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REVIEW PAPER

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Conservation threats and future prospects for the freshwater fishes of Ecuador: A hotspot of Neotropical fish diversity

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ABSTRACT

Freshwater fish communities in Ecuador exhibit some of the highest levels of diversity and endemism in the Neotropics. Unfortunately, aquatic ecosystems in the country are under serious threat and conditions are deteriorating. In 2018–19, the government of Ecuador sponsored a series of workshops to examine the conservation status of Ecuador's freshwater fishes. Concerns were identified for 35 species, most of which are native to the Amazon region, and overfishing of Amazonian pimelodid catfishes emerged as a major issue. However, much of the information needed to make decisions across fish groups and regions was not available, hindering the process and highlighting the need for a review of the conservation threats to Ecuador's freshwater fishes. Here, we review how the physical alteration of rivers, deforestation, wetland and floodplain degradation, agricultural and urban water pollution, mining, oil extraction, dams, overfishing, introduced species and climate change are affecting freshwater fishes in Ecuador. Although many of these factors affect fishes throughout the Neotropics, the lack of data on Ecuadorian fish communities is staggering and highlights the urgent need for more research. We also make recommendations, including the need for proper enforcement of existing environmental laws, restoration of degraded aquatic ecosystems, establishment of a national monitoring system for freshwater ecosystems, investment in research to fill gaps in knowledge, and encouragement of public engagement in citizen science and conservation efforts. Freshwater fishes are an important component of the cultural and biological legacy of the Ecuadorian people. Conserving them for future generations is critical.

KEYWORDS
biodiversity, conservation, Ecuador, endemism, freshwater fishes, Neotropics

1 | INTRODUCTION

Neotropical ecosystems are among the most biodiverse and ecologically important in the world. Few groups highlight the importance of the Neotropics more than the freshwater fishes. There are likely over 7000 species of freshwater fishes in South and Central America, which corresponds to approximately one in five fishes in the world or one in 10 vertebrates (Albert & Reis, 2011b). Freshwater fishes play crucial roles in their ecosystems, constitute important components of the historical and evolutionary legacy of the Neotropics, and are important sources of food and livelihoods for people (Albert & Reis, 2011a; Lo *et al*., 2020; Toussaint *et al*., 2016; van der Sleen & Albert, 2018). Unfortunately, Neotropical ecosystems are under serious threat, and knowledge of freshwater fishes and their conservation status lags behind that of other vertebrates (Anderson & Maldonado-Ocampo, 2011; Myers *et al*., 2000). Since freshwater fisheries typically generate only one tenth of the fisheries revenue compared to marine fishes, there is little economic incentive for governments to enforce conservation laws aimed at protecting them (FAO, 2018; Jiménez-Segura *et al*., 2016). The decline of Neotropical fishes disproportionally affects human populations in rural areas and indigenous people, which also makes it a social justice issue (Jiménez-Segura *et al*., 2016; Lo *et al*., 2020).

The threats that Neotropical fishes face have been increasingly recognized by ichthyologists and conservation biologists, resulting in several publications summarizing the vulnerable state of Neotropical fishes in different areas (Anderson & Maldonado-Ocampo, 2011; Jiménez-Segura *et al*., 2016; Lasso *et al*., 2015; Mojica *et al*., 2012; Pelicice *et al*., 2017; Reis *et al*., 2016). In 2018–19, *via* Acuerdo Ministerial 069, the government of Ecuador organized a series of workshops to generate national red lists of endangered species (Ministerio del Ambiente, 2019). The Freshwater Fishes Working Group reviewed 163 species and identified 35 species that were vulnerable, near threatened, endangered or critically endangered (Aguirre *et al*., 2019b). Although an important step forward, the work was greatly complicated by the lack of information because many species were deemed data deficient, highlighting the need for more research on the freshwater fishes of Ecuador. As the group discussed the conservation challenges for the freshwater fishes of Ecuador over several meetings, it became clear that their state was alarming and deteriorating across the country, much of the information needed to make decisions on the status of many species was not available, and the existing relevant literature was scattered and often difficult to access. Critically, with some exceptions (Jiménez-Prado *et al*., 2020; Jiménez-Prado & Vásquez, 2021; Loomis, 2017; Vélez Espino, 2003, 2006), there are few studies documenting how freshwater fish abundances, fisheries catches or geographic ranges have been affected by the environmental problems that aquatic ecosystems are experiencing. Available quantitative data on fish abundance and fisheries catches are typically based on short-term studies with a limited geographic scope that employ different methodologies, making trends difficult to decipher (Burgos-Morán *et al*., 2018; Jácome-Negrete *et al*., 2018; Revelo, 2010; Utreras, 2010).

In this review, we summarize current knowledge of the major conservation threats and prospects of the freshwater fishes of Ecuador. First, we present an overview of the geography of the major drainage basins in continental Ecuador. Second, we characterize the taxonomic and geographic distribution of the fish species for which concerns could be identified by the Freshwater Fishes Working Group. Third, we review the major factors causing the decline of freshwater fishes in Ecuador. Finally, we conclude by making recommendations for needed conservation actions.

2 | FISH DIVERSITY AND THE MAJOR DRIANAGE BASINS OF ECUADOR

Freshwater fishes constitute an important component of the biodiversity of Ecuador (Figure 1). In the most recent national list of the

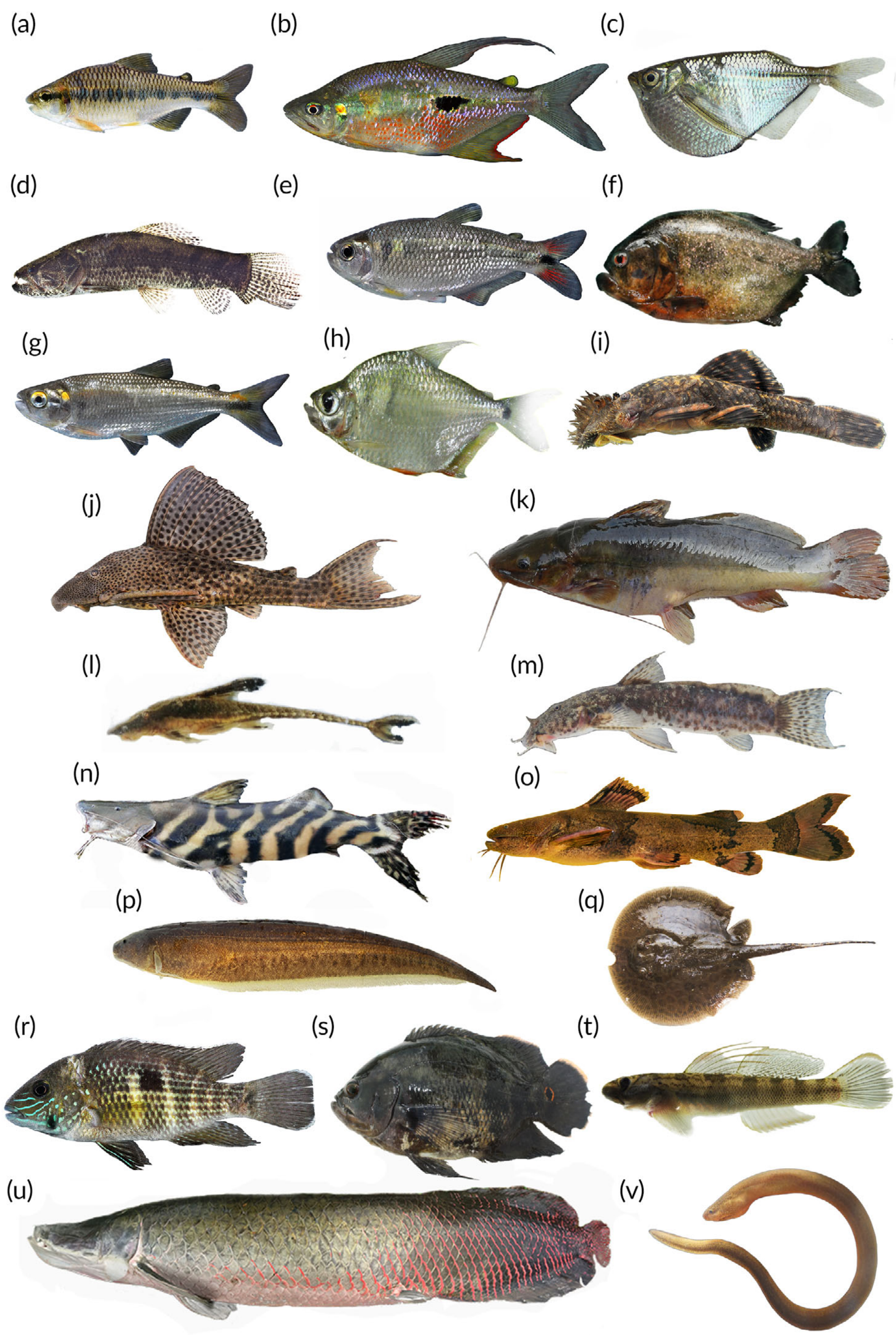

FIGURE 1 Representative Ecuadorian freshwater fish. (a) *Creagrutus kunturus*, (b) *Rhoadsia minor*, (c) *Gasteropelecus maculatus*, (d) *Hoplias malabaricus*, (e) *Eretmobrycon* sp., (f) *Pygocentrus nattereri*, (g) *Brycon* sp., (h) *Tetragonopterus argenteus*, (i) *Ancistrus clementinae*, (j) *Hypostomus* cf. *niceforoi*, (k) *Rhamdia cinerascens*, (l) *Sturisomatichthys frenatus*, (m) *Astroblepus* sp., (n) *Brachyplatystoma juruense*, (o) *Pseudopimelodus bufonius*, (p) *Brachyhypopomus palenque*, (q) *Potamotrygon motoro*, (r) *Andinoacara rivulatus*, (s) *Astronotus ocellatus*, (t) *Sicydium* sp., (u) *Arapaima gigas*, (v) *Synbranchus marmoratus*

freshwater fishes of Ecuador, Barriga (2012) included 951 species, most of which are in the Amazon region and the Amazon slopes of the Andes (Table 1). Since the publication of this list, new freshwater fish species have been described while others have been synonymized (*e.g.*, Arbour *et al*., 2014; Crampton *et al*., 2016; Lujan *et al*., 2015b; Provenzano & Barriga-Salazar, 2018; Tobes *et al*., 2020). Jimenez-Prado *et al*. (2015) updated the list for Western Ecuador, removing over 100 species listed in Barriga (2012) that are primarily estuarine. This resulted in a decline in the total number of primarily freshwater fish species to 836 (Table 1). Although the number of species will likely continue to change as new species are described and taxonomic revisions synonymize species, the general patterns are clear. The Ostariophysii dominate, as is the case in freshwaters throughout the world, with the Siluriformes (catfishes) and Characiformes (tetras and relatives) adding up to 694 species or about 83% of all Ecuadorian freshwater fishes. Within these orders, the most diverse families both on the western and Amazonian slopes of the Andes are the Characidae (tetras) and Loricariidae (suckermouth catfishes), with approximately 184 (22%) and 107 (12.8%) species respectively, representing over one-third of all freshwater fish in Ecuador (Table 1).

