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Conservation of migratory fishes in the Amazon basin

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Abstract

1. The Amazon basin hosts the Earth's highest diversity of freshwater fish. Fish species have adapted to the basin's size and seasonal dynamics by displaying a broad range of migratory behaviour, but they are under increasing threats; however, no study to date has assessed threats and conservation of Amazonian migratory fishes.
2. Here, the available knowledge on the diversity of migratory behaviour in Amazonian fishes is synthesized, including the geographical scales at which they occur, their drivers and timing, and life stage at which they are performed.
3. Migratory fishes are integral components of Amazonian society. They contribute about 93% (range 77–99%) of the fisheries landings in the basin, amounting to ∼US$436 million annually.
4. These valuable fish populations are mainly threatened by growing trends of over-exploitation, deforestation, climate change, and hydroelectric dam development.

Most Amazonian migratory fish have key ecological roles as apex predators, ecological engineers, or seed-dispersal species. Reducing their population sizes could induce cascading effects with implications for ecosystem stability and associated services.

5. Conserving Amazonian migratory fishes requires a broad portfolio of research, management, and conservation actions, within an ecosystem-based management framework at the basin scale. This would require trans-frontier coordination and recognition of the crucial importance of freshwater ecosystems and their connectivity.
6. Existing areas where fishing is allowed could be coupled with a chain of freshwater protected areas. Management of commercial and subsistence species also needs fisheries activities to be monitored in the Amazonian cities and in the floodplain communities to allow assessments of the status of target species, and the identification of management units or stocks. Ensuring that existing and future fisheries management rules are effective implies the voluntary participation of fishers, which can be achieved by increasing the effectiveness and coverage of adaptive community-based management schemes.

KEYWORDS
biodiversity, fisheries management, hydroelectric dams, overexploitation, societal importance, threats

1 | INTRODUCTION

Recent reviews have shown that most migratory animals across the planet are suffering major population declines, more so than related non-migratory species (Bauer & Hoye, 2014; Lennox et al., 2019). They have also emphasized the critical ecological role of animal migrations for ecosystem stability and functioning, and the universality of the causes driving their decline: habitat loss, barriers to migrations, overexploitation, and climate change. Animal migrations are notoriously difficult to define, and classic examples involving large-scale movements represent extreme cases rather than the rule (Dingle & Drake, 2007). Here, based on Dingle and Drake (2007), Lucas and Baras (2001), and McIntyre et al. (2016), migrations are considered as periodic or seasonal synchronized movements of adaptive value (critical for individual fitness and population persistence) between two or more separate habitats involving a large portion of the population and which are repeated within or across generations. Migratory species rely on multiple, distant but interconnected habitats during their life cycle, which has been termed 'triple jeopardy', illustrating their dependence on at least two distant habitats and on the corridor that relates them (McIntyre et al., 2016). Unlike flying or terrestrial animals, the movement of freshwater fishes is highly constrained by the linear and hierarchical structure of freshwater networks, and their migration corridors can be easily blocked by human causes. As a consequence, freshwater migratory fishes, which sustain vitally important fisheries for millions of people across the world, are among the most endangered of freshwater biota (Dudgeon et al., 2006).

Human impacts on migratory fish species are of growing concern in the Amazon basin, which hosts the world's highest freshwater fish species richness, with 2,406 species, representing 15% of the world's freshwater fishes (Jézéquel et al., 2020). Nearly all migratory fish species in the Amazon are considered to be potamodromous, migrating between different and often distant freshwater habitats to complete their life cycles. Many migratory movements are synchronized with the 'flood pulse' of Amazonian rivers (Junk, Bayley, & Sparks, 1989), which creates marked seasonal water-level variations to which fish species have adapted. The most conspicuous commercial species, such as the large and medium-sized Characiformes (e.g. *Prochilodus*, *Collossoma*) and the large goliath catfishes (e.g. *Brachyplatystoma*) perform medium- to long-distance migrations in the Amazon basin that have received most of the attention to date (Barthem & Goulding, 1997; Carolsfeld, Harvey, Ross, & Baer, 2003). However, the species that perform seasonal synchronized movements at local scales between the river channels and the flooded environments, such as many floodplain species, can also be considered migratory. This is because their non-random lateral movements involve the repetitive use of separate habitats that are essential to their feeding and reproductive success, and hence to the completion of their life cycles (Fernandes, 1997; Lucas & Baras, 2001; Osorio et al., 2011; Winemiller & Jepsen, 1998).

Given the diversity of Amazon fishes, the complexity of their life cycles, and the growing human pressures, there is a major need to synthesize critically available information to assess prospects for conserving Amazonian migratory fishes. This article addresses five questions: (i) What is the diversity of migratory behaviour among Amazonian fishes? (ii) What is the societal importance of migratory fishes in the Amazon basin? (iii) What factors threaten migratory species in the Amazon basin? (iv) What are the potential ecosystem impacts of extirpation or strongly reduced populations of migratory fishes in the Amazon basin? (v) What are the challenges in research, management, and conservation to preserve migratory species in the Amazon basin?

2 | DIVERSITY OF MIGRATORY BEHAVIOUR IN AMAZONIAN FISHES

2.1 | Diversity

The freshwater fish fauna of the Amazon (excluding its coastal zones) contains an estimated 2,406 valid species, including 1,402 endemic species representing 514 genera, 56 families, and 15 orders (Jézéquel et al., 2020). Of those, at least 172 species (~7.1% of all species in the basin) belonging to seven orders (~46.7%), 26 families (~46.4%), and 90 genera (~17.5%) perform potamodromous migrations (Supporting Information Table S1). Most migratory species belong to the orders Characiformes (60.5%) and Siluriformes (29.7%).

2.2 | Scales and types

The geographical scale of fish movements in the Amazon basin is often related to the direction of their migrations, which can be longitudinal (long and medium distance) or lateral (short distance) (Figure 1). Longitudinal migrations occur within the upstream–downstream gradient of rivers in both directions and can connect different parts of a river (upstream with downstream) or even the estuary or the main river channels with the headwaters (e.g. Andes,

