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# **ORIGINAL ARTICLE**



WILEY FISH and FISHERIES

# Ecosystem-based management of Amazon fisheries and wetlands

Michael Goulding<sup>1</sup> | Eduardo Venticinque<sup>2</sup> | Mauro L. de B. Ribeiro<sup>3</sup> | Ronaldo B. Barthem<sup>4</sup> | Rosseval G. Leite<sup>5</sup> | Bruce Forsberg<sup>5</sup> | Paulo Petry<sup>6,7</sup> | Urbano Lopes da Silva-Júnior<sup>8</sup> | Polliana Santos Ferraz<sup>9</sup> | Carlos Cañas<sup>1</sup>

<sup>1</sup>Wildlife Conservation Society (WCS), Bronx, New York

<sup>2</sup>Universidade Federal do Rio Grande do Norte (UFRN), Natal, Brazil

<sup>3</sup>Instituto Brasileiro de Geografia e Estatística (IBGE), Brasília, Brazil

<sup>4</sup>Museu Paraense Emilio Goeldi, Belém, Brazil

<sup>5</sup>Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

<sup>6</sup>The Nature Conservancy (TNC), Arlington, Virginia

<sup>7</sup>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

<sup>8</sup>Centro Nacional de Pesquisa e Conservação da Biodiversidade Amazônica – CEPAM/ Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, Manaus, Brazil

<sup>9</sup>Instituto Mamirauá, Tefé, Brazil

#### Correspondence

Michael Goulding, Wildlife Conservation Society (WCS), Bronx, NY. Email: mgoulding@wcs.org

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#### Abstract

Infrastructure development and overfishing in the Amazon make it imperative to define adequate scales for the ecosystem-based management of commercial fisheries and the wetlands on which they depend. We mapped fisheries and fish ecology data from Brazil, Peru, Bolivia and Colombia to an explicit GIS framework of river basins and mainstems. Migratory species account for more than 80% of the known maximum catches of commercial fisheries across the Amazon. Of these migratory species, we nominated six long-distance migratory fish taxa as flagship species to define the two main commercial fishery regions. The migrations of at least one goliath catfish species define a large-scale longitudinal link joining the Andes, Amazon Lowlands and Amazon River estuary. Migratory Characiforms demonstrate interbasin wetland connectivity between nutrient-rich and nutrient-poor rivers over at least 2 million km<sup>2</sup>, or about one-third of the Amazon Basin. We show that flooded forest area is the most important wetland variable explaining regional variations in migratory characiforme biomass as indicated by maximum annual fishery catches. The sustainable management of Amazon fisheries will require transnational cooperation and a paradigm shift from local community management alone to a more integrated approach that considers both rural and urban consumers and challenges, and the realistic life histories of migratory species.

#### KEYWORDS

catfishes, Characiforms, conservation, fish, flagship, migration

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# 1 | INTRODUCTION

The adequate scale of conservation in the Amazon has been of major interest since the 1980s, with most research focusing on upland rainforest and its role in the maintenance of terrestrial biodiversity and the regulation of regional climate (e.g., Laurance et al., 2002; Soares-Filho et al., 2010). In contrast, aquatic conservation in the Amazon has generally focused on floodplain fisheries and rural peoples. These efforts have been successful in managing some non-migratory species, such as the giant pirarucu (Arapaima spp., Arapaimidae) in some floodplain lakes, and developing cooperative actions at the local level in some non-protected areas and sustainable development reserves (McGrath, Castello, Almeida, & Estupiñán, 2015; Queiroz & Crampton, 1999). As more regional data became available and synthesized, however, it became apparent that migratory fish species accounted for most of the commercial catches in the Amazon (Barthem & Goulding, 2007). Considering the large regional scale of the fisheries sector in the Amazon, it also became apparent that isolated community management efforts alone were insufficient to manage commercial fisheries and the diverse wetlands on which they depend (Barthem & Goulding, 1997). Furthermore, widespread overfishing driven by the urban demand for fish (Tregidgo, Barlowa, Pompeub, Rochac, & Parrya, 2017) and large-scale infrastructure impacts (Castello & Macedo, 2015) present major management challenges, especially in an area as large as the Amazon.

Given that overfishing and/or environmental impacts threaten most fisheries around the world, experts now recognize ecosystembased management initiatives as necessary to meet the challenges of scale (e.g., Beard et al., 2011). The objectives of ecosystem-based fisheries might simultaneously attempt, albeit with trade-offs, to optimize the total fish yield of particular species, provide safeguards to overexploitation of species, provide long-term economic viability, conserve wetlands and their biodiversity, maintain a desirable ecosystem state, protect certain species and maintain various ecosystem services (Link, 2002). A first step is to define a convincing spatial context for the ecosystem-based framework. Migratory fish are the logical species to choose when defining aquatic ecosystem size and connectivity in the Amazon because their life cycles encompass various basins and wetlands across large areas.

The concept of fish migration has an ancient history in the Amazon, which is explicit in the commonly used words *piracema* (fish exit or movement in Tupi) in Brazil (Veríssimo, 1895) and *mijano* in Spanish-speaking countries (Silva & Stewart, 2017). References to migratory fishes in the Amazon usually pertain to common food species of medium to large size (Barthem & Goulding, 2007; Ribeiro & Petrere-Jr, 1990). Many small species are also recognized as migratory by local peoples, especially near cataracts and in small streams (<20 m width) where their movements are easily observed (Cabalzar, Lima, & Lopes, 2005; Chernela, 1985). Lateral migrations in and out of floodplains are also very important and probably account for the most movement of small (<15 cm as adults) and larger species (Cox-Fernandes, 1997; Goulding, Carvalho, &

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Ferreira, 1988). Fish also have historically been the most commercially valuable aquatic resources and are critical to food security in the Amazon; thus, they are of interest to a wide array of stakeholders over large areas (Almeida, Lorenzen, & McGrath, 2004). From a geographical and human cultural viewpoint, many fish migrations also include various countries, states/departments, protected areas and indigenous territories. Considering the large size of the Amazon Basin and the overwhelming importance of migratory species in the commercial fisheries, we present an explicit spatial framework designed to integrate flagship species, wetlands and interest groups in order to inform the development of ecosystembased management initiatives for the region.

