), (6) Nahualate (GT), (7) Lago de Atitlán (GT), (8) Madre Vieja (GT), (9) Coyolate (GT), (10) Achiguate (GT), (11) María Linda (GT), (12) Los Esclavos (GT), (13) Paz (GT, SV), (14) Cara Sucia (SV), (15) Grande de Sonsonate (SV), (16) Lago Coatepeque (SV), (17) Lempa (GT, SV, HN), (18) Mandinga-Comalapa (SV), (19) Jiboa (SV), (20) Estero Jaltepeque, (21) Jiquilisco Bay (SV), (22) Grande de San Miguel (SV), (23) Sirama (SV), (24) Goascaran (SV, HN), (25) Nacaome (HN), (26) Choluteca (HN, NC), (27) Negro (HN, NC); Gulf of Mexico (dashed basins):

(28) Alto Grijalva (GT, MX), (29) Lacantún* (GT, MX), (30) Chixoy* (GT, MX), (31) La Pasión* (GT, BZ), (32) Usumacinta main channel* (GT, MX), (33) San Pedro—Candelaria* (GT, MX); Atlantic Coast (darker-gray-shaded basins): (34) Hondo (GT, BZ, MX), (35) Mopán (GT, BZ), (36) north Belize (BZ), (37) central Belize (BZ), (38) Monkey (BZ), (39) Grande (BZ), (40) Moho (BZ), (41) Temash (BZ, GT), (42) Sarstún (GT, BZ), (43) Cahabón (GT), (44) Polochic (GT), (45) Lago de Izabal (GT), (46) Motagua (GT, HN), (47) Chamalecón (HN), (48) Ulúa (HN), (49) Leán (HN), (50) Cangrejal (HN), (51) Lis Lis (HN), (52) Aguán (HN), (53) Sico Tinto (HN), (54) Cangrejal, (55) Patuca (HN), (56) Warunta (HN), (57) Coco (HN, NC). (**B**) River basins in southern Central America. Pacific Coast (light-gray-shaded basins): (58) Estero Real (NC), (59) Pacific of Nicaragua (NC), (60) Tempisque (CR), (61) Nicoya Peninsula, (62) Bebedero (CR), (63) Barranca (CR), (64) Tárcoles (CR), (65) Pirrís (CR), (66) Térraba (CR), (67) Coto (CR, PN), (68) Chiriquí Viejo (PN), (69) Escarrea (PN), (70) Chico (PN), (71) Chiriquí (PN), (72) Fonseca (PN), (73) San Félix (PN), (74) Tabasará (PN), (75) San Pablo (PN), (76) Caté (PN), (77) San Pedro—Quebro (PN), (78) Tonosí (PN), (79) Guarare (PN), (80) La Villa (PN), (81) Parita (PN), (82) Santa Maria (PN), (83) Grande (PN), (84) Chame (PN), (85) Caimito (PN), (86) Matasnillo (PN), (87) Juan Diaz (PN), (88) Pacora (PN), (89) Bayano (PN), (90) Chimán (PN), (91) Sabanas (PN), (92) Marea (PN), (93) Sambú (PN), (94) Jaqué (PN), (95) Tucutí, (96) Tuira (PN), (97) Chucunaque (PN); Atlantic Coast (darker-gray-shaded basins): (98) Cartí (PN), (99) Mandinga (PN), (100) Cuango (PN), (101) Chagres (PN), (102) Lagarto (PN), (103) Indio (PN), (104) Platanal—Miguel de la Borda (PN), (105) Cocle del Norte (PN), (106) Belén (PN), (107) Veraguas (PN), (108) Concepción (PN), (109) Calovébora (PN), (110) Cricamola (PN), (111) Guariviara (PN), (112) Changuinola (PN, CR), (113) Sixaola (CR, PN), (114) Matina (CR), (115) Parismina (CR), (116) Tortuguero (CR, NC), (117) Sarapiquí (CR, NC), (118) San Carlos (CR), (119) Indio Maiz (NC), (120) San Juan (CR, NC), (121) Frío (CR, NC), (122) Lago de Nicaragua (NC, CR), (123) Blue Fields-Punta Gorda (NC), (124) Escondido (NC), (125) Kurinwas—Laguna Perlas (NC), (126) Grande de Matagalpa (NC), (127) Prinzapolka (NC), (128) Wawa—Kukulaya (NC), (129) Ulang (NC). * denotes river sub-basins that are part of the Usumacinta River drainage. Guatemala (GT), Belize (BZ), El Salvador (SV), Honduras (HN), Nicaragua (NC), Costa Rica (CR), and Panama (PN). River sub-basins boundaries and river network follow [10,11].

It has been hypothesized that the complex geological history of the region and biogeographic barriers, coupled with climatic shifts during the last glacial maximum, have played important roles in shaping present-day biodiversity patterns in Central America [6,9,12–14]. This is the case for freshwater organisms such as ostracods, crustaceans, other aquatic invertebrates, and vertebrates such as amphibians [15–21], but also fishes [22–27].

Central America holds a great diversity of species and is recognized within the world biodiversity hotspots [28]; moreover, two countries (Guatemala and Costa Rica) have been included in the group of like-minded megadiverse countries [29]. Notably, this region possesses an unique biota and habitats that are under several threats. These threats need to be considered when performing conservation assessments and developing recommendations in the region, particularly for the conservation and management of its unique freshwater fauna, including its fish assemblages. This is particularly true in the Anthropocene, which is characterized by an unparalleled human impact on the global environment, leading to dramatic declines in biodiversity and potentially the first mass extinction event attributable to a single species [30]. Nowhere is the biodiversity crisis more acute than in freshwater ecosystems [31,32]. Even though freshwater habitats cover less than 1% of the planet's surface, freshwater ecosystems support 11% of all animal species, including approximately half of the world's known fish diversity, and 5% of all plant species [33]. In addition, they provide critically important global ecosystem services that contribute to human welfare and livelihoods [34].

A global study documented five major threats for freshwater biodiversity, including overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species [35]. However, in most of these (very inclusive) analyses, the nature of particular issues found in geographically limited regions, such as Central America, are often overlooked. If we are to bend the curve and change the current trending loss in freshwater biodiversity [32], we must have sound scientific knowledge of the direct threats affecting freshwater biodiversity in different regions, and this knowledge must be used to inform effective conservation planning and in applying suitable conservation actions [36]. This study represents a major advance of the Global Freshwater Fish Assessment, an initiative that the IUCN's Freshwater Biodiversity Unit, in partnership with the Species Survival Commission (SSC), has been carrying out for the past 20 years. Our analysis includes the assessment of 227 previously Not Evaluated species and represents the first comprehensive assessment on the conservation status of 602 freshwater fish species native to Central America. As with other national and regional assessments [37–39], we expect that our work will serve as a baseline and key resource for local and regional governments, nongovernmental agencies, and researchers to catalyze fish and freshwater ecosystem conservation in the region.

2. Materials and Methods

2.1. Species Selection

For the assessment, we produced an updated list of the freshwater fishes of Central America based on the technical definition of a freshwater fish developed by the IUCN SSC Freshwater Fish Specialist Group, specifically "Freshwater fishes are species that live all, or a critical part of their lives in either freshwater inland or brackish estuaries." We started with the work of Reis et al. [40], which listed about 450 nominal taxa, complementing previous revisions, as cited above, updating our knowledge on the diversity of the region, and highlighting the need for more revisionary and integrative studies. More recent studies, published at the regional scale and focused on the biogeographical component, have provided comprehensive lists of the Central American fish fauna (mainly of the obligate freshwater taxa), or at least a significant portion of it. Among them, it is worth mentioning the contributions of Smith et al. [41], who listed a total of 170 species in 72 genera and 23 families for the area of lower Central America (i.e., Costa Rica and Panama); Matamoros et al. [42], who listed a total of 76 species in 35 genera and 10 families for the area of nuclear Middle America (Honduras, El Salvador, and Nicaragua); and Matamoros et al. [24], who listed a total of 525 species in 146 genera and 37 families for the entire region.

The species list was finalized by a group of experts actively working in the region during the assessment peer-review process, which occurred at the ABQ BioPark from 3 to 7 February 2020. Species were removed from the assessment process if (1) the species was identified as taxonomically invalid, (2) the species fell within the remit of a separate Red List Authority, or (3) the species was identified as non-native to the region. As a result of this analysis, 622 freshwater fish species were listed for Central America, which could be divided into 230 genera, 79 families, and 31 orders; of these, 103 species (16.5%) were primary freshwater (strict freshwater species), 188 species (30.2%) were secondary freshwater (fishes that have minimal tolerance to salinity, as in brackish waters), and 331 species (53.2%) were peripheral (freshwater fishes very tolerant to salinity, or marine species that spend part of their life in freshwaters).

