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AQUATIC ECOSYSTEM SERVICES

Review Paper

Ecosystem services generated by Neotropical freshwater fishes

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Abstract To understand how Neotropical freshwater fishes (NFF) benefit society, we conducted a broad literature survey to (i) map and list the ecosystem services (ES) generated by these organisms, and (ii) investigate how human activities have affected the ecosystem service chain. We found sound evidence that NFF contribute directly and indirectly to the generation of several provisioning, regulating, supporting, and cultural services. Provisioning services have been widely recognized, especially those related to fisheries, but this class also included ornamental fish, genetic pools, medicines, aquaculture, and bioindicators. Other services remain less understood and largely ignored by society. Regulating services included seed dispersal, decomposition, and top-down control, while supporting services included nutrient cycling, habitat quality, and ecosystem engineering. Cultural services associated with NFF included recreational fishing, tourism, fishkeeping, education, production of scientific knowledge, in addition to values linked to traditional communities, such as local knowledge, cosmology, and existential foundations.

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Human activities have negatively impacted the generation of ES, especially those related to fishing and food provisioning. This review indicates that Neotropical fishes benefit society in multiple ways, but it is imperative to improve our understanding about those benefits, and to increase conservation efforts directed to this important component of global biodiversity.

Keywords Biodiversity · Fishing · Local ecological knowledge · Nutrient cycling · Seed dispersal

Introduction

The diversity of Neotropical freshwater fishes (hereafter NFF) is extraordinary among vertebrates, unparalleled to any other zoogeographic region (Tonella et al., 2022). More than 6000 species have been described (Albert et al., 2020), representing about 1/3 of all freshwater fish species on the Planet (*sensu* Fricke et al., 2021). Such diversity, however, cannot be assessed solely by the number of species, as it entails a variety of forms, sizes, behaviors, distributions, and origins. These aspects naturally translate into high levels of phylogenetic and functional diversity (Toussaint et al., 2016), resulting in fish species generating important ecosystem functions and benefits to human societies (Taylor et al., 2006). These facets, however, have been little studied and understood (Vitule et al., 2017); ecosystem services (ES) have been an undervalued topic, probably because the concept is more recent, complex, and some dimensions are still difficult to assess/quantify (La Notte et al., 2017).

Ecosystem services represent the contact between natural resources and society (Díaz et al., 2015). Freshwater fish, in general, generate different services (Holmlund & Hammer, 1999) and contribute to multiple dimensions of human well-being (i.e., material, relational, and subjective; Cooke et al., 2016; McIntyre et al., 2016; IPBES, 2019). The importance of NFF to fishing and fishery products are well known, as they represent important economic resources for many countries and are exported worldwide. They also play an essential role in alleviating poverty in Latin America, as fish provide food, income, and capital for millions of families (FAO, 2018). However, NFF generate several other services, many of which are unrelated to fisheries but critical to support human activities. They include different types of provisioning, regulating, supporting, and cultural services (e.g., Taylor et al., 2006; Correa et al., 2007; Garnelo, 2007; Helfman, 2007; McIntyre et al., 2008; Olden et al., 2020), which generate direct and indirect benefits of economic and non-economic values. However, these services have received less attention than those related to fisheries and, in most cases, they remain largely unappreciated or even ignored by society. The common utilitarian view contributes to eclipse the perception of the multiple beneficial aspects associated with fish diversity (Obregón et al., 2018; WWF,

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2021). Improving our understanding about this topic is crucial considering the degradation of aquatic ecosystems and the erosion of NFF in the Anthropocene (Reis et al., 2016; Pelicice et al., 2017; Azevedo-Santos et al., 2021). The loss of fishery resources has been notorious (Hoeinghaus et al., 2009; Scarabotti et al., 2021), but lack of knowledge has made it difficult for society to assess the degradation and loss of other services provided by NFF. The scenario is unfavorable as public policies and development plans in Latin America (also globally) have not targeted the maintenance of ES critical to humanity. People generally are unaware of the concept of ES, and fail to recognize the benefits deriving from ecological processes that have no immediate economic relevance (Blanco et al., 2022).

Some reviews have examined the role of fish in providing ecosystem services worldwide (Holmlund & Hammer, 1999; Olden et al., 2020), but none has compiled studies on ES generated by NFF, so the actual extent of their benefits remains largely unknown. As there is a natural bias toward services related to fishing (e.g., Obregón et al., 2018; Olden et al., 2020), it is essential to identify and understand the existence of other services to clarify their occurrence, relevance, and gaps in knowledge, guiding research and sustainable policies. In this sense, this review aims to map the ES generated by NFF and understand how fish benefit society. Based on a broad literature survey, we sought evidence of ES considering the Millennium Ecosystem Assessment framework (MEA, 2005), which groups services into four classes, i.e., provisioning, regulating, supporting, and cultural. This review (i) organizes and lists the ES generated by NFF, and (ii) gathers evidence of how human activities have affected the ecosystem service chain provided by fishes. Our study clearly shows that fish contribute to the generation of several services far beyond those associated with fishing (Fig. 1), including services that are poorly known but critical for society.

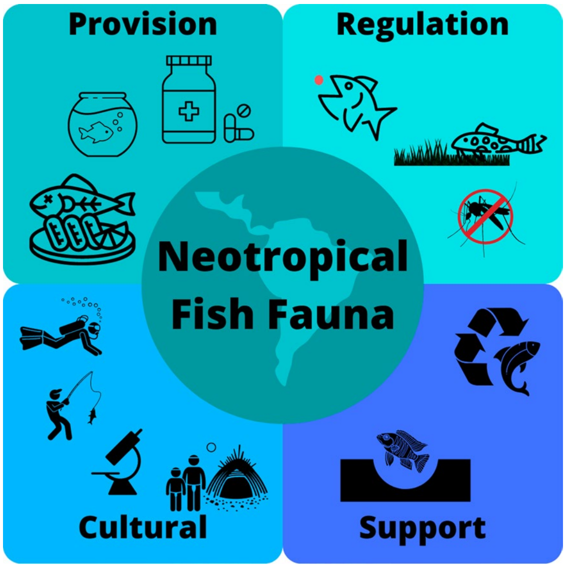

Fig. 1 Diagram illustrating some of the ecosystem services generated by Neotropical freshwater fishes. Provision: food, ornamental, and drug resources; Regulation: seed dispersal, herbivory, and pest control in natural environments; Support: nutrient cycling and ecosystem engineering; Cultural: traditional knowledge, scientific research, recreational fishing and ecotourism

Material and methods

We examined the existing scientific literature to synthesize the current knowledge about ecosystem services associated with NFF. This review is based on multiple and exhaustive literature surveys conducted on Web of Science (www.webofknowledge.com), Scopus (www.socpus.com), and Google (www.google.com). Different terms (and combinations) were employed, and they included "Neotropical," "South America," "fish," "freshwater," "service," "fishing," "fisheries," "nutrient," "dispersal," "cultural," among several others related to the ES topic. These surveys were conducted independently by each author between August 2021 and March 2022, and potential references were selected, debated, and eventually cited. Author's personal libraries were another source of references (scientific articles and books).