## 2 | METHODOLOGY

# 2.1 | Spatial context for the ecosystem-based management of migratory fish species

We developed a new classified river drainage network and scalable river basin hierarchy for the Amazon in order to map commercial fish catches, major river types, fish migrations, wetlands and other biological and limnological phenomena (Venticinque et al., 2016) (The complete database is available here: https://knb.ecoinformatics. org/#view/doi:10.5063/F1BG2KX8). In contrast to the Pfafstetter





river basin typology (e.g., Elesbon, Guedes, Amaral, Ribeiro, & Silva, 2011) commonly used by Amazon water authorities, our classification recognizes ecologically coherent spatial units referred to as mainstem basins, which include the main channels of major rivers, their associated floodplains and small tributaries that flow directly into these floodplains (Figure 1). Seven hierarchical basin levels from the largest to the smallest are referred to as Basin Level 1, Basin Level 2, etc. Basin Level 1 (Amazon drainage) includes the Amazon and Tocantins basins, both of which discharge into the estuary, and coastal areas north and south of the estuary that are influenced by Amazon discharge. Basin Level 2 delimits all tributary basins larger than 100,000 km<sup>2</sup> whose mainstems flow into the Amazon River channel and includes major tributaries, such as the Madeira

and Negro rivers. While not technically a basin, the Amazon River mainstem (238,000 km<sup>2</sup>) is also included as a single polygonal unit of Basin Level 2 due to its hydrological coherence and important ecological function in the system. The Amazon River mainstem consists of four main channel sections based on major fluvial geomorphological units and two estuary sections, all of which are similar in size to the Basin Level 4 sub-basins. For regional statistical analyses, we mapped fishery and wetland data to Basin Level 4 sub-basins (Figure 1). A first classification of river types (whitewater, blackwater and clearwater) in the Amazon for 6th-11th order tributaries of the Amazon was based on our own field data, the literature and qualitative visual analysis of high-resolution imagery (Venticinque et al., 2016).

To define the main commercial fishing region (Figure 1), we constructed a large data set based on historical fisheries catches from 188 urban fishing ports, 67 cities, 6 states and 4 countries in the Amazon region (database available at https://knb.ecoinformatics. org/#view/doi:10.5063/F1TB152P) (Venticinque et al., 2018). The Tocantins Basin was not included in the analyses because most of its commercial fish catch is associated with the large Tucuruí Dam reservoir, which has existed since the late 1980s. The maximum catch (t/year) of each species in each Basin Level 4 sub-basin was calculated by summing the historical maximum annual captures recorded in each of its cities, and this was considered a proxy of maximum known standing biomass of the species in each subbasin. The actual standing biomass would be some unknown larger amount since fishermen do not capture all fish. Approximately 79% of all available data could be mapped confidently to Basin Level 4 and mainstem sections, and only polygons that contributed to 99% of the total flagship species catch were included (Figures 2 and 3). There were insufficient data to calculate reliable catch per unit effort across the Amazon, but our main goal was to compare maximum yields regardless of fishing effort using extreme value statistics of total annual catches. Most cities are missing various years (<4 consecutive years) in the fisheries data, and the longest continuous data period for any site was 22 years. Thus, while these data provide no indication of current or sustainable fishing yields, they nevertheless provide a reasonable spatial indicator of the relative regional distribution of standing biomass.

### 2.3 | Interbasin migratory fish regions

The spatial distribution of life-history phases in migratory goliath catfishes was determined from length data obtained between 1982 and 2011 from commercial and experimental fisheries in Brazil, Peru, Colombia and Bolivia (Figure 4). Potential spawning



FIGURE 2 Candidate flagship species. Common names in Portuguese/Spanish. (a) Dourada/Dorado (*Brachyplatystoma rousseauxii*, Pimelodidae); (b) Piramutaba/ Manitoa (*Brachyplatystoma vaillantii*, Pimelodidae); (c) Curimatá/Boquichico (*Prochilodus nigricans*, Prochilodontidae); (d) Jaraqui/Yaraquí (*Semaprochilodus insignis*, Prochilodontidae); (e) Matrinchã/ Sábalo (*Brycon amazonicus*, Bryconidae); (f) Tambaqui/Gamitana (*Colossoma macropomum*, Serrasalmidae)



**FIGURE 3** Candidate interbasin migratory flagship species and the relative distribution of maximum known catches by Basin Level 4 subbasins and segments of the Amazon River mainstem

areas of goliath catfishes in the far western Amazon were extrapolated from level 4 basins (>10,000 and <100,000 km<sup>2</sup>) where studies have verified the presence of both mature adults and their

larvae in river channels (Barthem et al., 2017). The blackwater and clearwater tributaries used as feeding areas by interbasin migratory Characiforms are commercially fished primarily at their

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confluences with a whitewater river during spawning and dispersal migrations. Commercial fishery data are not a good indicator of migratory fish biomass in the nutrient-poor blackwater and clearwater rivers because catches made near confluences with whitewater rivers when the fish are migrating are often registered as coming from whitewater rivers. Field studies and fisheries data indicate that interbasin migratory Characiforms are relatively rare in blackwater and clearwater tributaries upstream of 300 km from their confluences with whitewater river mainstems (Ribeiro & Petrere-Jr, 1990). We thus truncated the tributary basins at 300 km upstream of their confluences with the whitewater river mainstems. In cases where natural or human-made barriers to fish migration exist, such as at major cataracts at the contact zone between the continental shields and alluvial floodplains or dams, sub-basins were also truncated at those points. The resulting blackwater and clearwater sub-basin polygons were then appended to the main commercial fisheries region to define the final interbasin migratory characiform region (Figure 4).

## 2.4 | Selection of flagship species

With approximately 2,500 species now recognized (Van-der-Sleen & Albert, 2017), the Amazon has the richest freshwater fish fauna in the world and there are many potential candidates WILEY-FISH and FISHERIES

for flagship species to target specific interest groups. Here, we focus only on selected migratory species that can inform the ecosystem-based management of fisheries to confront the impacts of infrastructure development and overfishing (Figure 4). The selection criteria include species that undertake longdistance interbasin migrations, they are among the historically most captured taxa, they are highly regarded in local cuisine, they command relatively high market prices, and they are currently or potentially vulnerable to overfishing and/or wetland degradation (Tables 1 and 2). Although body size has been emphasized elsewhere as a flagship species criterion (Ebner et al., 2016), we did not include it because the most important Amazonian commercial migratory food fishes are relatively large (>25 cm).

In addition to the criteria listed above, our selection also identifies 14 potential human-interest groups largely adapted from Ebner et al. (2016) (Table 1). It is beyond the purview of this paper to appraise the importance and geographical extent of each of these groups, and many of them will become more relevant when a larger selection of flagship species is available beyond just the long-distance migratory species considered here. Our principal target audiences are government resource managers, commercial fishers, water resource managers and environmentalists, as these groups will be essential to implement a pragmatic paradigm shift from local fisheries and wetland management only to a more realistic ecosystem-based perspective that considers the large-scale impacts of overfishing, headwater and wetland deforestation, dams and other far-reaching environmental influences.

