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Impacts of hydroelectric dams on fishes and fisheries in tropical rivers through the lens of functional traits

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We summarize observed and expected impacts of hydroelectric dams on tropical fishes and fisheries through the lens of fish functional traits and consequences of shifting functional diversity for social-ecological systems. Following impoundment, stocks respond to environmental changes differently according to their functional traits, resulting in fairly predictable shifts in assemblage functional structure. The most vulnerable species are those with traits adaptive for habitats with fast flowing water, structural complexity, flood pulsing or those requiring connectivity across basins to complete their life cycle. Shifts in assemblage functional trait distributions are accompanied by reduced fishery yields and impacts to other ecosystem services. Research employing a functional traits approach should enhance assessment of impacts of impoundments on biodiversity, fisheries and ecosystem services, especially for data-deficient systems.

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Introduction

Hydropower development represents a major threat to fish biodiversity and the maintenance of critically important fisheries worldwide [1,2], with potential to damage food security and rural livelihoods in tropical regions [3,4]. Hydroelectric dams impact spatio-temporal patterns of fish community structure and fisheries production by obstructing migration routes, altering sediment transport and water quality, promoting invasions by exotic species and biotic homogenization, and favoring generalist over specialist species [5,6•,7]. Large scale hydroelectric projects also can promote road construction, deforestation, mining, and urban development in surrounding regions, which may act synergistically with altered flow regimes to impact aquatic biodiversity and production. Our ability to predict responses of fish stocks to environmental changes caused by hydroelectric dams is critical for mitigating socioeconomic and ecological impacts of these projects, particularly in tropical regions where inland fisheries support livelihoods and food security for millions.

Tropical rivers support the highest freshwater fish diversity on Earth, with more than 8000 described fish species for the Neotropical region alone [8]. The Amazon Basin, for example, contains 2411 described fish species and at least 1089 endemic species, representing 16% of global freshwater fish diversity. Tropical rivers are experiencing a boom in hydroelectric development, with thousands of major dams and small hydropower plants already in operation, under construction, or planned for the coming decades [2,9•]. The rivers with greatest potential for hydropower expansion are often those containing the most morphologically and ecologically diverse fish faunas [10]. For example, river reaches impacted by controversial hydropower development projects within Brazil's Madeira and Xingu rivers [11] contained at least 800 and 450 fish species, respectively, many of which are endemic [12,13]. The maintenance of such high biodiversity depends critically on the seasonal flood pulse, which promotes the exchange of water, nutrients and organisms within a mosaic of channel and floodplain habitats [14]. Many of these same areas are home to human communities that depend heavily on fisheries for sustenance and livelihoods [15].

Whereas the negative impacts of impoundments have been well documented, predicting changes in fish assemblage structure and consequences for fisheries is challenging because of the high diversity and complexity of tropical rivers. Impacts from hydrologic alteration are unevenly distributed within fish assemblages, with certain species being severely impacted while others thrive in reservoirs created by dams. Shifts in species abundances affect ecological processes and important ecosystem services, such as nutrient cycling and fisheries production [16,17]. Does fish assemblage structure change in predictable ways following impoundment, and how do changes affect local fisheries? The answers to these questions are critical for assessing and mitigating impacts of hydroelectric development. While some studies have sought to integrate available knowledge for specific regions, most have focused on taxonomic responses [but see Refs. 18,19]. Generalizations that span taxonomic and geographic boundaries are urgently needed to keep pace with current hydropower development.

To address these questions, we review fish responses to river impoundment from the perspective of functional traits. A functional trait is any feature of an organism that affects performance or fitness, including those related to food acquisition (e.g. body size, mouth size and position), mobility and habitat use (e.g. body size and shape, fin size and position), metabolism (e.g. thermoregulation, salinity tolerance, hypoxia tolerance), reproduction (e.g. reproductive effort, parental investment in individual offspring), and defense tactics (e.g. crypsis, presence of armor or spines), among others [20,21•,22]. Traits and performance measures can be examined at the level of individual organisms or groups of species (i.e. functional groups). For example, traits associated with maximization of reproductive success can be combined to classify organisms according to functional groups based on life history strategies (i.e. syndromes defined by consistent patterns of trait intercorrelations). Functional traits influence environmental tolerances and habitat requirements, and dictate both species responses to a changing environment and their effects on ecosystem services [23,24•]. If species sharing similar traits display similar responses to environmental changes, a functional approach may improve our ability to quantify and predict impacts of dams on fish assemblages and fisheries across biogeographic regions [25]. Focusing specifically on large tropical rivers, we explore: (i) the potential of using functional traits to understand the impacts of hydrologic alteration on fishes and fisheries, (ii) patterns of functional responses to river impoundment (e.g. identifying functional traits of vulnerable or tolerant species), and (iii) some consequences of functional diversity changes for social-ecological systems.