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TABLE 1 Number of freshwater fish species by taxonomic family in Ecuador distributed along the western and Amazon slopes

Order	Family	Western slope	Amazon slope
Myliobatiformes	Potamotrygonidae	0 (0%)	6 (0.8%)
Osteoglossiformes	Osteoglossidae	0 (0%)	1 (0.1%)
Osteoglossiformes	Arapaimidae	0 (0%)	1 (0.1%)
Clupeiformes	Engraulidae	0 (0%)	3 (0.4%)
Clupeiformes	Pristigasteridae	0 (0%)	2 (0.3%)
Characiformes	Anostomidae	1 (0.9%)	24 (3.3%)
Characiformes	Bryconidae	5 (4.4%)	7 (1%)
Characiformes	Characidae	19 (16.8%)	165 (22.8%)
Characiformes	Curimatidae	5 (4.4%)	30 (4.1%)
Characiformes	Erythrinidae	2 (1.8%)	2 (0.3%)
Characiformes	Gasteropelecidae	1 (0.9%)	7 (1%)
Characiformes	Lebiasinidae	3 (2.7%)	15 (2.1%)
Characiformes	Parodontidae	2 (1.8%)	3 (0.4%)
Characiformes	Prochilodontidae	1 (0.9%)	2 (0.3%)
Characiformes	Chilodontidae	0 (0%)	2 (0.3%)
Characiformes	Crenuchidae	0 (0%)	12 (1.7%)
Characiformes	Hemiodontidae	0 (0%)	6 (0.8%)
Characiformes	Alestiidae	0 (0%)	1 (0.1%)
Characiformes	Serrasalmidae	0 (0%)	17 (2.3%)
Characiformes	Acestrorhynchidae	0 (0%)	6 (0.8%)
Characiformes	Cynodontidae	0 (0%)	4 (0.6%)
Characiformes	Ctenoluciidae	0 (0%)	3 (0.4%)
Gymnotiformes	Apteronotidae	1 (0.9%)	17 (2.3%)
Gymnotiformes	Gymnotidae	1 (0.9%)	7 (1%)
Gymnotiformes	Hypopomidae	1 (0.9%)	5 (0.7%)
Gymnotiformes	Sternopygidae	2 (1.8%)	8 (1.1%)
Gymnotiformes	Rhamphichthyidae	0 (0%)	4 (0.6%)
Siluriformes	Astroblepidae	14 (12.4%)	8 (1.1%)
Siluriformes	Cetopsidae	4 (3.5%)	8 (1.1%)
Siluriformes	Heptapteridae	4 (3.5%)	22 (3%)
Siluriformes	Loricariidae	12 (10.6%)	95 (13.1%)
Siluriformes	Pseudopimelodidae	3 (2.7%)	5 (0.7%)
Siluriformes	Trichomycteridae	4 (3.5%)	28 (3.9%)
Siluriformes	Aspredinidae	0 (0%)	14 (1.9%)
Siluriformes	Callichthyidae	0 (0%)	32 (4.4%)
Siluriformes	Pimelodidae	0 (0%)	43 (5.9%)
Siluriformes	Doradidae	0 (0%)	31 (4.3%)
Siluriformes	Auchenipteridae	0 (0%)	22 (3%)
Cyprinodontiformes	Poeciliidae	2 (1.8%)	0 (0%)
Cyprinodontiformes	Rivulidae	0 (0%)	7 (1%)
Beloniformes	Belonidae	1 (0.9%)	4 (0.6%)
Mugiliformes	Mugilidae	1 (0.9%)	0 (0%)
Cichliformes	Cichlidae	5 (4.4%)	34 (4.7%)
Perciformes	Haemulidae	1 (0.9%)	0 (0%)
Perciformes	Sciaenidae	1 (0.9%)	2 (0.3%)
Perciformes	Polycentridae	0 (0%)	1 (0.1%)

(Continues)

TABLE 1 (Continued)

Order	Family	Western slope	Amazon slope
Gobiiformes	Eleotridae	4 (3.5%)	0 (0%)
Gobiiformes	Gobiidae	7 (6.2%)	0 (0%)
Pleuronectiformes	Achiridae	4 (3.5%)	5 (0.7%)
Synbranchiformes	Synbranchidae	1 (0.9%)	2 (0.3%)
Syngnathiformes	Syngnathidae	1 (0.9%)	0 (0%)
Batrachoidiformes	Batrachoididae	0 (0%)	1 (0.1%)
Tetraodontiformes	Teraodontidae	0 (0%)	1 (0.1%)
Total=		113	725

Note: Percentages are the percentage of the total species richness for each family by slope. Data for the Western slope is from Jimenez-Prado *et al.* (2015) updated for new and synonymized species and data from the Amazon slope is from Barriga (2012).

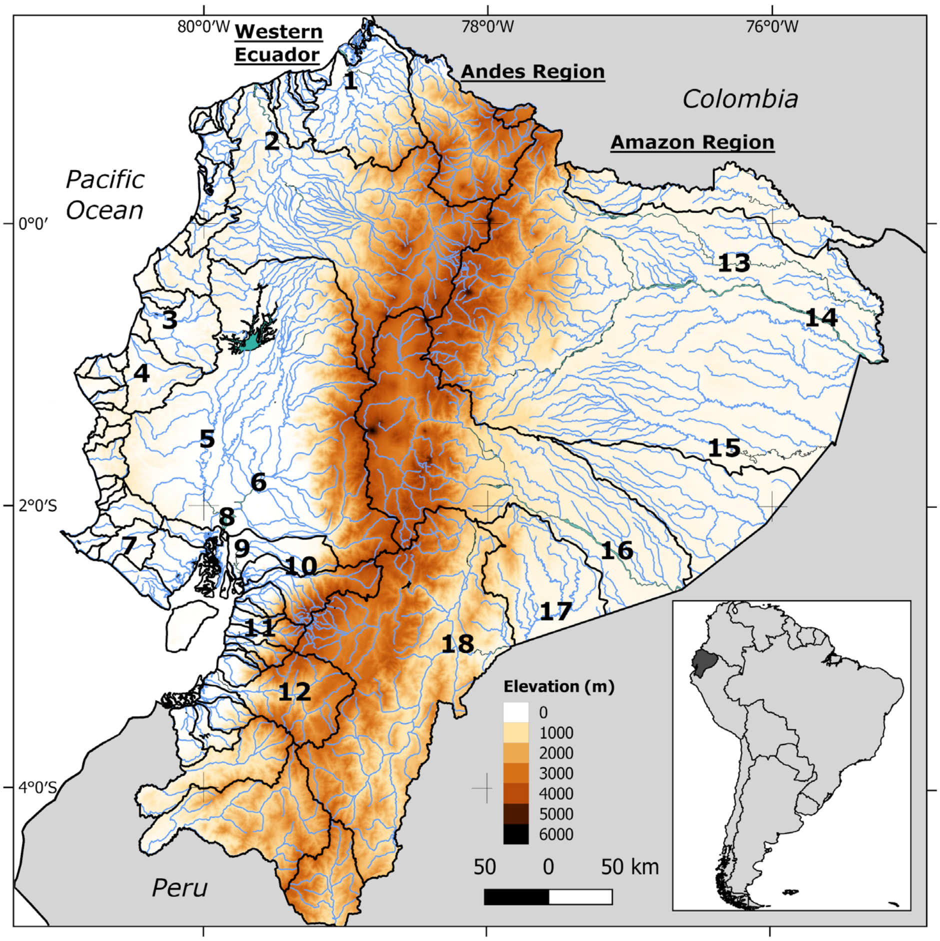

FIGURE 2 Map of Ecuador showing the major drainage basins. 1, Santiago-Cayapas Drainage; 2, Esmeraldas River; 3, Chone River; 4, Portoviejo River; 5, Daule River; 6, Babahoyo River; 7, Zapotal River; 8, Guayas River; 9, Taura River; 10, Cañar River; 11, Balao River; 12, Jubones River; 13, Aguarico River; 14, Napo River; 15, Curaray River; 16, Pastaza River; 17, Morona River; 18, Santiago River

Geographically, continental Ecuador is typically divided into three regions: (1) western Ecuador also known as the coastal region (*Costa*) included within the North Andean Pacific Slopes-Rio Atrato region, (2) the Andes Mountains region (*Sierra*), and (3) the Amazonian region (*Oriente*), which includes both the Amazonian lowlands and the western Amazon Piedmont (Abell *et al.*, 2008; Jimenez-Prado *et al.*, 2015) (Figure 2). These three regions are extremely different in their geological history, environmental characteristics and biotic communities (Barriga, 2012).

2.1 | Western Ecuador

Western Ecuador is characterized by its isolation, high levels of endemism and relatively low diversity (Figure 3a–d) (Jimenez-Prado *et al.*, 2015). The rise of the Andes Mountains drastically altered the aquatic landscape in the region, greatly influencing the climatic, geological and hydrological conditions (Jimenez-Prado *et al.*, 2015; Wolf, 1892). Other mountains, such as the *Cordillera Chongón-Colonche*,

FIGURE 3 Representative Ecuadorian rivers. (a) Mindo (Esmeraldas drainage), (b) Rio Palenque Reserve (Guayas drainage), (c) Abras de Mantequilla wetland (Guayas drainage), (d) Jubones River, (e) San Pedro River (high Andes near Quito), (f) Napo River, (g) Laguna de Limoncocha, (h) Curaray River

also play an important role in generating environmental variation and determining water flow patterns in the region. Western Ecuador has a pronounced humidity gradient going from extremely wet rainforest in the southern reaches of the Chocó in northwestern Ecuador, becoming seasonally dry forest southward until it transitions into near desert in northern Peru. This topographic and environmental complexity has resulted in high levels of endemism across taxonomic groups at micro-geographical scales, such that some plant species are known from single hill tops (Bonifaz & Cornejo, 2004; Dodson *et al*., 1985; Dodson & Gentry, 1978, 1991). Approximately 38% of freshwater fishes (43 of 112) are endemic (Jimenez-Prado *et al*., 2015), which is a high rate even for Neotropical ecosystems (Albert *et al*., 2011; Maldonado-Ocampo *et al*., 2012). The region includes a subset of the families present in the Amazon region, with estuarine groups being overrepresented (Table 1). Unfortunately, western Ecuador is the region of the country that has been most severely impacted by human development (Dodson & Gentry, 1991; Cuesta *et al*., 2017). It has the largest human populations and most of the land has been transformed to agricultural fields (Dodson & Gentry, 1991). The major drainage systems in Western Ecuador are listed below.

2.1.1 | The Santiago-Cayapas drainage system

This is the northernmost major drainage basin in western Ecuador and includes the Santiago and Cayapas Rivers and their tributaries in Esmeraldas Province (Table A). It is the region in western Ecuador with the greatest precipitation and includes the last remaining large tracts of primary rainforest in coastal Ecuador. There is an important transition in the ichthyofauna in the Santiago-Cayapas system, which includes divergent species not seen southward, such as the freshwater hatchet fish *Gasteropelecus maculatus* (Steindachner, 1879) (Figure 1c) and the characid *Roeboides occidentalis* Meek & Hildebrand 1916 (Jimenez-Prado *et al*., 2015). Jimenez-Prado *et al*. (2015) report 62 species of freshwater fishes from this drainage of which 15 (24.2%) are endemic.

2.1.2 | The Esmeraldas drainage system

This drainage is south of the Santiago-Cayapas and Mira drainages flowing from high in the Andes in a north-west direction and draining into the Pacific at the city of Esmeraldas. It receives a good deal of precipitation and includes some rainforest as well, although the forest and rivers have been greatly impacted by human development. Quito, the capital of Ecuador, and several small towns that cover a population of approximately 2 million inhabitants are located in the inter-Andean valley. Bodies of water in the highlands are severely affected by urban expansion and the lack of wastewater treatment from populations settled in the valley. The Esmeraldas basin is the second largest drainage in western Ecuador in terms of both area and water volume drained, and harbours an important freshwater fish fauna that varies substantially with elevation. The fish fauna is composed of some species that occur in the Guayas drainage (see below) and other rivers combined with some species that are unique to this drainage, such as the newly described pseudopimelodid *Microglanis berbixae* Tobes *et al*. (2020), or shared with the Santiago-Cayapas drainage. Jimenez-Prado *et al*. (2015) report 65 species of freshwater fishes from this drainage of which 17 (26.2%) are endemic to the drainage.

2.1.3 | Rivers of the northern coastal area

In the area between the mouths of the Esmeraldas and Guayas Rivers, there are small rivers running between the Coastal Mountain Range and the Pacific Ocean. The transition between humid and dry coastal forest appears to occur just north of the Chone River near Bahía de Caráquez (Wolf, 1892). However, there is an important pocket of humid forest south of the Chone River in the area between Puerto Cayo and Olón, where the coastal mountain chain lies in close proximity to the ocean. In this area, the Ayampe River holds water year round and is surrounded by lush forest (Fundación Jocotoco, 2020). South of Olón conditions get dry with the Peninsula of Santa Elena, including some of the driest habitats in Ecuador. Important rivers in this region include the Atacames, Muisne, Chone, Portoviejo, Ayampe and Zapotal. Reliable lists of the freshwater fishes in the region are not available although they are likely related to those in the Esmeraldas and Guayas basins, with low species diversity and an overrepresentation of estuarine species.

2.1.4 | The Guayas drainage system

The Guayas drainage basin is the largest drainage system in western Ecuador spanning an area of approximately 32,674 km^2 between the *Cordillera Chongon-Colonche* and the Andes Mountains in the provinces of Guayas and Los Rios (Gómez, 1989). The *Cordillera Chongon-Colonche* plays a key role in separating the Guayas drainage system from rivers along the coast and in funnelling the rivers south over a larger area towards the Gulf of Guayaquil. The Guayas River is formed by the union of its two major rivers near its mouth: the Daule and Babahoyo. The native vegetation in the lowlands of the Guayas basin has largely been replaced with agricultural fields (Dodson & Gentry, 1991). Because of its size and isolation, the Guayas drainage has both the highest number of freshwater fish species in western Ecuador (70 species) and the greatest percentage of endemic species (34.3%), including commercially important species like *Ichthyoelephas humeralis* (Günther, 1860) and *Leporinus ecuadorensis* Eigenmann and Henn, 1916 (Jimenez-Prado *et al*., 2015). Major rivers include the Guayas, Babahoyo, Daule, Vinces, Quevedo and Yaguachi.