# 2.5 | Migratory fish catches and wetlands by subregion

The ecosystem-based management of fisheries requires the conservation of major wetlands critical to fish survival, reproduction and growth at an adequate extent. Our analysis of the relation between migratory fish catches and wetlands focused only on Characiforms because of their overwhelming importance in commercial fisheries and direct connectivity to floodplain productivity. To test the importance of various wetlands for commercial fisheries, we divided the interbasin migratory characiform region into 10 subregions based on major geomorphological areas along the Amazon River mainstem (Dunne, Mertz, Meade, Richey, & Forsberg, 1998) and its major level 2 sub-basin areas (Venticinque et al., 2016). We categorized the fisheries and wetland data based on nine of these subregions (Figure 5). We excluded the Javari subregion from the analyses because little commercial fishing takes place there. We used the classification developed by Hess and Melack (Hess et al., 2015) for major vegetated wetland categories and the Water Body Dataset of the Shuttle Radar Mission (National-Geospatial-Intelligence-Agency Topography 2003/2015) for floodplain lake areas. For the analyses, we combined floodplain lakes and herbaceous communities into one class called floodplain lakes and all wetland forest types into a single flooded forest class. We further divided the flooded forests based

on their dominant sub-basin river type, with whitewaters representing nutrient-rich environments and blackwater/clearwater rivers representing nutrient-poor environments. For regression analysis, we scaled each subregion wetland area as a percentage of the total area of that wetland type in the interbasin migratory characiform region. Finally, stepwise multiple regression analyses of the maximum catches (t/year) of migratory characiform flagship species against major wetland types by subregion used the following models: whitewater river mainstem flooded forests, blackwater/clearwater tributary flooded forests, and whitewater river floodplain lakes that included herbaceous communities (Table 3). Criteria of variable removal were based on the probability of removal of 0.15 backwards. Blackwater and clearwater tributary lakes were not included in the analyses because they are neither nurseries nor important adult feeding areas for the migratory characiform flagship species. Owing to the fact that the species had different sampling sizes, model adjustment was evaluated by Adjusted Multiple R-squared. In addition, we used a power analysis for each regression (Table 3).

# 3 | RESULTS AND DISCUSSION

#### 3.1 | Context of Amazon fish migrations

Anadromous migrations (i.e., adult spawning migration is in a landward direction followed by the seaward migration of the juvenile in the life cycle) have drawn the most attention worldwide, especially the well-documented salmon migrations in the Northern Hemisphere (Lucas & Baras, 2001). Although most of the Amazon River is low-lying and without topographical barriers to migrations between the Amazon and the Atlantic, there are no known species that make large-scale anadromous migrations, which in general is true of tropical freshwater systems. At least six species of largely marine catfishes of the family Ariidae are common in the Amazon estuary (Barthem, 1985; Marceniuk & Menezes, 2007), including freshwater areas. The only ariid reported far upstream in a South American river is the New Granada sea catfish (Notarius bonillai, Ariidae) which occurs in the Magdalena River of Colombia, including its estuary (Marceniuk & Ferraris- Jr, 2003; Zúñiga-Upegui, Castro-Roa, García-Melo, García-Melo, & Herrada-Yara, 2006). Some ariid catfishes in Central America and southern Brazil migrate to estuaries or nearby lower courses of rivers to spawn in what appear to be short anadromous migrations (e.g., Gomes & Araújo, 2004; Yáñez-Arancibia & Lara-Dominguez, 1988). We have observed gravid ariids in fresh and brackish water fisheries in the Amazon estuary, and it is thus possible that they are also anadromous in this region. There are no reports of fish species in Amazonian rivers upriver of the estuary migrating to the sea to spawn (catadromous species). Mullet (Mugil, Mugilidae) spawn in open marine waters but feed in brackish or freshwater bays or inlets (e.g., González-Castro, Macchi, & Cousseau, 2011; Marin, Quintero, Bussière, & Dodron, 2003; Rivas, 1980). The Amazon estuary has at least four mullet species (Menezes, Nirchio, Siccharamirez, & Oliveira, 2015), and it is highly possible that one

Таха	Market name Po/Sp	Total Max catch (t)	% Max catch	Migratory	Trophic guild
Brachyplatystoma vaillantii	Piramutaba/Manitoa	24,409.2	14.23	Yes	Piscivore
Prochilodus nigricans	Curimatá/Boquichico	23,646.8	13.79	Yes	Detritivore
Mostly Hypophthalmus edentatus and H. marginatus, but also included H. fimbriatus	Mapará/Maparate	16,790.9	9.79	Yes	Planktivore
Brachyplatystoma rousseauxii	Dourada/Dorado	14,612.1	8.52	Yes	Piscivore
Colossoma macropomum	Tambaqui/Gamitana	13,877.1	8.09	Yes	Frugivore/zooplanktivore
Semaprochilodus insignis and S. taeniurus	Jaraqui/Yaraqui	13,018.1	7.59	Yes	Detritivore
Mostly Mylossoma aureum and M. duriventre, but also included other species of the genus Catoprion, Metynnis and Myleus	Pacu/Palometa	7,654.7	4.46	Yes	Omnivore/frugivore
Several species of the family Curimatidae, mostly of the genus Cyphocharax, Curimata, Potamorhina, Psectrogaster and Steindachneria	Branquinha/Yahurachi	5,930.0	3.46	Yes	Detritivore
Mostly Plagioscion squamosissimus, but also included other species of the genus Plagioscion, Pachypops and Pachyurus	Pescada/Corvina	5,771.2	3.37	۰.	Piscivore/crustivore
Several species of the genus Cichla	Tucunaré/Pavón	4,349.0	2.54	No	Piscivore
Several species of the family Anostomidae, mostly of the genera <i>Leporinus</i> , <i>Rhytiodus</i> and Schizodon	Aracu/Lisa	4,122.8	2.40	Yes	Omnivore
Triportheus albus, T. angulatus and T. elongatus	Sardinha/Sardina	3,521.5	2.05	Yes	Omnivore
Pseudoplatystoma fasciatum and P. reticulatum	Surubim/Doncella	3,315.1	1,93	Yes	Piscivore
Brycon amazonicus and B. cephalus	Matrinchã/Sábalo	2,531.8	1.48	Yes	Omnivore/frugivore
Piaractus brachypomus	Pirapitinga/Paco	2,390.9	1.39	Yes	Frugivore
Pseudoplatystoma tigrinum	Caparari/Doncella	2,276.5	1.33	Yes	Piscivore
Osteoglossum bicirrhosum	Aruanã/Arahuana	2,083.6	1.21	No	Omnivore
Several species of the family Loricariidae, mostly of the genus Liposarcus and Hypostomus	Acari-Bodó/Carachama	2,031.3	1.18	oN	Detritivore
Brachyplatystoma filamentosum (Lichtenstein, 1819) and B. capapretum Lundberg & Akama, 2005	Piraíba/Saltón	1,912.7	1.12	Yes	Piscivore
Several species of the family Anostomidae, mostly Anodus elongatus Agassiz, 1829 and the species of the genus Hemiodus	Charuto or Orana/Julilla	1,747.4	1.02	Yes	Algivore
Total		155,992.8	90.96		