Ecology from the perspective of functional traits: responses of functional diversity to environmental change

Trait-based approaches have become a central focus of community ecology because they facilitate inference about mechanisms driving community dynamics and thus provide an opportunity to increase generality and predictability of ecological responses to environmental variation [20,26]. Functional traits reflect adaptation to ecological conditions, with many traits having well-established form-function relationships [27] and displaying predictable variation along environmental gradients [28,29]. For example, fishes from many lineages that inhabit swift-moving water tend to possess similar adaptions to resist hydraulic forces, including narrow streamlined or dorso-ventrally compressed bodies, large pectoral fins, and reduced swim bladders [30]. Changes in environmental conditions (e.g. altered flow dynamics) will impact the advantages particular suites of traits confer and consequently affect species distributions and abundances [28].

Focusing on functional composition and diversity as a complement to strictly taxonomic approaches offers several advantages. Whereas fish species composition and diversity vary greatly among tropical river basins, mechanistic insights based on functional relationships may be transferable across biogeographic regions. Convergent functional trait patterns in relation to environmental gradients have been revealed for fish assemblages of temperate streams [31] as well as between temperate and tropical systems [32]. The functional composition of fish assemblages is strongly associated with spatial and temporal attributes of the flow regime [28,31]. Because river impoundments reduce the mean and variance of flows downstream, one might expect predictable shifts in the functional composition of fish assemblages. Even without loss of species, changes in species relative abundances can significantly alter functional diversity if functionally unique species become rare [33,34•,35].

A functional approach can aid biodiversity conservation and fisheries management by improving our ability to associate changes in species relative abundances or biomass with particular traits that in turn affect ecosystem services provided by fishes [21,36]. This response-and-effect framework links traits that determine how species respond to environmental gradients (i.e. response traits) with traits that affect other species and ecosystem processes (i.e. effect traits [23]). The resilience of ecosystem services to environmental change will depend on the relationships between diverse response and effect traits. Ref. [17] showed that reduced populations of migratory fishes following river impoundment reduced the economic value of fisheries yields due to correlations between migratory behavior, trophic ecology, cultural preferences, and species' market values. Understanding such relationships and the distribution of functional traits within natural species assemblages may allow resource managers to define targets aimed at maintaining or restoring ecosystem processes and services [20,37]. To that aim, there is an urgent need to improve the acquisition and accessibility of biodiversity monitoring data (including both taxonomic and functional assessments) as well as to determine which traits confer sensitivity of species to hydrologic disturbance (e.g. traits described in Table 2).

How does dam construction affect fish taxonomic and functional diversity?