Based on the evidence provided by the literature, we identified all ES associated with NFF and organized each service as provisioning, regulating, supporting, and cultural, following the framework of MEA (2005). The literature search also supported the investigation of impacts caused by human activities on the generation of ecosystem services.

Ecosystem services provided by NFF

We found sound scientific evidence (direct and indirect) that NFF generate a range of ES (Table 1 and

Fig. 2), including the four classes of MEA (2005). Some services are well known and widely recognized, such as those related to fisheries, fish production, and recreation. Other services deliver critical benefits to human activities (e.g., nutrient cycling, decomposition, seed dispersal), while many have cultural value. Some require further research to determine their mechanisms and relevance (e.g., pest control, invasion resistance), while others lack scientific evidence, either because they are probably not generated by fish (e.g., primary production), or because they have never been studied (e.g., water purification, soil formation, climate regulation). A quick search on the Web of Science database (https://www.webofknowledge.com), examining the scientific articles citing the main references in the field (i.e., Holmlund & Hammer, 1999), indicated that ES provided by NFF have received little attention: studies on NFF accounted for a small fraction of this literature (8.7% of the references; 334 papers on June 2022), and most of them are related to studies conducted in Brazil. Therefore, both the range of services and the role of fish are probably underestimated; some links remain undiscovered, whereas others are potential, but their demonstration is still a challenge.

Provisioning services

Provisioning services are the best studied and known. It includes several services related to fisheries, which play a key role in the provision of food and animal protein (Fig. 2A), generating income, and alleviating poverty in Latin America. Inland fishing is a global activity with strong social, environmental, and political significance (Lynch et al., 2016; FAO, 2018). In the Neotropical region, inland fisheries are found in every freshwater ecosystem (Fig. 3), involving different modalities (subsistence, recreational, artisanal, commercial, or industrial) and capturing a wide variety of species. This activity is important to countries that lack access to the ocean, such as Paraguay and Bolivia (Funge-Smith & Bennet, 2019), and remarkable in major rivers systems, such as the Magdalena-Cauca, La Plata, São Francisco, and Amazonas basins (Almeida et al., 2001; Petrere Jr. et al., 2002; Godinho & Godinho, 2003; Junk, 2007; FAO, 2015; Hallwass & Silvano, 2016; Lopes et al., 2016; Scarabotti et al., 2021), where it generates food, employment, and income for millions of people. Inland fisheries in the neotropics employ 3% of the employees around the world. This proportion is a small amount in comparison with South Asia and Africa (58 and 16%, respectively), but still generates around 500 thousand jobs (Funge-Smith & Bennet, 2019). Traditional communities rely strongly on fishery resources (Nietschmann, 1972; Gross, 1975; Santos & Alves, 2016), especially for their food security (Tregidgo et al., 2020), an aspect that confirms the social importance of NFF (e.g., FAO, 2018).

Migratory fishes (Fig. 2C, E) represent a valuable resource with great importance for inland fisheries and ecosystem functioning (Hoeinghaus et al., 2009; Flecker et al., 2010). Thousands of tons of migratory fish are landed annually in the Amazon region (Duponchelle et al., 2021) and in the La Plata Basin (Okada et al., 2005; Scarabotti et al., 2021), supplying regional markets and exports. Migratory fishes are iconic animals and include large catfishes [(e.g., *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *Brachyplatystoma rosseauxii* (Castelnau, 1855), *Zungaro zungaro* (Humboldt, 1821)] and characins [e.g., *Salminus brasiliensis* (Cuvier 1816), *Piaractus mesopotamicus* (Holmberg, 1887), *Prochilodus nigricans* Spix & Agassiz, 1829] (Barthem & Goulding, 1997; Carolsfeld et al., 2003). Small fish, a group highly diverse and widely distributed in the region (Castro & Polaz, 2020), also represent an important resource appreciated as food, bait, or ornamental. The ornamental fish industry moves billions of dollars annually (Dey, 2016), and the diversity of NFF has strong appeal (Sabaj-Perez, 2015; Evers et al., 2019; Ladislau et al., 2020; Tribuzy-Neto et al., 2020; Sousa et al., 2021; Novak et al., 2022); its potential is well-recognized (Axelrod et al., 1997), but often under-exploited (Pelicice & Agostinho, 2005). There are other economic uses of NFF, such as the manufacture of handicrafts, tools, and decorative objects (Fig. 2B) (Gonçalves et al., 2012; Olden et al., 2020), which involve, for example, the use of small Loricariidae and Serrasalmidae species, the tail of stingrays (Potamotrygonidae), catfish spines, and scales of pirarucu [*Arapaima gigas* (Schinz, 1822)]. The production of fish leather to make clothes, shoes and accessories has been appreciated in the market and in the fashion industry, especially due to its sustainability appeal; it may include farmed fish (e.g., *A. gigas*) or those captured by artisanal fisheries (e.g., *Prochilodus* spp.). Fishing by-products also have multiple

Table 1 Ecosystem services generated by Neotropical freshwater fishes

Ecosystem services	Evidence	Mechanism	Fish involved (examples)	Key References
1. Provisioning				
Food	Yes	Fish meat	Several species, including large pimelodids (e.g., *Pseudoplatystoma*, *Brachyplatystoma*) and characids (e.g., *Prochilodus, Piaractus, Salminus*, *Brycon*)	Petrere Jr. et al. (2002); Junk (2007); FAO (2018)
Fiber, fuel, and by-products	Yes	Fishery products	Several species, including the giant pirarucu (*Arapaima gigas*) and piranhas (*Serrasalmus*)	Barone et al. (2017); Olden et al. (2020)
Income	Yes	Employment, occupation, and economic value associate with fisheries	Several species	FAO (2018)
Ornamental	Yes	Ornamental fish industry and trade	Several species, including small characids (tetras), armored catfishes (Loricariidae), electric eels (Gymnotiformes), colorful cichlids, and stingrays (Potamotrygonidae)	Moreau & Coomes (2007); Lasso et al. (2016); Tribuzy-Neto et al. (2020)
Biochemicals	Yes	Biochemicals, drugs, active ingredients	Stingrays (*Potamotrygon*)	Magalhães et al. (2006); Cavali et al. (2022)
Medicines	Yes	Traditional medicine, zootherapy	Several species, including *Hoplias* and *Cichla*	Barros et al. (2012)
Genetic resources	Yes	Support for aquaculture, fisheries, and other goods	Several species, including *Colossoma macropomum, Piaractus mesopotamicus,* and *A. gigas*	Wasko et al. (2004); Oliveira et al. (2018); Val & Oliveira (2021)
Bioindication	Yes	Bioindicator of pollution and degradation	Several species	Chen et al. (2017); Carvalho et al. (2020); Gutiérrez & Agudelo (2020)
Fresh Water	No			
2. Regulating				
Seed dispersion	Yes	Dispersion of riparian plants	Several species, including *C. macropomum*, *P. mesopotamicus*, *Brycon orbygnianus*, *B. microlepis*, and *Astyanax*	Souza-Stevaux et al. (1994); Correa et al. (2007); Reys et al. (2009); Anderson et al. (2009)
Decomposition	Yes	Decomposition of coarse and fine material	Prochilodontidae, Curimatidae, and Loricariidae, with emphasis on *Prochilodus*, *Semaprochilodus*, and *Hypostomus*	Bowen (1983); Delariva & Agostinho (2001); Taylor et al. (2006)
Vegetation control	Yes	Periphyton control	Prochilodontidae, Curimatidae, and Loricariidae, with emphasis on *Prochilodus*, *Semaprochilodus*, and *Hypostomus*	Taylor et al. (2006); Winemiller et al. (2006)
Pest and disease control	Probable	Predation on vectors	Several species, especially small characids, catfishes, and cichlids	Oliveira et al. (2010); Tranchida et al. (2010); Azevedo-Santos et al. (2017)