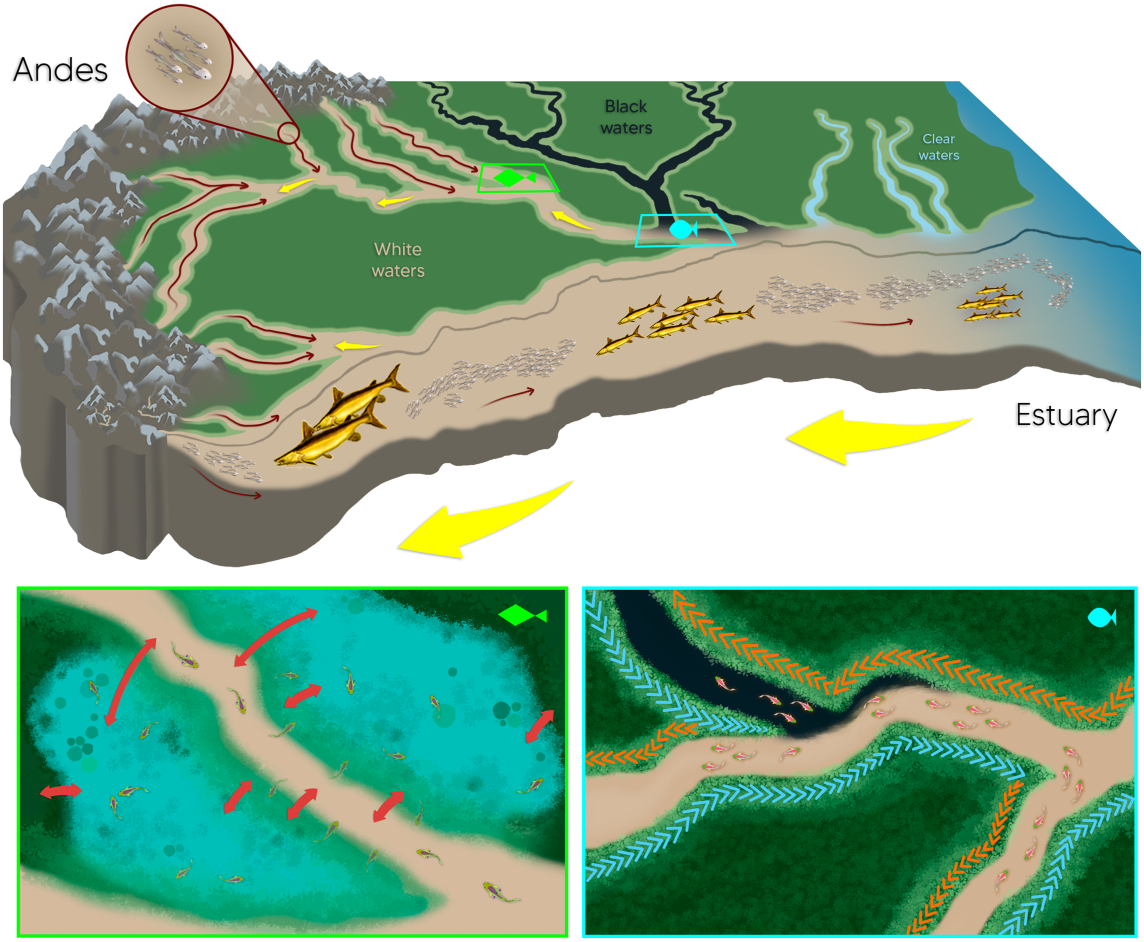

FIGURE 1 Illustration of the main fish migratory patterns in the Amazon basin (see Section 2 for details). The main graph represents the long-distance migrations (several thousand kilometres) of goliath catfishes, with larvae (brown loop) drifting down (brown arrows) from their hatching areas in the white waters of the Andean piedmont to their nursery areas in the Amazon estuary, where they will feed and grow a few years before migrating back to their breeding areas in the Andean piedmont (large and slender yellow arrows). The blue fish rectangle illustrates the medium-distance migrations (several hundred kilometres), exemplified by the *Prochilodus* spp. and *Semaprochilodus* spp. upstream movements (orange arrows) and downstream movements (blue arrows) between nutrient-poor black water and nutrient-rich white-water tributaries. The green fish rectangle illustrates the small distance lateral migrations (a few kilometres) performed by most species between main rivers and their floodplains, comprising a wide array of both permanently (oxbow lakes) and temporarily flooded environments (forests and savannahs)

Precambrian shields) or smaller tributaries (e.g. terra firme streams). Lateral migrations occur among habitats of river floodplains, including the main river channels and lakes, connecting channels, and various vegetated habitats, such as flooded forests (Fernandes, 1997; Osorio et al., 2011). Whereas a few species (e.g. *Brachyplatystoma*) perform only long-distance longitudinal migrations, some species perform both longitudinal and lateral migrations (e.g. Characiformes), and some perform mainly lateral migrations (e.g. Osteoglossiformes).

The longest longitudinal migrations known in freshwater ecosystems are performed by a group of large-bodied (1–3 m) goliath catfishes of the genus *Brachyplatystoma* (Barthem & Goulding, 1997; Barthem et al., 2017; Hauser, 2018; Hauser et al., 2019). One species, *Brachyplatystoma rousseauxii*, performs a trans-Amazonian round-trip migration of up ∼12,000 km between its hatching areas in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru and its nursery in the lower Amazon and estuary in Brazil (Barthem & Goulding, 1997; Barthem et al., 2017). In this exceptional migration, most adult fish return to the geographical area (sub-basin) where they were hatched (Duponchelle et al., 2016; Hauser et al., 2020), a process called 'natal homing'. Intermediate migrations on the scale of hundreds of kilometres are performed by several species of the orders Siluriformes, Characiformes, and Clupeiformes, for reproductive or feeding purposes between the floodplains and river channel, headwaters, and tributaries (see synthesis by Araujo-Lima & Ruffino, 2003; Diaz-Sarmiento & Alvarez-León, 2003; Figure 1). Some of the best-documented examples of these migrations come from the prochilodontids. Juveniles of *Prochilodus nigricans* are estimated to travel a minimum of 500 km upstream from floodplains towards western Amazonia (Silva & Stewart, 2017). Similarly, *Semaprochilodus* spp. travel up to 250 km upstream and downstream between nutrient-poor water where they feed and white-water river channels where they reproduce in central Amazonia (Ribeiro & Petrere, 1990).

Short migrations of only a few kilometres between habitats of the main river and the floodplains are usually referred to as lateral migrations. They are performed by most migratory Characiformes (Araujo-Lima & Ruffino, 2003; Diaz-Sarmiento & Alvarez-León, 2003; Fernandes, 1997; Goulding, 1980). Osteoglossiformes, such as *Arapaima*, have been shown to move synchronically through a total of eight distinct river floodplain habitats over the course of the flood pulse, closely following river water levels (Castello, 2008).

2.3 | Drivers

Fish migrate for three main purposes: reproduction, feeding, and survival; however, distinguishing among these drivers is often challenging (Lucas & Baras, 2001; McIntyre et al., 2016). In the Amazon basin, fish migrations are intimately linked to seasonal fluctuations of the hydrological regime (Goulding, 1980; Junk et al., 1989). Reproductive migrations of many Characiformes species are synchronized with the rainy season and rising waters, presumably to optimize environmental conditions for the hatching of eggs, growth of larvae and juveniles, and survival in general. Reproductive migrations can involve lateral movement between main channels and floodplains, such as in some piranha species, which lay their eggs on newly submerged vegetation (Uetanabaro, Wang, & Abe, 1993). In longitudinal reproductive migrations of Characiformes, adults of most species move downstream during rising waters from nutrient-poor black- or clear-water tributaries into white-water rivers' mainstems to spawn (Araujo-Lima & Ruffino, 2003; Diaz-Sarmiento & Alvarez-León, 2003; Ribeiro & Petrere, 1990). Longitudinal reproductive migrations of most large Siluriformes are carried out upstream, towards the Andean piedmont (Barthem et al., 2017; Barthem & Goulding, 1997; Duponchelle et al., 2016; Hauser et al., 2019; Hauser et al., 2020). White-water river mainstems mainly serve as highways for larvae drifting into nursery grounds located downstream in floodplains during the high-water season (Araujo-Lima & Oliveira, 1998; Lima & Araujo-Lima, 2004). White-water river floodplains and the estuary are also richer in nutrients and more productive than black- and clear-water systems, offering better conditions as nursery areas; juveniles of many migratory fish in the Amazon are only found in these habitats (Lima & Araujo-Lima, 2004).

Feeding migrations occur mostly during high waters, when, through lateral movements, adults of many frugivorous species (e.g. Serrasalmidae, Bryconidae) enter floodplains during high waters to benefit from the newly available habitat and feed on fruits falling from the inundated forest (Correa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015).

2.4 | Timing and fish life stages

Migrations occur at different life stages with different durations across the life span of Amazonian fish species. The trans-Amazonian migration of juvenile and sub-adult *B. rousseauxii* from their nursery areas (in the Amazon estuary and lower portion of the Amazon) to their adult feeding and breeding sites (in white-water tributaries of Bolivia, Colombia, Ecuador, and Peru) is a unique event that lasts for about 2 years. Once there, adults can move between different headwater tributaries, but they usually do not go back to central or lower Amazonia (Duponchelle et al., 2016; Hauser, 2018; Hauser et al., 2018). Another example, although this one lasts only a few weeks, is the ∼400 km upstream migration of juvenile pencil catfish, *Trichomycterus barbouri*, or chipi chipi, from the floodplains of the Beni River in Bolivia towards Andean foothill forest streams and rivers, where they will live as adults (Miranda-Chumacero, Álvarez, Luna, Wallace, & Painter, 2015). These examples are two of the most extreme cases in the length range of Amazonian migratory species: *B. rousseauxii* is one of the largest species in the Amazon basin, reaching over 1.5 m, although its length does not usually surpass 1.1 m length during its trans-Amazonian migration (Hauser et al., 2018), whereas *T. barbouri* measures no more than 3.3 cm when performing its spectacular upstream migration, which represents a much greater individual effort (Miranda-Chumacero et al., 2015).

Reproductive and feeding migrations performed seasonally at the adult stage usually occur each year for most species, which potentially spawn many times during their lives. Most migratory species in the Amazon basin are indeed iteroparous, as opposed to the semelparous reproductive strategy that consists of a single reproductive event during the lifetime, as exemplified by Gymnotiformes in the Amazon basin (Waddell et al., 2019) or more classically by some salmon species (Lucas & Baras, 2001). Some evidence, however, suggests that patterns of migration can change with age. In the central Amazon, adults of *Semaprochilodus* spp. travel between nutrient-poor tributaries and white-water rivers many times during the year. However, some of the larger *Semaprochilodus* that usually reach the most western tributaries no longer perform migration with age (Araujo-Lima & Ruffino, 2003). This is also true for some older *Colossoma macropomum* that do not migrate upstream during low water and stay in the floodplains (Goulding & Carvalho, 1982).