2.2. Distribution Mapping

Distribution maps are an important and required component of Red List assessments and can be used to inform priority sites or regions that are included within the range of at-risk species or groups of species. Using ArcGis 10.8 software [43], all species distributions were mapped to river and lake sub-basins as delineated by HydroBASINS [44], a globally standardized framework that delineates freshwater hydrological catchments at 12 resolutions and includes important information on hydrological connectivity. Delineation of species distributions to sub-basin scales is an established standard that has clear benefits for freshwater species conservation, given they represent well-defined and ecologically relevant management units.

Species distributions typically utilize HydroBASINS Level 08. However, species were mapped to finer-scale sub-basins to represent species distributions (HydroBASINS Level 12) more accurately when spatial data were available at sufficiently high detail or in cases of narrowly distributed endemic species. Preliminary distribution maps were digitized and reviewed to identify and rectify errors and dubious point localities.

When data were available, we used point localities (the latitude and longitude for a species collection event) to identify sub-basins known to contain a species. Georeferenced data were based on museum records from all major curated collections, mainly accessed through the Global Biodiversity Information Facility (GBIF), supplemented by expert experience and unpublished datasets. Additionally, when the occurrence of species in sub-basins for which their presence was not confirmed by any point localities, but was recorded in adjacent hydrologically connected sub-basins, we included those sub-basins as part of what we considered "inferred distributions." These inferred distributions relied on a combination of expert experience, inference of coarse-scale connectivity (e.g., HydroBASINS Level 06), and unpublished records that supported any potential distribution for those species.

2.3. Assessment of Extinction Risk

Species extinction risk was assessed according to the IUCN Red List Categories and Criteria: Version 3.1 at the global scale [45]. The IUCN Red List of Threatened Species is the world's most comprehensive information source on the global conservation status of plant, animal, and fungi, and is widely used to help inform conservation priority setting.

The IUCN Red List Categories and Criteria rely on five primary criteria with quantitative thresholds relating to biologically and ecologically relevant indicators of relative extinction risk. For a detailed explanation of the criteria that must be met for a species to be assessed under each category, please refer to the IUCN Red List Categories and Criteria: Version 3.1. Based on the quantitative thresholds and available data, we assigned one of the eight IUCN Red List categories [36]: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), and data deficient (DD), of which CR, EN, and VU are the threatened categories.

Reporting the proportion of threatened species in a taxonomic group requires consideration of species that fall into the data deficient category, as sometimes groups that are data-poor have a large proportion assigned to this category. Therefore, the reported percentage of threatened species for each group is presented as a best estimate that lies within a range of plausible values bounded by upper and lower estimates:

- Lower estimate = % threatened extant species if all DD species are not threatened, i.e., (CR + EN + VU)/(total assessed—EX);
- Best estimate = % threatened extant species if DD species are equally threatened as data-sufficient species, i.e., (CR + EN + VU)/(total assessed—EX—DD);
- Upper estimate = % threatened extant species if all DD species are threatened, i.e., (CR + EN + VU + DD)/(total assessed—EX).

2.4. Classification of Threats

For this study, the major threats affecting each species were coded using the IUCN Threats Classification Scheme [36]. Major threats were categorized into several threat bins that included pollution, agriculture and aquaculture, biological resource use, natural systems modifications, invasive and other problematic species and diseases, residential and commercial development, energy production and mining, transportation and service corridors, climate change and severe weather, and human intrusions and disturbance.

3. Results

3.1. Diversity and Distribution

The Central American freshwater ichthyofauna includes 622 species from 230 genera, 79 families, and 39 orders reported up until 2020, with 107 species that are endemic to a single country and 193 species endemic to the region. The overall checklist includes 103 primary fishes (17%), 188 secondary fishes (30%), and 331 peripheral fishes (53%). These numbers are reflected clearly in Figure 2, where it is evident that coastal areas have the highest species richness, due to the dominance of peripheral and secondary fishes. This is also evident in areas of Panama and Costa Rica, while highlands in Nicaragua, Honduras, El Salvador, and Guatemala generally exhibit lower species richness.

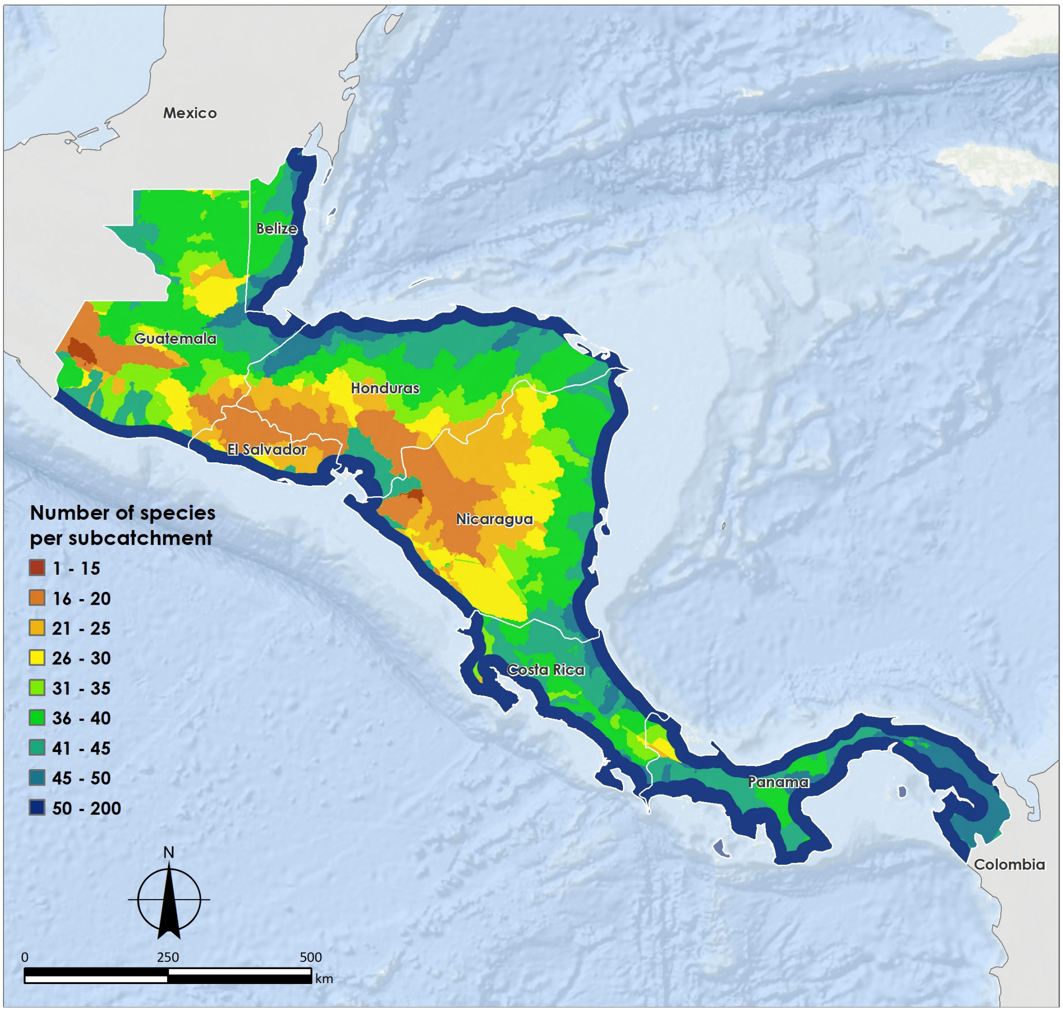

Figure 2. Species richness distribution map for Central American freshwater fishes. Dark blue represents highest richness areas.

Species endemism in Central America is mapped in Figure 3. In this map it is evident that the largest number of endemics are found in Panama, where there are 50 species that represent 24% of the total species. Panama is followed by Costa Rica and Nicaragua with 17 and 13 species, respectively.

3.2. Species Conservation Status

A total of 602 species (97% of the total checklist) have been assessed under the IUCN Red List criteria since 2005, with 68% (425 species) assessed within the last five years. A small proportion of the checklist (20 known species) remain Not Evaluated (NE), including 6 regional endemic species in Guatemala (3 species), Panama (2 species), and Belize (1 species). However, given a 96.8% coverage of freshwater fishes that occur in Central America, the results presented herein represent a robust analysis of extinction risk, and the region is considered comprehensively assessed.