Table 1 (continued)

Ecosystem services	Evidence	Mechanism	Fish involved (examples)	Key References
Pollination	Probable	Control of insects that prey upon pollinators	Unknown	No study in the Neotropical region, but see Knight et al. (2005)
Invasion resistance	Probable	Niche opportunities and resource release	Several species, probably involving community-level effects	Isaac et al., 2014; Fitzgerald et al. (2016); Bezerra et al. (2019); Santos et al. (2021),
Climate	Probable	Biomass accumulation and uptake of methane carbon	Several species, probably involving community-level effects	No empirical evidence, but see Sanseverino et al. (2012)
Water purification	Probable	Algae control via cascading effects	Grazers (e.g., Prochilodontidae, Curimatidae, and Loricariidae) and top predators (e.g., *H. malabaricus*)	Taylor et al. (2006); Mazzeo et al. (2010)
Erosion	No			
Natural hazard protection	No			
3. Supporting				
Nutrient cycling	Yes	N/P cycling	Several species	McIntyre et al. (2008); Small et al. (2011)
Provision of habitats	Yes	Environmental control and ecosystem engineers	Grazers (e.g., *Prochilodus*) and nest builders (e.g., cichlids)	Taylor et al. (2006); Winemiller et al. (2006); Mormul et al. (2012); Bessa et al. (2021)
Soil formation	Yes	*Terra Preta* in the Amazon	Several species	Kern et al. (2017)
Primary production	Probable	Indirect effects of top predators on consumers, and benthivorous fish revolving the substrate	Several predators (e.g., *H. malabaricus*) and benthivorous fish (e.g., *Prochilodus,* cichlids)	Taylor et al. (2006); Mazzeo et al. (2010); Mormul et al. (2012)
Water cycling	No			
Production of Oxygen	No			
4. Cultural				
Recreation and esthetic values	Yes	Recreational and sport fisheries, aquarium hobbyists and snorkeling	Several species, including large pimelodids (e.g., *Pseudoplatystoma*), characids (e.g., *Brycon*, *Salminus*), peacock basses (*Cichla*), and several small ornamental characids, catfishes, poecilids, and cichlids	Arce-Ibarra & Charles (2008); Barcellini et al. (2013); Freire et al. (2016); Bessa et al. (2017)
Education and inspiration	Yes	Fishkeeping and scientific knowledge	Several species	Diogo et al. (2008); Tonini et al. (2016); Albert et al. (2018)
Knowledge system	Yes	Local ecological knowledge (LEK)	Several species	Silvano et al. (2008); Hallwass et al. (2020); Baird et al. (2021); Pereyra et al. (2021)
Spiritual and religious	Yes	Cosmology, taboos, and connections with Nature	Several species	Harp (1994); Garnelo (2007); Alves et al. (2012)

Table 1 (continued)

Ecosystem services	Evidence	Mechanism	Fish involved (examples)	Key References
Sense of place	Yes	Identity and sense of belonging	Several species	Garnelo (2007); Moreira & Colombier (2019)

The organization was adapted from MEA (2005)

uses, including oil and meal to feed other animals, and exports (head, tails, and bladders) to attend international markets (Barone et al., 2017). We emphasize also that inland fisheries develop complex production chains, involving different equipment (e.g., vessels, engines, fishing gears), activities (e.g., transport, storage, processing) and stakeholders (e.g., fishers, retailers, export), which employ millions of people directly and indirectly.

Although all fishing modalities target some main species (Freire et al., 2016; Hallwass & Silvano, 2016), inland fisheries in the Neotropical region are essentially multi-specific, especially small-scale artisanal activities (Tregidgo et al., 2021). Thus, the high diversity of NFF must create an insurance effect for fisheries, dumping oscillations of specific stocks against disturbances and natural variation, an important mechanism to maintain fishery production. This service is reasonable in situations of stock depletion due to overfishing, when underexploited stocks compensate for diminishing returns (e.g., Myers & Worm, 2003). Insurance effects may also work in regulated rivers, when migratory species decline and the fishery system adapts to exploit sedentary species (Agostinho et al., 2016).

Fish diversity also constitutes an important genetic pool (Wasko et al., 2004; Hillsdorf & Hallerman, 2017), serving as a subsidy for several activities. It supplies aquaculture stocks with wild fish (Oliveira et al., 2018; Torati et al., 2019) and offers regional alternatives for aquaculture development (Fonseca et al., 2017; Lima Junior et al., 2018; Dávila-Camacho et al., 2019; Val & Oliveira, 2021). However, the potential use of NFF in aquaculture has been greatly overlooked, given the predominance of non-native fish in the aquaculture industry, such as carps [e.g., *Cyprinus carpio* Linnaeus, 1758, *Ctenopharyngodon idella* (Valenciennes, 1844)], African clariid catfishes [*Clarias gariepinus* (Burchell, 1822)], and tilapias [*Oreochromis niloticus* (Linnaeus, 1758)] (Azevedo-Santos et al., 2011; Valenti et al., 2021). One important exception is the tambaqui *Colossoma macropomum* (Cuvier, 1816), a species native to the Amazon, which represents about 20% of fish production in Brazil (Valenti et al., 2021). Neotropical fishes also generate goods related to the provision of chemical and medicinal compounds (Alves & Rosa, 2006; Magalhães et al., 2006; Padilla et al., 2012; Cavali et al., 2022), although these products remain less studied