3 | SOCIETAL IMPORTANCE OF MIGRATORY FISHES IN THE AMAZON BASIN

Freshwater fish have long been one of the most important protein sources for Amazonian people. The historical and cultural importance of migratory species, as well as their nutritional value and contribution to food security, have been well documented (see Supporting Information). What remains unclear is the contribution of migratory fishes to total fish catch in the basin, although migratory Characiformes and Siluriformes represent about 83% (46% and 37% respectively) of the annual commercial landings of migratory and non-migratory fish species in the Amazon basin (Goulding et al., 2019).

Owing to the absence of official fisheries statistics in most Amazonian countries, estimates of total Amazonian fish landings are far from complete. More than a decade ago, the total commercial fisheries landings in the Amazon basin, excluding the Tapajós, Xingu, and upper Negro river basins, was estimated at 173,000 t yr^{-1} (Barthem & Goulding, 2007). Using this estimate and the approximate percentage contribution of the different Amazonian regions provided by the same authors, the contribution of different categories of migratory fish species in fisheries landings for the main Amazonian regions has been estimated (Table 1). Using such data, their economic value in 2019 was also estimated from the mean price per kilogram of these species in the different regions (Figure 2). Long-distance migratory fish, medium-distance large-sized Siluriformes, medium-distance large-sized Characiformes, medium-distance small-sized species, and short-distance or resident species were distinguished, as these groups attract different market prices.

For the portion of the fish catch that is landed in ports, migratory species average ~93% of total landings in the Amazon basin (Table 1), but there are marked regional differences, with their contribution peaking at over 99% in the border between Brazil, Colombia, and Peru and being lowest in the clear-water basins draining the Precambrian shields, such as the Tocantins River (~77%). The Amazon estuary, the lower Amazon, upper Solimões, lower Tocantins, and the Colombian Amazon fisheries have higher contributions of Siluriformes species in the landings, whereas the lower Solimões, upper Amazon, middle Negro, and middle Madeira have more contribution of the Characiformes species (Table 1, Figure 2). The contribution of migratory species to fish landings, albeit still high, is relatively lower in the upper Madeira in Bolivia (~81%, owing to the important contribution of the introduced *Arapaima*). The introduced *Arapaima* spp. account for most landings of the short-distance migrating or resident species in the upper Madeira.

According to Barthem et al. (1997), the fisheries sector in the Brazilian Amazon generates a total annual income between US

TABLE 1 Relative contribution of the different categories of migratory fish species, per region, to total fisheries landings in the Amazon basin, based on total Amazonian landings of 173,000 t yr^{-1} and the percentage contribution of each region to these total landings (Barthem & Goulding, 2007)

	Total landings (%)	Mean landings	LD (%)	MDLS (%)	MDLC (%)	MDS (%)	SD-R (%)
Estuary (Belém)	28	48,440	47	0.5	0.3	49.6	2.6
Lower Amazon	7	12,110	22.3	7.9	5.5	61.7	2.6
Central Amazon (Manaus)	29	50,170	9.9	12	5.1	70.2	2.8
Madeira	2	3,460	9.9	6.7	2.0	72.6	8.8
Upper Madeira	2	3,460	2.7	36.8	23.8	18.4	18.3
Purus-Juruá	4	6,920	31.2	21.7	1.4	41.6	4.2
Border area Brazil, Colombia, Peru	7	12,110	43.7	29.7	0.3	25.7	0.6
Peru	16	27,680	2.3	6.2	1.6	85.4	4.5
Tocantins	5	8,650	0	0	0	76.5	23.5

Note: For details about the data and methods, see Supporting Information Table S2.

Abbreviations: LD, long-distance migratory species correspond to goliath catfishes (*Brachyplatystoma* spp.); MDLC, medium-distance large-sized Characiformes correspond to *Colossoma macropomum* and *Piaractus brachypomus*; MDLS, medium-distance large-sized Siluriformes correspond to all other large migratory catfishes (*Pseudoplatystoma* spp., *Zungaro zungaro*, *Phractocephalus hemioliopterus*, *Calophysus macropterus*, etc.); MDS, medium-distance small-sized correspond to most other smaller Characiformes (*Prochilodus* spp., *Semaprochilodus* spp., *Brycon* spp., etc.); SD-R, short-distance and resident species (*Arapaima* spp., *Plagioscion squamosissimus*, most cichlid species, etc.).

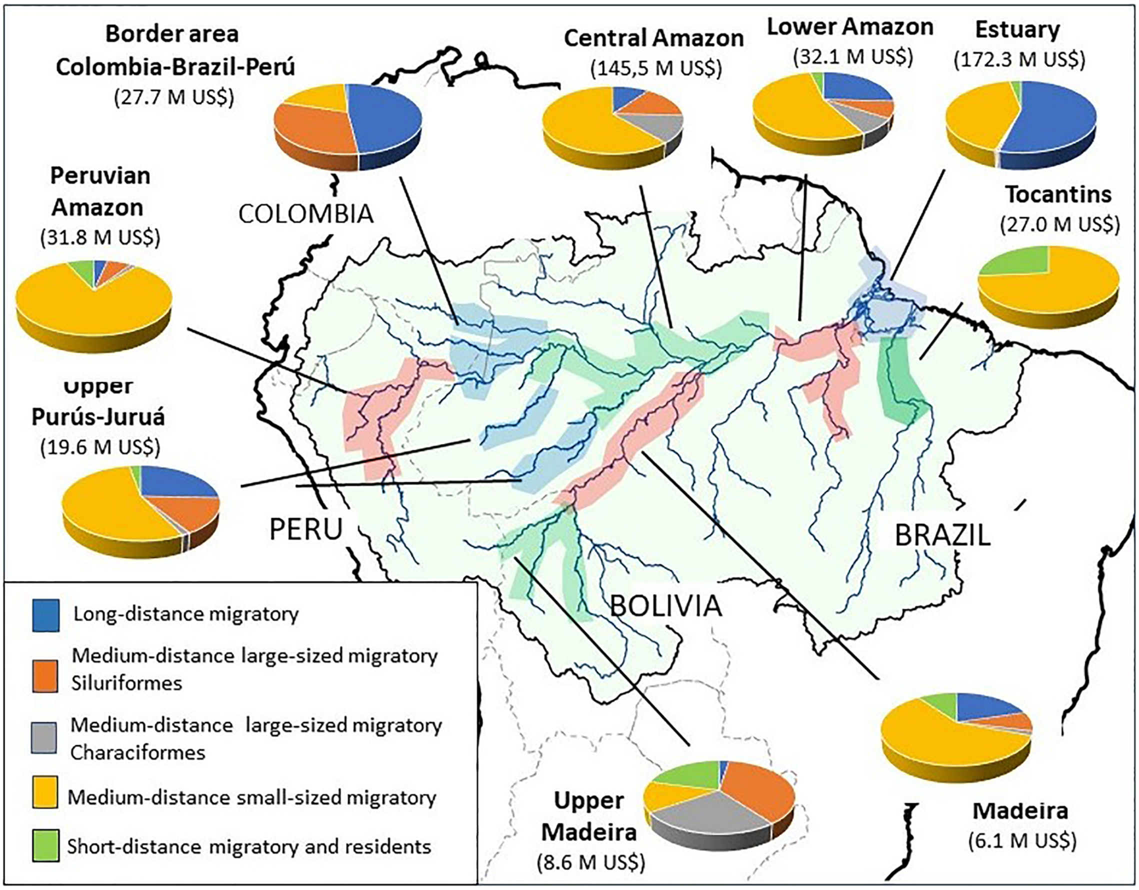

FIGURE 2 Relative economic contribution, per region, of the different categories of migratory fish species to total fisheries landings in the Amazon basin. The mean estimated economic contributions (in millions of US$) of the region's landings are in parentheses. For details about the data and methods, see Supporting Information Table S2

$100 million and US$200 million and employment for 168,000 people, and migratory fishes are the major part of the catch. Van Damme, Carvajal-Vallejos, Camacho, Muñoz, and Coronel (2011) estimated the yearly monetary value of migrating fish species in the Bolivian Amazon at about US$3 million. Here, total fisheries landings in the Amazon basin represented >US$470 million (Figure 2). Migratory species in all four categories (excluding short-distance migrating or resident species) average ~93% of total landings and therefore account for approximately US$436 million out of the estimated US$470 million provided annually by landed Amazonian fisheries.