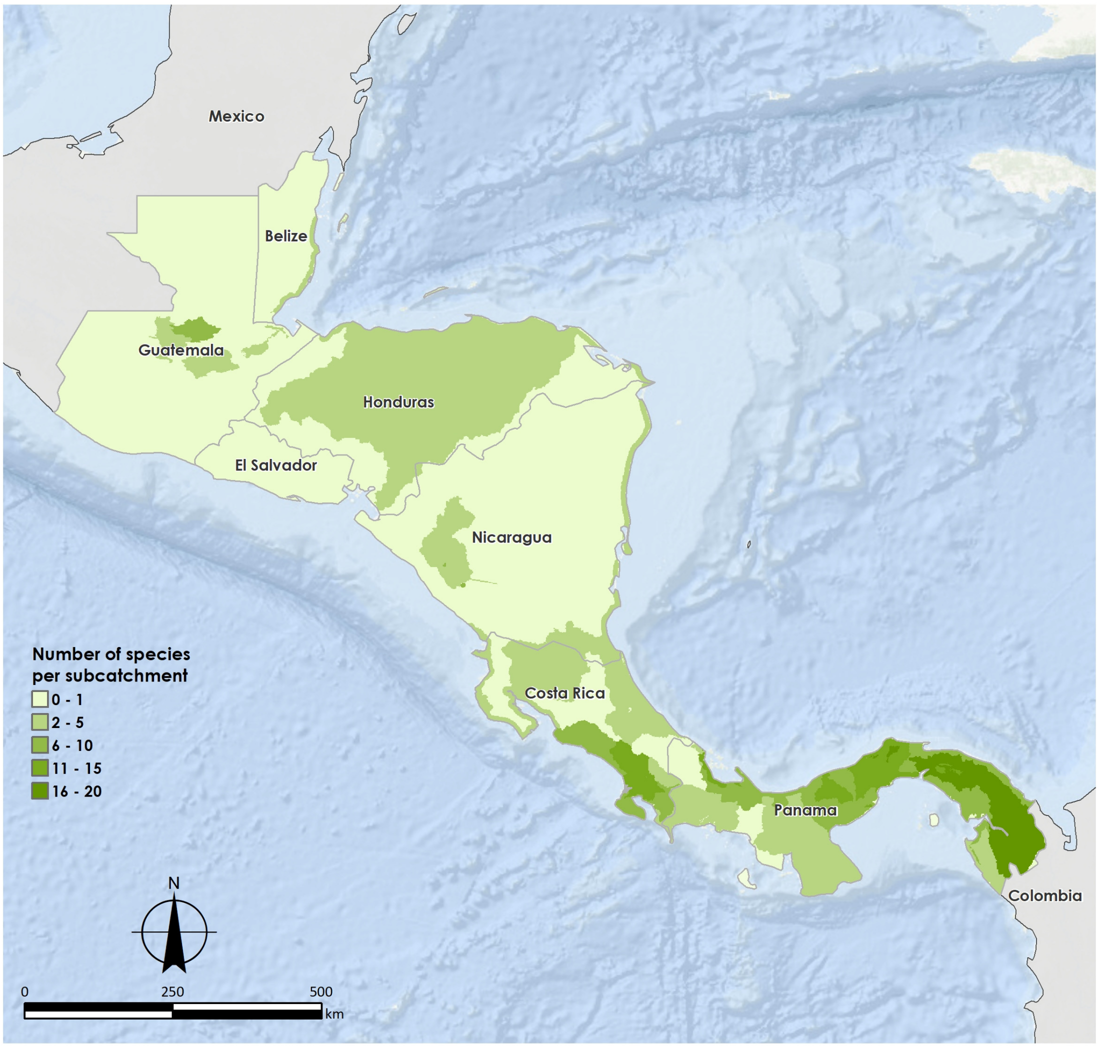

Figure 3. Endemic freshwater fish species richness distribution map for Central America. Dark green represents highest richness areas.

According to the assessment, in the most optimistic scenario (lower estimate), 91 species (15%) are considered "Threatened with extinction" (Supplementary Materials Table S1). The best estimate includes 18% of the species. If assuming all "Data Deficient" (DD) species are threatened (upper estimate), the percentage of species increases to 28%. Overall, 8% of the species are classified as "Vulnerable", 5% as "Endangered", and 2% as "Critically Endangered" (Table 1). Species that are classified as "Least Concern" (LC) represent 68% of the assessed species. Over 50% of the of 91 threatened species identified in this assessment are distributed between Costa Rica and Panama (Figure 4), with 51% being secondary species, 21% primary, and 16% peripheral. Most of the DD species are peripheral fishes, with the largest numbers (15–17) present in the Pacific region (Figure 5).

The 602 Central American freshwater fishes assessed include 31 orders and 79 families. The most diverse families are Cichlidae (80 spp.), Poeciliidae (70 spp.), Characidae (46 spp.), and Gobiidae (38 spp.). Threatened species were found in only 20 of the 79 fish families registered for Central American freshwaters, corresponding to 91 species. A total of 8 families comprise over 50% of the species classified as threatened, and the most numerous families have the most threatened species, including 28% of cichlids, 26% of poeciliids, and 37% of characids (Supplementary Materials Table S2).

Table 1. Central American freshwater fishes classified under the global IUCN Red List Category and Criteria methodology.

IUCN Red List Category	Number of Species	Number of Endemic Species
Critically Endangered	15	12
Endangered	29	16
Vulnerable	47	28
Near Threatened	24	6
Least Concern	409	15
Data Deficient	78	20
Extinct	0	0
Extinct in the wild	0	0
Not evaluated	20	6
Total species assessed	602	97

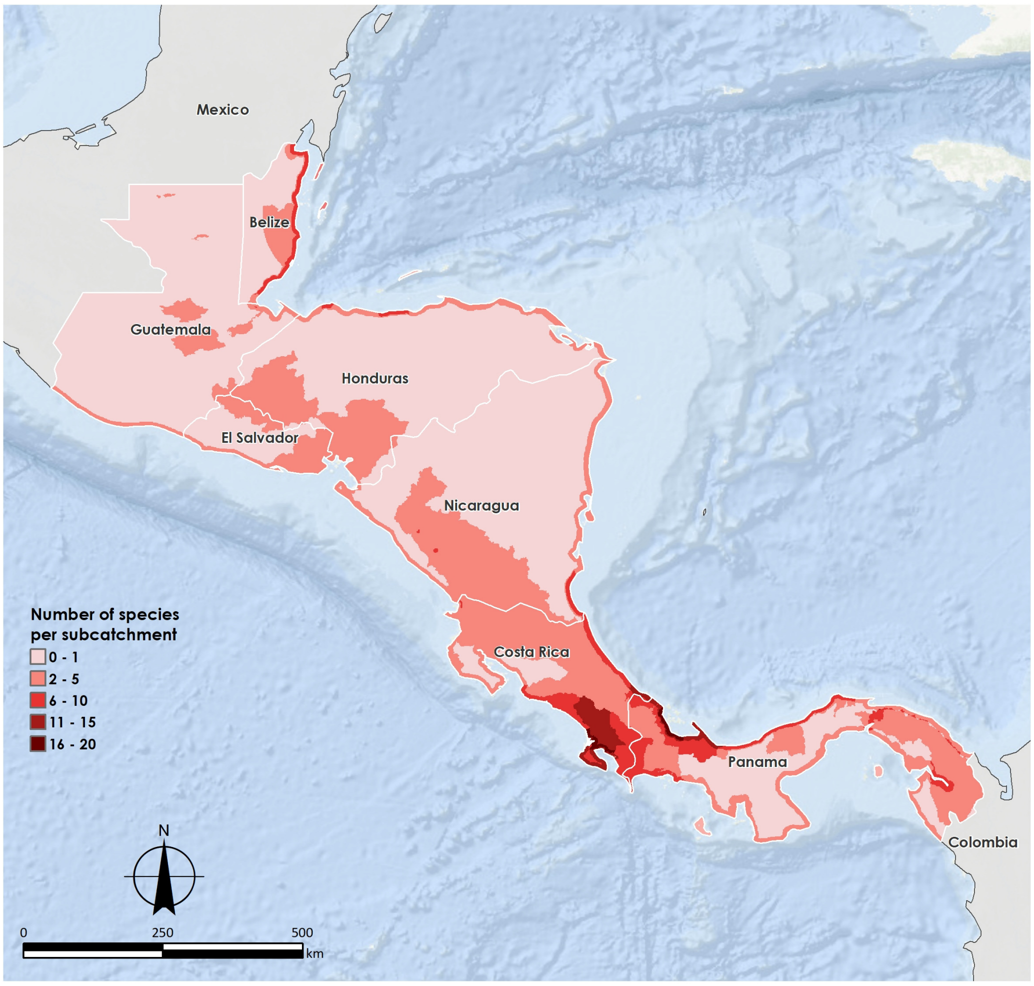

Figure 4. Threatened freshwater fish species richness distribution map for Central America. Dark red represents highest richness areas.