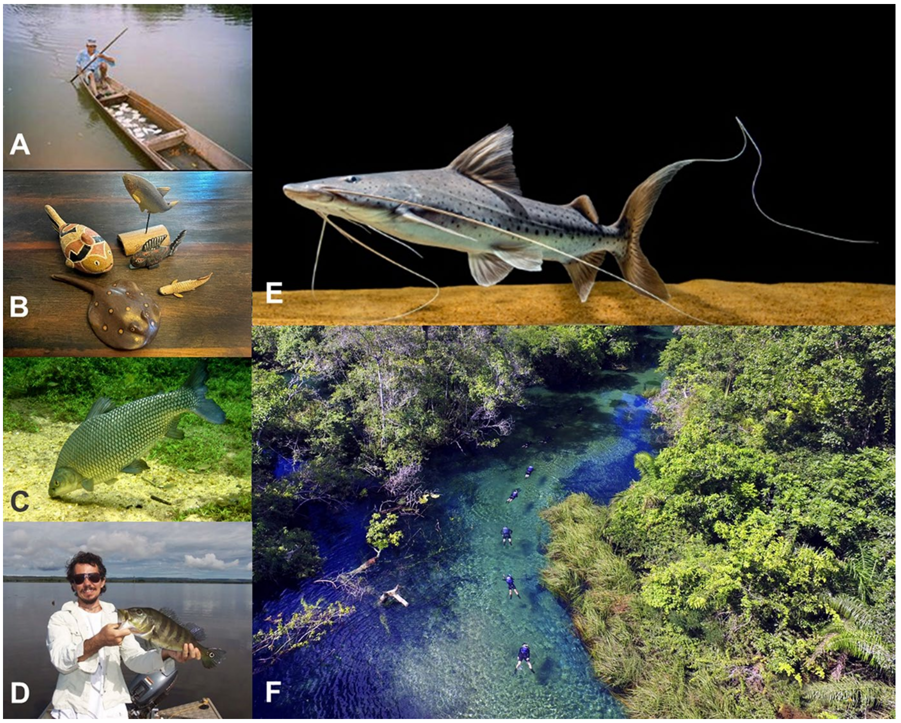

Fig. 2 Multiple ecosystem services generated by Neotropical freshwater fishes. **A** = artisanal fisheries; **B** = handmade decorative objects inspired by different fish species; **C** = detritivorous fish [*Prochilodus lineatus* (Valenciennes 1837)] with effects on decomposition, nutrient cycling and ecosystem engineering; **D** = recreational fishing (*Cichla piquiti* Kullander & Ferreira 2006); **E** = large migratory catfish [*Brachyplatystoma filamentosum* (Lichtenstein 1819)] appreciated by artisanal, commercial, and recreational fisheries; **F** = snorkeling to observe fish in the wild. Source: the authors

Fig. 3 Artisanal fishery conducted in inland ecosystems of the Neotropical region. **A** = artisanal fishers using hook and line in the Mato Grosso Pantanal; **B** = cast-net fishing in the Jequitinhonha River; **C** = industrial fishing in the lower Amazon; **D** = cast-net fishing in rapids of the Xingu River; **E** = artisanal fisher using seines in the Itaipu Reservoir, Paraná River. Source: the authors

and understood. The use of fish in healing practices and health issues is more common in traditional communities, or in those whose access to conventional medicine is more restricted (Thé et al., 2003; Barros et al., 2012).

Neotropical fishes (the species or the community) have also been used as tools in impact assessment and monitoring studies, working as bioindicators of environmental quality. Most species have specific ecological requirements, especially rheophilic and migratory fish, being sensitive to human impacts and constituting sentinels of environmental change. They have been useful to indicate impacts emerging from land conversion (e.g., Carvalho et al., 2017; Chen et al., 2017; Guimarães et al., 2022), deforestation (Arantes et al., 2018; Prudente et al., 2018), fishing (Doria et al., 2017; Röpke et al., 2022), river regulation (Araújo et al., 2018), climate change (Lopes et al., 2017; Borba et al., 2021), and environmental contamination (Maggioni et al., 2012; Viana & Lucena Frédou, 2014; Schulz & Martins-Junior, 2001; de Carvalho et al., 2020; Gutiérrez & Agudelo, 2020; Henriques et al., 2021; Pinto et al., 2021). However, protocols to use NFF as bioindicators are still incipient, requiring more research and development.

Regulating services

NFF contribute with the generation of services associated with ecosystem functioning, with direct and indirect benefits to society. For example, seed dispersal represents an essential service, probably of wide occurrence. Several species consume fruits in riparian areas of rivers, lakes, and floodplains (Fig. 4), contributing to seed dispersal and the maintenance of riparian vegetation (Souza-Stevaux, 1994; Correa et al., 2007; Reys et al., 2009; Horn et al., 2011; Barbosa & Montag, 2017). The relative importance of fish compared to other vertebrates is unknown, but the diversity of frugivorous species is disproportionally high in the Neotropical realm (ca. 104 species from 17 families; Correa et al., 2007), indicating that seed dispersal is a common service (Anderson et al., 2009). Another essential ES generated by fish is the