Much of the fish harvested in the Amazon, however, is consumed in river communities and is never 'landed' into markets, a phenomenon common to most inland fisheries worldwide (Fluet-Chouinard, Funge-Smith, & McIntyre, 2018). As an example, it is estimated that almost 600,000 t yr^{-1} of fish are consumed throughout the Brazilian Amazon (Isaac & Almeida, 2011) and 29,000 t yr^{-1} in the Colombian Amazon (Agudelo, 2015), which together are about three times as much as the commercial landings reported for the Amazon basin (Barthem & Goulding, 2007). Although fish consumed in urban centres may partly come from marine fisheries or aquaculture, these figures indicate a strong underestimation of Amazonian catches estimated by landing statistics (Fluet-Chouinard et al., 2018). Estimates of these 'hidden' subsistence fish catches vary, but they are of the same order of magnitude, or more, as the estimates of fish landings previously provided herein (Crampton, Castello, & Viana, 2004). Bayley (1998) used the data from Batista, Inhamuns, Freitas, and Freire-Brasil (1998) to re-estimate total fish catch in the Amazon basin at ~450,000 t yr^{-1}. Although migratory species still dominate subsistence catches, some sedentary species belonging to the Cichlidae and Loricariidae families can sometimes account for half or more of the catches (Batista et al., 1998; Castello, McGrath, Arantes, & Almeida, 2013; Castello, McGrath, & Beck, 2011). The figures provided here offer just a glimpse of the importance of migratory fishes to Amazonian people, but further studies with current data that also include subsistence fisheries will help to refine quantitative estimates.

4 | THREATS TO MIGRATORY SPECIES IN THE AMAZON BASIN

The main threats to freshwater fish in the Amazon are similar to those menacing freshwater biodiversity and fishes worldwide: overexploitation, flow and habitat modification by hydropower development, deforestation, and climate change (Carpenter, Stanley, &

Zanden, 2011; Dudgeon et al., 2006; Xenopoulos et al., 2005). Some acknowledged or potential threats, such as pollution, waterways, non-native species, or exploitation by the ornamental trade, are detailed in Supporting Information. Importantly, most of these threats interact synergistically, further aggravating their individual impacts (Anderson et al., 2019; Forsberg et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016).

4.1 | Overexploitation

Historically, overharvesting has been the most important driver of freshwater ecosystem degradation in the Amazon basin (Castello, McGrath, Hess, et al., 2013), and this affects many important migratory fish species. Catches of the largest, most commercial, species are declining in most regions of the basin. This trend started with *Arapaima* spp. (Veríssimo, 1895), which was overharvested to the point of being placed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora II list of endangered species (Castello & Stewart, 2010; Castello, Stewart, & Arantes, 2011). Although basin-wide evidence of overfishing is still rare, many trait-based studies over the last few decades have offered evidence for regional overfishing of most large, high-valued species, such as the second-largest scaled fish of the Amazon, *C. macropomum* (Campos, Garcez, Catarino, Costa, & Freitas, 2015; Isaac & Ruffino, 1996), several large catfishes such as *Brachyplatystoma vaillantii*, *B. rousseauxii* (Agudelo et al., 2013; Alonso & Pirker, 2005; Garcia Vasquez et al., 2009), *Pseudoplatystoma tigrinum* and *Pseudoplatystoma fasciatum* (=*Pseudoplatystoma punctifer*, Isaac, Ruffino, & McGrath, 1998; Ruffino & Isaac, 1999), and *Pinirampus pirinampu* (Sant'Anna, Doria, & Freitas, 2014). Owing to their basin-wide migrations, *B. rousseauxii* and *B. vaillantii* are particularly at risk: whereas their adult populations are already heavily fished or overexploited in the lower (Araújo Cruz, 2020) and upper Amazon basin (Agudelo et al., 2013; Garcia Vasquez et al., 2009; Petrere, Barthem, Agudelo, & Gomez, 2004), juveniles of these species at present support the largest Amazonian industrial fishery in the lower Amazon (Alonso & Pirker, 2005; Barthem & Goulding, 2007). Overharvesting, however, is no longer limited to large species and was recently also suggested to affect regionally some of the smaller Characiformes that now make up most of the catches, such as *P. nigricans* (Bonilla-Castillo, Agudelo, Gómez, & Duponchelle, 2018; Catarino, Campos, Garcez, & Freitas, 2014) or *Psectrogaster* spp. (Garcia Vasquez, Vargas, Sánchez, Tello, & Duponchelle, 2016).

The depletion of stocks of large-bodied species is the inevitable adjustment of tropical fish communities to increasing fishing effort (Bayley & Petrere, 1989). This common phenomenon in fisheries worldwide, where large, long-lived species are progressively replaced in the landings by smaller, short-lived species with higher production/biomass ratios, is referred to as the ‘fishing down’ process (Welcomme, 1995) or the ‘fishing down the food web’ process, which also predicts declining trophic levels in the catches (Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998). The decline of mean catches of the largest commercial species is already observed in several regions of the Amazon basin: in Brazil for *C. macropomum* (Barthem et al., 1997; Garcez & Freitas, 2011), *Arapaima* spp. (Castello & Stewart, 2010; Cavole, Arantes, & Castello, 2015), *B. filamentosum* (Petrere et al., 2004); in Peru for several of the largest species, such as *Arapaima* spp., *B. rousseauxii*, *C. macropomum*, and *Piaractus brachypomus* (Garcia Vasquez, Tello, Vargas, & Duponchelle, 2009); and in Colombia for *B. filamentosum*, *B. rousseauxii*, and *Pseudoplatystoma* spp. (Agudelo, Sánchez, Rodríguez, Bonilla-Castillo, & Gómez, 2011). Declining mean size of target species or increasing proportions of immature specimens in fisheries catches are also common signs of overexploitation, although difficult to observe because they require accurate, though seldom available, long-term size data (Froese, 2004). Castello, McGrath, Hess, et al. (2013) showed a strong, historical decline in the mean lengths of harvested species between 1895 and 2007 in the Brazilian Amazon. In the Colombian Amazon, the proportion of immature individuals in the catches is frequently >50% for many large catfishes, and these proportions have increased in recent decades (Agudelo, Bonilla-Castillo, Gómez, Salvino, & Trujillo, 2012). The same is observed for *C. macropomum* (Garcez & Freitas, 2011) and *Arapaima* spp. (Cavole et al., 2015) in Brazil.

4.2 | Dams

There are currently about 158 hydroelectric dams in operation or under construction in the Amazon basin and about 351 new dams are planned in the next 30 years, including 21 large dams below 400 m elevation (Almeida et al., 2019). Hydropower infrastructure is arguably the most rapidly growing threat, with important potential for altering connectivity and biodiversity loss, including in the Andean portion of the basin (Anderson et al., 2018; Finer & Jenkins, 2012; Forsberg et al., 2017; Latrubesse et al., 2017; Latrubesse et al., 2021).

Hydroelectric impoundments have impacts on migratory fishes at different scales, from local extinction of species that cannot adapt to reservoirs and dam-tailwater conditions, to basin-wide extirpations of migratory species (Freeman, Pringle, Greathouse, & Freeman, 2003; Pringle, Freeman, & Freeman, 2000). The most evident effect of dams on Amazonian fishes is the disruption of migration routes (Agostinho, Gomes, Santos, Ortega, & Pelicice, 2016; Ribeiro, Petrere, & Juras, 1995; Santos, 1995). Although most studies have been carried out in the heavily fragmented Paraná and Paraguay basins, they show that despite financial investments and engineering efforts in the construction of fish passes, these are largely ineffective in the re-establishment of routes, free upstream and downstream movements of young and adults, and regional recruitment (Agostinho et al., 2007; Lira et al., 2017; Pompeu, Agostinho, & Pelicice, 2012). In the Amazon basin, otolith microchemistry analyses have provided clear evidence that fish passes in the recently constructed Jirau and Santo Antônio dams on the Madeira River do not currently permit upstream passage of sub-adult *B. rousseauxii* returning from the lower Amazon estuary (Hauser, 2018) and prevent former movement of *Brachyplatystom* *platynemum* between the upstream and downstream reaches of the dams (Hauser et al., 2019).