**TABLE 1** The most important fish taxa historically in Amazon commercial fisheries as indicated by maximum known catches

Note. Highlighted taxa indicate proposed candidate migratory flagship species.

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<b>TABLE 2</b> Proposed flagship species and potential interest g	roups
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Таха	Brachyplatystoma vaillantii, B. rousseauxii	Prochilodus nigricans	Colossoma macropomum	Semaprochilodus insignis, S. taeniurus	Brycon amazonicus
Interest group					
Artisanal commercial fishers	E	E	E	E	E
Aquarists	СМ	СМ	CM	СМ	СМ
Industrial-scale fishermen	E				
Fishmongers (Urban markets, refrigeration plants)	E	E	E	E	E
Subsistence fishers	F	F	F	F	F
Indigenous peoples		F	F	F	F
Scientists	СМ	СМ	CM	СМ	СМ
Environmental managers	СМ	СМ	CM	СМ	СМ
Water resource users	СМ	СМ	CM	СМ	СМ
Non-governmental organiza- tions (NGOs)/ environmentalists	СМ	СМ	СМ	СМ	СМ
Aquaculturalists			E, GB		E, GB
Aquarists	СМ				
General public	IW	F	IW		
Restaurants/Regional cuisine	E, C	С	С	С	С

Note. C: cultural (highly regarded flavour, restaurants); CM: conservation/management; E: employment; F: food; GB: gene bank; IW: iconic wildlife.

or more of these taxa undertake short-distance anadromous migrations, but little is known about their life histories (Barthem, 1985). The bull shark (*Carcharhinus leucas*, Carcharhinidae) and the largetooth sawfish (*Pristis pristis*, Pristidae) have been captured at least 3,000 km upstream in the Amazon, although they are considered to be opportunistic and not obligatorily migratory (Garrick, 1982; Thorson, 1974; Werder & Alhanati, 1981). The presence of newly born individuals (0.6–0.8 m length) of both species in the brackish and freshwater of the Amazon coast indicates they can use the Amazon estuary as a nursery area. Telemetry investigations in the Fitzroy River, Western Australia, also show that large-tooth sawfish can use freshwater as a nursery for large juveniles (0.9–2.5 m length) (Whitty et al., 2017).

If enough were known about the life histories of Amazonian fishes, hundreds of species might be considered migratory under a broad definition of migration (e.g., Chapman et al., 2012). Fish studies that have included some combination of floodplain lakes, river channels and flooded forests show that there are massive seasonal movements of large numbers of species between these major habitats (Cox-Fernandes, 1997; Cox-Fernandes & Petry, 1991; Goulding et al., 1988; Petry, Bayley, & Markle, 2003). There have been no successful long-distance fish tagging experiments for the Amazon. Nevertheless, the nature of fish migrations can be inferred from the direct observation of fisheries operations (Barthem & Goulding, 1997; Goulding, 1981; Ribeiro & Petrere-Jr, 1990) and catch data (Petrere-Jr, 1985). These observations are further supported by ichthyoplankton sampling in river channels (Araujo-Lima & Ruffino, 2004; Barthem et al., 2017; Cañas & Pine, 2011) and migratory fish otolith chemistry related to river chemistry (Hegg, Giarrizzo, & Kennedy, 2015; Hermann, Stewart, Limburg, & Castello, 2016).

All Amazon migratory fishes of commercial importance in inland waters are potadromous species; that is, they migrate in rivers and they complete their entire life cycle in freshwater. Fish migration studies in freshwater usually focus on upstream or downstream movements of schools in river channels (See Carolsfeld, Harvey, Ross, & Baer, 2003). Because spawning occurs in river channels, currents or active swimming transport eggs, larvae and juveniles downstream, resulting in the upstream migration of subadults or adults at some life cycle stage to counterbalance the displacement of offspring (Araujo-Lima, Silva, Petry, Oliveira, & Moura, 2001). Our focus here is not only on species that migrate in river channels but also that undertake longdistance interbasin migrations centred on the Amazon River and its major tributaries. The life-history areas of these species thus define the minimum area for ecosystem-based management initiatives. We refer to these taxa as interbasin migratory species, and they present two main migration types: continental-scale goliath catfish migrations and long-distance characiform migrations. The long-distance migratory Characiforms (order Characiforms) and catfishes (order Siluriformes) account for approximately 83% (46% and 37%, respectively) of the maximum-recorded annual commercial catches (t/year) of migratory and non-migratory species in the region (Table 1).

### 3.2 | Candidate flagship migratory species

Flagship taxa are iconic species used to promote conservation awareness (Caro, 2010). Criteria for the selection of flagship

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**TABLE 3** Power analysis and Pearson correlations based on stepwise multiple regressions of major wetlands and maximum commercial catches of interbasin migratory characiform flagship species