All species in the families Anguillidae (one species), Lacantunidae (one species), Megalopidae (one species), and Pristidae (two species) stand out by having 100% (five) of their species threatened. These include species such as *Pristis pectinata* and *P. pristis* that are predominantly marine but use freshwaters to reproduce (i.e., Lake Nicaragua) [46,47]. Families with approximately 50% of their species diversity that were categorized as threatened include Sphyrnidae (2 species), Serranidae (2 species), Profundulidae (6 species), and Rivulidae (19 species), with the latter having 52.6% (10) species threatened distributed in Central America. Within Rivulids, eight of the threatened species are considered endangered, and one species, *Cynodonichthys kuelpmanni*, is considered critically endangered. *Cynodonichthys kuelpmanni* is only known to be distributed at the type locality, the Cordillera Central, 20 km from Punta Peña, Bocas del Toro, Panama, where extensive agriculture and agrochemicals have severely altered the habitat of this watershed [48,49]. Families with approximately 30% of species threatened include Lebiasinidae, Cichlidae, and Characidae. Among the cichlids, six species are endemic to Lake Apoyo in Nicaragua, including *Amphilophus astorquii*, *A. chancho*, *A. flaveolus*, *A. globosus*, *A. zaliosus*, and *A. supercilius*, all of which are assessed as critically endangered due to the introduction of the piscivorous bigmouth sleeper (*Gobiomorus dormitor*) [50,51]. At least 9 families contain between 5% and 25% species classified as threatened, and species of 59 families are classified under data deficient, least concern, or near threatened.

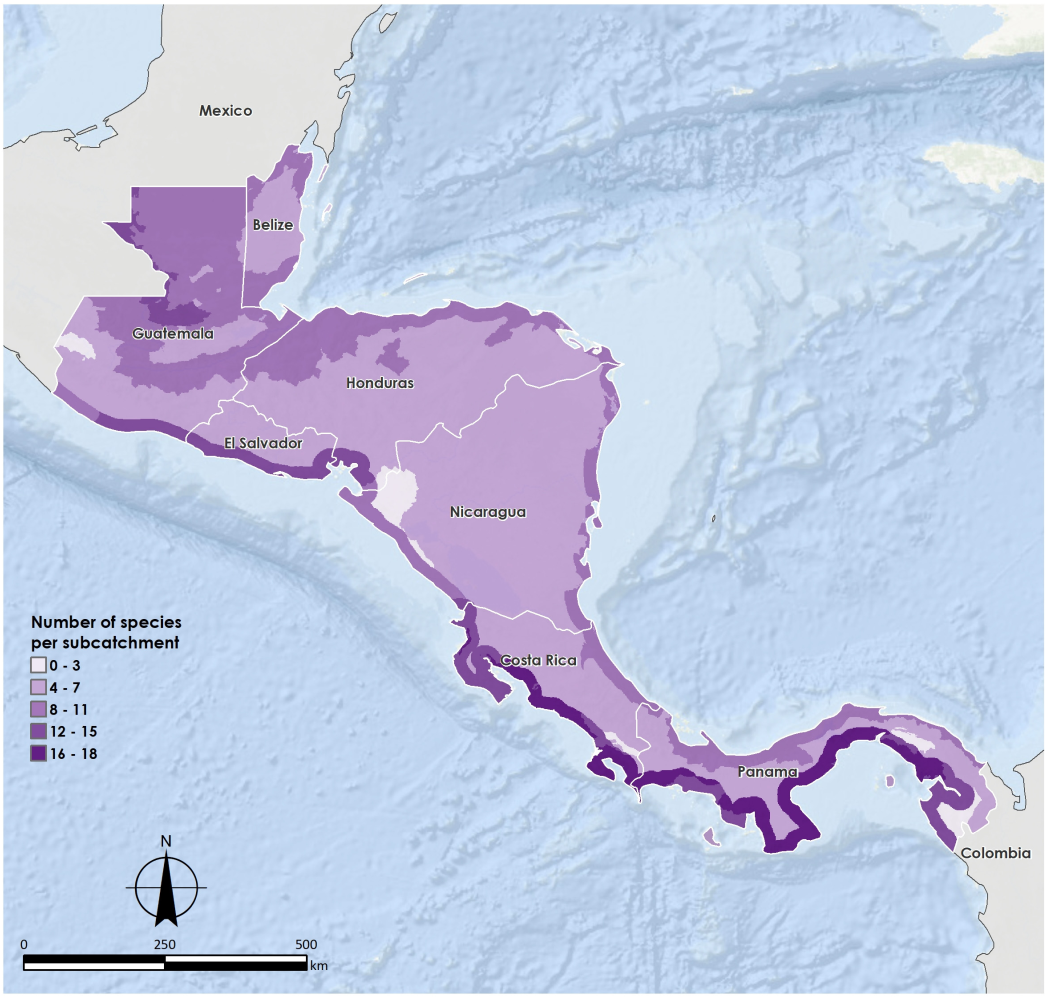

Figure 5. Data-deficient freshwater fish species richness distribution map for Central America. Dark purple represents highest richness areas.

Often, threatened species (e.g., *Poeciliopsis santaelena*, *Xiphophorus signum*, *Scolichthys iota*, *Astyanax kompi*) have only been known to be distributed in localities that are vulnerable aquatic habitats impacted by a suite of localized threats that include agricultural production of annual and perennial non-timber crops, mining and quarrying, droughts, dams and water management, and the introduction and establishment of invasive species, among others. In contrast, most of the diversity classified as peripheral (e.g., Clupeiformes, Beloniformes, Mugiliformes, Pleuronectiformes) is widely distributed across coastal habitats and is generally categorized as being at a very low risk of extinction, despite a relatively low number of species distributed in Central America for some groups.

3.3. Major Threats

The major threats impacting the Central American ichthyofauna are presented in Figure 6. Pollution was identified as one of the major threats for both species categorized as threatened (71.4%; Figure 2) and for all Central American freshwater fishes (44.5% Figure 2). The main sources of pollution in Central America are agricultural and forestry effluents, including livestock ranching, which affect 62.6% of threatened species and 32.6% of all species in the region. Domestic and urban wastewater affect 40.7% of threatened species and 26.4% of all species in the region. Industrial and military effluents affect 20.9% of threatened species and 22.3% of all species in the region. Particular species are threatened by mining activities affecting whole ecosystems (e.g., Lake Izabal) [52] and oil spills (e.g., Trans-Panama Oil Pipeline) [53]. Although 5% of all species in the region are reportedly threatened by garbage and solid waste, the true percentage might be higher for species inhabiting areas where urban and rural development is prevalent [54]. Additionally, research that focuses on microplastic pollution and other forms of solid waste pollution in freshwater fishes remains lacking in Central America [55–57], and new information will undoubtedly contribute to a better understanding of the impacts of these potential threats.

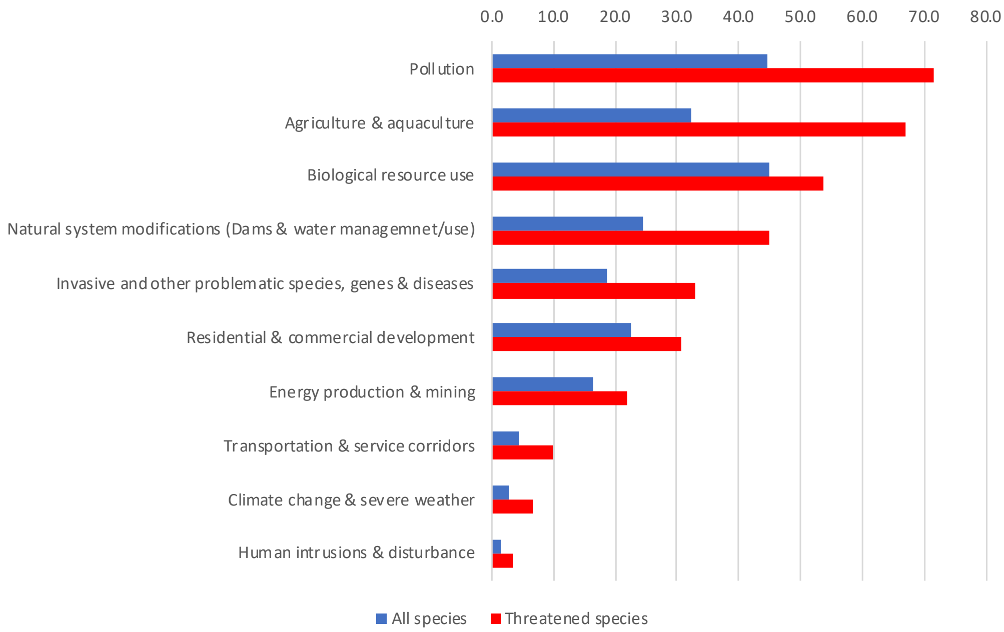

Figure 6. Major threats to freshwater fishes in Central America, with an emphasis on overall and threatened species.