2.1.5 | The southern coastal system

South of the Guayas River along the coast there is a series of small rivers with steep slopes that run short distances between the Andes Mountains and the Pacific Ocean (Valdiviezo-Rivera *et al*., 2018b). The freshwater fishes in this region seem to be mostly a subcomponent of those present in the Guayas drainage system, enriched for species adapted to mountain streams. However, Barriga (2012) recognized a distinct biogeographic zone for freshwater fishes in the southern portion of this region, the Catamayo zone, spanning from the Jubones River just north of the city of Machala southward to northern Peru. This region is recognized as an important hotspot of endemism for other groups, suggesting that there has been significant historical isolation (Aguirre *et al*., 2016; Cucalón Tamayo, 2019; Tapia-Armijos *et al*., 2015). Major rivers in this system include the Taura, Cañar, Bulubulu, Balao, Jubones and Santa Rosa.

2.2 | The Andes region

The Andes have played a fundamental role in shaping the ecology and evolution of Ecuador's flora and fauna. They divide the lowlands into western and Amazonian regions that harbour largely distinct fish faunas (Barriga, 2012). Rivers along the western slopes of the Andes drain relatively short distances to the Pacific while those on the eastern slopes constitute tributaries that eventually drain into the Atlantic Ocean through the Amazon River. Andean rivers are characterized by fast-flowing water and very rapid habitat transitions due to the steep slopes, resulting in high levels of biological diversity and endemism (Anderson & Maldonado-Ocampo, 2011). Fish diversity tends to be highest at mid and low elevations in Andean streams, and the fish communities transition with elevation (Aguirre *et al*., 2016; Jimenez-Prado *et al*., 2015). The Andean catfish genus *Astroblepus* (Figure 1m) predominates at high elevations, together with introduced species like the rainbow trout *Onchorhynchus mykiss* (Walbaum, 1792) and brown trout *Salmo trutta* Linnaeus, 1758 (Anderson & Maldonado-Ocampo, 2011; Maldonado *et al*., 2011). The Andes region has been severely impacted by anthropogenic factors for hundreds of years with much of the natural forest having been substituted for agricultural fields, non-native timber plantations and pastures (Sierra, 2013). Many large cities lacking proper wastewater treatment are located in the Andes, and introduced trout are highly detrimental to native species (Vimos *et al*., 2015). There has also been an increase in dam construction in recent years (Anderson *et al*., 2018). The major rivers of the Ecuadorian Andes are discussed in the sections on Western Ecuador and the Amazon region (see above and below). The Andes are also peppered by stunning natural lakes, lagoons and ponds of tectonic, glacial and volcanic origins, such as Laguna San Pablo, Yaguarcocha, Yanacocha, Papallacta, Quilotoa, Tambo and Colta (León Velasco, 2010; Nieto, 2008). Some of these are or were inhabited by native species like *Astroblepus* spp., but many have been stocked with introduced species such as rainbow trout, carp, goldfish and largemouth bass, threatening the native fishes and possibly driving some to local extinction (Casallas & Gunkel, 2001; Terneus Jácome, 2014; Vélez Espino, 2003).

2.3 | The Amazon region

The largest remaining forests and greatest number of freshwater fish species in Ecuador are found in the Amazon region. Although it rains throughout the year, precipitation increases between March and July, resulting in seasonal flooding and a hydrological cycle with highly variable water levels (Galacatos *et al*., 1996, 2004; Junk *et al*., 2007; Silva & Stewart, 2017). The lowlands harbour the characteristic fish diversity of the Amazon basin, including large pimelodid catfishes, a great diversity of characiforms, suckermouth catfishes, cichlids, osteoglossiforms and myliobatiforms, among many others. The Amazon Piedmont region is characterized by rapid turnover of habitats and fishes. Despite a number of recent studies on the diversity of the ichthyofauna in the region (Barriga, 2012; Barriga, 1986; Barriga *et al*., 2016; Galacatos *et al*., 1996; Hidalgo & Rivadeneira-R, 2008; Nugra-Salazar *et al*., 2016; Rivadeneira *et al*., 2010; Rodríguez-Galarza *et al*., 2017; Stewart *et al*., 1987; Valdiviezo-Rivera, 2012), there have been no systematic reviews of the entire fauna and much remains to be learned about the ecology of most species. Much of the region lacks roads but road construction is accelerating (Articulación Regional Amazónica, 2011; Charity et al., 2016), and there is a growing number of threats, including oil and mineral exploitation, deforestation and growing human populations (Lessmann *et al*., 2016; López *et al*., 2013; Sierra, 2000).

Barriga (2012) divided rivers in the Amazonian region into biogeographic zones for freshwater fishes. Above 600 m, he identified the High Napo, High Pastaza, Upano-Zamora and Chinchipe zones, while for the lowlands he recognized the Napo-Pastaza and Morona-Santiago zones. The major drainages in this region are listed below.

2.3.1 | The Aguarico River

The Aguarico River is a tributary of the Napo River and is the northernmost major drainage in the Amazonian region, draining an area of approximately 12,000 km^2 (León Velasco, 2010). It originates in the Cordillera Oriental of the Andes and is formed by the confluence of the Cofanes, Azuela and San Miguel Rivers. The Aguarico proper is a turbid whitewater river with a high load of suspended solids that winds through the Amazonian lowlands forming an abundance of oxbow lakes and floodplain pools (Saul, 1975). Although a complete species list is not available, fish diversity appears substantial (Borman *et al*., 2007; Ibarra & Stewart, 1989; Saul, 1975; Vriesendorp *et al*., 2009). In August 2017, the Cuyabeno Wildlife Production Reserve, which forms part of the Aguarico River drainage, was included in the Ramsar Convention (Ramsar 2018).

2.3.2 | The Napo River

The Napo drainage is the largest and most important drainage in the Ecuadorian Amazonian region, draining an area approximately of 30,600 km^2, and is a main tributary of the upper Amazon (Nieto, 2008). Although there is much to be learned about the freshwater fishes in this drainage, it is one of the better studied drainages of the Ecuadorian Amazon because of the classic studies by Stewart *et al.* (1987, 2002) and Ibarra and Stewart (1989), who collected 222 fish community samples between 200 and 2500 m in elevation. More recent studies include Valdiviezo-Rivera (2012) and Valdiviezo-Rivera *et al.* (2018a), who created a field guide of the fishes of the Limoncocha Lagoon. The diversity of freshwater fishes in the Napo is by far the highest in Ecuador (Galacatos *et al*., 1996; Ibarra & Stewart, 1989; Saul, 1975; Stewart *et al*., 2002; Valdiviezo-Rivera *et al*., 2018a), with Barriga (2012) reporting 680 fish species for the drainage.

2.3.3 | The Curaray River

This river drains an area approximately of 18,000 km^2 (León Velasco, 2010) and is a tributary of the Napo drainage, sharing part of its ichthyofauna and habitat characteristics in lowlands and flooded forest areas (Jácome-Negrete, 2013). Studies of the fishes in this region have focused on the use of fishes by native people and have documented species richness and occurrence in the middle and low parts of the drainage (Guarderas *et al*., 2013; Jácome-Negrete, 2013).

2.3.4 | The Pastaza River

The Pastaza River is formed by the union of the Patate and Chambo Rivers and is a tributary of the Marañon drainage in Peru (Rivadeneira et al., 2010). It drains an area of approximately 40,000 km^2. Other important rivers in the drainage include the Topo, Palora and Bobonaza. Rivadeneira *et al.* (2010) compiled information on the fishes of the Pastaza drainage and reported 142 species occurring between 300 and 2840 m in elevation. They also indicated that 31 new species have been described from this basin, a little under half of which (14) appear to be endemic. Very little is known otherwise about the ecology of most species. Unfortunately, the upper Pastaza drainage has been significantly impacted by dam construction and the lowlands by oil extraction. At the border with Peru, the Pastaza is a Ramsar protected site (Articulación Regional Amazónica, 2011; Macedo & Castello, 2015).

2.3.5 | The Morona River

The Morona River originates on the eastern side of the Kutukú protected forest area, one of the largest protected areas in Ecuador (CARE *et al.*, 2012). It is a tributary of the Marañon River. There is very little published about the freshwater fishes in this river since it is relatively far from large human populations and oil extraction activities. However, this drainage is likely threatened by illegal mining activities (Fierro, 2015).

2.3.6 | The Santiago River

The southernmost major drainage in the Ecuadorian Amazon is the Santiago River drainage, which drains an area of approximately 15,400 km^2 (León Velasco, 2010). This drainage is structurally complex because of its proximity to rivers running along the foothills such as the Upano and Paute Rivers in the central Ecuadorian Amazon and the Zamora River in the south. These rivers merge in an important biodiversity hot spot known as the Kutukú-Cóndor corridor (CARE *et al.*, 2012), which includes some remarkably diverse ecosystems harbouring many undescribed terrestrial and aquatic species (Schulenberg & Awbrey, 1997). This has also been a region of historical conflict over land disputes between Ecuador and Peru (Schulenberg & Awbrey, 1997). Recent years have seen the development of new mining operations and dam construction, which have stimulated efforts to study the fishes in the region (Barriga, 1997; Nugra *et al.*, 2018).

3 | THE THREATENED FRESHWATER FISHES OF ECUADOR

It is clear that the freshwater fishes of Ecuador are under grave threat (Barriga, 2012; Celi & Villamarín, 2020; Jimenez-Prado *et al.*, 2015). At least one marine species that enters freshwater, the critically endangered largetooth sawfish *Pristis pristis* (Linnaeus, 1758), seems to have gone functionally extinct in Ecuador and is now extremely rare or locally extinct (Dulvy *et al.*, 2016; Mendoza *et al.*, 2017). The Andean catfish *Astroblepus ubidiai*, the only native fish in the high Andes of Imbabura Province in northern Ecuador, is considered critically endangered after having gone through a severe range contraction driven by multiple anthropogenic factors. It is now known only from a few isolated localities (Arguello & Jimenez-Prado, 2016; Vélez Espino, 2003, 2006). In north-western Ecuador, *Astyanax ruberrimus* seems to have been locally extirpated from the Atacames basin after the construction of a dam (Jiménez-Prado *et al.*, 2020), while the native poeciliid *Pseudopoecilia fria* seems to have been displaced to the upper reaches of the Atacames basin after the introduction of the exotic poeciliid *Poecilia gilli* (Jiménez-Prado & Vásquez, 2021). In the Puyango drainage in southern Ecuador, an unidentified loricariid previously consumed by people in the area was reported to have gone locally extinct by Tarras-Wahlberg *et al.* (2001), possibly due to mining pollution. Given the lack of historical data and systematic research, the cases described above may be just the tip of the iceberg. It is possible that many other fishes have gone locally extinct or that undescribed species have been lost.

The Endangered Freshwater Fishes Working Group evaluated the status of 163 freshwater fish species in Ecuador (Aguirre *et al.*, 2019b). Unfortunately, a lack of information resulted in 66 of these 163 species (40.5%) being deemed data deficient (DD). Additionally, many of the species that were not evaluated lacked sufficient data to even be considered for evaluation so the real number of species in the DD category is likely much greater. Of the remaining species, 62 were categorized as least concern (LC), 15 as vulnerable (VU), 13 were categorized as near threatened (NT), six as endangered (EN) and one as critically endangered (CR) (Table 2). Geographically, the greatest number of species, 22, was from the Amazon region, where unregulated fisheries pressures and habitat degradation resulted in concerns being identified for 16 pimelodid catfishes. The threats were deemed severe enough that five of these were categorized as endangered in Ecuador. From the Andes region, concerns were only identified for four species, although the only species categorized as critically endangered, *Astroblepus ubidiai* (Pellegrin, 1931), is from this region (Arguello & Jimenez-Prado, 2016; Mena-Valenzuela & Valdiviezo-Rivera, 2016; Vélez Espino, 2003, 2006). The remaining nine species for which concerns could be identified were from Western Ecuador. Only one species from this region, the characid *Pseudochalceus bohlkei* Orcés, 1967 from Esmeraldas province (Orcés, 1967), was categorized as endangered in Ecuador. Given the lack of data, it is likely that more species may be threatened, although it is also possible that some of the species listed in Aguirre *et al.* (2019b) are in better condition than currently recognized. Directed studies are urgently needed to improve our understanding of the threats to Ecuador's freshwater fishes.