Power analysis					
Таха	Observed effect size (f2)*		Test power**		
All taxa	1.494		0.791		
Semaprochilodus insignis and S. taeniurus	19.408	19.408		1.000	
Brycon amazonicus	2.533		0.958		
Colossoma macropomum	2.164		0.638		
Prochilodus nigricans	0.422		0.299		
*f2 = R2/(1–R2) **Cohen "default" = 0.8					
Cohen large effect size $f2 \ge 0.35$					
Regressions					
Effect	Coeff ± Std. error	Std. Coef	t	p-value	
Four characin taxa together					
Constant	3.027 ± 0.191	0	15.849	0	
Whitewater river flooded forest	$0.055 \pm 0.022$	0.575	2.464	0.049	
Whitewater river floodplain lakes	0.018 ± 0.009	0.467	2.004	0.092	
$(r^2 \text{ adj} = 0.599; N = 9; F = 6.978; p = 0.027)$					
Semaprochilodus insignis and S. taeniurus					
Constant	1.733 ± 0.093	0	18.643	<0.001	
Black/clearwater river flooded forest	$0.315 \pm 0.025$	0.978	12.481	<0.001	
$(r^2 \text{ adj} = 0.951; N = 9; F = 155.769; p < 0.001)$					
Brycon amazonicus					
Constant	2.115 ± 0.085	0	24.858	<0.001	
Black/clearwater river flooded forest	0.125 ± 0.027	1.034	4.718	0.003	
Whitewater river floodplain lakes	$-0.015 \pm 0.006$	-0.508	-2.319	0.06	
$(r^2 \text{ adj} = 0.717; N = 9; F = 11.138; p = 0.010)$					
Colossoma macropomum					
Constant	2.623 ± 0.194	0	13.551	<0.001	
Whitewater river flooded forest	0.079 ± 0.023	0.864	3.436	0.026	
(r <sup>2</sup> adj = 0.684; N = 6; F = 11.808; p = 0.026; filter = 95% of total capture)					
Prochilodus nigricans					
Constant	2.455 ± 0.363	0	6.769	<0.001	
Whitewater river flooded forest	$0.086 \pm 0.041$	0.621	2.094	0.074	
(r <sup>2</sup> adj = 0.297; N = 9; F = 4.386; p = 0.074)					

species are often arbitrary and ad hoc, and well-defined candidates for freshwater systems are scarce, although a recent example for Australia at a continental and regional scale is promising (Ebner et al., 2016). The identification of target conservation audiences is crucial for meaningful flagship species recognition (Veríssimo et al., 2014). Five of our candidate migratory flagship taxa are among the six with the highest maximum historical catches (t/year) recorded, and all command relatively high market prices (Figure 4 and Table 1). Four taxa have been widely exploited, as indicated by their relatively high maximum catches in the first and second quartile regional divisions (Figures 3 and 5). Although planktivorous catfishes of the genus Hypophthalmus (Pimelodidae) were among the six most captured taxa and are migratory (Merona, Juras, Santos, & Cintra, 2010; Ribeiro, Petrere-Jr, & Juras, 1995), we have no evidence that they undertake long-distance interbasin migrations, one of the criteria we used to define a flagship species for an ecosystem-based framework. Although matrinchã (*Brycon amazonicus*, Bryconidae) is only 14th on the market taxa list of the most captured species, we nominate it as a flagship candidate because it is one of the favourite food species and a connecting species between large river floodplains and upland rainforest streams. In addition, matrinchã is the migratory species that occupies the largest number of habitats in the Amazon Basin.





Based on published studies, all six of our proposed candidate flagship taxa are overfished or now highly vulnerable to growth overfishing, which is a fishing level that exceeds the maximum yield per recruit. Growth overfishing for two species of goliath catfishes, dourada (*Brachyplatystoma rousseauxii*, Pimelodidae) and piramutaba (*Brachyplatystoma vaillantii*, Pimelodidae), and the large characiform tambaqui (*Colossoma macropomum*, Serrasalmidae), occurred as early as the 1990s, if not somewhat earlier (Alonso & Pirker, 2005; Batista & Isaac, 2012; Isaac & Ruffino, 1996). The fruit- and seed-eating tambaqui was once the most important commercial fish species in the western Amazon (Petrere-Jr, 1985) and the first threatened with the near commercial extinction of adults. A combination of the uncontrolled gillnet fishing of young fish in whitewater river floodplains by local communities (Isaac & Ruffino, 1996; Sousa & Freitas, 2010) and wetland deforestation in the Amazon River floodplain downriver of the Negro River confluence (Renó, Novo, Suemitsu, Renno, & Silva, 2011) is likely the major factor affecting its decline. Based on length and weight data in the central Amazon, curimatá (*Prochilodus nigricans*, Prochilodontidae) is now heavily fished (Catarino, Campos, Souza, & Freitas, 2014). Matrinchã was not considered to be overfished in the central Amazon based on data collected between 1994 and 2002 (Santos-Filho & Batista, 2009), although the present dominance of this species in the large Manaus market from aquaculture strongly suggests that overfishing has occurred in a manner similar to that observed for tambaqui. Possible growth overfishing of jaraqui (*Semaprochilodus insignis* and *Semaprochilodus taeniurus*, Prochilodontidae) was recognized as early as the late 1980s (Batista & Isaac, 2012; Ribeiro & Petrere-Jr, 1990) but subsequent seine mesh agreements led to recuperation of stocks. The lack of data since then, however, leaves the present situation unclear.

# 3.3 | Continental-scale migratory goliath catfish region

Goliath catfishes undertake the only known continental-scale migrations in the Amazon. The migrations of dourada, piramutaba, babão (Brachyplatystoma platynemum, Pimelodidae) and zebra catfish (Brachyplatystoma juruense, Pimelodidae) involve movements from the eastern or central Amazon where nurseries are located, to the western Amazon where spawning occurs in river channels (Barthem et al., 2017; Cañas & Pine, 2011; Hegg et al., 2015; Hermann et al., 2016). Continental-scale migrations span at least 75% of the length of the Amazon Basin and, in the case of dourada, at least 90% of the length of the basin stretching from the Andes to the Amazon River estuary and plume (Figure 6). The upstream movements of large subadults and adults to reach spawning areas may take several years, but the downstream movements of offspring from spawning to nursery areas are undertaken in a few weeks at most (Barthem et al., 2017) (Figure 6). Although goliath catfish spawning areas have only been recorded in a few headwater basins in or near the Andes, mature adults have been registered in all major rivers in or near (<300 km) the Andes in Colombia, Ecuador, Peru and Bolivia (Barthem, Goulding, Forsberg, Cañas, & Ortega, 2003; Cañas, 1999; Cañas & Pine, 2011; García, Vargas, Tello, & Duponchelle, 2012; Lasso et al., 2011; Van-Damme, Carvajal-Vallejos, Rua, Córdova, & Becerra, 2011). It thus appears safe to assume that some combination of goliath catfish species spawns from just north of the equator in Colombia to at least 17°S in Bolivia. A small quantity of mature dourada is also known to fishermen and was verified by us to occur in the upper Branco River, a semi-turbid tributary of the Negro River associated with the Guiana Shield in Brazil and Guyana. There are no data to indicate whether Branco River and western Amazon populations are genetically isolated.