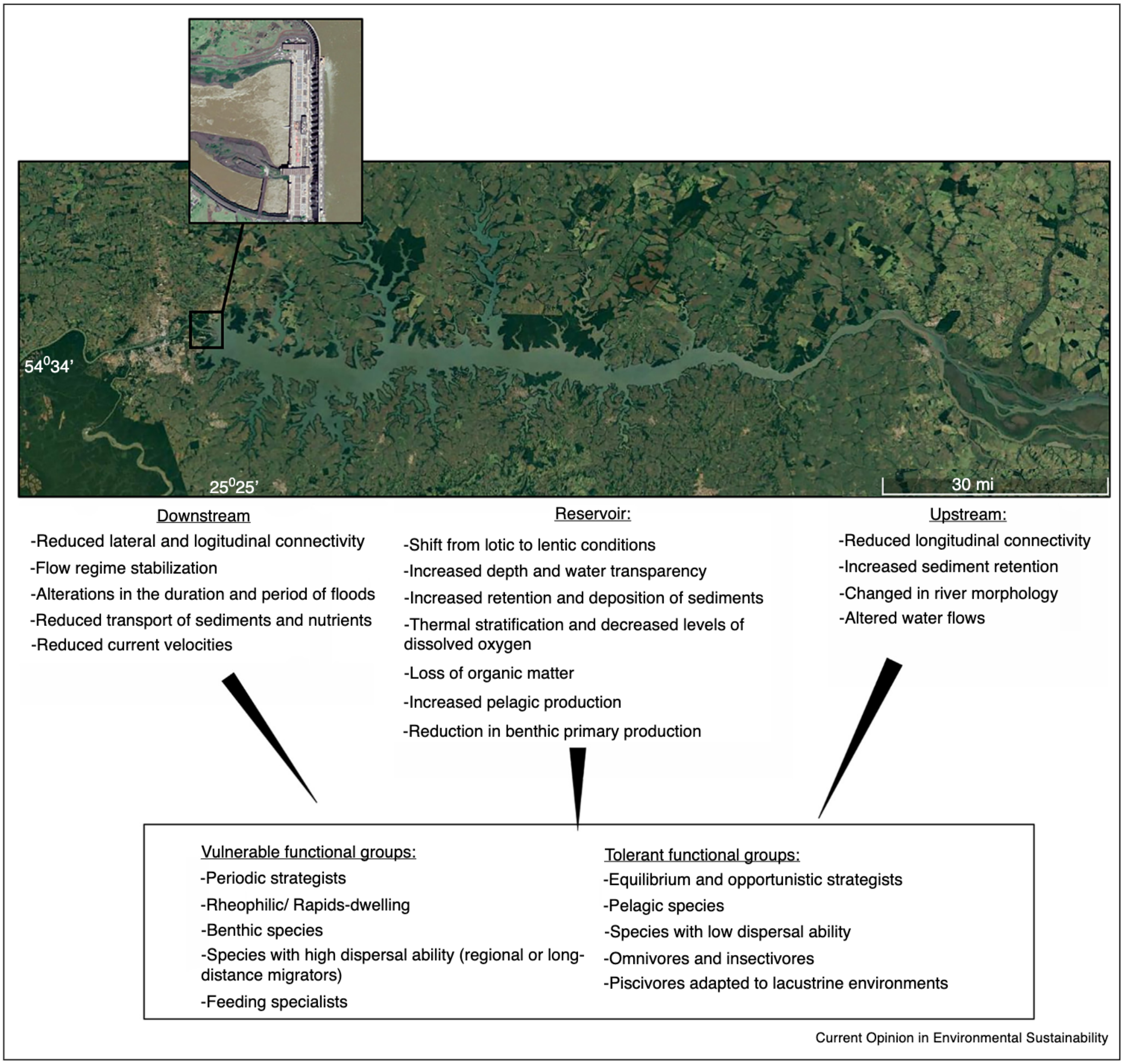
Despite advances in trait-based approaches [e.g. 23,36] few studies have analyzed the impacts of dams on functional diversity in tropical rivers [38•,39,40•]. We go beyond these studies and compile information from the scientific literature documenting shifts in diet, growth and other indicators of organism and population performance, as well as trends in assemblage composition and species diversity to assess functional responses to dam construction in several large tropical rivers of South America, Asia, Australia and Africa. Because fish assemblages are influenced by multiple abiotic environmental factors (e.g. discharge, geomorphology, surface area, depth, and habitat structural complexity), biotic factors (e.g. species pool, dispersal ability), and the design, age and operational features of dams [19], there is large potential for variation in responses of fish assemblages to impoundment. The timing and magnitude of dam impacts on taxonomic and functional assemblage structure likely vary depending on specific features of the dam and river reach. For example, horizontal bulb turbines employed in run-of-river dams or the vertical axis turbines used in large reservoirs differ in their environmental impacts and would be expected to illicit different responses by affected fish assemblages. In addition, series of reservoirs within a given sub-basin would have synergistic ecological impacts. Despite inevitable differences across case studies, here we emphasize broad patterns of functional responses; examples of site-specific responses can be found in the literature cited herein. Our exploration of functional responses to river impoundment focuses mainly on local (i.e. reservoir) and regional (upstream and downstream of the dam) patterns because most studies have analyzed impacts at these scales. The cumulative effect of multiple dams at the river-basin scale remains poorly understood and represents a key area for future research.