4 | THE FACTORS CAUSING THE DECLINE OF ECUADOR'S FRESHWATER FISHES

As human populations have grown and technology has made it easier to exploit natural resources, the pressure on Ecuadorian aquatic ecosystems has increased, resulting in a variety of threats for the

TABLE 2 Critically endangered (CR), endangered (EN), near threatened (NT) and vulnerable (VU) freshwater fishes of Ecuador identified by the national endangered freshwater fishes working group (Aguirre *et al*., 2019b)

Order	Family	Species	Nat. cat.	Eval. crit.	Glob. Cat.	Region
Myliobatiformes	Potamotrygonidae	*Potamotrygon motoro*	NT	NA	DD	AMZ
Osteoglossiformes	Osteoglossidae	*Osteoglossum bicirrhosum*	NT	NA	NE	AMZ
Osteoglossiforme	Arapaimidae	*Arapaima gigas*	VU	B2ab(iii)	DD	AMZ
Characiformes	Curimatidae	*Potamorhina altamazonica*	NT	NA	NE	AMZ
Characiformes	Curimatidae	*Pseudocurimata boehlkei*	VU	B1b(iii)c(i)	DD	WE
Characiformes	Curimatidae	*Pseudocurimata boulengeri*	NT	NA	NE	WE
Characiformes	Prochilodontidae	*Ichthyoelephas humeralis*	NT	NA	NE	WE
Characiformes	Prochilodontidae	*Prochilodus nigricans*	VU	A2ad + 4ad	NE	AMZ
Characiformes	Anostomatidae	*Leporinus ecuadorensis*	NT	NA	NE	WE
Characiformes	Serrasalmidae	*Mylossoma duriventre*	NT	NA	NE	AMZ
Characiformes	Characidae	*Grundulus quitoensis*	VU	D2	NE	AND
Characiformes	Characidae	*Pseudochalceus bohlkei*	EN	B2b(iv)c(i)	NE	WE
Characiformes	Characidae	*Pseudochalceus longianalis*	VU	NA	NE	WE
Siluriformes	Cetopsidae	*Paracetopsis esmeraldas*	NT	NA	NT	WE
Siluriformes	Pimelodidae	*Brachyplatystoma filamentosum*	VU	A2a,d + A4a,d	NE	AMZ
Siluriformes	Pimelodidae	*Brachyplatystoma juruense*	VU	A2d + 4d	NE	AMZ
Siluriformes	Pimelodidae	*Brachyplatystoma platynemum*	EN	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Brachyplatystoma rousseauxii*	EN	A2d + 4d	LC	AMZ
Siluriformes	Pimelodidae	*Brachyplatystoma tigrinum*	VU	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Brachyplatystoma vaillantii*	EN	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Calophysus macropterus*	VU	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Leiarius marmoratus*	VU	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Phractocephalus hemioliopterus*	VU	A2d + 4d	NE	AMZ
Siluriformes	Pimelodidae	*Pinirampus pirinampu*	EN	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Platynematichthys notatus*	NT	NA	NE	AMZ
Siluriformes	Pimelodidae	*Pseudoplatystoma punctifer*	EN	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Pseudoplatystoma tigrinum*	VU	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Sorubimichthys planiceps*	NT	NA	NE	AMZ
Siluriformes	Pimelodidae	*Zungaro zungaro*	VU	A2d + A4d	NE	AMZ
Siluriformes	Pimelodidae	*Batrochoglanis transmontanus*	VU	B1ab(iii)c(ii)	LC	AMZ
Siluriformes	Astroblepidae	*Astroblepus mindoensis*	NT	NA	NT	AND
Siluriformes	Astroblepidae	*Astroblepus ubidiai*	CR	NA	CR	AND
Siluriformes	Astroblepidae	*Astroblepus vaillanti*	NT	NA	DD	AND
Cichliformes	Cichlidae	*Andinoacara sapayensis*	VU	A3c + B1b(iii)c(i)	DD	WE
Gobiiformes	Gobiidae	*Sicydium rosenbergii*	NT	NA	NT	WE

Note: Nat. cat. is the national category assigned by the working group, Eval. crit. are the IUCN criteria used to assign the national category, Glob. cat. is the IUCN global category for the species (DD, data deficient; NE, near endangered), and Region is the region of Ecuador in which the species occurs (AMZ, Amazon region; AND, Andean region; WE, Western Ecuador).

freshwater fishes that vary regionally. Below, we review some of the major threats.

4.1 | Habitat loss through physical alteration of rivers

Habitat loss in aquatic ecosystems in Ecuador is caused by many factors, among which the physical alteration of the river bottom and banks is one of the most severe (Figure 4). Freshwater fishes have evolved over geological time scales to inhabit portions of rivers with certain sets of environmental and physical characteristics. Logs, woody debris, rocks, fallen leaves, macrophytes, natural caves, *etc*., are often required for routine activities such as procuring food and for reproduction (Angermeier & Karr, 1984; Grenouillet *et al*., 2002; Lo *et al*., 2020; Wright & Flecker, 2004; Zeni & Casatti, 2014). When the physical substrate of the river is altered, the affected portion of

FIGURE 4 Physical destruction of river banks and bottom caused by the removal of gravel for construction. Pictures from the Guayas River basin in western Ecuador

the river often becomes a very poor or unusable habitat for native species. The loss of required habitat for reproduction can be particularly severe and result in the local extinction of sensitive species (Aarts *et al*., 2004). River alteration can also facilitate colonization by invasive species, which are often more tolerant of poor environmental conditions (Bates *et al*., 2013; Casatti *et al*., 2009). The movement of bottom materials can affect downstream portions of the river, increasing turbidity and burying fish habitat in silt (Berkman & Rabeni, 1987; Lo *et al*., 2020). Importantly, the damage is often not obvious when seen from land.

The use of heavy machinery for the removal of river gravel for construction is common throughout Ecuador (León-Ortiz, 2017; Matamoros-Ramírez, 2013) and is poorly controlled. Removal of gravel and rocks by heavy machinery can results in a total loss of natural habitat conditions. Artisanal miners can also take advantage of the movement of the substrate to illegally mine the impacted river stretches, resulting in further contamination of the river (Matamoros-Ramírez, 2013). There are also concerns about possible unforeseen impacts of large megaprojects on rivers. For example, Ecuador lost one of its iconic waterfalls, *Cascada de San Rafael*, in February 2020, just a few years after the completion of the nearby massive Coca-Codo-Sinclair hydroelectric project. Evidence indicates that the hydroelectric project substantially increased erosion rates in the Coca River (Escuela Politecnica Nacional, 2020), and concerns have been raised about the project's potential influence on the waterfall collapse (Cobo, 2020). No studies to date have examined the impact of the physical alteration of river substrates on Ecuadorian freshwater fishes.

4.2 | Deforestation

Deforestation impacts aquatic ecosystems in a number of ways. It increases soil erosion, which increases turbidity and sedimentation, and causes contaminants to enter streams (Jones *et al*., 1999; Webb *et al*., 2004; Wood & Armitage, 1997). In the Ecuadorian Amazon, erosion in deforested areas is causing the release of natural mercury, which is biomagnified in food webs and accumulates in large fish that are consumed by indigenous people (Mainville *et al*., 2006; Moreno Vallejo, 2017; Webb *et al*., 2004; WHO, 2011). Deforestation also changes water temperature and light conditions (Castelle *et al*., 1994; Ilha *et al*., 2018; Macedo *et al*., 2013; Pusey & Arthington, 2003), reduces levels of litter detritus and increases periphyton (Bojsen & Jacobsen, 2003; Lorion & Kennedy, 2009), reduces habitat complexity (Lo *et al*., 2020), affects hydrological processes (Iñiguez-Armijos *et al*., 2014), is associated with the increase of introduced species in streams (Jones *et al*., 1999; Pusey & Arthington, 2003), and affects alpha and beta diversity, community composition, and ecosystem function (Bojsen & Jacobsen, 2003; Iñiguez-Armijos *et al*., 2014; Lo *et al*., 2020; Lorion & Kennedy, 2009; Pusey & Arthington, 2003; Zeni *et al*., 2019). Deforestation has even been associated with morphological changes in fish (Ilha *et al*., 2018).

Deforestation in Ecuador has been severe (Dodson & Gentry, 1991; Mosandl *et al*., 2008; Sierra, 2000; Tapia-Armijos *et al*., 2015). Although the proportion of the deforested area and timing of deforestation varies substantially by region (Ministerio del Ambiente, 2017; Sierra, 2013), Ecuador had the highest average annual rate of deforestation in Latin America between 1990 and 2012 (Armenteras & Rodríguez Eraso, 2014). Using satellite imagery, González-Jaramillo *et al*. (2016) reported that forests covered 11,871,700 ha or 48.1% of the surface area of continental Ecuador in 1986, declining to 10,368,500 ha or 36.8% by 2008. Data from Ecuador's *Ministerio del Ambiente* are more optimistic. They report that 50.7% of the area of continental Ecuador or 12,631.198 ha remained covered by native forests in 2016 and that deforestation rates show a declining trend from 129.943 ha/year of native forest lost between 1990–2000 to 94.353 ha/year in 2014–16 (Ministerio del Ambiente, 2017). High rates of population growth in Ecuador have been one of the main factors. Population size more than quadrupled from an estimated 4 million people in 1957 (Dodson & Gentry, 1991) to over 17 million by 2018 (The World Bank, 2020).

Regionally, deforestation has been most severe in Western Ecuador, where as much as 70% of the original forest has been lost

(Cuesta *et al*., 2017). Patches of primary forest remain in the very north-western region of Ecuador close to the Colombian border, scattered along the steep slopes of hills and in small reserves. The construction of an elaborate road system in the mid-twentieth century made the rapid deforestation of the region possible. Deforestation was exacerbated by the implementation of land reform laws in the 1960s that allowed the confiscation of "unproductive" land for redistribution to landless peasants, encouraging deforestation on privately owned land to avoid seizure (Dodson & Gentry, 1991). The very high levels of endemism in the region make the loss all the worse (Barriga, 2012; Bonifaz & Cornejo, 2004; Dodson & Gentry, 1991; Jimenez-Prado *et al*., 2015). The Andes region has also suffered severe deforestation such that approximately 40% of the original vegetation has been lost (Cuesta *et al*., 2017). Much of the remaining primary forest in the region occurs in areas with extremely steep slopes that are inappropriate for agriculture or harvesting timber or in small preserves (Marian *et al*., 2020; Mosandl *et al*., 2008; Tapia-Armijos *et al*., 2015; Wunder, 1996). Villages, towns and cities in the region are often packed in small valleys, exacerbating demands on nearby natural resources. Large indigenous populations predominate in this region and have modified the Andean landscape for centuries (Mosandl *et al*., 2008). Native forest and páramo habitat have largely been replaced with non-native tree monocultures of *Pinus*, *Eucalyptus*, *Cupressus*, *etc*., increasing habitat homogeneity and changing the environmental conditions (Buytaert *et al*., 2007; Hofstede *et al*., 2002; Marian *et al*., 2020; Wunder, 1996). The rapid habitat transitions that occur with elevation make the Andes extraordinary centers of biological diversity (Anderson & Maldonado-Ocampo, 2011; Hamilton, 1995; Homeier *et al*., 2010; Myers *et al*., 2000). Fish species adapted to a narrow range of environmental conditions in mountain streams may be particularly susceptible to local extinction when habitat conditions degrade. The Amazon region has the most remaining original vegetation and the most diverse freshwater fish communities (Barriga, 2012). However, it is experiencing some of the highest rates of deforestation (Lessmann *et al*., 2016; Myers, 1993; Sierra, 2000; Southgate *et al*., 1991). Deforestation has been worst in the northern Amazon region where oil deposits are largest. Myers (1993) identified the Napo region as one of 14 global deforestation fronts. As is the case in the coastal region, government land reform initiatives encouraged deforestation by colonists (Sierra, 2000; Wunder, 1996). Road construction for oil extraction and a population growth rate that is double the national average are aggravating the problem (López *et al*., 2013).

Only two studies have directly examined the effects of deforestation on Ecuadorian fish communities and both were conducted in the Amazonian region. Bojsen and Barriga (2002) studied fishes in 12 sites in headwater streams of the upper Napo River catchment that were in relatively good condition. Half of these sites were in forested areas and half were in deforested areas. They did not find a significant effect of deforestation on species richness, but beta diversity was higher among forested than deforested sites, indicating that deforestation may homogenize fish diversity across communities. The percentage of rare species was also positively associated with canopy cover. Total fish density was actually higher in deforested sites but the communities changed from being dominated by omnivorous and insectivorous characiforms in forested sites to periphyton-feeding loricariids in deforested sites. Bojsen (2005) further examined the effect of deforestation on the diet and condition of three characids in small streams of the Napo basin. The impact of deforestation depended on the ecology of the species, with species depending on terrestrial invertebrates and exhibiting less diet flexibility being most severely impacted. Thus, even in streams that are still in relatively good condition, deforestation may change the composition of fish communities and their ecosystem functions, as well as impact the viability of vulnerable rare species with narrow habitat preferences (Bojsen, 2005; Lo *et al*., 2020). When deforestation is accompanied by severe stream habitat degradation, the impact on fish communities can be catastrophic. Studies conducted on macroinvertebrate communities in Ecuador have been more common and have similarly demonstrated the importance of native forest cover on water quality, species diversity, community structure and the presence of sensitive taxa (Arroyo & Encalada, 2009; Bücker *et al*., 2010; Damanik-Ambarita *et al*., 2016; Guerrero Chuez *et al*., 2017; Iñiguez-Armijos *et al*., 2014, 2016, 2018; Urdanigo *et al*., 2019). Much more work is needed on the effects of deforestation on Ecuadorian freshwater fish communities.