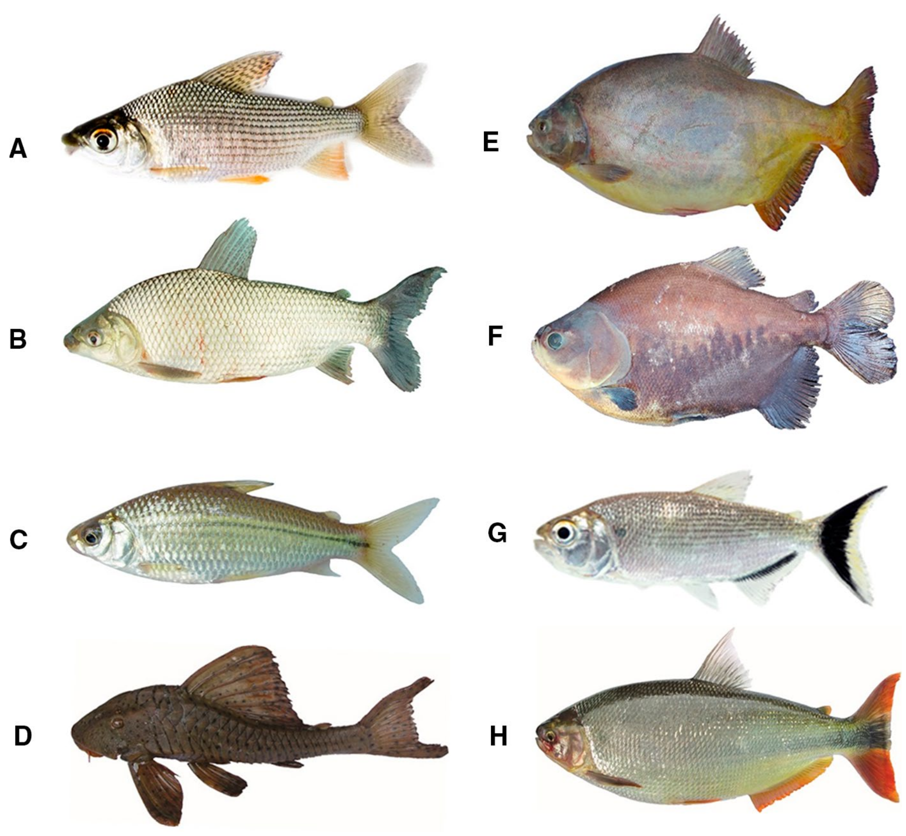

Fig. 4 Detritivorous fish that scrape substrates and contribute to decomposition, nutrient cycling, and environmental quality: *Prochilodus nigricans* (**A**), *Prochilodus lineatus* (**B**), *Steindachnerina brevipinna* (Eigenmann & Eigenmann 1889) (**C**), and *Hypostomus cochliodon* Kner 1854 (**D**). Frugivorous and omnivorous fish that contribute to seed dispersal: *Piaractus mesopotamicus* (**E**), *Colossoma macropomum* (**F**), *Brycon falcatus* Müller & Troschel 1844 (**G**), and *Brycon microlepis* (**H**). Fish size not to scale. Source: Angelo A. Agostinho, Carla S. Pavanelli, and Leandro M. Sousa

decomposition of organic matter. Many NFF specialized in feeding on detritus and decaying organic matter (Bowen, 1983), such as Prochilodontidae, Curimatidae, and Loricariidae (Fig. 4). These fishes consume particulate material and debris deposited on bottom and other substrates (Fig. 2C), acting directly on the decomposition of organic matter and nutrient cycling (Delariva & Agostinho, 2001; Vanni et al., 2002; Taylor et al., 2006). Other fish contribute indirectly to the decomposition process, such as scavengers [e.g., piranhas, the catfish *Calophysus macropterus* (Lichtenstein 1819), and some trichomycterid and cetopsid catfishes] and generalists that fragment plant and animal food in the water column (e.g., small characins) or revolve the substrate (e.g., cichlids, stingrays, and catfishes). These processes accelerate decomposition by making resources available to other consumers and decomposers, which are especially important along the river continuum (Vannote et al., 1980).

Another relevant service occurs through herbivory and the control of vegetation growth. Although the consumption of living plants (except flowers, fruits, and seeds) is not typical among NFF (Goulding, 1980; Okeyo, 1989). However, this service assumes great relevance in the control of filamentous algae and periphyton, affecting nutrient dynamics, habitat quality, and system state. Experiments show that fish that scrape substrates (i.e., Loricariidae, *Prochilodus*; Fig. 4) exert strong control over periphyton and algae, affecting a series of physical and chemical parameters, in addition to nutrient release, carbon cycling, sediment deposition, and primary production (Flecker, 1996; Taylor et al., 2006; Winemiller et al., 2006). As these fish are abundant and widely distributed in river systems of South America, they must have strong effects on ecosystem functioning and dynamics, keeping rivers and lakes in a certain regime (Mormul et al., 2012).

Many regulating services potentially generated by NFF are controversial or lack sound evidence, demanding more research. For example, the use of fish as biocontrol agents has been a frequent strategy, and several researchers argue that it has positive effects on macrophytes and mosquitoes-borne diseases control (Roux & Robert, 2019). Some species, such as the Trinidadian Guppy *Poecilia reticulata* Peters, 1859, have been extensively used in the control of mosquitoes that transmit diseases, such as malaria and dengue. Although this approach has theoretical and empirical bases (i.e., many fish consume insect larvae), its practical relevance is controversial as a biocontrol tool (Tranchida et al., 2010; Azevedo-Santos et al., 2017). In addition, biocontrol programs have caused the introduction of several non-native fish in tropical and subtropical regions of the world, especially small Poeciliidae (El-Sabaawi et al., 2016). However, the role of native fish controlling some species of Simuliidae and Culicidae in natural conditions cannot be ruled out, as many small fish prey upon insect larvae, with potential to exert demographic control over certain inconvenient blackflies and mosquitoes (e.g., *Simulium* spp., *Culex quinquefasciatus* Say, 1823) (Ibarra-Trujillo & García-Alzate, 2017). The predation of fish on insect larvae can positively affect other services, such as pollination. Experimental evidence indicates that fish can indirectly facilitate the reproduction of terrestrial plants by reducing the abundance of dragonfly larvae in lakes, which prey on pollinating insects as adults (Knight et al., 2005). This indicates a possible service; however, no study investigated the interaction between NFF and pollination. Another potential service is biotic resistance to biological invasion. Some studies suggest that impacted systems, such as regulated rivers or deforested streams, are more susceptible to bio-invasion (Casatti et al., 2009; Pelicice et al., 2018; Bezerra et al., 2019; Santos et al., 2021). The erosion of fish diversity may open space and release resources for invaders, and some studies have indicated the potential of fish to control non-native organisms (Cantanhêde et al., 2008; Oliveira et al., 2010; Isaac et al., 2014). However, the relationship seems to be complex, as other factors mediate biotic resistance or acceptance, such as the origin and ecological traits of the invader, environmental filters, and invasion windows (Fitzgerald et al., 2016; Santos et al., 2018a, b; Muniz et al., 2020). Finally, one cannot ignore the possible role of fish in carbon sequestration and, consequently, in climate regulation. For example, by incorporating carbon from methane in wetlands (Sanseverino et al., 2012), fish biomass may affect this important greenhouse gas emission. No study has demonstrated this process, but considering that some fish accumulate high biomass in certain ecosystems, especially fish occupying lower trophic levels (e.g., *Prochilodus* and some highly abundant curimatids), the methane sink service seems plausible.

Apparently, some regulation services are not performed directly by NFF, such as water purification, erosion control, and protection against natural disasters. However, one cannot exclude the possibility that fish indirectly affect the generation of these services. For example, algivorous fish and top predators potentially contribute to algae control (through direct and indirect cascading effects), affecting ecosystem properties and supporting some regimes (e.g., clear water state; Scheffer & Carpenter, 2003). This process has been observed in mesocosm experiments, where cascading effects induced by *Hoplias malabaricus* (Bloch, 1794) contribute to improving water quality (Mazzeo et al., 2010).