Available evidence on the effect of dams mainly focuses on the large, long-distance migratory species, which are usually most at risk (Agostinho et al., 2016; Arantes, Fitzgerald, Hoeinghaus, & Winemiller, 2019). For long-distance migrants, such as goliath catfishes and other longitudinal migrants, any dam on their migration routes will interfere by isolating their breeding areas from feeding and nursery areas (Agostinho, Pelicice, & Gomes, 2008; Ribeiro et al., 1995), depleting resident populations above the dams, with unlikely long-term chances of persistence (e.g. for *B. rousseauxii* in the Madeira; Hauser, 2018; Van Damme et al., 2019). Large catfish fisheries usually decline upstream and downstream of dams, as was observed above the Tucuruí dam on the Tocantins River (Ribeiro & Petrere, 1988; Ribeiro et al., 1995). The same was observed below (Santos, Pinto-Coelho, Fonseca, Simões, & Zanchi, 2018) and above (Van Damme et al., 2019) the Jirau and Santo Antonio dams in the Madeira River. The fisheries of smaller, mid-distance detritivorous and frugivorous migratory species first increased in the river channels upstream and downstream of the Tucuruí (Ribeiro et al., 1995) and Peixe Angical dams in the Tocantins River shortly after their construction but declined afterwards (Monaghan, Agostinho, Pelicice, & Soares, 2020). In the Jamari River, fisheries of migratory Characiformes also strongly declined after construction of the Samuel dam (Santos, 1995).

As Andean tributaries supply most (>90%) of the organic and inorganic materials transported by Andean-origin lowland Amazonian rivers, they control various geomorphological processes, such as river meandering and floodplain formation in river sections downstream (Filizola & Guyot, 2009; McClain & Naiman, 2008). Therefore, even dams located upstream of fish migration routes can affect migratory species by reducing sediment and nutrient supplies (Forsberg et al., 2017) and altering the hydrological migratory cues and the physico-chemical spawning cues to which the fish are adapted (Agostinho et al., 2008; Bailly, Agostinho, & Suzuki, 2008; Freitas et al., 2012; McIntyre et al., 2016). Modification of flow regimes, and especially of flood duration, can also strongly affect recruitment and juvenile survival in migratory species (Bailly et al., 2008). Alteration of granulometry and geomorphology usually result in decreased abundance of bottom-feeding species, such as the migratory Curimatidae, as observed below the Samuel, Tucuruí, and Itaipu dams (Agostinho, Júlio, & Petrere, 1994; Santos, 1995). Modifications to channel morphology reduce the frequency of adjacent oxbow lakes and the connectivity with the floodplain, together with reduced nutrient supply and thus decreased primary production (Forsberg et al., 2017). This can also have severe impacts on the mid-distance migrants that are the primary and secondary consumers making up the bulk of fisheries in the Amazon basin (i.e. most commercial Characiformes species; Barthem & Goulding, 2007). For example, the collapse of the migratory planktivorous *Hypophthalmus* spp. fishery and general decreased catches in the lower Tocantins River were attributed to a reduction in nutrient supply and phytoplankton biomass following the Tucuruí dam construction (de Mérona, Juras, dos Santos, & Cintra, 2010). By reducing variability, intensity, and amplitude of the downstream flood pulse, and by modifying geomorphology, dams also disrupt lateral connectivity between river channels and floodplains (Forsberg et al., 2017). Migratory fishes that seasonally migrate laterally to floodplain habitats then have fewer opportunities to colonize flooded forest habitats that play key roles as nursery and feeding areas, ultimately affecting fisheries (Castello, Bayley, Fabré, & Batista, 2019; Castello, Isaac, & Thapa, 2015). For example, a 37% reduction in maximum flooded area in the Loreto Region, Peru, following the construction of large dams would result in an 88% decline in annual fish yield (Forsberg et al., 2017).

Newly formed reservoirs associated with the development of hydroelectric dam construction usually change environmental conditions towards more lentic waters, which favours non-migratory species at the expense of the former migratory species that populated the river channels (Agostinho et al., 2008, 2016; Arantes, Fitzgerald, et al., 2019). Another major impact of large reservoirs, such as Tucuruí, Balbina, Samuel, or Sinop, is their strong filter effect on the movements of larvae and juveniles of migratory species drifting downstream. These young stages, adapted to migrating in running, oxygenated waters, are suddenly faced with huge stagnant lake-like water bodies with low oxygen concentration caused by decomposing vegetation, and the presence of many predatory species they do not normally encounter, such as piranhas and predatory cichlids (Pelicice, Pompeu, & Agostinho, 2015).

4.3 | Deforestation

Deforestation is usually linked to agriculture and cattle ranching in the Amazon basin, but it is also frequently associated with other human activities, such as mining, hydroelectric dam construction, and road building (Anderson et al., 2018; Forsberg et al., 2017; Lees et al., 2016; Malhi et al., 2008). Its effects can differ within the affected area and downstream. Deforestation in the uplands typically increases water runoff and sediment loads carried downstream by the rivers, altering geomorphological and biochemical processes with consequences on soil erosion and biological productivity of aquatic ecosystems (Coe, Costa, & Soares-Filho, 2009). Local deforestation can have regional implications: strong deforestation in the Tocantins and Araguaia basins resulted in increased water discharge by 25% and shifted flood pulse timing by a month in these rivers (Coe et al., 2009). Increased flood amplitude and decreased flood duration caused by local deforestation tend to augment erosion in the river channels and reduce water transparency (Winemiller, Marrero, & Taphorn, 1996). More violent floods result in the washing out of substrate and associated benthic algae and organisms on which migratory detritivores feed (Flecker, 1996). Adjacent lakes also tend to become shallower and muddier by the increased sedimentation (Winemiller et al., 1996). Reduced water transparency directly affects algal and zooplankton production in floodplain lakes, which are important nursery areas for most Amazonian migratory and non-migratory fish species (Pringle et al., 2000). In the Venezuelan

Andean piedmont, where deforestation was particularly acute and diminished connectivity with downstream floodplains, the abundance of migratory fishes, including *Prochilodus* spp., was severely reduced (Winemiller et al., 1996). Deforestation usually also reduces the input of large wood in local streams, depleting fish species richness and abundance, including many migratory species, with potential consequences for fisheries and ecosystem functioning (Wright & Flecker, 2004). Recent analyses of stable isotopes demonstrated that terrestrial plant material and arthropods were the most important items contributing to migratory fish biomass in the oligotrophic Apaporis River floodplains in Colombia, emphasizing the importance of seasonally flooded forests for sustaining fisheries in the Amazon basin (Correa & Winemiller, 2018). Adverse impacts of deforestation on fish species richness, diversity, abundance (Arantes et al., 2018; Freitas et al., 2018), biomass and functional diversity (Arantes, Winemiller, et al., 2019), and on fishery yield of migratory species (Castello et al., 2018) have also been shown.

4.4 | Climate change

As they rely on multiple geographically separated habitats that are changing at different rates and in different ways, migratory fish species are likely to be strongly affected by climate change with potential desynchronization of the favourable conditions between the habitats at the start and at the destination (Lennox et al., 2019). Climate change in the Amazon basin is expected to alter hydrological dynamics by changing patterns of rainfall (Castello & Macedo, 2016; Malhi et al., 2008, 2009). Increased discharge and extent of inundation are projected in western Amazonia, with the opposite trend in the central and eastern parts (Sorribas et al., 2016). Increased frequency and intensity of extreme events, such as floods and droughts, are also expected (Zed et al., 2016). One of the first studies on the potential impacts of climate change on Amazonian fishes predicted potential species loss of up to 12% in the Amazon and 23% for the Tocantins basins, although there was no indication of whether or not the species affected were migratory (Xenopoulos et al., 2005). Reduced river discharge and drought have been shown to affect fish population size-structure, community composition, and reproduction (Frederico, Olden, & Zuanon, 2016; Röpke et al., 2017, 2019). Hydrological shifts, and river droughts in particular, can reduce the availability of migratory corridors between critical habitats, such as river channels and floodplains, directly affecting migratory species (Röpke et al., 2017). As water volume decreases, its temperature may increase and its oxygen concentration drop, becoming detrimental or lethal for fish species (Ficke, Myrick, & Hansen, 2007; Frederico et al., 2016). As energy allocation in adult fish is divided between maintenance metabolism, growth, and reproduction (Wootton, 1998), increased amounts of energy spent in compensating for unfavourable thermal conditions will come at the expense of energy expenditure for growth and reproduction, while also increasing susceptibility to disease (Ficke et al., 2007; Freitas et al., 2012). The toxicity of pollutants to fish tends to increase with water temperature, as does the bioaccumulation of mercury (Ficke et al., 2007). In lentic environments, such as floodplain lakes, increased temperature could enhance eutrophic conditions and stimulate explosive macrophyte development, modifying food web dynamics and ultimately affecting the fishes that depend on them (Ficke et al., 2007).