4.3 | Wetland and flood plain degradation

Neotropical wetlands constitute a critical habitat for many freshwater fish species. Seasonal rains often result in the formation of highly productive floodplains that many fish species have evolved to use as nursery habitat or feeding grounds during portions of their life cycle (Davies & Walker, 2013; King *et al*., 2003; Winemiller, 2004; Winemiller & Jepsen, 2004). These floodplains can contribute to maintaining the biodiversity of the whole river ecosystem, provided that connectivity is maintained (Aarts *et al*., 2004). Despite all the ecosystems services floodplains provide, dams, water transfers and abstractions, and conversion of land to agricultural fields have modified the natural flood regimes of rivers and their associated floodplains, resulting in a loss of crucial fish habitat and, subsequently, a reduction in fish production and diversity (Welcomme & Halls, 2004; Winemiller & Jepsen, 1998).

In Ecuador, floodplains and wetlands cover an area of approximately 15,000 km^2 at elevations below 500 m in elevation, of which 61% is in the Amazon region (DINAREN, 2002). Seasonally flooded forests cover an area of over 8600 km^2 in the Amazon and another 363 km^2 are covered by grasslands and farmlands. Fortunately, much of the natural flooded forest in Ecuador's Amazonian region is still standing. However in the coastal region there are approximately 5800 km^2 of seasonally flooded land, of which only 7.4% still harbours native vegetation. Most flood plains in the coastal region have been converted to rice fields, banana plantations, grassland for cattle, sugar cane plantations and maize fields. To stop cultivated areas from getting flooded in the rainy season, dams, dikes and canal systems have been constructed throughout the region, which has resulted in a loss of approximately 82.6% of the floodplain habitat (DINAREN, 2002).

Abras de Mantequilla (AdM, Figure 3c) is one of the most important wetlands remaining in Western Ecuador (Alvarez-Mieles, 2019) and provides insight into the consequences of the degradation of Ecuador's floodplains. AdM is located at the center of the Guayas River basin in the lowlands-coastal area of Western Ecuador and is a river-wetland system that experiences marked predictable seasonality. During the wet season (January–April), the system floods and expands before decreasing dramatically in the dry season, with water remaining only in the main channels (Alvarez-Mieles, 2019). The wetland was declared a Ramsar site in March 2000 and is a valuable site for freshwater fishes, supporting at least 22 species, including commercially important species (Alvarez-Mieles, 2019; Ochoa Ubilla *et al*., 2016; Ramsar,). Macrophytes, which provide shelter from predators, food, and spawning and nursery grounds (Agostinho *et al*., 2007; Alvarez-Mieles, 2019; Meerhoff *et al*., 2007; Meschiatti *et al*., 2000), are abundant at AdM, with the floating macrophyte *Eichornia crassipes* (Pontederiaceae), commonly known as 'water hyacinth', representing around 80% of the total macrophytes biomass in the wetland, and *Salvinia auriculata* Aubl. 1775, *Pistia stratiotes* Linnaeus 1753, *Ludwigia peploides* (Kunth) P. H. Raven, *Lemna aequinoctialis* Welwitsch 1859, *Paspalum repens* P. J. Bergius and *Panicum frondescens* G. Mey, also being relatively common (Alvarez-Mieles, 2019). Characids like *Eretmobrycon festae* (Boulenger 1898), *Rhoadsia altipinna* Fowler 1911 and *Landonia latidens* Eigenmann and Henn 1914 are the most abundant fishes representing between 87% and 89% of the total littoral fish abundance, and are an important source of food for commercially important fish species. Other important endemic characids like *Phenacobrycon henni* (Eigenmann 1914), *Iotabrycon praecox* Roberts 1973 and *Hyphessobrycon ecuadoriensis* Eigenmann and Henn 1914 occur in the area, albeit at lower densities, as do fisheries species like *Andinoacara rivulatus* (Günther 1860), *Mesoheros festae* (Boulenger 1899), *Pseudocurimata boulengeri* (Eigenmann 1889), *Brycon dentex* Günter 1860 and *Ichthyoelephas humeralis* (Günther 1860) (Alvarez-Mieles *et al*., 2019). Ochoa Ubilla *et al*. (2016) specifically studied the community composition and size structure of commercially important native fishes in AdM and reported that *I. humeralis* and *Pseudocurimata* spp. were the most abundant fisheries species. The abundance of *I. humeralis*, a migratory and ecologically important species that is highly valued as a food fish in rural areas of the Guayas basin (Prado España, 2012), highlights the importance of wetlands like AdM. In addition, Revelo (2010) reported that 70% of fish collected in the region between January and March (peak wet season) are in an advanced stage of sexual maturity. Although fishing is prohibited during 2 months in the peak spawning period (Revelo, 2010), this is very difficult to enforce and the movement and congregation of fishes makes them extremely vulnerable to overfishing during this period.

With the loss of most of the natural floodplain area in Western Ecuador, it is likely that many native freshwater fishes have been greatly affected and some species may not be able to recover even if other problems are resolved. Finding ways to restore floodplain habitat will be an important challenge for future conservation efforts.

4.4 | Agricultural and urban water pollution

In Ecuador, high population growth rates and economic need have led to rapid increases in agricultural production and urban expansion, often resulting in the uncontrolled influx of pollutants to freshwater ecosystems (Borbor-Cordova *et al*., 2006; Donoso & Rios-Touma, 2020) (Figure 5). Plantations and cities often border rivers, facilitating the influx of agrochemicals, sediments and untreated waste water (Donoso & Rios-Touma, 2020; Universidad Agraria del Ecuador, 2011). Solid waste is sometimes dumped directly into streams. Some pollutants are poorly soluble in water and adhere to sediments, allowing them to persist at contaminated sites for long periods (Abellán, 2006). Others are fat soluble and can be biomagnified as they rise through the food web, reaching very high concentrations in apex predators (Abellán, 2006). No studies have directly examined the effects of agricultural or urban pollutants on freshwater fishes in Ecuador, but water quality and macroinvertebrate data provide evidence that this is likely a serious problem.

The Guayas River basin in western Ecuador illustrates the potential magnitude of the problem. It constitutes the most important agricultural center in Ecuador, with approximately 68% of national crops grown there, and harbours some of the largest human populations, including Guayaquil, the largest city in the country (Borbor-Cordova *et al*., 2006). Fertilizers and pesticides are applied in great quantities and leach into rivers, and untreated waste water flows into rivers throughout the basin (Borbor-Cordova *et al*., 2006; Deknock *et al*., 2019; Ribeiro *et al*., 2017; Universidad Agraria del Ecuador, 2011). As a consequence, the Guayas basin includes some of the most degraded aquatic ecosystems in the country (Dodson & Gentry, 1991), threatening freshwater fish communities with high rates of endemism (Jimenez-Prado *et al*., 2015). High levels of bacterial coliforms surpassing permitted limits have been commonly reported close to cities (Robinson Vera, 2015; Valencia Díaz, 2018). Damanik-Ambarita *et al*. (2016) examined water quality at 120 sites throughout the basin using macroinvertebrate indices and found compromised water quality at sites on arable land and bad water quality at sites in residential areas. Low oxygen levels (<5 mg/l) have been reported in the Daule River and may be a product of releases of anoxic water from the Daule-Peripa impoundment combined with eutrophication from fertilizer leaching and the influx of untreated waste water (Universidad Agraria del Ecuador, 2011). Deknock *et al*. (2019) examined pesticides from water samples taken at 181 sites throughout the Guayas basin and found detectable levels at 60% of sites, with cudusafos, butachlor and pendimethalin being the most common detectable pesticides. Banana and rice plantations were implicated as the likely sources. Banned pesticides like lindane, endrin and heptachlor have also been detected (Universidad Agraria del Ecuador, 2011). Mero *et al*. (2019) found levels of cadmium exceeding recommended limits (>0.67 mg/kg) in sediment, as well as

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FIGURE 5 Pollution is a serious problem affecting rivers throughout Ecuador. (a) Many cities and towns are on the shores of rivers, resulting in a constant flow of waste into rivers. View of the city of Vinces on the Vinces River. (b) Small contaminated stream in Portovelo

in the water hyacinth *Eichhornia crassipes* and the snail *Pomacea canaliculata*, in the Guayas, Babahoyo and Daule Rivers, and Carpio Rivera (2016) reported cadmium contamination in the Chimbo River, south-eastern Guayas basin.

Similar problems are affecting rivers throughout the country. In the upper Napo basin of the Amazon region, Vellosa Capparelli *et al*. (2020) found concentrations of several metals, including Hg, Cd, Cu and Pb, above permissible limits, and associated these with the presence of nearby gold-mining operations, nonfunctional municipal landfills, urban centers and fish-farming operations. The Teaone River, a highly impacted tributary to the Esmeraldas River with about 50% of its watershed area converted to agricultural land, exhibits excesses of phosphates in its main channel that are likely associated with human activity (Molinero *et al*., 2019). Lack of wastewater treatment is a common problem in Ecuador, such that even the capital Quito treats less than 10% of the waste water that it generates (Castillo Pazmiño, 2012; Donoso & Rios-Touma, 2020). Studies of the San Pedro–Guayllabamba–Esmeraldas Rivers, which receive waste waters from Quito, found persistence of pollutants like carbamazepine and acesulfame throughout the watershed, while other emerging organic pollutants, such as caffeine, sulfamethoxazole, venlafaxine, *O*-desmethylvenlafaxine and steroidal estrogens, were detectable but degraded as they moved downstream (Voloshenko-Rossin *et al*., 2014). Similarly, Donoso and Rios-Touma (2020) found some of the highest concentrations reported for suspended microplastics, as well as significant concentrations in sediment of the Guayllabamba River. With all the reported problems, studies on the effects of agricultural and urban pollutants on freshwater fishes throughout Ecuador are urgently needed.

4.5 | Mining

Artisanal mining, which is common in Ecuador, is typically poorly regulated and can cause severe environmental damage due to the poor safety practices employed. New policies and changes in existing mining laws in Ecuador have resulted in the development of large-scale industrial mining that is also causing serious problems (Adler Miserendino *et al*., 2013; López *et al*., 2013; Wildlife Conservation Society, 2020). In addition, the government of Ecuador increased mining concessions from about 3% to 13% of Ecuador's land area in 2016–17, threatening the roughly 30% of the total land area protected by Bosques Protectores included in these new concessions (Roy *et al*., 2018).

The southern Andes of Ecuador are rich in gold deposits along both their western and eastern slopes (Appleton *et al*., 2001; Ramírez Requelme *et al*., 2003; Tarras-Wahlberg *et al*., 2001). On the western side, large gold deposits near the populations of Portovelo-Zaruma, Ponce Enriquez and Puyango have been exploited for hundreds of years and constitute some of the most important mining lands in the country (Adler Miserendino *et al*., 2013; Betancourt *et al*., 2005; Tarras-Wahlberg *et al*., 2001). They are also significant sources of contamination, especially of mercury. Much of the mining in the area is artisanal and performed with poor environmental safety practices including illegal dumping of waste directly into rivers (Adler Miserendino *et al*., 2013). As a consequence, water turbidity typically increases close to mining operations, and mercury is relatively common in suspended particulate matter and bottom sediments in the region (Appleton *et al*., 2001; Tarras-Wahlberg *et al*., 2001). Levels of cyanide, mercury and other metals in rivers often exceed environmental quality criteria (Appleton *et al*., 2001; Betancourt *et al*., 2005; Mora *et al*., 2016; Tarras-Wahlberg *et al*., 2001), strongly affecting fishes, which sometimes disappear completely close to mining operations and decline in abundance farther downstream. In the only published study reporting mercury concentrations in freshwater fishes from the region, Tarras-Wahlberg *et al*. (2001) documented the disappearance of an unidentified loricariid (suckermouth catfish) previously consumed by locals in the Puyango catchment, and found mercury levels above recommended limits in native cichlids and characiform fishes. Nonetheless, mercury levels in inhabitants of the region appear to be relatively low, possibly because the transformation of elemental mercury into toxic methyl-mercury appears to be low (Betancourt *et al*., 2005).

Mineral exploitation is widespread in the Amazon region (López *et al*., 2013). Exploitation of large gold deposits on the eastern side of the Andes in Zamora Chinchipe province, southern Ecuador, especially in Nambija and Chinapintza, has caused significant environmental problems. Although Amazonian river sediments can have naturally elevated levels of mercury (Mora *et al*., 2019; Webb *et al*., 2004), several studies have documented mercury concentrations in rivers close to mining operations that are several times background levels, including the Congüime, Nangaritza, Nambija, Zamora and Yacuambi Rivers (González-Merizalde *et al*., 2016; López-Blanco *et al*., 2015; Mora *et al*., 2018, 2019; Ramírez Requelme *et al*., 2003). Elevated concentrations of other metals like lead and manganese have also been documented (González-Merizalde *et al*., 2016; Mora *et al*., 2018, 2019), as have elevated concentrations of metals in people in the area (González-Merizalde *et al*., 2016). In the Cordillera del Cóndor, Santiago River basin, several large-scale mines are clearing large tracts of rainforest and displacing indigenous people (Federación Internacional por los Derechos Humanos, 2017; Pérez, 2019). Studies directly examining the impacts on freshwater fishes are urgently needed.