Agriculture and aquaculture impact a substantial percentage of threatened species (67%) and a considerable percentage of all freshwater species in the region (32.4%). The main threat is agro-industry farming, which affects 57.1% of threatened species and 24.8% of all species in the region, followed by small-holder farming, affecting 13.2% of threatened species and 5.1% of all species in the region. Most impacts are directly related to the clearance of natural habitats for agricultural development, timber plantations, and cattle ranching [58], which also contributes to habitat degradation through pollution and losses in vegetative cover. Palm oil monocultures have increased considerably in the region, particularly in Guatemala, Honduras, and Costa Rica [59,60], and have contributed to increases in pollution, erosion, and water extraction.

Biological resource use or natural resource exploitation, including logging and wood harvesting, is a threat to more than half of threatened species (53.9%) and nearly half (45.0%) of all Central American freshwater fishes. Impacts associated with logging and wood harvesting are mostly related to clearings for agriculture, pastureland, and coastal development. These processes normally include a reduction in tree coverage, which leads to reduced dry-season flow rates [61], increased water temperatures [62], and overall declines in habitat quality and complexity. In this same category, fishing and harvesting of aquatic resources is a threat to approximately 54% of threatened species and 45% of all species in the region. Species that were identified as threatened by fishing are primarily broadly distributed and marine-associated species such as the cubera snapper (*Lutjanus cyanopterus*), American eel (*Anguilla rostrata*), or elasmobranchs such as the sawfishes (*Pristis* spp.) and the hammerhead shark (*Sphyrna lewini*). Most of these species are impacted by large-scale harvest, and only a few species are impacted by subsistence use.

Natural system modifications, mainly through dams and water management/use (e.g., agricultural diversion dams, hydroelectric power generation) affect nearly half of all threatened species (45.1%) and nearly a fourth of all Central American freshwater fishes (24.6%). Large dams that are utilized in the production of hydroelectric power were identified to affect 24.2% of threatened species and 7.6% of all species, mostly through the diversion of river flow and the obstruction of migration routes for species such as the mountain mullet (*Dajaus monticola*), bobo mullet (*Jotorus pichardi*), and machaca tetras (*Brycon costaricensis* and *B. guatemalensis*) [63], among others.

Finally, the threats posed by invasive alien species are among the most important, least controlled, and least reversible of human impacts on freshwater ecosystems [64]. In the present assessment, 33.0% of threatened species and 18.6% of all species in the region were identified to be impacted by non-native species (e.g., through direct predation or competition, food-chain disruption, ecosystem modification). The direct effects of invasive alien species are often unclear given the difficulty of studying biotic interactions in complex aquatic systems. However, the establishment of species such as the Nile tilapia (*Oreochromis niloticus*) and other related species, the armored catfishes (*Hypostomus* cf. *niceforoi* and *Pterygoplichthys pardalis*), largemouth bass (*Micropterus salmoides*), and common carp (*Cyprinus carpio*) is common in the Central American region, and the presence of these species can potentially affect local biodiversity and ecosystems in negative ways [65–69].

Information on the distribution of the Central American ichthyofauna at a fine scale is still lacking throughout most of the region. Furthermore, local, and regional studies that examine the effects of existing threats (e.g., microplastic, lack of wastewater management, non-native fishes) on freshwater ecosystems and their biodiversity are scarce [50]. However, some negative effects have been clearly observed. Scientific studies are urgently recommended even when undisturbed habitat might be unavailable for comparative analysis. The lack of knowledge regarding freshwater biology in Central America hinders our ability to make data-driven informed decisions regarding conservation and management of aquatic ecosystems in the region, including large-scale projects such as interoceanic canals as well as "smaller" water capture projects for irrigation or pond aquaculture. Laws regulating pollution remain active in all countries, but the extent to which they are successfully fulfilled and reinforced varies across countries [70].

4. Discussion

4.1. Comparison with Other Freshwater Fish Assessments

Our work adds 227 new freshwater fish species assessments, and to date 11,937 freshwater fish species have been assessed using IUCN Red List methodology [71], which represents 65.2% of about 18,290 valid species of freshwater fishes [72]. In order to compare our findings with global and regional trends, we analyzed the percentage of the Central American freshwater ichthyofauna across four IUCN categories (extinct and extinct in the wild; critically endangered, endangered, and vulnerable; near threatened and least concern; and data deficient) and contrasted our results with global data corresponding to 11,937 freshwater fish species evaluated by the IUCN Red List [71] and with other comprehensive assessments for different regions and countries [37–39] (Figure 7).

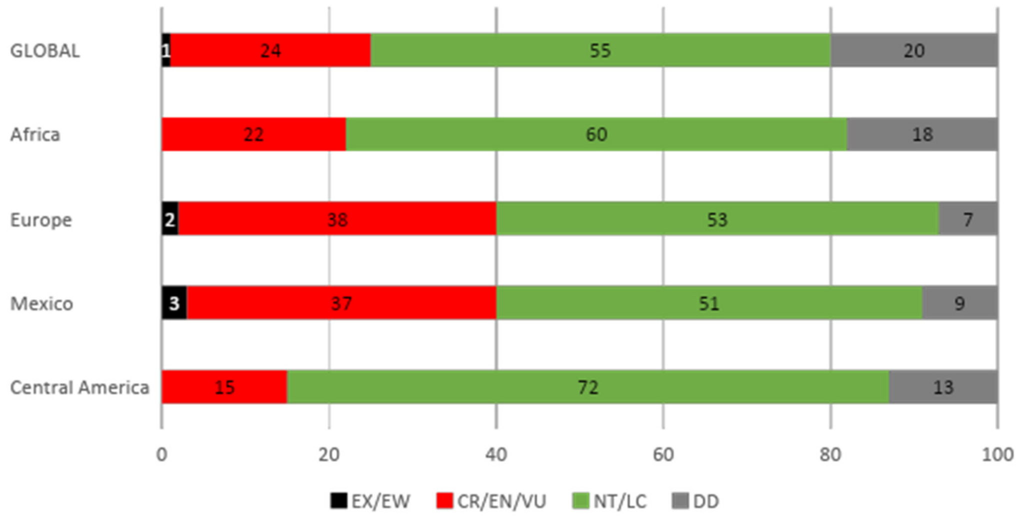

Figure 7. Percentage of freshwater fish species in four categories, globally, for selected regions, and for Central America (for global, see [71]; for Europe, see [37]; for Africa, see [38]; for Mexico, see [39]).

Compared to the extinction risk of freshwater fishes reported in neighboring countries (e.g., Mexico) or other regions (e.g., Africa) where IUCN assessments have been published (Figure 3), the Central American ichthyofauna is relatively well-preserved, as at least 72% of the species do not meet the threshold criteria for a threatened category, which is higher than the global estimate (55%) and regional estimates, particularly for Europe (53%) and Mexico (51%). We found 15% of Central American freshwater fishes to be threatened, which is 9% below the global estimate, and approximately 20% lower than the regional estimates in Europe and Mexico. It is important to highlight the lack of species that are considered extinct or extinct in the wild in Central America, compared to 3% and 2% of extinctions in Mexico and Europe, respectively. The percentage of data-deficient species in Central America is 7% below the global estimate and 5% below the African estimate. However, the percentage of species considered data-deficient in Central America (13%) is higher than those from Europe and Mexico with 7% and 9% of species categorized as data-deficient, respectively.

Peripheral species account for a large percentage of freshwater ichthyofaunal diversity in Central America (53%). Given that many of these species exhibit broad ranges, they generally exhibit a higher proportion of least concern species when compared to secondary and primary freshwater fishes. Therefore, their inclusion in our analysis may artificially lower the overall percentage of threatened freshwater fishes in the region, making comparisons with other regional assessments (e.g., Europe) difficult when the definition of a freshwater fish varies across studies. To test the impact that the inclusion of peripheral species had on our results, we carried out the same analysis presented above, but included only primary and secondary Central American fish species in our analysis. Results show that the proportion of threatened species (CR/EN/VU) increased from 14% to 26%, yielding a percentage that is closer to the global average threatened percentage for freshwater fishes (24%), but still 14% lower than the 38% of species occurring in Europe (Figure 7) that fall into a threatened category [37]. These data further support the perception that the Central American freshwater fish fauna is relatively well-preserved when compared to other regions where comprehensive analyses are available.

In response to the IUCN's Species Survival Commission's (SSC) interest in going beyond Red List Assessments by adopting an "Assess—Plan—Act cycle" and a goal that "every species that needs conservation attention is covered by an effective plan of action" [73], we briefly discuss the status of endemic species by country to highlight the need for endemic species conservation at the national level, according to Dunn et al. [74]. For example, *Poecilia teresae* is a threatened species endemic to Belize, and therefore effective conservation planning and action must include local actors at the national level.