#### 3.4 | Long-distance migratory characiform region

The common nexus among interbasin long-distance migratory Characiforms is that their movements for spawning and upstream dispersal centre on nutrient-rich whitewater rivers (e.g., Arauio-Lima & Goulding, 1997; Ribeiro & Petrere-Jr, 1990; Silva & Stewart, 2017) (Figures 7 and 8). The floodplains of whitewater rivers are also their nurseries (Figure 8) because of the relatively high primary production associated with nutrients brought downstream from the Andes or from headwaters associated with the Fitzcarrald Arch, a low hilly region in the upper Purus and Juruá basins (Melack & Forsberg, 2001; Regarda et al., 2009). Many, if not most, of the long-distance migratory characiform species, however, are not restricted to whitewater rivers but also migrate into and out of nutrient-poor blackwater and/or clearwater rivers that large subadults and adults use as feeding areas (Correa & Winemiller, 2018; Goulding, 1980; Ribeiro & Petrere-Jr, 1990). Based on the main commercial fisheries area and migratory areas outside of it, the interbasin migratory characiform region occupies an area of  $2,015,414 \text{ km}^2$ , or nearly one-third of the Amazon Basin (Figure 4), of which approximately 225,596 km<sup>2</sup> (11.2%) is wetlands. Of these wetlands, flooded forests cover 189,775 km<sup>2</sup> (84.1%), herbaceous communities cover 21,806 km<sup>2</sup> (9.7%) and floodplain lakes at intermediate water levels cover 14,015 km<sup>2</sup> (6.2%). The whitewater rivers account for 71.9% of the flooded forests in the interbasin migratory characiform region, followed by flooded forests of blackwater and clearwater tributaries, which represent 28.1%. Most of the interbasin migratory Characiforms of major commercial importance



**FIGURE 6** Dourada/Dorado migration from the estuary to the far western Amazon based on empirical observations of differential size classes captured in commercial fisheries, experimental ichthyoplankton sampling and otolith chemistry related to river chemistry. Red points show data locations



**FIGURE 7** (a) Major Amazon river types based on visual characteristics and general chemistry. Most whitewater rivers have headwaters in the Andes and carry heavy sediment loads. Blackwater and clearwater rivers arise in the lowlands and transport relatively few sediments and are nutrient-poor. (b) Confluence of the whitewater Amazon River and the blackwater Negro River. (c) Confluence of the whitewater Madeira River and the clearwater Machado River showing fishermen using a seine to capture migratory Characiforms during dispersal migrations





are widely distributed in this area, although some species, such as curimatá and pacu (*Mylossoma* spp., Serrasalmidae), are missing from at least some blackwater rivers such as the Negro (Goulding et al., 1988). The Madeira Rapids were a barrier to jaraqui, although jaraqui escama grossa (*Semaprochilodus insignis*, Prochilodontidae) was introduced upstream of the cataracts in the 1980s and has now

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spread widely in the Guaporé/Itenez and Mamoré basins of Brazil and Bolivia (Van-Damme et al., 2011).

The available genetic evidence indicates little differentiation in the populations of interbasin migratory Characiforms within the interbasin migration region we defined (Machado, Willis, Teixeira, Hrbek, & Farias, 2016: Santos, Ruffino, & Farias, 2007). In contrast to the interbasin migratory goliath catfishes, interbasin migratory Characiforms spawn throughout the Amazon Basin wherever there are whitewater rivers, and especially near their confluences with blackwater and clearwater confluences (Figure 7). Each annual upstream dispersal migration event places mature fish farther upstream. Some species. such as the jaraquis, become rare near the Andes, at least as indicated by fisheries data (Anderson, Montoya, Soto, Flores, & McClain, 2009). Based on detailed studies of jaraqui, annual migrations that include spawning and dispersal movements in nutrient-poor tributaries and the Amazon River mainstem can extend for 1,300 km in the Central Amazon, with upstream annual displacements in whitewater rivers of 300 km (Ribeiro & Petrere-Jr, 1990). Numerous ichthyoplankton studies in whitewater river channels also confirm massive downstream displacement of migratory characiform larvae until they enter floodplain nurseries (Araujo-Lima & Oliveira, 1998; Araujo-Lima & Ruffino, 2004; Lima & Araujo-Lima, 2004).

### 3.5 | Flagship characiform species and wetlands

Based on previous statistical analyses that showed that commercial fishermen historically targeted the areas with the most productive floodplains (Petrere-Jr, 1983), we expected a priori that the production of regional commercial fisheries would correlate with whitewater river floodplain areas, but with which wetlands in those areas had yet to be determined. Modern satellite imagery has permitted the relatively accurate mapping of major Amazon wetland types (Hess, Melack, Novo, Barbosa, & Gastil, 2003; Hess et al., 2015; Melack & Hess, 2010). Within the migratory characiform region, flooded forests and lakes (including their herbaceous communities) are the dominant floodplain wetlands. We expected a priori that regional fisheries production would correlate with lake areas of whitewater river floodplain because of their known role as nurseries (Bayley, 1988; Leite, Silva, & Freitas, 2006; Mounic-Silva & Leite, 2013; Petry et al., 2003). The correlation between flooded forest areas and their river types across the Amazon was less clear. Experimental gillnet studies and commercial fish landing analyses in different areas of the Amazon reported that fish abundance and/or diversity was most associated with flooded forest area (Arantes et al., 2017; Castello et al., 2017; Lobón-Cerviá, Hess, Melack, & Araujo-Lima, 2015). An experimental gillnet investigation of 15 floodplain lakes of the Central Amazon floodplain correlated fish species richness with the extent of shrub vegetation during the high water period and the extent of aquatic herbaceous communities and open waters during the low water season (Freitas et al., 2018).

Although the number of subregions (N = 9) we used to detect the regional importance of wetland type in fisheries production (Figure 5) was low for regression analyses, a power analysis indicated that the sample size effect of all regressions exceeded the minimum value considered to be acceptable (Table 3) (Cohen, 1988). More specifically, the power analysis for tambaqui indicated intermediate acceptability (0.638), but it indicated elevated acceptability for all four taxa considered together (0.791), jaraqui (1.000) and matrinchã (0.958), thus assuring interpretive validity for these four cases. Power analysis for curimatá (0.299) alone indicated the lowest degree of confidence for the various flagship species considered in the fisheries production and wetland regression analyses.