The negative effects of mining have also been reported for many years in Esmeraldas Province in north-western Ecuador (Figure 6) (Rebolledo & Jiménez-Prado, 2013). Illegal mining in the region has increased substantially since 2008 and largely occurs in the proximity of rivers, causing severe habitat degradation and conflict between miners and residents. It is estimated that approximately 57% of the original forest in the area has been affected (Lapierre Robles & Aguasanta Macías, 2019). By 2012, the mined area included 5709 ha directly subjected to mining activity and an area of 224,284 ha affected indirectly (Rebolledo & Jiménez-Prado, 2013). In a study carried out between 2015 and 2017 involving 32 sample sites along the Santiago-Cayapas River basin, all streams and estuaries sampled showed very high concentrations of aluminium and iron throughout the study period (Lapierre Robles & Aguasanta Macías, 2019). An estimated 4800 mining pools containing contaminated water have been left open in Esmeraldas Province (Moreno-Parra, 2019). Besides the serious damage to the physical structure of river banks, the high turbidity resulting from mining limits the entry of light into the water, severely affecting the growth of filamentous algae and phytoplankton. As a consequence, herbivorous bottom-feeding fishes like the loricariids *Chaetostoma marginatum* Regan 1904 (guañas), *Sturisomatichthys frenatus* (Boulenger 1902) (*palo secos*) and *Rineloricaria jubata* (Boulenger 1902) (mantequeros), and the freshwater gobies *Awaous transandeanus* (Günther 1861) (babosos) and *Sicydium* sp. (ñemes), are forced to consume detritus, ingesting metals present in high proportions in sediments as well. Elevated concentrations of metals have been detected in *C. marginatum*, an important food fish for local people in the upper Bogotá, Santiago basin (Rebolledo & Jiménez-Prado, 2013). Arsenic (0.5 mg kg^{-1}) was also detected in *Gobiomorus maculatus* (Günther 1859) (*Cagua de Concepción*) and mercury (0.2 mg kg^{-1}) in *Strongylura fluviatilis* (Regan 1903) (*Cherre*) (Rebolledo & Jiménez-Prado, 2013), both of which are also consumed locally.

FIGURE 6 Damage from mining operations. Santiago-Cayapas River drainage, Esmeraldas province, northwestern Ecuador

4.6 | Oil extraction

Large oil deposits were discovered in the Amazon region of Ecuador in the 1970s, and oil production became the main export for Ecuador by 2011 (Lessmann *et al*., 2016). Unfortunately, these oil deposits are under some of the most biodiverse Neotropical rainforest in the world and in territories inhabited by indigenous people (López *et al*., 2013). Oil extraction has a long history of causing accidental oil spills, leaching or improper dumping of waste products, loss of wildlife and health issues for local people (Anderson *et al*., 2019; Bass *et al*., 2010; Lessmann *et al*., 2016). Past oil-related environmental problems in Ecuador have resulted in large international lawsuits against oil companies and significant conflicts between oil interests and indigenous people (Cely, 2014; Moreno Vallejo, 2017). Indirect problems associated with oil extraction, like road construction, can also cause severe problems (Espinosa *et al*., 2018; Suárez *et al*., 2013). In the 2010s, the government of Ecuador launched a significant expansion of oil extraction activities, reviewed in Lessmann *et al*. (2016). Although the government initially sought international support to leave oil in the earth in environmentally sensitive areas like the Ishpingo-Tambococha-Tiputini (ITT) oil field in a remote section of Yasuní National Park, lack of international support made this inviable. Instead, many new blocks in Ecuador's southern Amazon region have been opened for oil concessions. Consequently, approximately 68% of the Amazon rainforest region now consists of oil extraction blocks. What is worse, the oil blocks occur within biologically rich reserves like Yasuní National Park, Cuyabeno Wildlife Reserve, Limoncocha Biological Reserve and Cofán Bermeo Ecological Reserve. Only about 16% of the Ecuadorian Amazon is now protected in nature reserves free of oil blocks (Lessmann *et al*., 2016).

There is surprisingly little research directly examining the impacts of oil extraction on fishes of the Ecuadorian Amazon. Moreno Vallejo (2017) examined contaminants associated with oil extraction in tissues from detritivorous loricariids and the predator *Hoplias* *malabaricus* (Bloch 1794) in rivers of the northern Amazon impacted by oil extraction and rivers of the southern Amazon where oil is not extracted. He did not find significant differences between regions but did find significant differences among sites, including in metals like Co, Ba, Cd and Hg, which he associated with oil spills. This is consistent with elevated Hg levels found in *H. malabaricus* collected near an oil spill site in the Corrientes River, Peruvian Amazon (Webb *et al*., 2015). In Moreno Vallejo's (2017) study, Hg levels were higher in *H. malabaricus* than in the loricariids, likely due to bioaccumulation in the predator *vs*. the primary consumer, and As and Hg concentrations were above permitted levels, indicating significant risks for human populations. Levels of Ba, Cd and Pb were particularly high in the Conde and Payacu Rivers. Mena Olmedo (2016) used a similar approach to examine contaminants in tissues of the freshwater prawn *Macrobrachium brasiliense* (Heller 1862), and also found elevated values at some sites.

4.7 | Dams

One of the most serious threats to Neotropical rivers is the continued construction of dams that impede the movement of fishes and sediments, and alter the abiotic and biotic conditions of rivers (Agostinho *et al*., 2008; Anderson *et al*., 2018; Baxter, 1977; Carvajal-Quintero *et al*., 2017; Sanz Ronda *et al*., 2009; Timpe & Kaplan, 2017; Winemiller *et al*., 2016; Zarfl *et al*., 2015). While some industrialized countries are removing their dams to restore natural ecosystem functions (O'Connor *et al*., 2015), hundreds of new dams are under construction or planned in some of the most biodiverse tropical countries (Anderson *et al*., 2018; Winemiller *et al*., 2016; Zarfl *et al*., 2015). Dam construction throughout Ecuador has accelerated in the last few decades as increasing hydroelectric power became a major government objective (Anderson *et al*., 2018; López *et al*., 2013) (Figure 7).

Problems associated with dams have been reported throughout Ecuador. In the Santiago River basin in the Ecuadorian southern Amazon region, the Paute Integral Hydroelectric Complex has been operating for more than 30 years (CELEC EP HIDROPAUTE, 2013). As occurs in other artificial reservoirs, the Centrales Molino and Mazar impoundments provide habitat for introduced species, accumulate sediment and have anoxic bottom water, which may affect species downstream when it is periodically released (El Comercio, 2009). Alteration of natural water flow patterns can also be severe (Figure 7d). In northern Ecuador, a hydroelectric power plant located in Manduriacu (border of Imbabura and Pichincha provinces) has been implicated in environmental problems downstream. The plant became operational in March 2015 (La Hora, 2016) and is supplied by the Guayllabamba River, which collects sewage from the entire city of Quito and its surroundings, and drains into the Blanco River, Esmeraldas basin. Since May 2016, there have been at least three massive fish kills linked to the release of water and accumulated sediments from the impoundment (La Hora, 2016). In the Atacames River drainage, a small coastal drainage basin in coastal Esmeraldas Province, two dams were built in the 2000s to collect water for irrigation. Unfortunately, the dams have become barriers for some species. In 2012, large numbers of *Astyanax ruberrimus* Eigenmann 1913, a characid known locally as *tacuana*, were documented attempting to migrate upstream, presumably for reproductive purposes, but could not pass the dam (Jiménez-Prado, 2012). Although other factors could be at play, by 2016 *A. ruberrimus* was no longer found in the Atacames basin and is possibly locally extinct there (Jiménez-Prado & Vásquez, 2021).

The Guayas basin in Western Ecuador harbours the largest artificial impoundment in the country, the Daule-Peripa multipurpose project, located 10 km upstream of the town of Pichincha at the confluence of the Daule and Peripa Rivers. The Daule-Peripa dam and associated structures were built in the 1980s to store water for agricultural use, for the transfer of water to water-deficient areas and for the generation of hydroelectric power (CELEC EP, 2013). It has a water storage capacity of 6000 m^3 and covers approximately 27,000 ha at capacity (CELEC EP, 2013). Despite its size, there has been very little published research on its impacts on fish communities in its area of influence. As is often the case for artificial impoundments, the Daule-Peripa impoundment harbours relatively large populations of edible fishes that are exploited by local fishermen (Aguirre *et al*., 2013; Baxter, 1977). However, much of the deep waters are anoxic and their release has been associated with low oxygen levels detected in the Daule River (Universidad Agraria del Ecuador, 2011). It is also an important component of a canal system for transferring water throughout much of the central portion of Western Ecuador, from Daule-Peripa west to the Peninsula of Santa Elena, south to the Chongón impoundment close to Guayaquil and east to the Baba River (CELEC EP, 2013), which has the potential to allow gene flow between previously unconnected fish populations in western Ecuador. Another more recent dam has been constructed in the eastern side of the Guayas basin on the Baba River (Cruz, 2013). Monitoring by the Instituto Público de Investigación de Acuicultura y Pesca suggests that species exhibiting migratory behaviours, such as *bocachico* (*I. humeralis*), *dama de montaña*, *dama blanca*, and *sábalo* (*Brycon* spp.), dica (*Pseudocurimata* spp.), *etc*., appear to be declining there (Willan Revelo, pers. obs.). The plight of the prochilodontid *I. humeralis*, a migratory species that is endemic to the Guayas basin and is one of the commercially most important freshwater fishes in Western Ecuador, is particularly concerning. At the start of the rainy season in Western Ecuador (November–December), *I. humeralis* forms large schools to begin its upstream migration, making it vulnerable to over exploitation. Monitoring data indicate that it has declined substantially upstream of the impoundment since the dam was constructed and fishing activities have largely ceased (Willan Revelo, pers. obs.). General environmental degradation in the area may also be playing a role.

The impacts of dams may not be limited to ecological processes. The transformation of a river into an artificial impoundment is a major form of habitat transformation resulting in substantial change in selective regimes. Several studies have documented significant

FIGURE 7 Dams have been constructed in rivers throughout Ecuador and more dams are planned. (a) View of impoundment formed by Daule-Peripa Dam, upper Guayas basin (western Ecuador). (b) Dam in the Baba River, Guayas drainage basin (western Ecuador). (c) Impoundment formed by the Chongon Dam outside of the city of Guayaquil (western Ecuador). (d) Daniel Palacios Dam (Paute Integral Hydroelectric Complex) showing river without water (Andes)

morphological changes associated with adaptation to conditions in artificial impoundments in other areas (Haas *et al*., 2010; Palkovacs *et al*., 2007; Svozil *et al*., 2020), including genetic changes (Franssen, 2011, 2012). Significant divergence in body shape between river and artificial impoundment populations has been reported in the predatory fish *Hoplias microlepis* (Günther 1864), with impoundment populations generally being more robust and differing in fin placement and size (Aguirre *et al*., 2013; Granda Pardo & Montero Loayza, 2015). Even greater changes in body shape may be occurring in the more active predatory fish *Brycon alburnus* Günther 1859 (Windsor Aguirre, unpublished data). Although phenotypic plasticity is likely at play, some genetic adaptation may also be occurring as has been observed in other populations subjected to strong selection (Bell & Aguirre, 2013; Hendry & Kinnison, 1999). If so, the flow of alleles favoured in artificial impoundments into river populations would be of concern given the potential for these alleles to be maladaptive in river habitats given the ecological differences between these habitats.

4.8 | Overfishing

Freshwater fisheries are widespread throughout Ecuador, and fishes are an important and often inexpensive source of protein for people in rural areas (Barnhill Les *et al*., 1974; Revelo & Laaz, 2012; Utreras, 2010) (Figure 8). Unfortunately, freshwater fisheries in Ecuador are often difficult to regulate, making overexploitation a constant threat. There are also few published data on long-term trends in freshwater fisheries catches, making it extremely difficult to assess the magnitude of the problem. However, it is broadly recognized that fisheries catches for commercially important species, like large Amazonian catfishes, have declined (Jácome-Negrete *et al*., 2018; Utreras, 2010).

In Western Ecuador, freshwater fisheries have been most important in the Guayas River basin, where catches are largely locally consumed (Barnhill Les *et al*., 1974; Revelo, 2010; Revelo & Laaz, 2012). The most important fisheries species in the Guayas basin include *Ichthyoelephas humeralis*, *Pseudocurimata* spp. and *Brycon* spp.

(Figure 1g), *Hoplias microlepis* (*guanchiche*), *Dormitator latifrons* (Richardson, 1844) (*chame*), *Leporinus ecuadorensis* (*ratón*), *Mesoheros* and *Andinoacara* (Figure 1r) (*viejas*), *Rhamdia* (Figure 1k) (*barbudo*), and introduced tilapia (Barnhill Les *et al*., 1974; Revelo, 2010). Although monitoring of the fisheries has been sporadic, fishermen universally indicate that major fisheries species have declined. The lack of long-term data makes the magnitude of the problem unclear. Fisheries in Los Ríos province have been followed most closely and show clear evidence of decline (Instituto Nacional de Pesca, 2012; Prado *et al*., 2012; Revelo, 2010; Revelo & Laaz, 2012). Use of illegal fishing gear like gill nets or illegal mesh sizes likely exacerbates the problem (Revelo, unpublished data).