Panamanian freshwater endemic fishes account for 24% of the total number of species recorded in the country (207 species). Among these endemic species, 18 are classified under a threatened category (9 VU, 5 EN, and 4 CR). Due to a lack of information, the extinction risk of 13 species could not be accurately assessed, and these are classified as DD. Nicaraguan endemic fish species include 7% of the total reported species in the country (196 species); of these species, 12 are classified under a threatened category (5 VU and 7 CR), accounting for 92% of the endemic species in the country. Costa Rican endemic species comprise 6.4% of the total species recorded for the country (264 species); among these endemic species, 88% are classified under a threatened category (9 VU and 6 CR), and only 2 species are classified as DD. Guatemala possesses 13 endemic species from three families: Poeciliidae (9 species), Cichlidae (2 species), and Characidae (2 species). These Guatemalan endemic freshwater fishes comprise 5% of the total number of species (249 species) recorded for the country. Eight of these species (*Poecilia rositae*, *Rocio spinosissima*, *Scolichthys iota*, *Xiphophorus signum*, *Pseudoxiphophorus attenuatus*, *P. cataractae*, *P. diremptus*, and the enigmatic cichlid *Amphilophus margaritifer*) are classified under a threatened category (4 VU, 3 EN, and 1 CR), representing 62% of the endemic species in the country. Four endemic species in Guatemala (*Astyanax baileyi*, *A. dorioni*, *Pseudoxiphophorus obliquus*, and *Scolichthys greenwayi*) are classified as DD, and the livebearer *Pseudoxiphophorus litoperas* is classified as least concern (LC). In Honduras (168 species), 4% of the freshwater fishes are endemic and 2 are classified as threatened, including the Mojarra Hondureña (*Chortiheros wesseli*) classified as VU and the Olomina de Ulúa (*Tlaloc portillorum*) classified as EN. In Honduras, there is one endemic species classified as DD (*Amphilophus hogaboomorum*). As discussed above, Belize contains one endemic species (*Poecilia teresae*), and it is considered EN due to land use change, deforestation, mining activities, and dams that have modified aquatic ecosystems where it occurs [75]. Finally, in El Salvador, none of 122 freshwater fish species reported for the country are endemic. For a spatial representation of endemism in Central America, see Figure 3.

4.2. Analysis of Major Threats

Several authors have carried out revisions of the major threats that impact freshwater biodiversity [35,76], which have helped to contextualize the current freshwater biodiversity crisis [32]. Although threats are classified in different categories, it is well-known that stressors act in synergy to impact freshwater species [64], but for practical purposes, these are discussed separately in the following sections.

4.2.1. Pollution

Pollution is the major stressor for threatened freshwater fish species in Central America, affecting an alarming 71.4% of species assessed as threatened (Figure 6). These findings are consistent with observed declines in water quality associated with anthropogenic activity over the past two centuries, with a notable increase in nutrient discharge in the 1960s and subsequent acceleration of eutrophication processes [77]. Both point and nonpoint sources of pollution are relevant issues affecting the quality of water bodies. Industrial and domestic sewage are subjected to minimal or no treatment prior to their discharge into natural waterways. Nonpoint agricultural runoff is an important contributor to increases in nutrients and persistent organic pollutants in rural areas.

Studies on the effects of pollution in Central American freshwater bodies are relatively scarce [78], but there is a limited body of information for some localities in Guatemala [52,79–81], El Salvador [82,83], Honduras [84,85], and Costa Rica [86,87]. Studies focusing specifically on the effects of pollutants on freshwater fishes are virtually nonexistent (but see Oliva-Hernández et al. [56], Ortiz et al. [57]). However, this small body of research provides insight into the pervasiveness of pollutants throughout the region, and in many cases, inferences can be drawn to conclude that widespread pollution is resulting in continuing declines in habitat quality.

Persistent organic pollutants, herbicides, insecticides, urban waste dumps, fecal matter, heavy metals, and emerging pollutants such as hormones and antibiotics are some of the substances which severely alter the quality of freshwater ecosystems [77]. Algal blooms are becoming more frequent due to the increase of nutrients (e.g., Lake Atitlán and Lake Amatitlán in Guatemala; Cerrón Grande reservoir in El Salvador) [77–79,88], and several ecosystems are undergoing eutrophication [89]. Every year, local communities report fish kills likely related to the sugarcane, banana, and palm oil industry in Guatemala [90] and Costa Rica [91,92]. These various sources of pollution, limitations in water treatment, and a lack of compliance in response to regulatory frameworks are prevalent throughout Central America [93–98].

The adverse effects of pollution on the health and behavior of freshwater fishes have been widely documented [99–101]. Pollution can lead to hypoxia and increased acidity, which in turn have been shown to negatively impact fish reproduction, hatchling survival, growth, immune systems, and in many cases result in mass mortality events. In natural systems, fishes are exposed to a suite of interacting pollutants which may amplify their negative effects on individual fitness [102].

Specific examples of species affected by pollutants in the region are provided in the published Red List assessments, such as *Rocio spinosissima*, an endangered cichlid endemic to the Polochic River and Lake Izabal drainage in the Atlantic slope of Alta Verapaz and Izabal in Guatemala [103]. Major pervasive threats to this species include industrial pollution associated with mining activities, agrochemicals, and urban discharges, as well as recreational and industrial development [52,104,105]. In the Sixaola River Basin, an international river basin on the Caribbean slope of Costa Rica and Panama, nine species (*Cynodonichthys rubripunctatus*, *Astyanax anai*, *Hyphessobrycon bussingi*, *Amatitlania kanna*, *A. myrnae*, *Cribroheros bussingi*, *C. rhytisma*, *Eretmobrycon gonzalezi*, *Phallichthys quadripunctatus*) are endangered due to widespread pesticide pollution and raw sewage discharge from rural areas [91]. In some cases, pesticide runoff has resulted in concentrations that cause extensive fish kills [92].

4.2.2. Agriculture and Aquaculture

Impacts from agriculture and aquaculture are related to other threats presented herein, since the expansion of agriculture leads to biological resource use, clearance of forests, and transformation of natural ecosystems into plantations or farming pools. Agriculture also contributes to pollution, mostly through pesticides, herbicides, fertilizers, and livestock manure that run off into water bodies. Aquaculture is oftentimes a source of propagules for non-native species, many of which have been introduced through both deliberate and accidental occurrences [106,107]. In Panama, species introduced for aquaculture purposes represent 64% of non-native species introductions [108].

The main threats to freshwater fish biodiversity categorized under "Biological resource use" are logging and wood harvesting as well as deforestation and forest degradation. Logging and wood harvesting are related to agricultural expansion. Some of the negative effects caused by agricultural expansion are the loss of water recharge and natural damping zones, increases in erosion and sedimentation rates [61,97], reduced dry-season flow rates [109], and declines in the availability and quality of suitable habitat.

Deforestation and forest degradation are considered some of the world's most pressing land change challenges [110]. Central America has experienced rapid deforestation during the last century, particularly between the 1960s and 1980s [111]. Although recent assessments suggest that some parts of the region are exhibiting ongoing forest recovery, this has been proven to vary across the seven countries comprising the region, with the least developed countries experiencing rapid deforestation and the most developed countries (Panama and Costa Rica) showing woody vegetation gain and more stable forest cover configuration [111].

Some examples of species affected by deforestation and land use change as a result of agricultural expansion and associated increases in sedimentation include *Tlaloc portillorum*

(EN), a species known to inhabit only the headwaters of the Ulúa and Nacaome River basins on the Atlantic and Pacific slopes of Honduras, respectively [112]; *Amphilophus lyonsi* (EN), which is restricted to the Pacific versant of southern Costa Rica and western Panama, occurring from the Coto to the Dupí River drainage [113,114]; eight species (*Cynodonichthys siegfriedi* EN, *Cynodonichthys uroflammeus* EN, *Pterobrycon myrnae* EN, *Poeciliopsis paucimaculata* EN, *Imparfinis lineatus* EN, *Pseudocheirodon terrabae* Vu, *Cribroheros altifrons* Vu, and *Eretmobrycon terrabensis* Vu) from the Térraba River drainage on the Pacific slope of southwestern Costa Rica [61,115,116]; and finally, *Priapichthys puetzi* (CR), which is known to inhabit two collection localities in the Guarumo River drainage in Bocas del Toro Province, Panama [117]. Also, agricultural expansion has had negative impacts to vegetation and water availability at Ramsar Site Complejo Barra de Santiago in Cara Sucia basin in El Salvador. The Cara Sucia basin is the only the watershed where *Atractosteus tropicus* (EN locally) is known to be present in El Salvador [118].