River impoundment affects environmental conditions upstream (e.g. new lentic habitat within the reservoir body) and downstream (e.g. altered flow regime) of the dam, and fragments the river network longitudinally and laterally (Figure 1). The combined effects of altered environmental conditions and fragmentation of riverscapes result in significant changes in fish assemblage structure and functional diversity in large rivers (Table 1). Such shifts are associated with traits that convey either tolerance or vulnerability to the new ecological conditions of the impacted system (Tables 2). Although changes in ecological conditions in dammed rivers depend on multiple factors (e.g. water quality, geomorphology, sediments) that are varied and complex, certain changes that occur both upstream and downstream of impoundments are acute and fairly obvious [41].

In *impounded reaches*, that is, within the newly formed reservoir, changes in functional trait distributions within the fish assemblage are fairly predictable because dams cause a shift from lotic to lentic conditions (Figure 1). An initial pulse of decomposition of terrestrial vegetation, nutrients, and aquatic production in newly flooded areas (a so-called *trophic surge*) supports increased abundance and biomass of trophic groups able to take advantage of these resources, particularly detritivores, omnivores and insectivores, plus some piscivores that benefit from increased availability of prey [42]. Species richness may increase initially if species colonize from diverse habitats submerged within the area of the new reservoir (e.g. floodplain lakes and tributaries, flooding of biogeographic barriers) and non-native species are introduced (e.g. stocking of lentic-adapted species). When a reservoir inundates cataracts that form a barrier between freshwater faunal regions [43], it allows invasion of the upstream reach by species from the downstream region, some of which may possess unique functional traits. This was the scenario documented when Itaipu Reservoir flooded the Sete Quedas Falls on the Paraná River in Brazil [44]. Over time, levels of dissolved oxygen often decline, particularly at the bottom of the reservoir. In the impounded area, organic matter is lost due to oxidation, sedimentation, biological assimilation, and downstream export, leading to a reduction in benthic primary production [45]. A well-mixed riverine water column can become thermally stratified in the reservoir. These changes lead to precipitous declines of both taxonomic and functional diversity (Table 1). In general, the most vulnerable species are those possessing functional traits associated with rapidly flowing water, periodic flow pulses, and habitat complexity (Table 2). Obligate rheophilic species (i.e. preferring to live in running water) with traits such as dorso-ventrally flattened bodies, dorsally located eyes, inferior mouths and large pectoral and pelvic fins (Table 2) may be extirpated when rapids are submerged within the reservoir (Figure 1). Migratory fishes with periodic life history strategies depend on natural flow regimes to trigger migration and reproduction as well as to increase chances of successful recruitment, and these fishes become rare or disappear altogether following dam construction. Benthic species decline due to habitat loss and metabolic stress caused by the low concentrations of dissolved oxygen at the bottom of the reservoir. Many traits characteristic of benthic species, such as dorso-ventrally compressed bodies, inferior mouths and reduced swim bladders, are maladapted for swimming and feeding in the water column of reservoirs.

Omnivores often become the dominant trophic guild in newly formed reservoirs, with large herbivores and invertivores usually being negatively impacted. In addition to changes in dominance of trophic guilds, studies have reported dietary shifts. For example, in the Tocantins Basin the relative importance of fish as a food resource increased whereas detritus was consumed less (see Table 1 for additional examples). Increased open-water area provides favorable habitat and foraging opportunities for pelagic fishes (e.g. *Plagioscion* spp.) and visually oriented pursuit predators (e.g. *Cichla* spp.). Some species of

Figure 1



Examples of impacts due to dam construction and consequent lateral and longitudinal fragmentation of the river network, and vulnerable or tolerant functional groups through the river network (see details of traits and examples in Table 2). Map shows a section of the Paraná River after the construction of Itaipu Dam (insert), Brazil. Itaipu, like other dams in tropical rivers, altered environmental conditions and imposed a physical barrier to fish movement. Longitudinal and lateral connectivity with the floodplain was reduced both upstream and downstream, negatively affecting access to spawning and feeding grounds ([e.g. 17,19,51,87]). The dam may also function as an ecological trap, because even if the constructed fish passage were to allow upstream migration to suitable spawning and nursery habitats, recruits are unlikely to migrate downstream through the reservoir and turbines to populate areas below the dam. Image source: Google Earth (Image Landsat/Copernicus).