Potential shifts in the range of migratory species to cope with expected temperature increases will be reduced or hampered by the fragmentation of river networks that result from hydroelectric dams and other infrastructure development in the Amazon basin (Myers et al., 2017). This situation is likely to be worse in the Andean portion of the basin, where most dams have been built or are planned (Anderson et al., 2018), interacting with climate change to decrease species ranges and prevent them from reaching suitable climatic areas in some regions (Herrera-R et al., 2020).

Global warming and reduced oxygen are also expected to reduce fish body size significantly owing to fundamental ecological and metabolic principles (Cheung et al., 2013; Sheridan & Bickford, 2011). Declining body size could also lead to ecosystem alteration through trophic cascade for predatory species (Estes et al., 2011) or through disruption of carbon flows for detritivorous species (Taylor, Flecker, & Hall, 2006). The synergistic effects of climate-driven and fishing-induced reductions of fish size could further aggravate such potential impact.

5 | POTENTIAL ECOSYSTEM IMPACTS OF THE LOSS OF MIGRATORY SPECIES

Most Amazonian migratory fish species have crucial ecological roles, given their functions as apex predators, ecological engineers, or seed-dispersal species. They often provide significant subsidies from one component of the ecosystem to another, so that the depletion of their stocks or populations could have different but additive and potentially marked consequences for Amazonian aquatic food webs.

Community-level studies have emphasized the crucial ecological role of top predators in terrestrial and aquatic ecosystems (Estes et al., 2011; Heithaus, Frid, Wirsing, & Worm, 2008). Top-down effects are expected in food webs when entire functional groups of predators are depleted, as was demonstrated for several, often migratory, top predatory fish species (Heithaus et al., 2008; Myers, Baum, Shepherd, Powers, & Peterson, 2007). A similar scenario is likely to happen with the decline of the large predatory catfish community of the Amazon basin. ECOPATH models indicated strong cascading effects of the removal of the largest *Brachyplatystoma* species, including an important biomass increase of their fish prey with a concomitant decrease in invertebrate biomass and increase in macrophyte biomass (Angelini, Fabré, & da Silva, 2006; Lima, 2017). They also showed that *B. rousseauxii* was one of the most sensitive components; that is, responsible for major ecosystemic alteration in the case of stock depletion. Trophic cascades are strongest where they involve large, mobile vertebrate predators (Borer et al., 2005). There is, thus, little doubt that the decline of large, long-distance migratory catfishes will have profound effects on the structure and functioning of food webs in the Amazon basin.

Migratory fishes are known to provide trophic subsidies to different river systems and can strongly influence the structure of local habitats and communities through feeding and breeding activities (Bauer & Hoye, 2014). Despite the existence of highly diversified migratory fish communities, including long-distance migrations, the role of fish movements in nutrient transport and their effects on local food webs has received little attention so far in the Amazon basin, particularly for large predators (Winemiller & Jepsen, 1998). There is evidence, however, that middle-sized migratory species of the family Prochilodontidae have a significant role in Amazonian food web dynamics. Prochilodontid fish of the genera *Prochilodus* and *Semaprochilodus* feed on detritus, algae, and associated microorganisms and are important prey for larger piscivorous species (Hoeinghaus, Winemiller, Layman, Arrington, & Jepsen, 2006). Experimental in situ exclusions and enclosure of *Prochilodus mariae* in Venezuela resulted in major changes in benthic organic matter and algal and invertebrate communities, and hence in community and ecosystem attributes (Flecker, 1996; Taylor et al., 2006). These studies demonstrated that *Prochilodus* are a functionally dominant engineering species capable of structurally modifying their habitats and influencing pathways of energy and nutrient flux in ecosystems. Prochilodontids also perform complex large-scale migrations between different river systems, migrating to rich floodplains during high waters for spawning and returning to often nutrient-poor tributaries in the low water period (Ribeiro & Petrere, 1990). As such, these migratory detritivores play important roles in energy and biomass transfer to species higher in the food chain, providing subsidies that allow larger piscivores to support higher population densities than would normally be possible in oligotrophic waters (Hoeinghaus et al., 2006; Winemiller & Jepsen, 1998). They also allow increased ecological efficiency and the connection of food webs over different spatial scales (Hoeinghaus et al., 2006; Winemiller & Jepsen, 1998). Besides *Prochilodus* and *Semaprochilodus* spp., several other migratory characiform species feeding relatively low on the food chains, such as *Anodus* spp., *Brycon* spp., *C. macropomum*, *Mylossoma* spp., and *Triportheus* spp. only reproduce in white-water rivers, whereas they inhabit all types of water as adults (Lima & Araujo-Lima, 2004). This transfer of basic primary production by migratory species from nutrient-rich white-water rivers into oligotrophic (clear‐ or black-water) ecosystems might, therefore, be a widespread phenomenon in the Amazon basin.

Another crucial ecological aspect of many Amazonian migratory fishes is their frugivory and associated ability to disperse seeds (ichthyochory) and improve their germination process, participating in the spatial distribution and diversity of riparian forests –see Correa, Costa-Pereira, et al. (2015) for a review. Although seed dispersal was initially believed to be ensured essentially by birds and mammals, the last few decades have provided strong evidence that fishes are major participants in this process (Correa, Costa-Pereira, et al., 2015; Correa, Winemiller, López-Fernández, & Galetti, 2007; Goulding, 1980; Horn et al., 2011) and may have been the first vertebrate dispersers in the Neotropics 70 million years ago (Correa, Costa-Pereira, et al., 2015). As most tree species fruit during the high-water season, when fish invade the flooded forest to feed, seed dispersal is likely to result from a long process of mutually beneficial co-adaptation (Correa, Costa-Pereira, et al., 2015; Goulding, 1980; Silva Ferreira, Fernandez Piedade, de Oliveira Wittmann, & Franco, 2010). There are approximately 150 known frugivorous fish species from 17 families and six orders in the Neotropics (Horn et al., 2011), most of which occur in the Amazon basin. These fish species consume at least 566 species of fruits and seeds from 82 plant families (Correa, Costa-Pereira, et al., 2015). As the most effective seed dispersal agents are large-bodied fish species, which are the most targeted by fisheries (Correa, Costa-Pereira, et al., 2015), fish overharvesting can potentially also threaten plant biodiversity and conservation (Correa, Araujo, et al., 2015).

6 | CHALLENGES IN RESEARCH, MANAGEMENT, AND CONSERVATION

Considering the diversity of fish migrations and the scales at which they occur in the Amazon basin, conservation of migratory fish species would ideally require the implementation of a riverscape approach, similar to that proposed by Fausch, Torgersen, Baxter, and Li (2002). Given the state of ecological knowledge, however, the growing human pressures on natural resources (water, fish, and other aquatic biota), and the lack of environmental commitment and coordination between government agencies of Amazonian countries, advocating only such a comprehensive strategy would be utopic. Tackling this challenge calls for a more pragmatic approach, setting different levels of possible actions.

6.1 | Research

Whereas fisheries statistics have been collected historically in some of the main fishing areas (Manaus, Santarém, Belém in Brasil, Iquitos, Pucallpa, and Puerto Maldonado in Peru; Leticia and Puerto Leguizamo in Colombia), many such data collection systems no longer exist. This scarcity of data collection represents a major challenge to conservation by preventing assessments of fish population status. There is an urgent need to monitor fisheries activities (landings by species, size distributions) not only in all urban centres, but also in river fishing communities where a large portion of the catch is consumed. Improving our knowledge on the migratory behaviour of most species is also a prerequisite for designing appropriate conservation measures in the face of growing human pressures. Ecological information on routes, habitat use, timing and environmental conditions are missing for most migratory species in the Amazon. Several recent studies mentioned in this review are using new otolith microchemistry or improved telemetry techniques that bring new possibilities to complement traditional approaches in understanding migratory patterns (see Hermann et al., in press). The use of these techniques should be encouraged.

In addition to improved knowledge of fish migratory behaviour, perhaps the greatest need lies in identifying management units (i.e. stock definition) for all exploited taxa. Such a goal is at present daunting, given the general scarcity of fisheries monitoring data and population genetic studies. That scarcity is only matched by a generalized paucity of researchers and investments in research on Amazonian fishes, pointing to the need to boost research via increased funding and incentives to work on Amazonian fishes.