Fisheries in the Amazon region are important as a critical source of food and because of the cultural importance of fishes to indigenous peoples of the region (Guarderas *et al*., 2013; Guarderas & Jácome-Negrete, 2013; Jácome-Negrete, 2013; Jácome-Negrete & Guarderas, 2005). The Amazon River fishery is a multispecies fishery with at least 36 species known to be exploited. Fisheries species composition differs among rivers, with the quantity and diversity being greatest in the Napo and Morona Rivers (Burgos-Morán *et al*., 2018). The greatest pressure is directed towards the large catfishes, especially pimelodids and loricariids, which make up approximately half of the species fished, and 50%–70% of the biomass (Burgos-Moran *et al*., 2011; Utreras, 2010; Utreras *et al*., 2012). Since fisheries catches are not properly monitored, there are no reliable annual catch data, only general tendencies derived from Amazonian market sales records and survey data collected from fishermen. These indicate a general decrease in the supply of Amazonian fish and unsustainable fishing practices. The situation of large catfishes seems particularly precarious (Utreras, 2010), but other groups are likely being affected. For example, Loomis (2017) conducted a survey of fisheries catches from the Limoncocha Lagoon over several weeks in April and May of 2017 and compared the results, based on 756 specimens from 23 species that were recorded, to catches reported from a 2002 census. Cynodontids, which had been highlighted in 2002 as a potential bioindicator of the health of the Limoncocha Lagoon, were completely absent from the 2017 catches. In addition, five of the top 10 species listed as having the highest nutritional/sale value in 2002 were also not collected in 2017 (*Calophysus macropterus*, *Leiarius marmoratus*, *Hypostomus micropunctatus*, *Brycon melanopterus* and *Potamorhina latior*). Although a longer study with temporal replication is needed to verify the results, these findings are disturbing. Data on important fisheries related to subsistence and recreational activities are not collected, despite estimates suggesting that these generate larger catches than commercial operations. Subsistence fishing is estimated to contribute approximately 250% more of the total fisheries catch than commercial fishing, while sport-fishing contributes between 3% and 5% of the total catch (Burgos-Moran *et al*., 2011).

FIGURE 8 Overfishing threatens native freshwater fishes throughout Ecuador. (a) Fishing net placed in the Guayas drainage basin, western Ecuador. (b) Fishes in a market of the Amazonian region

Overexploitation of Amazonian fisheries disproportionally affects indigenous people that have depended on fish in the region for 1000 of years. There are 10 indigenous nationalities in the Ecuadorian Amazon (Cofan, Secoya, Siona, Waorani, Shiwiar, Andoa, Sápara, Achuar, Shuar and Kichwa) that use over 100 fish species in their territories for a variety of purposes including for food, as bait and fishing amulets, to manufacture tools for hunting and other artefacts, for medicinal purposes and in rituals (Burgos-Morán *et al*., 2018; Wildlife Conservation Society, 2012). Indigenous groups carry out fishing tasks in an artisanal way, using simple fishing gear such as hooks, nylon nets, fishing rods, harpoons and arrows. However, sometimes they use ichthyotoxic plants like barbasco (*Lonchocarpus nicou*), insecticides or even dynamite (Bremner & Lu, 2006; Burgos-Morán *et al*., 2018; Durango Tello, 2013; Sirén, 2011; Wildlife Conservation Society, 2012). The *per capita* consumption of fish differs greatly within and among indigenous nations and is influenced by the altitudinal range at which indigenous communities are established within a river basin, with communities at lower elevation tending to consume more fish (Bustamante & Sierra, 2007; Descola, 1996; Durango Tello, 2013; Vasco & Sirén, 2019; Wildlife Conservation Society, 2012).

Developing better monitoring practices for freshwater fisheries throughout Ecuador will be critical to ensure their long-term viability, as well as the health of aquatic ecosystems.

4.9 | Introduced species

The negative effects of non-native species has been well documented (Cucherousset & Olden, 2011; Gozlan *et al*., 2010; Gozlan & Newton, 2009; IUCN, 2009). Barriga (2012) identified 13 species of fish introduced in Ecuador including salmonids, cyprinids, several poeciliids, a centrarchid and several cichlids (Figure 9). Native Ecuadorian fish species have also been introduced to new regions, like the Cachama *Piaractus brachypomus* (Cuvier 1817) and Paiche *Arapaima gigas* (Schinz 1822) (Figure 1u), which have been introduced from the Amazon region to Western Ecuador (the latter into culture facilities) (Barriga, 2012; Revelo & Laaz, 2012), and the cichlid *Andinoacara rivulatus* (Figure 1r), which is native to Western Ecuador and has been introduced to the Amazon region (Nugra *et al*., 2018).

Several African Tilapia species (*Oreochromis* spp.) have been introduced to Neotropical ecosystems, including Nile *O. niloticus* (Linnaeus 1758), blue *O. aureus* (Steindachner 1864), Mozambique *O. mossambicus* (Peters 1852) and Tanzania tilapia *O. urolepis* (Norman 1922), as well as their hybrids (Figure 9a). Tilapia are established in lowland rivers throughout Ecuador (Barriga, 2012; Jácome *et al*., 2019). *O. mossambicus* was the first tilapia species introduced to Ecuador in 1965 in Santo Domingo de los Colorados (Western Ecuador) (Ovchynnyk, 1967). It escaped from captivity shortly after and some recaptured individuals were introduced to the Yaguarcocha Lake in northern Ecuador (Marcillo Gallino & Landívar Zambrano, 2008). *O. niloticus* was introduced from Brazil in 1974 and red tilapia hybrids were introduced in the 1980s (Marcillo Gallino & Landívar Zambrano, 2008). Tilapia are now a major aquiculture species in Ecuador with a peak production of 27,315,395 lbs achieved in 2007, converting Ecuador into the largest tilapia producer in Latin America (Jácome *et al*., 2019). Established tilapia populations occur throughout the country and are especially common in disturbed aquatic ecosystems (Barriga, 2012; Jimenez-Prado *et al*., 2015; Revelo & Laaz, 2012). For example, artisanal fishermen in the Guayas River basin often collect *Oreochromis* spp. in large numbers and at larger sizes than native fish, and they are also frequently captured in artificial impoundments and estuaries (Laaz *et al*., 2009; Mejia Burgos, 2015; Pacheco-Bedoya, 2012). Although there has been concern about the ecological impact of tilapia on Ecuadorian ecosystems for decades, published studies on its ecological impact are sparse.

Rainbow trout (*Oncorhynchus mykiss*) are native to Pacific watersheds of North America from Alaska to Mexico (Figure 9b). Since 1874, they have been introduced to all continents except Antarctica for sport fishing and aquaculture. In Ecuador, the introduction of rainbow trout began in 1932 in rivers, streams and lakes of the inter-Andean region (Illescas Merchán, 2011), and they have become a popular recreational fishing and food fish (Calero & Villavicencio, 2016; Gallardo Pólit, 2012; Mora *et al*., 2009; Nugra Salazar, 2014). Over 200 hatcheries distributed in 12 provinces exist in Ecuador, producing a total of 982.3 tons per year, which represents revenues of ~US $2,678,997 (Morales Lozada, 2013; Salazar Duque *et al*., 2019; Tognelli *et al*., 2016). Rainbow trout in Ecuador typically inhabit streams from 1200 m to over 3000 m above sea level, where they feed mainly on benthic organisms, insects, molluscs, fish eggs and

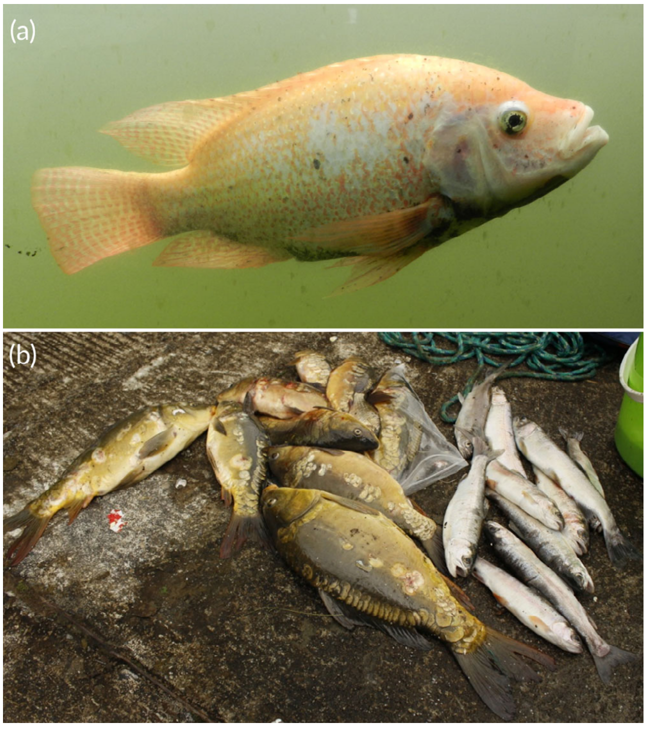

FIGURE 9 Introduced species. (a) Tilapia, *Oreochromis* sp., were intentionally introduced as an aquaculture species in the 1970s and now occur throughout Ecuador. (b) Carp *Cyprinus carpio* is a widely introduced ornamental species, while rainbow trout, *Oncorhynchus mykiss*, is a major sport and food fish that is very common in cold, high-elevation Andean streams

small fishes (Anchacaisa Velasco, 2015). They are hardy and can survive in different habitats, spawn readily, grow quickly and are tolerant of a wide range of environmental conditions. Water temperature is one of the major limiting factors. Although they can withstand wide temperature ranges, spawning and growth occur primarily within a narrower range of 9–14°C (FAO, 2009). Rainbow trout threaten native species including fish and amphibians by altering trophic networks and directly feeding on native fish species (Krynak *et al*., 2020; Martín-Torrijos *et al*., 2016; Tognelli *et al*., 2016; Vimos *et al*., 2015; Vimos Lojano, 2010). They have been implicated in the decline of endemic *Astroblepus* in Cajas National Park (Davila Cevallos & Garces Acosta, 2007; Gobierno Autonomo Descentralizado Cuenca, ETAPA, 2018) and the endemic, critically endangered frog *Atelopus nanay* Coloma 2002 (Programa de las Naciones Unidas para el Desarrollo Gobierno de Ecuador, 2018).

Less widely distributed non-native species can also cause problems. The largemouth bass *Micropterus salmoides* (Lacepède 1802), native to North America, was introduced into Lago San Pablo (San Pablo Lake), the second largest lake in Ecuador located approximately 100 km north of Quito, for sport fishing around 1964 and has been implicated in the decline of populations of the critically endangered *Astroblepus ubidiai* (Arguello & Jimenez-Prado, 2016; Meschkat, 1975; Restrepo-Santamaría & Álvarez-León, 2013). Residents of the area indicate that largemouth bass occur throughout the lake and neighbouring streams, where they feed on fish, insects and vegetation. Locals use largemouth bass as a food fish and for medicinal purposes, and indicate that the size and number of fish has declined in recent years (Katherin Miranda, pers. comm.). Non-native Poeciliids were widely introduced to Ecuador for mosquito control in the early 1970s (WHO, 2003) and as ornamental species to this day. Non-native poeciliids appear to be quite frequent in some basins, where they can have severe impacts on native species. This appears to be the case for *Poecilia gilli* (Kner, 1863), which has displaced *Pseudopoecilia fria* (Eigenmann & Henn, 1914) from the low and mid-basin regions of the Atacames River (northwestern Ecuador), and has also been implicated in morphological changes observed in the surviving populations, such as a decrease in body size and the anterior displacement of the pectoral fin (Jiménez-Prado *et al*., 2020). Studying the impacts of introduced fishes on the ecology and evolution of native species is a major direction of future research.

4.10 | Climate change

Although concerns about climate change often focus on its effects at high latitudes, tropical ecosystems are also under serious threat (Báez *et al*., 2016; Herzog *et al*., 2011; Vuille *et al*., 2008). Changes in climate and precipitation patterns, changes in the frequency and intensity of flooding and droughts, the impact of rising sea levels on low-lying coastal areas, and the effects of rising temperatures on high-elevation Andean ecosystems are major concerns for freshwater fishes (Kaufman, 2019). Most research on this topic in Ecuador has focused on high-elevation Andean ecosystems, where the temperature has risen approximately 0.1°C every decade for the last 70 years, and models predict temperature increases of as much as 4.5–5°C by the end of the 21st century (Vuille *et al*., 2008). Moreover, declines in glacial runoff in the Ecuadorian Andes are expected to be among the most pronounced in the world (Cauvy-Fraunié *et al*., 2016). Melting glaciers are a serious risk for these ecosystems because of the resulting changes in water temperature, and water flow volume and timing (Buytaert *et al*., 2006). They also constitute a serious threat for the water security of human populations in the region (Vuille *et al*., 2008).