4.2.3. Biological Resource Use

Artisanal small-scale and subsistence fisheries in freshwaters are relatively common in Central America [119,120]. However, most fisheries lack sustainability assessment or proper management [121] (but see Quintana and Barrientos [120] and Quintana et al. [122]). Overfishing is commonly the first disturbance in the historical progression towards fisheries collapse, followed by or in tandem with other factors, such as pollution and eutrophication, mechanical habitat destruction, introduced species, and climate change. Evaluating the direct effects of fishing pressure on the health of a population can be difficult, given complex system responses and often the presence of interacting stressors. Despite these uncertainties, there is ample evidence that overfishing is a significant factor in the decline in numerous species populations [123].

Examples of species threatened by fisheries are largely limited to broadly distributed peripheral species that are included within well-studied and widespread single- or multi-species commercial fisheries [124], both as target species and as bycatch. Three of these species are elasmobranchs (assessed by Kyne et al. [125]) that utilize nearshore estuarine habitat, and therefore may be more vulnerable to fishing pressure when compared to their marine counterparts due to proximity to coastal human populations, limited volume, and relatively unstable physical chemistry [126]. Two of these three species are sawfish (*Pristis pristis* and *P. pectinata*), which, due to their rostrum, are easily entangled in nets and difficult to remove without mortality [127]. Once considered a separate species, the sawfish of Lake Nicaragua was abundant in the 1960s but has been considered critically endangered or even locally extinct since the early 1980s because of uncontrolled fishery pressure [125,128]. In Costa Rica, fishing pressure on secondary and peripheral species such as *Parachromis dovii*, *Parachromis managuensis*, *Joturus pichardi*, and *Atractosteus tropicus*, has resulted in population declines due to overfishing in recent years, to the point that temporary bans on harvest have been established for some species [129].

4.2.4. Dams and Other Natural System Modifications Relating to Water Management/Use

Dams have contributed significantly to human development in the recent past, and their derived benefit to society has been considerable. However, in many cases, an unacceptable and often unnecessary price has been paid to secure those benefits, especially in social and environmental terms, by displaced peoples, downstream communities, taxpayers, and the natural environment [130]. Currently, 77% of the total water discharge of the 139 largest river systems in the northern third of the world is strongly or moderately affected by fragmentation from dams, interbasin diversions, and irrigation withdrawal. Humans currently appropriate half of the estimated 40,700 km^3 of annual global runoff [131,132], resulting in severe impacts on the world's freshwater biota, which has contributed to the endangerment of several freshwater fishes globally.

Over the past 30 years, Central America has experienced a substantial increase in the number of dams constructed for hydroelectric power production, and many social and environmental impacts from these dams have been documented [133]. Currently, there are 187 operating dams in Central America dedicated to energy production, 34 under construction, and another 205 projected to be built in the coming years [133,134]. Several locally endemic and migratory species of freshwater fishes are threatened by damming infrastructure in Central America. Included in this list are *Poecilia teresae* (EN), from the Mountain Pine Ridge in Cayo, Belize; *Poecilia rositae* (EN), endemic to the Cahabón and Polochic drainages in Guatemala; several species of Poeciliids of the genera *Pseudoxiphophorus*, *Scolichthys*, and *Xiphophorus* endemic to the upper reaches of the Usumacinta River in northern Guatemala; and *Chortiheros wesseli* (VU), endemic to a limited number of rivers in the Papaloteca River drainage on the Atlantic slope of northern Honduras [135,136].

Anderson et al. [63] highlight that threats to freshwater ecosystems from dams and natural system modifications are not limited to the effects of mega-projects. The authors highlight the threats of a high number of hydroelectric generation projects across the region, which include river fragmentation, stream dewatering, and downstream hydrological alterations, as well as cumulative effects of multiple dams within a single river basin. For example, eight hydropower dams were built in the Sarapiquí River Basin during the 1990s, and an evaluation showed fragmentation and reduced downstream flow caused by these projects [137]. The effects of one dam in this system (Doña Julia Dam) were studied closely, showing that fish assemblages differed between sites directly above and below the dam, suggesting fragmentation, restriction of migratory fishes' movement, and an increasing domination of opportunistic fishes in the upper sections of the river [138]. The risks to freshwater organisms from the high number of hydroelectric power projects should be adequately assessed to determine the extent to which they affect movement between upstream and downstream reaches, particularly for migratory diadromous species, and to inform adaptive management strategies such as fish ladders, artificial side channels, or increased flow in diverted streams [139]. Alteration of species composition could substantially affect community structure and biotic interactions as well as ecosystem processes [63,137,138].

4.2.5. Invasive Species

Introductions of alien species are among the most important, least controlled, and least reversible of human impacts on the world's ecosystems, strongly affecting their biodiversity, biogeochemistry, and economic benefits. The impact has been such that Strayer [64] suggested that the Anthropocene is facilitating a new era in which all continents are connected as a "New Pangaea" through human activities.

There are no analyses of invasive fish introductions or establishment events for the whole of Central America. National checklists are scarce, except for Guatemala, where Elías et al. [69] published a synthesis of non-native fishes in that country, and Panama, where González [108] describes in detail the diversity, origin, and current status of the 15 invasive fish species present in Panamanian freshwaters. To obtain data on invasive fishes documented in the region, the Global Invasive Species Database (GISD) was utilized to generate a report on the occurrence of invasive freshwater fishes in the seven Central American countries, producing 50 records for 14 species [140]. Results from GISD were collated with occurrences of an additional 15 invasive species reported throughout the primary literature [108,121,141–148], resulting in a total of 29 invasive fish species reported in the region (Supplementary Materials Table S3).

The total number of non-native fish species found in Central American freshwaters (29 species) is relatively low when compared to other regions, such as Europe (195 species) [149] or countries such as Mexico (104–118 species) [39] and the United States (536 species, including several hybrids and translocated species) [150]. Panama and Costa Rica stand out, with 15 and 13 established non-native species [146], respectively. In Guatemala, 12 established non-native species have been reported [69]. Honduras contains eight established non-native species, Nicaragua contains five species, El Salvador contains four species, and Belize one.

African tilapias in the genus *Oreochromis* have been intentionally and unintentionally introduced in over 100 countries outside of their native ranges, and Central American countries [69,106,107], where at least four species (*Oreochromis aureus*, *O. mossambicus*, *O. niloticus*, and *Oreochromis* sp.) are widely established, are no exception. Establishment of these fishes as a protein source for rural communities is well-studied in Nicaragua, where Mckaye et al. [151] identified an early stage of the invasion and McCrary et al. [106] later documented how the species has become widely established and might be responsible for disease outbreaks in native cichlid populations. In the northern countries of Central America, Esselman et al. [107] have documented the expansion of tilapia at an initial establishing rate of 2 km per year followed by a rapid expansion of 30 km per year until the expansion slowed. Canonico et al. [67] reviews the effects of tilapia introduction on native diversity, but scientific studies in Central America are still lacking. Escape from aquaculture farms during floods is likely a primary dispersal mechanism for these species [106,107].

Another group of invasive species present in the region are Loricariids, also known as South American armored catfishes or plecos. Plecos from the genus *Pterygoplichthys* have been reported in El Savaldor (JEB Pers. Obs.), Belize [152], Honduras [153], Costa Rica [154], and Guatemala [121,155,156], where they are widely established. A second Loricariid genus, *Hypostomus*, has been reported in Guatemala [69], Nicaragua [143], and Costa Rica [146]. Moreover, another catfish species, the striped catfish or panga (*Pangasianodon hypophthalmus*), has been recently introduced in wetlands in the northern Caribbean of Costa Rica in a border area with Nicaragua [146]. Negative effects of plecos and the panga have been documented in other introduced regions and include extreme changes in water quality and nutrients [157] and severe reductions in native fish populations [158,159].

Few other invasive species have been scientifically studied in the region, and their impacts, establishment success, and rates of spread remain mostly unknown. The introduction of the predator *Cichla monoculus* in Lake Gatún in Panama has resulted in negative effects on native prey and subsequent disruptions within the food web [66,144], including changes in the trophic position of the native predator *Hoplias microlepis* through niche competition [160]. Cruz [161] documented the introduction of *Micropterus salmoides* into Yojoa Lake in Honduras and its subsequent depletion of native fauna, a scenario also reported for Lake Atitlan in Guatemala [66]. In both Honduras and Panama, these fishes were introduced in an attempt to boost the sport fishing experience, principally for foreigners living in these countries. More recently, Elías et al. [145] reported the presence of another South American non-native species, the Pacu, *Piaractus brachypomus*, in Lago Petén Itzá, Guatemala, but there is no evidence of its establishment. In Costa Rica, Angulo [154] also reported another species of Pacu (*Colossoma macropomum*) which was introduced for fishing purposes and to control populations of some exotic mollusks in culture ponds. However, in recent years, several observations have been reported, which suggests uncontrolled population growth and spread into non-targeted areas.