6.2 | Management

For fishes that are harvested for commercial or subsistence purposes, a key challenge is ensuring compliance with existing management limits. Management of such species is at present almost entirely based on restrictive measures, such as minimum size of fish, gears and mesh size limitations, closed season and areas, quotas, and control of access. Minimum size measures are followed in fisheries with a specific target, such as the *Arapaima* fishery in managed lakes or the *Brachyplatystoma* trawl fishery in the estuary (Barthem, da Silva, Raseira, Goulding, & Venticinque, 2019). However, they are almost impossible to implement in all fisheries, given their multi-gear and multispecies nature, the vast areas involved, and the severe underfunding and understaffing of management agencies responsible for fisheries. For *Arapaima*, nearly 77% of the catch in weight in the lower Amazon region has been estimated to be illegal (Cavole et al., 2015). Spawn-at-least-once limits, such as size and season limits, are among the most important management measures because they ensure stock recruitment (Myers & Mertz, 1998). The usefulness of a closed season is debated in the Amazon. It is often associated with monetary compensation for fishers in Brazil, which can have adverse effects as a measure to protect fish stocks (Corrêa, Kahn, & Freitas, 2014). Owing to the complexity of many species' migratory behaviour, the choice of the closed season is complicated and considered of little value in central Amazon fisheries, where most commercial fish species reproduce during the flooding period and are much less accessible to fishing gears than during the low water period (Barthem et al., 2019; Ribeiro & Petrere, 1990). Yet, previous studies on overfished stocks of Amazonian migratory species have suggested that compliance with existing size and season limits would enable those stocks to recover (Castello et al., 2019; Castello, Stewart, & Arantes, 2011; Isaac & Ruffino, 1996). Recently, a 5-year complete fishing interdiction for *C. macropomum* was proposed to foster stock recovery (Barthem et al., 2019).

Over the last three to four decades, community-based management (CBM) has grown to encompass numerous communities in virtually all rivers of the Amazon and represents a major conservation movement. CBM has proved an effective tool for mitigating threats on some migratory species, such as *P. nigricans* (Anderson, Montoya, Soto, Flores, & McClain, 2009), *C. macropomum* (Arantes & Freitas, 2016), and especially on *Arapaima*. There are now ~500 fishing communities implementing CBM for *Arapaima* in the Amazonas state alone (Campos-Silva, Hawes, & Peres, 2019). Where studies have been made, populations of *Arapaima* and of other migratory species have recovered from overexploitation by increasing abundance (Campos-Silva et al., 2019; Campos-Silva & Peres, 2016; Castello et al., 2019). Catch per unit effort is also generally higher in lakes with CBM than in lakes without, as is mean body length of target species, including long-distance migratory species, even though these management schemes are at the small, local scale (Almeida, Lorenzen, & McGrath, 2009; Castello, Stewart, & Arantes, 2011). As CBM often involves conservation of floodplain habitats, it provides benefits to migratory species that depend on these (Isaac et al., 1998). Limiting fishing and implementing reserves in the floodplains, where most migratory species spend a critical part of their lives, could also be a complementary solution (Barthem et al., 1997). The conservation of migratory fishes therefore requires strengthening and further supporting the development not only of CBM schemes but also of centralized government agencies.

A detailed, integrated management system for goliath catfishes (*B. rousseauxii* and *B. vaillantii*) has previously been proposed for Brazil (Fabré, Barthem, Carvalho, & Angelini, 2005), including the estuary where most exploited individuals are immature, but only very few of the recommendations have been implemented so far. For long-lived migratory species, the effects of overfishing could be reduced by using simple indicators that have been proposed as alternatives to conventional stock assessment models: the median length of catches, the proportion of mature individuals in the catches, the proportion of fish caught at the optimum length, and the percentage of old, large individuals ('mega-spawners'; Froese, 2004). The proportion of these mega-spawners in the catches draws on the increasing evidence that in long-lived, late-maturing species, large, old fish play major roles in the persistence of a population (Berkeley, Chapman, & Sogard, 2004; Birkeland & Dayton, 2005; Froese, 2004). Ideally, there should be no single mega-spawner in the catches. However, in complex multispecies fisheries, such as those of the Amazon basin, mesh-size regulation would not be effective in reducing the upper size limit of catch for many species. Keeping a proportion of 30–40% of megaspawners in fisheries landings, which reflects a healthy stock (Froese, 2004), might be a more practical solution. In Peru (Garcia Vasquez A., unpublished data), and in some locations in Colombia too, the largest *Brachyplatystoma* specimens are angled by hook and line, which may allow specific management strategies to achieve this goal. Again, this would require the implementation, in all countries, of appropriate fisheries statistics (catch and effort), including length monitoring on a few selected target species, to assess the effect of the proposed solutions. The targeted species could change every 2 years to provide robust statistics for monitoring the stock health every 4–6 years for each large target species.

The ecosystem-based fisheries management that is internationally proposed for marine resources (Pikitch et al., 2004) might also help conserve medium- and long-distance migratory fish species in the Amazon. Ecosystem-based fisheries management has two main goals: satisfying societal and human needs for food and economic benefits while conserving the structure, diversity, and functioning of ecosystems. Such an approach has been promoted in the Amazon through two main mechanisms: CBM (see earlier) and basin-wide management. The basin-wide approach to ecosystem-based fisheries management uses iconic long- and medium-distance migratory goliath catfishes and characin species. Goulding et al. (2019) proposed using the particular life histories of these migratory species to link crucial spawning, feeding, and nursery habitats across vast environmental connectivity gradients in the Amazon basin: from Andean tributaries, lowland rivers, and their floodplains down to the Amazon estuary. They advocated that the basin scale is the appropriate framework for ecosystem-based management of fisheries in the Amazon and its wetlands and emphasized the need to maintain hydrological connectivity in the Amazon basin. This can only be achieved through the recognition of the crucial importance of freshwater ecosystems and their connectivity at the whole Amazon basin scale, which implies transfrontier coordination. Harmonized management of transboundary waters is recognized as a priority (Castello, McGrath, Hess, et al., 2013; Pelicice et al., 2017), and the Amazon Cooperation Treaty Organization might be the right place to propose solutions (Latrubesse et al., 2017).

6.3 | Conservation

Not even the best available research and fisheries management framework can alone conserve Amazon migratory fishes in the face of current trends of deforestation, climate and hydrological change, and construction of dams. There is an urgent need to minimize, and to the extent possible avoid, the adverse impacts that such trends are producing. As discussed elsewhere, however, there are no basin-wide coordinated efforts to assess and manage the progression of such threats on aquatic ecosystems of the Amazon. There are policies relevant for aquatic conservation in most countries of the basin, including protected areas, regulation on forests in private properties, water resource management, and environmental licensing of hydropower dams. Together, however, these policies have limited capacity to curb current trends, largely because they ignore the role of hydrological connectivity in freshwater ecosystem structure and functioning (Anderson et al., 2019; Castello & Macedo, 2016; Leal et al., 2020).

Although, to some extent, the numerous protected areas can be seen as the paradigm in Amazon conservation, they were primarily designed to preserve terrestrial ecosystems and are largely ineffective in protecting aquatic ecosystems and biota (Azevedo-Santos et al., 2019; Castello, McGrath, Hess, et al., 2013; Frederico, Zuanon, & De Marco, 2018; Leal et al., 2020). This situation also holds true for the Andean portion of the basin (Anderson et al., 2019), where the breeding grounds of many migratory species are located. There are very few aquatic reserves in the Amazon basin (e.g. Mamirauá and Piagaçu-Purus in Brazil and Pacaya-Samiria in Peru), but these have proved effective in replenishing the populations of overexploited migratory species such as *Arapaima* or *C. macropopum* (Arantes & Freitas, 2016; Ortega & Hidalgo, 2008). Nevertheless, important habitats for the life cycle of migratory fishes, such as spawning, nursery, and feeding areas, are currently not protected. The white-water river floodplains are the most important habitats for commercial migratory fish species, but less than 1% are under integral protection and 15% are under some level of management (Goulding et al., 2019). Encounters between white-water and clear-water or black-water tributaries are other very important areas for migratory species that might warrant inventory and protection (Barthem et al., 2019). The Amazon estuary, which holds crucial nursery areas for goliath catfishes, should also be a major target for conservation; but again, most of the detailed recommendations provided in the integrated management system proposed by Fabré et al. (2005) are not implemented. Owing to the connected nature of river networks, reserves, even when they are effective at preserving freshwater biota, remain highly susceptible to human activities occurring upstream in the catchment, such as damming, deforestation, and pollution (Fausch et al., 2002). Human disturbances downstream can also have effects far upstream, through the action of migratory species (Fausch et al., 2002).