small fast-growing fishes with opportunistic life history strategies thrive in new reservoirs, especially within the littoral zone (e.g. tetras of the family Characidae in the Neotropics, mud carps of the family Cyprinidae in Asia), and small clupeids (*Limnothrissa miodon*, known locally as 'kapenta') often are introduced and quickly dominate pelagic zones of reservoirs in Africa. In regulated rivers, species with relatively long generation times, low reproductive effort, and high investment per offspring (e.g. *Cichla* spp. and other equilibrium life history strategists)

Table 1

Patterns frequently observed for fishes and fisheries in relation to dam construction, with examples from tropical rivers

Frequent patterns	Example or evidence	References
Shifts in assemblage composition and structure	Observed in the Amazon (Madeira and Tocantins Rivers) and Paraná River basins, Brazil; Lancang-Mekong River Basin, China; Shoalhaven River, Australia; Volta Lake and Lake Kariba, Africa	[46,68,7,69,70,39]
Functional simplification or homogenization of assemblages	Observed reduction in the functional space occupied by species in the Paraná River, Brazil; increases in numerical dominance in the middle and upper Tocantins River, simplification of fish assemblages in reservoirs in the Qiantang and Lancang-Mekong Rivers basins in China	[47,7,69,38•]
Short-term increases, followed by long-term decreases, in total richness and abundance	Observed in fish assemblages in the Amazon (e.g. Tocantins and Madeira rivers) and Paraná River basins, Brazil	[71,70,39]
Shifts in diet	*Mylossoma duriventre* shifted from frugivorous to insectivorous in the Madeira River, Brazil; *Ctenopharyngodon idellus* shifted diet from plants to algae in the Han River, China; *Leporinus friderici* shifted diet from, predominately, vegetal material and organic matter to terrestrial arthropods in the Serra da Mesa reservoir in the Tocantins River, Brazil; increased relative importance of fish and decreased importance of detritus as food resource in the Tucurui Reservoir, Tocantins River, Brazil	[72,73,70], unpublished results in Ref. [38•].
Shifts in food web structure	Increases in niche breadth (i.e. dietary diversity) in the newly formed reservoir in the Paraná River, Brazil; decreases in planktivores, herbivores, and detritivores, and concomitant increase in piscivore abundance in the Tocantins River, Brazil; decrease of top predators in the Paraná, São Francisco, Iguaçu and Paranapanema Rivers, Brazil; shifts in the relative importance of benthic (detritus and algae) to pelagic (phytoplankton) production sources supporting primary consumers in the Paraná River Basin, Brazil	[60,74,38•]
Reduced body size	Reduction in mean size of species in the Paraná, São Francisco, Iguaçu and Paranapanema Rivers, Brazil; reduction in sizes of young-of-the-year fishes in Hanjiang River, China	[71,17,40•]
Decreasing in fishery yields of high market value species	Observed in the Paraná and Amazon basins, Brazil (e.g. Itaipu Reservoir in the Paraná River, Tucurui Reservoir in the Tocantins River, and Madeira River after completion of Jirau and Santo Antonio dams), and in rivers in Asia (e.g. Xinanjiang and Fuchunjiang dams in the Qiantang River and dams in the Zhujiang [Pearl] River, China; Pak Mun Dam, Mekong Basin, Thailand; Nam Theun Hinboun Dam, Mekong Basin, Laos) and Africa (e.g. Senegal River)	[75,46,51,17,76,74, 19,38•,77]
Changes in composition of fishery	Increased dominance of omnivorous (e.g. *Pterodorus granulosus*) and piscivorous (e. g. *Plagioscion squamosissimus*) species in Itaipu Reservoir, Paraná River, Brazil; increased dominance of the piscivorous *P. squamosissimus* and decreases in the dominance of the planktivorous *H. marginatus*, herbivorous *Myleus* and *Methynnis* spp., and detritivorous *Semaprochilodus brama* in the lower Tocantins River, Tucurui Dam, Brazil; Landings of *Tenualosa ilisha* declined after Farakka Dam construction, River Ganges, India; in the Kafue River reservoir above Kafue Gorge Dam (Zambia), the large surface area and shallow water of the reservoir benefitted tilapia species that now form a major part of the commercial catch	[78,17,74,19,38•]
Increased fishing effort required to maintain catch	Total fishing effort almost doubled after Itaipu Reservoir construction in the Paraná River, Brazil	[17]
Local extinctions	Chinese shad *(Tenualosa reevesi)* is extinct in the Qiantang River; Chinese sturgeon (*Acipenser sinensis*), endemic Yangteze sturgeon (*Acipenser dabryanus*), sailfin sucker (*Myxocyprinus asiaticus*), and Chinese paddlefish (*Psephurus gladius*) declined drastically and were locally extinct in some locations of the river after Gezhouba Dam construction in the Chang Jiang [Yangtze] River; several species declined or disappeared after construction of the Pak Mun Dam, Mekong River Basin, Thailand; *Tenualosa ilisha* was commercially extinct from the Ganges River after the completion of the Farakka Dam	[79,80,75,81,82,18]
Shifts in species' behavior (e. g. migration, reproduction patterns)	Migratory species that previously ascended to upper reaches of the Chang Jiang [Yangtze] River now reproduce below the dam; Colder water downstream of dams delayed spawning for several species in rivers in China; Unexpected patterns of habitat use were observed in the Salto Caxias Reservoir, Iguaçu River, Brazil (e.g. benthic species became abundant in the pelagic zone during the filling phase of the reservoir).	[47,19]
Increased records of non-native species	Observed in the Capivara Reservoir, Paranapanema River, and Itaipu Reservoir, Paraná River, Brazil; in many reservoirs in India (e.g. tilapia, *Oreochromis mossambicus,* and silver carp *Hypophthalmichthys melitrix*) and the Lancang-Mekong River Basin in southeast Asia (e.g. *Neosalanx taihuensis* and nonnative species of Cyprinidae)	[69,83]