Invasive fish species have the potential to severely impact species in isolated water bodies, as is the case for Lake Xiloá in Nicaragua, where the introduction of tilapias (*Oreochromis* sp.) threatens five endemic species (*Atherinella jiloaensis* (CR), *Amphilophus viridis* (VU), *A. xiloaensis* (VU), *A. amarillo* (VU), and *A. sagittae* (VU) [106].

Translocations, or the movement of species among aquatic systems within the region, can be similarly detrimental, as is the case for the bigmouth sleeper (*Gobiomorus dormitor*), a predatory species which was introduced into the isolated Lake Apoyo on the Pacific slope of Nicaragua in 1991 by local fishermen. Predation by this species is the primary threat to an endemic flock of six cichlid species (*Amphilophus astorquii*, *A. chancho*, *A. flaveolus*, *A. globosus*, *A. zaliosus*, and *A. supercilius*) [51]. There is evidence that tilapias have also played a role in the *Amphilophus* flock threat status [50,51]. The jaguar cichlid, *Parachromis managuensis*, has been translocated into Lake Gatun in Panama [144], as well as in other body waters in Costa Rica [154], but there is no evidence of its impact. Some other species (e.g., *Atherinella chagresi*, *Megalops atlanticus*, and *Vieja maculicauda*) have managed to move through the Panama Canal, colonizing new environments and potentially causing alterations in local food webs [162]. It is important to highlight that translocations are poorly understood, and their impact on ecosystems and their species assemblages in Central America are not well-documented.

4.2.6. Residential and Commercial Development

As in many other regions, surface waters most affected by urban and industrial pollution in Central America are those located in or adjacent to highly populated and urbanized areas. Such is the case for the Tárcoles River Basin in Costa Rica, which represents only 4% of the country's territory but includes 60% of the population and 85% of industrial activity [163]. The same authors describe a similar situation in the Acelhuate River in the metropolitan area of San Salvador City in El Salvador and around Lake Amatitlán, an important part of the urban area of Guatemala City.

One example of extinction risk associated with residential and commercial development is that of the fin-joined goby (*Gobulus birdsongi*), a critically endangered mangrove-dependent species known to inhabit only one locality that contains two mangrove streams on the Pacific slope of the Panama Canal, with an area of occupancy that is estimated to be less than 10 km^2. This species is threatened by continued coastal development and removal of mangrove habitat and has not been observed in recent years [164].

4.2.7. Energy Production and Mining

Mining activities are a major source of pollutants that directly affect the quality of water, soil, and air, subsequently impacting livelihoods and biodiversity. Mining is a very important economic activity in Central America, with an average of 14% of land area subjected to mining concessions across Nicaragua, Honduras, and Guatemala, with the highest proportion of 31% being in Honduras [165]. In El Salvador minor illegal extraction is possible to occur. In general terms, gold (Au), silver (Ag), lead (Pb), and zinc (Zn) are the most commonly extracted. Iron (Fe), lead (Pb), mercury (Hg), cadmium (Cd), arsenic (As), and cyanide are the main contaminants associated with mining and refinery processes. The use of mercury (Hg) and arsenic (As) compounds in mining activities and the use of large amounts of water for shale oil exploitation are causing downstream pollution in soils and waters [166].

One example of a critically endangered species affected by mining activities in Central America is the Olomina *Cynodonichthys keulpmanni*, known to inhabit only its type locality at the foot of the Cordillera Central, near the town of Punta Peña in Bocas del Toro Province, Panama. Among other threats, extractive mining activities may affect subpopulations occurring within the Ngäbe-Buglé Comarca [167].

4.2.8. Transportation and Service Corridors

Historically, Central America has been viewed as a potential shipping corridor between the Atlantic and Pacific oceans, a link which would amount to significant economic value. The most successful of all attempts to connect these oceans is the Panama Canal, completed in 1914 and expanded in 2016.

Assessments in the Panama Canal have documented an interchange of faunas between the Pacific and Atlantic oceans [41]. The more recent Panama Canal expansion has also produced a higher number of marine species in Lake Gatun (R. González pers. comm., 2020). For the most part, these projects lack environmental impact evaluations properly addressing the potential consequences such man-made modifications might have on freshwater biodiversity and the connectivity of its waters. A study in Lake Bayano, Panama, reported that 5 years after the dam was built, freshwater species in the lake decreased by 79% [168].

In 2013, the Nicaraguan government also sought to complete an interoceanic connection project known as the Nicaraguan Canal. Multiple scientists have vocalized major concerns about the completion of the Nicaragua Canal without proper investigation into the project's impacts on native freshwater biodiversity [169–172]. Härer et al. [172] highlighted that the construction of the Nicaraguan Canal would join two drainages that have been historically separated and whose fish faunas differ substantially, threatening to promote biotic homogenization and the loss of diversity.

4.2.9. Climate Change and Severe Weather

Freshwater aquatic ecosystems are as vulnerable to global change as terrestrial and marine ecosystems [173]. In a global-scale assessment, Sala et al. [174] found both lentic and lotic ecosystems to be the most sensitive to land use change, exotic species, and climate change. In a study evaluating hydrological climate change projections for the 2050–2099 period, Hidalgo et al. [175] found median significant reductions in precipitation (as much as 5–10%) and runoff (as much as 10–30%) in northern Central America. Therefore, the prevalence of severe drought in this sub-region may increase significantly in the future under current climate change projections. They also concluded that northern Central America could warm as much as 3 °C during 2050–2099, and southern Central America could see a temperature increase as high as 4 °C during the same period, and that the projected dry pattern over Central America is consistent with a southward displacement of the Intertropical Convergence Zone (ITCZ).

Examples in Central America of freshwater fish species affected by climate change are scarce. The impacts of climate change in aquatic taxa in the region remain an open question, and species with restricted distributions are likely under serious threat. For example, climate change models predict that the suitable habitat for the microendemic cichlid *Chortiheros wesseli* in Honduras could decrease as a result of localized climate change driven by habitat modification [176]. Another species under risk is the Santa Elena livebearer (*Poeciliopsis santaelena*), a vulnerable species endemic to the Potrero Grande River within the Santa Elena Peninsula, on the northern Pacific coast of Costa Rica within the Pacific of Nicaragua basin (Fig. 1B). This species is restricted to a single threat-based location, given extreme drought conditions in recent years, which are likely to be exacerbated by climate change. This threat has the potential to drive this species to a higher threatened category in the immediate future, and complete desiccation of its habitat may result in extirpation [177].

5. Conclusions

This study represents an important contribution to the understanding of the number of freshwater fish species inhabiting the Central American isthmus (622), but also highlights that further research is still needed to better understand the status of the freshwater ichthyofauna the region. Although this is the first comprehensive analysis of the conservation status of Central American freshwater fishes, at least 20 species remain unassessed, and there are another 78 data-deficient species for which there is too little information to accurately assess their extinction risk. One key finding is that the percentage of threatened species is relatively lower than that found in other regions and countries previously evaluated. While this statistic is encouraging, it is important to note that there are 91 threatened species, 15 of which are critically endangered, and to our knowledge, there are no specific conservation actions in place to secure their persistence. It seems that governmental and NGO investment in freshwater conservation in the region is still in its infancy, and these funding sources remain focused primarily on terrestrial and marine ecosystems. Most existing conservation initiatives (e.g., laws, regulatory frameworks) are poorly enforced, and the primary threats continue to pervade or appear to be increasing in magnitude and scope. Additionally, there are several large megaprojects that have been projected for the region, including dams in several countries and the interoceanic Nicaraguan canal, which could have a severe deleterious impact on the fish fauna and other aquatic organisms in the region.

Our assessment provides critical baseline data on the direct threats to the freshwater ichthyofauna in the region and represents an important first step towards the formulation of effective conservation planning and action initiatives. One key result of this work is the formalization of a working group to advance the development of deliberate conservation activities, and thanks to this effort, we have also established alliances with international organizations with which we hope to develop a joint strategy for the conservation of the freshwater fishes of Central America.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14100793/s1, Table S1. Summary of Central American freshwater fishes' conservation status under IUCN Red List Categories: critically endangered (CR), endangered (EN), and vulnerable (VU). Tolerance to salinity is included as primary (Pri), secondary (Sec), and peripheral (Per). Countries of distribution and endemism are shown as Guatemala (G), Belize (B), El Salvador (EL), Honduras (H), Costa Rica (CoR), Nicaragua (N), and Panama (P). Table S2: Global IUCN Red List Status of Central American freshwater fishes by taxonomic family. Table S3. List of non-native species by country. Countries of distribution and endemism are shown as Guatemala (G), Belize (B), El Salvador (EL), Honduras (H), Costa Rica (CoR), Nicaragua (N), and Panama (P). * Denotes translocations.

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