Supporting services

NFF directly affects nutrient cycling, as they consume different resources (i.e., detritus, plants, and animals), which are digested and recycled as nitrogen and phosphate compounds. This service is essential for maintaining aquatic food webs, and releasing nutrients to primary producers and consumers. Nutrient excretion and cycling are universal processes, although excretion rates vary between fish species and communities (McIntyre et al., 2007, 2008; Small et al., 2011). Moreover, fish are important agents of decomposition, as mentioned before; several species specialized in feeding on detritus and dead organic matter, while small generalist characids, catfishes, and cichlids contribute to mobilizing and fragmenting resources. This process is particularly important in polluted systems, where fish assimilate carbon from untreated domestic sewage (Carvalho et al., 2020). Scrapers (e.g., *Prochilodus*; Fig. 2C) seem to have strong effects on the environment and regime states (Mormul et al., 2012), affecting ES related to nutrient cycling, microhabitat provision, and water quality. These fish act as ecosystem engineers, with strong top-down control over periphyton and phytoplankton assemblages, affecting nutrient input to the water column (Flecker, 1996; Winemiller et al., 2006; Campos-Silva et al., 2021), the physical structure of microhabitats, and invertebrate dispersion (Flecker, 1992; Flecker & Taylor, 2004). Other ecosystem engineers include fish that modify the substrate by building nests (Bessa et al., 2022), or fish that affect chemical processes in karstic environments (Corrêa et al., 2018). Therefore, fish play a key role in nutrient cycling and habitat quality through different paths and functions.

Fish do not generate some critical supporting services, such as oxygen production, water cycling, and primary production, but they can potentially affect their performance. For example, piscivorous fish can affect primary production through cascading effects (e.g., Campos-Silva et al., 2021), as also demonstrated in controlled experiments (Schindler et al., 1997; Mazzeo et al., 2010). Other services need further investigation. For example, although fish diversity is not directly involved in soil formation, areas of *terra preta* (black soil) in the Amazon were produced due to the historical deposition of organic material, including fish remains, carried out by traditional communities during the past several thousand years (Kern et al., 2017). These fertile soils are preferred for small-scale agricultural activities, presenting high concentration of organic carbon, phosphorus, calcium, magnesium, zinc, and manganese. In this case, there is a clear connection between *terra preta* and NFF, although the process may no longer occur due to the historical reduction of indigenous populations over the last centuries.

Cultural services

Neotropical fishes generate a range of cultural services with effects at different spatial scales (i.e., local, regional, and global). Recreational services associated with fishing activities are highly appreciated. Recreational fishing (Fig. 2D) is widespread in the Neotropical region (Freire et al., 2012, 2016), found in different environments where it uses simple gears (e.g., hook, line and rod) to capture different fish species (low selectivity), mostly small-sized. The activity is economically accessible and provides leisure and food, playing an important social role. Sport fishing represents a more specialized segment, which takes advantage of the presence of many large-sized species and predatory fish. The economic sector moves billions of dollars in products, equipment, and tourism, attracting anglers from all over the world. The activity is widespread in the Neotropical region, but some localities are hotspots of sport fishing, such as the Brazilian Pantanal, the lower Paraná River, coastal rivers, and several Amazonian tributaries, such as the Araguaia, Negro, and Tapajós rivers. For example, the recreational value of the region surrounding Aruanã town, Araguaia Basin (Brazil), was estimated at US$ 7.6 billion per year (Angelo & Carvalho, 2008). Similarly, the economic value of recreational fishing focused on snooks (*Centropomus* spp.) in the lower Ribeira de Iguape River (Brazil) was estimated at US$ 2 million (Barcellini et al., 2013). Iconic species appreciated by recreational and sport fisheries include peacock basses (*Cichla* spp.), large catfishes (e.g., *Pseudoplatystoma* spp., *Brachyplatystoma* spp.), pirarucu (*A. gigas*), and several characiforms (e.g., *Salminus* spp., *Brycon* spp., *Piaractus* spp., *C. macropomum*, *Megaleporinus* spp.).

The high diversity of shapes, colors, sizes, behaviors, and evolutionary histories connect NFF with touristic, esthetic, educational, and scientific values. Snorkeling to observe freshwater fishes [e.g., *S. brasiliensis*, *Brycon microlepis* Perugia, 1897, small tetras)] in situ is an important activity in the surrounding highlands of the Brazilian Pantanal (Lima et al., 2014) (Fig. 2F). In some cities, 80% of the tourists are motivated to visit underwater trails in headwater streams, which may raise up to 48% of the revenues associated with tourism (Barbosa & Zamboni, 2000). Snorkeling has also brought economic development and infrastructure to local communities, such as roads and employment (Guimarães & Zavala, 2009). The activity is still small-scale, but has grown in the Neotropical region (Bessa et al., 2017). The ornamental charm of NFF is another important service (Fig. 5), supporting a global ornamental industry (Evers et al., 2019; Valenti et al., 2021). Ornamental NFF are highly appreciated worldwide (Axelrod et al., 1997), supporting hobbyists in the USA, Europe, and Asia, with intense exports of wild fish from the Amazon (Tribuzy-Neto et al., 2020) and Central America (Dávila-Camacho et al., 2019). Fishkeeping, when performed in a correct and sustainable form, is also connected with education—as observed in public aquaria, gardens, ornamental ponds, and scientific collections (Tonini et al., 2016). We emphasize the role NFF in the production of scientific knowledge, as they have served as models to understand physiological issues (e.g., Baldisserotto et al., 2019; Pelster et al., 2021), behavior (e.g., Kowalko, 2020), comparative anatomy (e.g., Diogo et al., 2008), vertebrate evolution (e.g., Monteiro et al., 2018), environmental degradation (e.g., Azevedo-Santos et al., 2021),