When the four flagship characiform taxa were considered together, the regression model indicated whitewater mainstem flooded forest as the most significant wetland indicator of fisheries production upriver of the estuary, followed by whitewater floodplain lakes ( $r^2$  adj = 0.599; N = 9; F = 6.978; p = 0.027) (Table 3). The speciesspecific regression results for three of the flagship characiform taxa, however, do not reflect the relative collinearity of floodplain lake and flooded forest area in the western Amazon because the large floodplain lake area of the eastern Amazon is not linearly correlated with fisheries production (Figure 9). A more local study that focused on the eastern subregion indicated that floodplain forest cover was more correlated with fish yield than aquatic macrophytes associated with lakes (Castello et al., 2017).

The individual regression models for three of the selected flagship species agree with empirical data studies of wetland use by large subadults and adults. For tambaqui, whitewater mainstem flooded forest explains 68% of the variance in its capture abundance (r<sup>2</sup> adj = 0.684; N = 6; F = 11.808; p = 0.026; filter = 95% of total capture). Tambagui is one of the most unusual migratory fishes in the Amazon because of its possession of numerous gill rakers, which are associated with a zooplanktivorous diet in whitewater river floodplain lakes and molar-like teeth used for feeding on fruits and seeds in flooded forests after just a few months of age (Araujo-Lima & Goulding, 1997). The detritivorous jaraquis are closely related, have similar life histories and produce hybrids in the wild (Ribeiro, 1984). Blackwater and clearwater river flooded forests explained 95% of the catch variance for these species ( $r^2$ adj = 0.951; N = 9; F = 155.769; p < 0.001) and 72% for matrinchã  $(r^2 \text{ adj} = 0.717; N = 9; F = 11.138; p = 0.010)$ . Prior to 1 year of age, jaragui leave their whitewater river floodplain nurseries and migrate to blackwater and clearwater rivers (Ribeiro & Petrere-Jr, 1990). There they feed on detritus derived from vascular plants and periphyton in flooded forests (Benedito-Cecilio, Araujo-Lima, Forsberg, Bittencourt, & Martinelli, 2002; Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993; Leite, Araújo-Lima, Victoria, & Martinelli, 2002). The migratory pattern of matrinchã is similar to that of jaraquis, although matrinchã is omnivorous as a large subadult and adult with a preference for fruits and seeds and is more dependent on rainforest streams as low-water refuges (Borges, 1986; Lima, 2017).

No wetland variable strongly explained the variance in the maximum capture of curimatá, although the area of whitewater



**FIGURE 9** (a) Flooded forest (feeding areas) and floodplain lake areas (nurseries) are highly correlated in most subregions of the interbasin migratory characiforme region when the Eastern Amazon is not included in the regression. (b) When the Eastern Amazon is included, its extremely large floodplain lake area skews the correlation

river mainstem flooded forest explained 30% of the variance ( $r^2$  adj = 0.297; N = 9; F = 4.386; p = 0.074). Carbon isotope analyses of fish flesh related to algae, vascular plant material and herbaceous plants indicate that there is great spatial variability along the Amazon River floodplain in the ultimate carbon sources in the detritus on which curimatá feeds (Benedito-Cecilio et al., 2002). There are no empirical data on the regional detritus composition along the Amazon River floodplain that might indicate spatial differences in curimatá productivity. Maximum catches of curimatá occur in the far western and eastern subregions, the former with relatively small floodplain lakes and the latter with large lakes (Figure 2).

#### 3.6 | Scale management challenges

The continental-scale migratory goliath catfish species are the most challenging to manage because of the enormous life-history areas they occupy and the various countries involved. There is the possible perception that protecting their spawning areas in western Amazon headwaters in Andean countries, where little commercial fishing occurs, would provide little benefit to the peoples that live there and only enhance downstream fisheries, including industrial-scale operations in the Amazon River estuary where most of the commercial catch occurs. This perception, however, would be shortsighted because migratory fish species also provide the most solid scientific example for local peoples, NGOs and others to use as an environmental argument to confront the negative impacts of infrastructure development on western headwater sub-basins that could have far-flung downstream consequences on fisheries and wetlands in general (Forsberg et al., 2017). Mitigating the impacts of infrastructure on headwater sub-basins would strengthen ecosystem services related in general to water quality, aquatic biodiversity and wetlands. Furthermore, the adult populations of most migratory goliath catfishes represent first-class food fishes exploited to various extents in the Andean countries farther downstream of the spawning areas (Agudelo-Córdoba et al., 2013; Garcia-Vasquez et al., 2009). Because goliath catfishes also undertake the longest freshwater fish migrations in the world, this makes them inherently interesting to a wide public audience interested in Amazon wildlife. Finally, goliath catfishes represent a wildlife focal point to promote transnational cooperation for Amazon conservation and infrastructure mitigation, perhaps with greater utilization and participation in the United Nation's Convention of the Conservation of Migratory Species.

The outstanding features of the interbasin migratory characiform region are its size, or nearly one-third of the Amazon Basin based on the sub-basin and mainstem areas we defined, and its vast wetlands dominated by flooded forests. We showed that the commercial fisheries production of flagship Characiforms correlates with the area of flooded forests (also see Castello et al., 2017) and whitewater river floodplain lakes. The interbasin migratory Characiforms have evolved to use the nutrient-rich floodplains of whitewater rivers as their nurseries and whitewater river channels as spawning habitats and dispersal corridors. Several species also migrate to nutrient-poor blackwater and clearwater tributaries, a phenomenon that represents not only a major transfer of energy but also dynamic terrestrial-aquatic trophic linkages (Correa & Winemiller, 2018; Ribeiro & Petrere-Jr, 1990; Winemiller & Jepsen, 2004). Some species of migratory Characiforms also represent a high biomass of flooded forest seed predators and dispersers (Anderson, Nuttle, Rojas, Pendergast, & Flecker, 2011; Correa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015; Goulding, 1980). The characiform flagship species thus contribute to several ecosystem services that bridge river types, including regulating (interbasin energy balance), supporting (seed dispersal agents), provisioning (prey for other fishes, dolphins and humans) and cultural (highly valued species). One of the candidate flagship species, matrinchã, represents connectivity not only between whitewater river floodplain nurseries and blackwater/clearwater tributaries (Leite, 2004), but also to upland rainforest, the streams of which it uses as refuge habitats during the low water season (Borges, 1986).