New studies have evaluated whether it is possible to create new protected areas (Azevedo-Santos et al., 2019; Frederico et al., 2018) or re-draw protected-area boundaries to improve protection of freshwater ecosystems. Creation of chains of protected areas could help maintain most migratory species by protecting them from harvest and protecting their habitats in various locations across the basin (Barthem et al., 1997; Bayley & Petrere, 1989; Crampton et al., 2004; Hurd et al., 2016). A recent study demonstrated that taking into account both terrestrial and freshwater biodiversity data for conservation planning could greatly improve benefits for freshwater biodiversity (including fish), with only negligible losses for terrestrial biodiversity (Leal et al., 2020). However, although the need for such re-evaluations is clear, to our knowledge there is no effort to enable them. In fact, many protected areas in the Amazon have been and continue to be reclassified and degazetted (Anderson et al., 2018), further limiting their effectiveness with respect to migratory fishes.

6.4 | Considerations about hydropower development in the Amazon basin

One of the most important issues highlighted in this review, as in previous studies (Anderson et al., 2018; Castello, McGrath, Hess, et al., 2013; Hurd et al., 2016), is the urgent need to preserve natural flow regimes and connectivity among river basins and between river channels and their floodplains. However, even the best fisheries regulations, provided they are enforced, will not be effective if dams disrupt flow regimes and connectivity. Dams also promote deforestation, which in turn further favours climate change. As the main driver disrupting connectivity is the construction of dams, the conservation of the Amazon's aquatic biota – of migratory fishes in particular, and of the many ecosystem services they provide – requires regional reconsideration of the sustainability of large-scale hydroelectric development in the Amazon basin and halting hydropower expansion. There are cleaner, cheaper alternative energy sources for Amazonian countries that are likely to become even more cost-effective in the near future with technological development and under the projected changes in climate (Kahn, Freitas, & Petrere, 2014). Dam development in the Amazon basin, when unavoidable, should at least be carried out considering spatially explicit prioritization methods that trade-off energy power and biodiversity loss under different scenarios (Almeida et al., 2019; McIntyre et al., 2016; Ziv, Baran, Nam, Rodríguez-Iturbe, & Levin, 2012) in order to lower environmental costs. In river basins already affected by dams, accumulated evidence emphasizes the imperative necessity of preserving free-flowing tributaries for maintaining reproduction of migratory fish (Casarim, Prado, Loures, & Pompeu, 2018; Marques, Dias, Perbiche-Neves, Kashiwaqui, & Ramos, 2018).

In the Amazon basin, environmental impact studies prior to building infrastructure were usually not conducted for existing dams because these were built before baseline data were available (Castello, McGrath, Hess, et al., 2013). As for the newly erected ones, such studies are seldom properly done, with insufficient planning, funding, and realization time. In addition, environmental impact studies should be carried out by renowned public universities and research institutes instead of private consulting firms in order to ensure the independence of results from conflicting interests. For hydropower plants already constructed, such as the Madeira or Tocantins dams, there is an urgent need to modify fishway technology to ensure a safe passage for migratory fish species while blocking the colonization of invasive species. This can only be achieved through coordination of researchers, engineers, and dam operatives to develop ad hoc technologies adapted to Amazonian species. In other parts of the world, many recent research efforts have focused on reducing the fragmentation effect of dams by devising selective fish passage systems that exploit species differences in physical ability, spawning behaviour, and sensitivity to various sensory stimuli (Birnie-Gauvin, Franklin, Wilkes, & Aarestrup, 2019; Lennox et al., 2019; Silva et al., 2018). In the Amazon basin, where such technology is not available and where fish pathways are currently ineffective, governments should foster strong investments in research and engineering projects focusing on similar approaches. This, in turn, requires promoting and financing further research on the ecology of many migratory species as such knowledge is an unavoidable prerequisite to successful fishways (Pompeu et al., 2012; Silva et al., 2018) and to the establishment of conservation measures (Barthem et al., 2019).

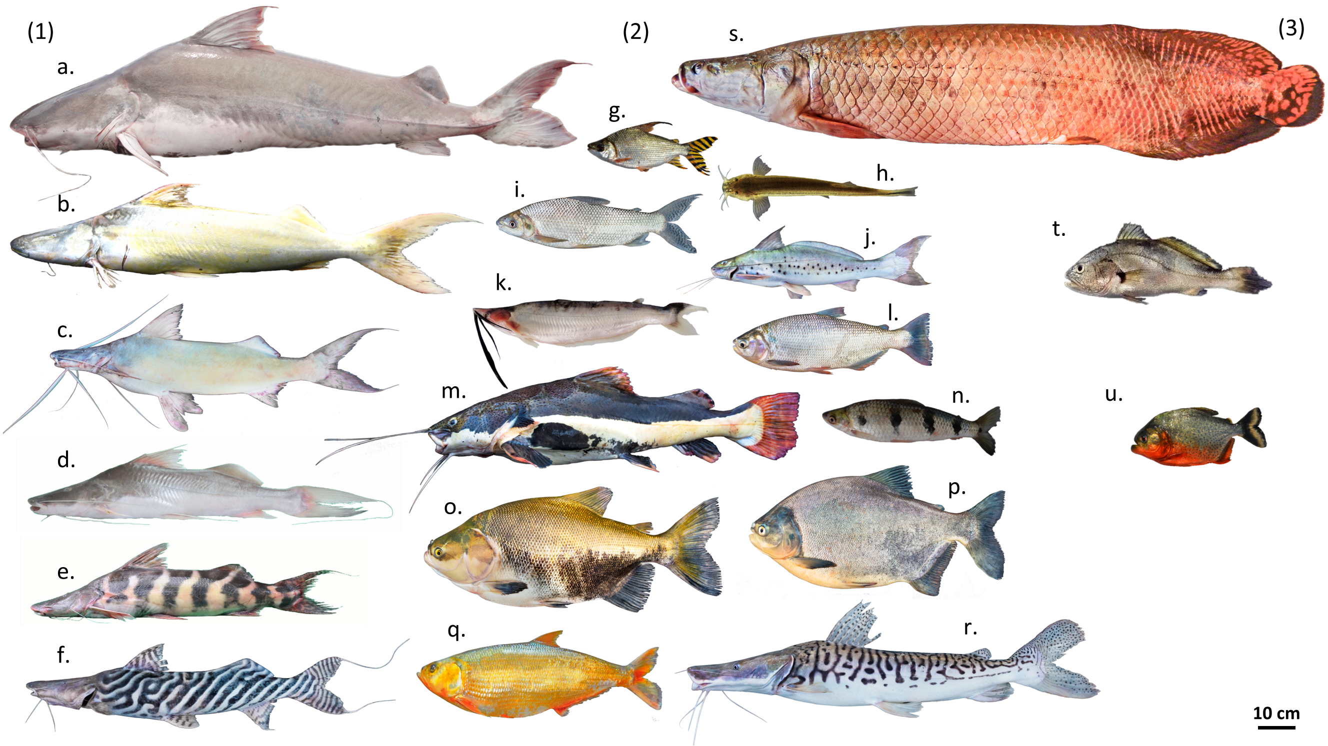

FIGURE 3 Examples of species belonging to the three main categories of migrations (most of which are cited in the text). (1) Long-distance migrations: (a) *Brachyplatystoma filamentosum*, (b) *Brachyplatystoma rousseauxii*, (c) *Brachyplatystoma platynemum*, (d) *Brachyplatystoma vaillantii*, (e) *Brachyplatystoma juruense*, (f) *Brachyplatystoma tigrinum*. (2) Medium-distance migrations: (g) *Semaprochilodus insignis*, (h) *Trichomycterus barbouri*, (i) *Prochilodus nigricans*, (j) *Calophysus macropterus*, (k) *Hypophthalmus fimbriatus*, (l) *Brycon amazonicus*, (m) *Phractocephalus hemioliopterus*, (n) *Schizodon fasciatus*, (o) *Colossoma macropomum*, (p) *Piaractus brachypomus*, (q) *Pellona flavipinis*, (r) *Pseudoplatystoma tigrinum*. (3) Short-distance migrations: (s) *Arapaima* sp., (t) *Plagioscion squamosissimus*, (u) *Pygocentrus nattereri*. For the sake of available space and visibility of small species, large species reaching over 1 m lengths (a, b, l, q, r, s) are not represented to their maximum length, unlike small and medium species. The scale does not apply to *T. barbouri* (h), given its very small size at migration (∼30 mm). Photo credits: (a), (d), (e) García Dávila et al. (2018); (b) Fernando Carvajal-Vallejos; (c), (f), (i), (j), (l), (m), (o), (p), (r) Aldo Echeverria; (h) Guido Miranda (WCS); (g), (k), (n), (t)–(w) Arantes, Winemiller, et al. (2019); (q), (s) Daniel Barroso

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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