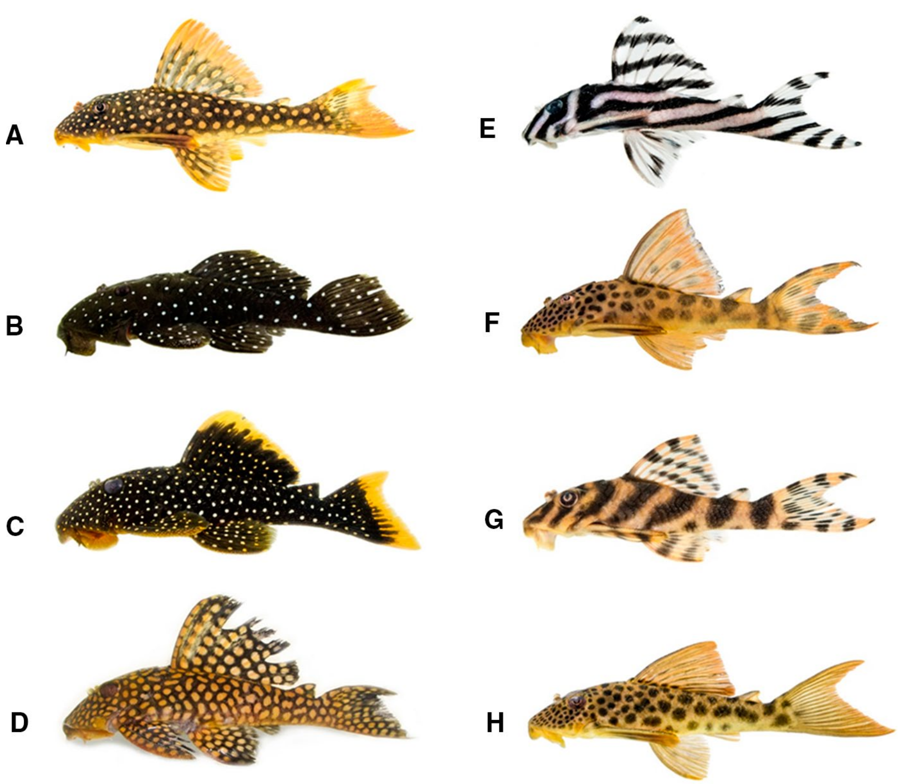

Fig. 5 Diversity of ornamental armored catfishes from the Amazon Basin: *Scobinancistrus aureatus* Burgess 1994 (**A**), *Parancistrus nudiventris* Rapp Py-Daniel & Zuanon 2005 (**B**), *Baryancistrus xanthellus* Rapp Py-Daniel, Zuanon & de Oliveira 2011 (**C**), *Baryancistrus niveatus* (Castelnau 1855) (**D**), *Hypancistrus zebra* Isbrücker & Nijssen 1991 (**E**), *Peckoltia sabaji* Armbruster 2003 (**F**), *Peckoltia vittata* (Steindachner 1881) (**G**), and *Peckoltia feldbergae* (de Oliveira, Rapp Py-Daniel, Zuanon & Rocha 2012) (**H**). Fish size not to scale. Source: Leandro M. Sousa

evolutionary processes, and geological history (e.g., Dagosta & De Pinna, 2017; Albert et al., 2018).

The diversity of NFF is also connected to a series of cultural values related to traditional communities, indigenous groups, and artisanal fishers. These services are among the most relevant benefits generated by NFF, as they have historical roots and developed deep connections with people. The historical importance of fishing for many cultures has supported intimate relationships between people and fish, which has constituted a rich source of sustenance, inspiration, and guidance for men and women (Garnelo, 2007; Cruz-Garcia et al., 2019; Cubillos-Cuadrado et al., 2019; Moreira & Colombier, 2019). Fish is a common source of local ecological knowledge (LEK), playing a key role in the understanding of natural resources, ecological relationships, and the order of Nature (Costa-Neto et al., 2002; Moura & Marques, 2007; Silvano et al., 2008; Carvalho Junior et al., 2011; Braga & Rebelo, 2014). Traditional cultures usually have extensive knowledge about different aspects of NFF, including species identification, behavior, and distribution (Hallwass et al., 2020; Pereyra et al., 2021), being able to indicate potential ES performed by NFF, such as seed dispersal (Silvano et al., 2008) and the structure of food webs (Pereyra et al., 2021). Local knowledge is also valuable to assess environmental impacts, for instance, pollution (Silvano & Begossi, 2016) and river regulation (Hallwass et al., 2013; Baird et al., 2021). Fish also appear in the cosmological systems of many cultures (Harp, 1994; Garnelo, 2007; Oliveira, 2017; Alves et al., 2012; Castro & Barros, 2020), affecting customs and offering a sense of belonging, religious basis, and existential foundations. It is worth noting that the cultural value of NFF is not restricted to traditional communities, as humans naturally appreciate Nature from spiritual and esthetic motivations (Wilson, 1986).

Human impacts and the loss of ES

The impacts of human activities on fish diversity have been well documented (Reis et al., 2016; Pelicice et al., 2017, 2021), including changes in species abundance, diversity patterns, and community structure. However, the consequences on the generation of ES have been less investigated and understood, except for inland fisheries. Multiple stressors, in particular the construction of dams, land conversion, irrigation, mining, species invasion, pollution, and overfishing, have impacted services associated with fishing, causing economic and social losses (Petrere et al., 2004; Hoeinghaus et al., 2009; Agostinho et al., 2016; Kwak et al., 2016; Tregidgo et al., 2017, 2021; Doria et al., 2021). The degradation of fishing resources is widespread, with negative effects on the structure and size of fish stocks, target species, yield, income, costs, and fishing systems, among other indicators. For example, long-term monitoring indicates that main stocks have declined in the La Plata Basin (Rabuffetti et al., 2020; Scarabotti et al., 2021), while fishers recognize that stocks of target species have collapsed in the lower São Francisco basin (D'Ávilla et al., 2021). Even in more pristine regions, such as the Amazon, fishery resources have been degraded or lost (Petrere Jr. et al., 2004; Santos et al., 2018c; Van Damme et al., 2019). The loss of fishery resources has affected the generation of cultural services, such as LEK, since traditional communities have been forced to live in modified environments with altered fish diversity, often with non-native fish (Hallwass et al., 2013; Catelani et al., 2021). Services associated with recreational fisheries have also been degraded, especially in areas affected by dams or overfishing, resulting in the loss of target species with recreational and esthetic value. Signs of vulnerability or even deterioration have been reported even in remote regions that traditionally support high-quality fisheries, such as the Rio Negro basin (Holley et al., 2008; Lubich et al., 2021). The fishing activity itself has impacted NFF (e.g., Petrere Jr. et al., 2004; Tregidgo et al., 2017). Recreational fishing, for example, has affected native fish populations in coastal rivers and brackish waters, due to the lack of official monitoring programs and management strategies that do not consider spatial ecology and biological requirements (e.g., sequential hermaphroditism and diadromous behavior of snooks, *Centropomus* spp.) (Garrone-Neto et al., 2018). Conflicts between anglers and artisanal fishers have been frequent in different basins, which intensify in degraded environments and mosaics of protected areas, including indigenous lands, with economic and cultural losses for both sides, especially due to the loss of fishing grounds and opportunities for collaborative management (Freire et al., 2016; Motta et al., 2016; Garrone-Neto et al., 2018).