may outcompete formerly dominant periodic strategists and come to dominate the large-piscivore guild. Species with traits associated with low dispersal ability but good maneuverability near submerged branches and aquatic vegetation (e.g. deep-body with broad fins), including sedentary or short-distance migrators, also tend to increase in abundance.

Alteration of environmental conditions affects patterns of taxonomic and functional assemblage structure differentially across the river depending on distances upstream or downstream from the dam. Assemblage functional trait distributions may be also affected by the presence of dams at distant locations within the river basin. Although less predictable than responses within reservoirs, some of the same traits affected by a reservoir also respond at locations far from the dam. *Upstream* of reservoirs, impacts on migratory periodic strategists can prevail for many kilometers leading to decline in their abundance (e.g. *Brachyplatystoma flavicans*, *Phractocephalus hemiliopterus* and *Pinirampus pirinampu* in the middle-upper Tocantins River after the Tucurui Dam was built in the lower part of the river [46]). Dams also create barriers that can result in the concentration of migratory fishes in free-flowing stretches and tributaries [19]. Species adapted to life in rapids (e.g. benthic and rheophilic species) may persist if sufficient lotic habitat is maintained somewhere within the altered fluvial landscape [47].

Downstream from dams, cumulative effects of diminished peak discharges, stabilized water levels, and reduced transport of sediments and current velocities (Figure 1) negatively affect rheophilic fishes as well as long-distance migratory species and periodic strategists that rely on flood pulses for successful reproduction and recruitment (e.g. *Semaprochilodus* spp. in the Tocantins River, Brazil). In some cases, species possessing traits that facilitate long distance migrations (e.g. large muscle mass, long caudal peduncle, high aspect ratio of caudal and pectoral fins) were reported to increase in abundance in areas close to the dam, likely due to the dam blocking their attempts at upstream migration [19]. However, this functional group has generally been reported to decline in downstream reaches in the long term [e.g. 46,47]. Fishes with limited physiological tolerance to low temperatures disappear in reaches where dams release cold water from the hypolimnion (e.g. shad *Tenualosa reevesi* in Asian rivers, Table 1). Other populations show compensatory mechanisms to these changes in water temperature (e.g. delayed reproduction, slower growth in several species below the dams on the Qiantang and Han Rivers in China). Losses of species and their associated traits have generally resulted in functional simplification of assemblages both downstream and upstream of dams, with implications for the functioning of rivers and provision of important services, as we discuss below.