Research on the effects of climate change on freshwater fish communities in Ecuador is sparse. Studies conducted on macroinvertebrate communities at high-elevation sites close to glacial influence indicate the potential for strong but variable effects (Cauvy-Fraunié *et al*., 2014, 2015, 2016; Jacobsen *et al*., 2014). With the exception of *Astroblepus* spp. and *Grundulus quitoensis* Roman-Valencia, Ruiz & Barriga, 2005, native fish species in Ecuador mostly occur below 2200 m (Maldonado *et al*., 2011), that is, relatively far downstream from where glacial influence is strongest. Nonetheless, Neotropical fishes are strongly influenced by hydrological cycles and temperature changes (Correa & Winemiller, 2018; Oberdorff *et al*., 2015; Silva & Stewart, 2017), thus, many high and mid-elevation Andean fish species may be affected (Herrera-R *et al*., 2020; Kaufman, 2019). Fish in small mountain streams also have limited opportunities for habitat tracking and dispersal (Herrera-R *et al*., 2020; Taniwaki *et al*., 2017). Recent studies from other areas suggest a range of potential impacts including changes in the distribution of species and trophic assemblages (Garzke *et al*., 2019; Herrera-R *et al*., 2020), the age of sexual maturity (Shahjahan *et al*., 2017), metabolic rates (Petitjean *et al*., 2019), nutrient composition (Colombo *et al*., 2019), contaminant absorption (Schartup *et al*., 2019) and alterations in sex ratios (Fernandino & Hattori, 2019). Rarer cold water species at high elevations are likely to be impacted the most (Buisson *et al*., 2008; Herrera-R *et al*., 2020), suggesting that high-elevation *Astroblepus* spp. (Figure 1m) may be particularly vulnerable. In Ecuador, there are 24 recognized species of *Astroblepus*, of which 17 are listed as endemic (Barriga, 2012). Very little is known about the ecology or distribution of most species of Ecuadorian *Astroblepus*, a problem that is made worse by the taxonomic uncertainties plaguing this genus (Ochoa *et al*., 2020; Schaefer *et al*., 2011). Given the magnitude of the threat and the high rates of endemism, studies on the impacts of climate change on Andean fishes are urgently needed, as is a comprehensive taxonomic review of the genus *Astroblepus* in the Ecuadorian Andes.

Rising seawater levels or increasing storm intensity can also threaten freshwater fishes in low-lying coastal areas, including the small drainages west of the coastal mountain ranges that may be inhabited by locally adapted populations or endemic species (Aguirre *et al*., 2019a; Cucalón Tamayo, 2019; Jiménez-Prado & Aguirre, 2021). We are not aware of studies on this topic in Ecuador.

5 | PROSPECTS AND RECOMMENDATIONS

The threats to the freshwater fishes of Ecuador are diverse and widespread. Many aquatic ecosystems throughout the country have already been severely degraded. Unless drastic actions are taken, the long-term prospects are not good. Below we make recommendations for actions needed to ensure the long-term preservation of Ecuador's freshwater fishes.

5.1 | Enforce existing conservation laws

Ecuador's Constitution is among the most progressive on Earth in terms of the conservation of nature and specifically indicates that the government shall protect the right of the people to live in an ecologically healthy environment and will guarantee the preservation of nature. It also advocates for the conservation of ecosystems and biodiversity, the prevention of environmental contamination, the recovery of degraded natural spaces, the sustainable management of natural resources and the establishment of a national system of protected areas to maintain biodiversity and ecosystem services (Asamblea Constituyente, 2008; Mila Maldonado & Yánez Yánez, 2019). However, these laws are often not enforced, negatively affecting all Ecuadorians, especially the poor in rural areas that rely the most on the ecosystem services that healthy rivers provide. The government of Ecuador must work with local communities to prioritize the conservation of freshwater ecosystems as mandated by the Constitution and invest significant resources to enforce existing environmental laws. This means increasing investment in existing institutions like the Instituto Público de Investigación de Acuicultura y Pesca and the Ministerio del Ambiente y Agua, and expanding their ability to work with law enforcement agencies like the Unidad de Protección de Medio Ambiente (UPMA) to enforce conservation laws. It would also be beneficial to find ways to increase collaboration between these institutions and the Instituto Nacional de Biodiversidad (INABIO), Red Ecuatoriana de Ictiología (REI), universities and environmental organizations to improve identification of regulatory priorities.

5.2 | Restore degraded aquatic ecosystems

Recognizing the state of the world's ecosystems, ambitious goals have been set globally for their restoration (Suding *et al*., 2015). Many of Ecuador's aquatic ecosystems are also severely degraded so conserving them in their current state is not enough. Efforts must be made to restore them. Several studies have aimed to identify priority conservation areas for Ecuador and can help guide these efforts (Campos *et al*., 2013; Cuesta *et al*., 2017; Lessmann *et al*., 2014; Sierra *et al*., 2002). In addition, Ecuador's existing national protected areas system includes nearly 20% of its area (Cuesta *et al*., 2017) and constitutes another base from which restoration efforts can be expanded. However, large-scale conservation efforts developed for terrestrial landscapes often neglect aquatic ecosystems (Anderson & Maldonado-Ocampo, 2011; Myers *et al*., 2000), so restoration efforts that prioritize the needs of aquatic ecosystems will be critical. The nature of rivers also complicates restoration efforts because problems in the upper portions of drainage basins may affect sites far downstream and some ecologically important fishes are migratory. Thus, approaches at the scale of the drainage basin are needed, and the national government or organizations that can coordinate actions across provinces must assume leadership roles. In addition, restoration efforts often involve restocking programs for locally or ecologically extinct species (Aprahamian *et al*., 2003). Because of the very high levels of endemism in Ecuador, any such efforts should carefully assess the evolutionary history of the populations involved to avoid introducing fish with maladaptive alleles (Landínez-García *et al*., 2020).

5.3 | Establish a national monitoring system for freshwater fishes

A serious problem impeding conservation efforts in Ecuador is the lack of standardized historical data on the natural baseline for freshwater ecosystems. Monitoring of freshwater fishes in Ecuador has often been sporadic, regional, based on different methods and focused primarily on commercially important species. As a consequence, there are almost no data on changes in abundance, fisheries catches or geographic ranges for the freshwater fishes in Ecuador, making it very difficult to quantify how severely freshwater fishes have been impacted by the degradation and loss of aquatic habitat throughout the country. Many aquatic ecosystems are already severely degraded so it is also difficult to understand what has been lost without standardized baseline data of what the ecosystems were like prior to the degradation. The societal perspective on what is natural also shifts over time. Because younger generations have only known ecosystems in their degraded states they will often mistake this for natural, and baselines continue to shift generation after generation as ecosystems degrade (Jackson *et al*., 2011; Pauly, 1995).

One of the most important conservation actions that can be taken is to establish a standardized national monitoring system for freshwater ecosystems. This would establish a baseline that can be used from this point forward to monitor changes in species ranges, abundance, size distribution, reproductive output and timing, the introduction of non-native species, and emergence of fish diseases. Dedicated monitoring programs like these are routine in other countries, and provide invaluable information on the health and changes in aquatic communities. The monitoring system could be developed by investment of resources within an existing government agency like the Instituto Público de Investigación de Acuicultura y Pesca, the Ministerio del Ambiente y Agua or the Instituto Nacional de Biodiversidad. Alternatively, an independent program could be developed with universities, research institutions or non-profit organizations. Publishing the data would be important to allow interested parties to help monitor trends.

5.4 | Fill gaps in knowledge of natural history, ecology and taxonomy

With some notable exceptions (*e.g*., Barnhill Les *et al*., 1974; Herrera-Madrid *et al*., 2020; Valdiviezo Rivera *et al*., 2017; Vélez-Espino, 2003), there are very few detailed studies on the natural history and ecology of most Ecuadorian freshwater fishes. There are also uncertainties about the distribution of some species (Aguirre *et al*., 2014, 2017; Meza-Vargas *et al*., 2019; Valdiviezo Rivera, 2014; Valdiviezo-Rivera *et al*., 2020) and significant taxonomic uncertainty in many groups (*e.g*., Arbour *et al*., 2014; Lujan *et al*., 2015a; Provenzano & Barriga-Salazar, 2018; Román-Valencia *et al*., 2013, 2015; Tan & Armbruster, 2012; Tobes *et al*., 2020). A factor complicating taxonomic research is the lack of support for natural history collections. Although there are established fish collections [*e.g*., Escuela Politécnica Nacional (Barriga Salazar & Argüello, 2019) and the Instituto Nacional de Biodiversidad], most fish collections in Ecuador are maintained by individual researchers with little support. There are also poorly explored regions in Ecuador, like the small drainage basins on the western slopes of the Cordillera Chongón-Colonche and some tributaries in the Amazon region. One possible avenue to stimulate needed research would be for Ecuadorian and international ichthyologists to cooperate on the development of a comprehensive book on the fishes of Ecuador. Progress in this direction has already been made with the publication of a book on the fishes of Western Ecuador (Jimenez-Prado *et al*., 2015) and of a field guide to the fishes of the Amazon, Orinoco and Guianas (van der Sleen & Albert, 2018). Although completing the necessary work on Ecuador's Amazonian fish species would require considerable effort, it is possible and would constitute a major step forward for Ecuadorian and Neotropical ichthyology.

Accessibility to many tools that are critical for biodiversity research is improving significantly. Methods for DNA sequencing are now extremely robust, and new low-cost genomic sequencing technologies are emerging that allow the creation of mobile genomics laboratories (Krehenwinkel *et al*., 2019). Studies employing molecular markers with Ecuadorian freshwater fishes are still relatively sparse and constitute a major direction for future growth (Cucalón Tamayo, 2019; Cucalón Tamayo & Bajaña Zambrano, 2015; Escobar-Camacho *et al*., 2015; Loh *et al*., 2014; Lujan *et al*., 2015b; Malato *et al*., 2017; Vu *et al*., 2013). Other biodiversity research tools like geographic information systems (Menéndez-Guerrero & Graham, 2013) and geometric morphometrics (Aguirre & Jiménez Prado, 2018; Zelditch *et al*., 2012) require minimal laboratory resources and can provide great insights into the ecology and evolution of freshwater fishes. There is also a growing open science movement that has made sophisticated data science tools openly available online (Jézéquel *et al*., 2020; National Center for Biotechnology, 2021; Python Software Foundation, 2021; R Core Team, 2021; SlicerMorph, 2021). The increase in accessibility to these tools provides an opportunity to fill substantial knowledge gaps on the ecology and evolution of Ecuadorian freshwater fishes. In addition, funding for natural history and taxonomy has been in decline in the United States and Europe for some time (Dalton, 2003; Futuyma, 1998; Wägele *et al*., 2011; Yong, 2016). The resulting voids must be filled. International collaborations should help transfer expertise to Ecuadorian ichthyologists to ensure the long-term viability of biodiversity research in Ecuador.

5.5 | Promote community outreach and citizen science

Mobilizing citizens to advocate for the sustainable management of natural resources is critical for long-term conservation efforts. Ecuador has a rich history of community outreach for biological research and conservation (de Koning *et al*., 2011; Ministerio del Ambiente del Ecuador, 2010). However, the low income levels in the country can complicate public engagement. Facilitating public participation in income-generating activities related to natural ecosystems (Stronza & Pêgas, 2008) and clearly communicating the economic value of the ecosystem services (Wallace, 2007) is vital. For example, communities that depend on ecotourism for income tend to be particularly fierce advocates for natural landscapes. Work with fishing cooperatives to promote sustainable management and report external threats to fishing stocks could help conserve these. Recreational fishermen can also play important roles as advocates for the conservation of aquatic ecosystems when properly engaged (Granek *et al*., 2008) and represent an underutilized resource in Ecuador. In recent years, citizen science has emerged as a powerful platform for data collection and public engagement (Aceves-Bueno *et al*., 2015; Golinelli *et al*., 2015). The Instituto Nacional de Biodiversidad has promoted citizen science initiatives and entered into an accord in 2019 with the Academy of Natural Sciences of California and the National Geographic Society to administer the iNaturalist network in Ecuador (INABIO, 2019). This has resulted in range expansions, discovery of species that were thought extinct, new records of non-native species and broad collection of phenological data. There are also multinational efforts like the Citizen Science for the Amazon project, which aims to track migrations of Amazonian fish (Citizen Science for the Amazon, 2021). Promoting citizen science projects on freshwater fishes could be a powerful tool to fill knowledge gaps on their distribution and ecology, and help promote public engagement.

6 | CONCLUSIONS

The freshwater fishes of Ecuador are severely threatened by a number of anthropogenic factors and many aquatic ecosystems have already been severely degraded. A lack of information complicates efforts to estimate the magnitude of the problem but immediate action is clearly needed, including enforcement of existing environmental laws, restoration of degraded aquatic ecosystems, development of a national monitoring system, increased investment in research, and promotion of public participation in research and conservation efforts. Freshwater fishes are an important component of the biological and cultural legacy of the Ecuadorian people. Conserving them for future generations is vital.

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