The migratory flagship species clearly illustrate how spawning, nursery and feeding areas exist along vast environmental connectivity gradients in the Amazon. The migratory flagship species spawn in river channels but very few of these habitats are protected in the Amazon or even given explicit wetland status (Cunha, Piedade, & Junk, 2015), as has been proposed by the Ramsar Convention (Mathews, 1993), to which all Amazonian countries are signatories. The nurseries of goliath catfishes occur in river channels or open waters of the estuary, and those of the flagship characiform species occur in floodplain waters. Only approximately 15% of the whitewater river floodplains are under some level of management, and this is mostly under the conservation category of sustainable use, with <1% under integral protection. There are three notable sustainable development reserves: Mamirauá (12,500 km<sup>2</sup>) at the confluence of the Caquetá-Japurá and Amazon rivers, Piagaçu (10,000 km<sup>2</sup>) along the lower Purus River in Brazil and Pacaya-Samiria (20,000 km<sup>2</sup>) between the Ucayali and Marañón rivers in Peru. Indigenous territories represent approximately 17% of the main commercial fishing area but largely occur outside of the whitewater river nursery areas. The blackwater/ clearwater sub-basins linked to the main commercial fishing region function as feeding areas for large subadults and adults contain two national parks, Anavilhanas (3,500 km<sup>2</sup>) and Jaú (22,720 km<sup>2</sup>), both in the lower Negro Basin. Despite their protected status, these parks are similar in function to sustainable development reserves because humans exploit fish and other resources in them.

# 3.7 | Infrastructure impacts, climate change and flagship species

Considering river impoundment (dams) and deforestation as the major impacts, the main fishing regions we defined have already suffered major impacts from two large dams on the Madeira River in Brazil and deforestation of the Amazon River floodplain downriver of its confluence with the Negro River. There is still no evidence that goliath catfishes use the fish passages constructed around the Santo Antônio Dam on the Madeira; thus, new annual recruits cannot reach headwater-spawning areas in Bolivia and Peru. The long lentic environments now upstream of the dams could also affect the capacity of the larvae and juveniles to move downstream, since these fish depend on currents to support their downstream migration. FISH and FISHERIES

The Amazon River floodplain downriver of the mouth of the Negro River has been heavily deforested, with at least 3,500 km<sup>2</sup> removed for agricultural activities since the late 1970s, and likely much more than that since the 1930s due to jute farming and livestock ranching (Goulding, Smith, & Mahar, 1996; Renó et al., 2011). The lower Amazon River floodplain undoubtedly has important nurseries, and wetland deforestation may in part be responsible for the drastic decline in some species, such as the highly frugivorous tambagui (Isaac & Ruffino, 1996), which was once the most important commercial species. Importantly, however, the remaining forest is still critical to fish production (Castello et al., 2017). The blackwater and clearwater sub-basin areas (446,320 km<sup>2</sup>) upstream of the main commercial fishing area, to which many species migrate partially or permanently after reaching large subadult stages, have suffered relatively little deforestation. The most notable impact is the Balbina Dam reservoir (2,300 km<sup>2</sup>) near Manaus, which is located on a small blackwater river, but the impoundment has had relatively little impact on regional commercial fisheries.

All of the main Andean tributary basins are experiencing headwater deforestation for agricultural expansion and have booming mining activities in the mountainous regions and hydrocarbon exploitation in the adjacent lowlands (Finer, Jenkins, Pimm, Keane, & Ross, 2008). To date, there are no large dams on major Andean tributaries. Most concern is centred on potential high-walled storage dams for the Marañón, Ucayali and Beni rivers, and their potential downstream impacts on wetlands and fisheries if the hydrological, sediment and nutrient cycles are heavily modified (Anderson et al., 2018; Forsberg et al., 2017; Latrubesse et al., 2017). Proposed channel straightening and/or dredging of the Amazonas, Ucayali, Marañón and Huallaga rivers in Peru are also of concern and will soon reach the environmental impact assessment stage.

In addition to overfishing and wetland degradation, an ecosystembased framework also needs to consider the effects of climate change that could exacerbate direct human-related impacts. Climate models predict wetter conditions (+9-18%) in the next 70-80 years in the western Amazon and drier conditions in the east (Sorribas et al., 2016). If the predicted conditions prevail, then there would be increased mean and maximum river discharge in the northwestern Andes-Amazon tributaries and an increased inundation extent of western floodplains. The central and eastern Amazon would have decreased river discharges, and a smaller inundation extent is predicted for the central (-15.9%) and lower Amazon (-4.4%) during low water periods. There is historical evidence for severe decadal drought and flood conditions, with major recent droughts and extreme low water periods along the Amazon River mainstem in 1997, 2005 and 2010 (Marengo, Tomasella, Alves, Soares, & Rodriguez, 2011). Extreme low water seasons reduce floodplain lake areas, and anecdotal data indicate that commercial fishing intensifies, as fish are much easier to catch in smaller and shallower waterbodies (Tomasella et al., 2013). Fishers also correlate intense upstream migrations of the flagship and other migratory species with extreme low water periods; thus, migratory fish in general also become more vulnerable to fisheries and a large number of piscivores in shallower and narrower river channels.

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4 | CONCLUSION

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In this paper, we propose that migratory species are a promising focal point to promote aquatic ecosystem-based conservation in the Amazon. National legal definitions of migratory fish species, however, are vague, although Brazil, Peru, Ecuador and Bolivia are signatories to the United Nations sponsored Convention on the Conservation of Migratory Species of Wild Animals. The Convention of Migratory Species defines transnational migrations as occurring when "the entire population or any geographically separate part of the population of any species... a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries" (United-Nations-Environment-Programme 1979). Our candidate flagship species all qualify as transnational migratory species. Our results provide key insight, via fish migrations and correlations between fish catch and wetlands, into longitudinal and lateral ecosystem linkage among the Andes, lowland river types and the Amazon River estuary. Our results demonstrate that Amazon fisheries management needs to consider the life cycle areas of migratory species and the critical importance of whitewater river floodplain nurseries and flooded forests of all river types. Considering the large size of the Amazon and the long-distance fish migrations involved, we suggest that a basin and mainstem spatial context is the most auspicious framework for large-scale ecosystem-based management of the fisheries in the Amazon and the wetlands on which they depend. We defined two major interbasin migratory regions, each with challenges pertaining to specific interest groups, and especially government environmental management agencies charged with fisheries and wetland protection. We suggest that flagship species provide a means to generate greater interest in fisheries management and conservation at the large scales now needed to confront the challenges of overexploitation and environmental degradation. An "Amazon Basin Fisheries and Wetlands Management Commission," or something similar, is needed to help coordinate and regulate fishery harvests of transboundary migrants and the wetlands on which they depend.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interests.

# ORCID

Michael Goulding D http://orcid.org/0000-0002-7609-6470

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