Human activities have affected the generation of other ES and functioning. A series of experiments have demonstrated how the selective removal of scrapers causes intense changes in nutrient cycling, affecting environmental conditions and primary production (Flecker, 1996; Taylor et al., 2006; Winemiller et al., 2006). Some fish, such as *Prochilodus* and *Brachyplatystoma*, are particularly vulnerable to human stressors such as overfishing and dam regulation, as they are migratory, rheophilic, and targeted by fisheries (Oliveira et al., 2015; Van Damme et al., 2019; Lopes et al., 2019). The selective removal of *Prochilodus* stocks, an ongoing process (Baigún et al., 2013; Catarino et al., 2019), has great potential to induce cascading ecosystem changes. Other studies reveal how the erosion of fish diversity affects nitrogen and phosphorus cycling, indicating that non-random extinctions, driven by species identity, size, and biomass (typical effects of fisheries), are more likely to remove species important for nutrient cycling (McIntyre et al., 2006). The decline of frugivorous migratory fish [e.g., *C. macropomum*, *Brycon orbignyanus* (Valenciennes, 1849)] has been a growing concern (Costa-Pereira & Galetti, 2015; Tonella et al., 2019), with negative effects on seed dispersal. Deforestation, river regulation, and fishing have impacted their stocks causing depletion and size reduction; however, larger frugivorous fish have disproportionate importance for seed dispersal, as they disperse more seeds of different species, and seeds have greater chances of germination (Correa et al., 2015; Costa-Pereira & Galetti, 2015; Barbosa & Montag, 2017; Araújo et al., 2021). Therefore, the selective removal of this guild should have a strong effect on the regeneration and maintenance of riparian forests and floodplains, with deleterious consequences for ecosystem functioning and biodiversity conservation. This scenario points to possible tradeoffs and conflicts among different ES, as the same group of fish may support multiple services (i.e., fishing and seed dispersal), a problem that could be minimized with fishery management and protected areas (Nagl et al., 2021). Potential conflicts in the use of services represent an important knowledge gap. They deserve more research effort, especially to understand the dispute among stakeholders and different fishing modalities, and their interaction with the provision of non-economic services (e.g., seed dispersal, LEK). It is essential to consider that provisioning services delivered by NFF can promote important bridges between regulating and cultural services. It has been shown that the implementation of community-based fisheries management in the Amazon lowlands, based on the controlled and sustainable exploitation of pirarucu *A. gigas*, favors multiple fish species (and other organisms), and help to reconcile human welfare, biodiversity conservation, and its positive effects on ecosystem functioning (Campos-Silva et al., 2018).

The impact of invasive species on ES remains poorly investigated, but the topic deserves attention as it entails complex tradeoffs between positive and negative consequences for different stakeholders. Multiple non-native species currently invade the Neotropical region (Garcia et al., 2018; Bueno et al., 2021; Doria et al., 2021; Elías et al., 2022; Franco et al., 2022), which have promoted relevant changes in fish diversity in some scenarios (e.g., Pelicice & Agostinho, 2009; Attayde et al., 2011; Vitule et al., 2012; Bezerra et al., 2019). Changes in ES are, therefore, expected. In fact, a recent study revealed how the invasion of the peacock bass *Cichla kelberi* Kullander & Ferreira, 2006 changed the composition of ecosystem functions and services potentially generated by small fish (Leal et al., 2021), indicating that the erosion of diversity is directly related to the degradation and loss of ES. Furthermore, development plans have relied only on specific economic gains emerging from introductions, ignoring the loss of other services and the associated economic, social, and environmental costs (Magalhães et al., 2018). In this regard, it is essential to understand how invasive fish that generate immediate economic services for aquaculture (e.g., tilapia, carp) and fisheries (e.g., genus *Cichla*, *Arapaima*, *Micropterus, Oncorhynchus*) affect the maintenance of ES generated by native diversity, and how positive/negative effects translate to each stakeholder. For example, the invasion of Nile tilapia *O. niloticus* is prone to cause several impacts on native biodiversity (Canonico et al., 2005), and this exotic fish generates lower per capita income for artisanal fisheries (Novaes & Carvalho, 2013).

The understanding of how the loss of NFF affects the generation of ES is still deficient, pointing to the need for further research. The focus must go beyond services associated with fisheries since NFF are involved in the generation of several other services with no directly perceived economic value, but are critical for the functioning of ecosystems, traditional communities, and economic activities. The loss of cultural links remains widely ignored by resource management and development plans (e.g., Chiaravalloti & Dyble, 2018), although cultural services are highly vulnerable to environmental degradation. This topic deserves more attention, considering that fish are essential to maintaining social cohesion and identity in traditional societies, affecting the social organization and governance forms. Indigenous and traditional people usually have weak political representation and resilience against large-scale environmental changes (Doria et al., 2018), while they are highly dependent on the fishery resources and other values associated with fish and aquatic ecosystems. Furthermore, the continuous degradation of LEK has resulted in massive cultural losses in the form of valuable empirical and traditional knowledge acquired through the historical interaction between humans and fish. The loss of LEK implies the loss of valuable information about biodiversity, ecosystem functioning and services, which may include data currently unavailable to science, such as long-term abundance trends and species extirpations (Hallwass et al., 2013, 2020). The loss of LEK also negatively impacts the implementation of community-based management strategies and conservation actions that depend on the engagement of local communities.

It is also important to assess the economic value of ES (e.g., Siikamäki et al., 2015; Costanza et al., 2017) using broader quantitative approaches and considering services not linked to immediate economic returns. Few studies have assessed the value of NFF, and they have examined services with direct monetary benefits (e.g., Angelo & Carvalho, 2008; Tribuzy-Neto et al., 2020; Valenti et al., 2021). It is essential to inform society about the direct and indirect economic benefits emerging from NFF, considering that economic and social development has occurred under activities that damage ecosystems, such as energy production and agriculture, which underestimate or ignore the importance of ES for human well-being (Auerbach et al., 2014; Blanco et al., 2022). This aspect is fundamental if we consider that human activities depend on some critical services (e.g., water production, nutrient cycling, and climate regulation), which until recently have not been realized by society. This perspective needs revision, especially because developing nations, home to a disproportionate fraction of biodiversity (particularly freshwater fish), do not prioritize the maintenance of ES and sustainability (Pelicice, 2019). The inclusion of ES in development policies represents a fundamental action toward a more sustainable agenda and compliance with the Sustainable Development Goals of the United Nations.

Conclusion

This article is the first review of ecosystem services generated by Neotropical freshwater fishes, the most diverse assemblage of vertebrates on Earth. We found robust evidence that fish diversity benefits society in multiple ways through the generation of provisioning, supporting, regulating, and cultural services. The importance of fish for ecosystem functioning is irrefutable since the group colonized virtually all inland aquatic environments in the Neotropical region, where they mobilize energy, accumulate biomass, integrate trophic levels, and interact with humans. However, the current understanding of ES generated by NFF is strongly biased toward fishing activities, which represent a small fraction of existing services. Such bias is reasonable as inland fisheries benefit millions of families by providing food, income, livelihood, capital, and other products. However, the bias eclipses other services, which remain poorly investigated or even unknown to science and society, including critical services for humanity. Therefore, it is imperative to improve our understanding of this topic, which includes questions on how human activities affect ES, and how its loss affects society. Unfortunately, the current knowledge is significantly limited, as we lack answers to basic questions, e.g., how does the loss of certain species (or reductions in abundance and diversity) affect the generation of services? How do specific human actions affect the generation of specific services? What is the economic value of NFF? The loss of ES in the Anthropocene seems to be the norm and predicting its consequences will be fundamental to implementing sustainable policies that protect the natural capital and human activities, which will depend on specific scientific advances in this topic.

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Conflict of interest There is no conflict of interest to declare.

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