Some of the consequences of changing functional diversity on social-ecological systems

Despite arguments that expanded aquatic habitat in reservoirs should enhance fishery production, there is increasing evidence that impoundments impact functional composition and diversity of fish assemblages and reduce the value of fisheries. This discrepancy likely results from trade-offs between short-term benefits and long-term negative impacts, as well as cultural preferences and traditions that affect fishery valuation. Many native and introduced short-lived, fast-growing fishes thrive in reservoirs (e.g. carps, tilapias; see above and Tables 1, 2). Non-native lentic-adapted species are often introduced in attempts to boost fisheries production [19,47]. Increased abundance of lentic-adapted species and small fast-growing fishes can enhance overall fish production (total biomass); however, high yields for individual stocks sometimes are unsustainable in the long term, with stocks of high cultural and economic value often being the first to collapse [48] (Table 2). As large, long-lived species, including migratory fishes and apex predators, are depleted, fisheries exploit smaller species with more resilient populations, a phenomenon referred to as 'fishing down' [49,50]. This process can be further exacerbated over time as fishing effort intensifies to compensate for reduced value of stocks. Thus, the initial period of trophic surge in a newly formed reservoir tends be followed by declines in total yields, catch-per-unit effort, and fishery value [17,51]. These effects are not limited to the reservoir proper, and often extend to reaches upstream and downstream of dams. For example, studies have documented 70% declines in catch-per-unit effort in the Tocantins River after the completion of the Tucurui Dam, 39% declines in the mean annual catch in the Madeira River after the completion of the Santo Antônio and Jirau dams, and loss of 50% of fisheries yields (nearly 11 250 metric tons per year) following damming and loss of connectivity between Lake Guiers and the Senegal River (Table 1).

A shift from a fishery dominated by periodic strategists to one with equilibrium and opportunistic strategists may increase the vulnerability of fisheries to collapse. In natural rivers, the most valuable stocks tend to be species with periodic life histories having high compensatory potential in reproductive output that facilitates fitness and population persistence in the face of large-scale variation in recruitment [52]. Many large periodic strategists migrate to spawn in seasonally inundated floodplains and exhibit delayed maturation, high fecundity, and multiple annual spawning bouts over a relatively long lifespan. Years with optimal conditions for spawning and recruitment (e.g. large or long duration flood pulses) result in strong year classes and 'storage' of individuals across years via long lifespans that compensate for weak year classes during years with unfavorable conditions [53].

Table 2

Functional groups and functional traits most vulnerable, tolerant and showing variable response to hydroelectric dam construction and examples of impacts

Functional groups		Functional Traits	Examples	References
More vulnerable				
Life history strategies	Periodic	Long generation time, large body size, high batch fecundity, low investment per offspring (e.g. no parental care), low juvenile survivorship with large interannual and spatial variation in recruitment, usually perform migration	Declined in the Paraná and Amazon basins (e.g. Jaraquis *Semaprochilodus* spp. in the lower Tocantins River) in Brazil, the Sinnamary River in French Guiana, and in rivers in China (e.g. paddlefish and sturgeons in the Yangtze River)	[47,74,38•]
Habitat use strategies	Rheophilic/ rapids-dwelling	Streamlined, elongate bodies, dorsally located eyes, inferior mouths, large pectoral fins, dorso-ventrally flattened bodies, reduced swim bladders	Declined in multiple reservoirs in the Paraná River and in the reservoir and downstream of a dam in the upper Tocantins River, Brazil. High mortality of rheophilic species (e.g. *Baryancistrus xanthellus*) observed immediately after reservoir formation on the Xingu River, Brazil. Several rheophilic fish species disappeared from Chinese rivers after they were dammed	[75,84,39,12,38•]
	Benthic species	Relatively wide bodies, dorsally located eyes, inferior mouths, relatively slow swimmers. A few benthic species (e.g. *Hoplias malabaricus*) have terminal or superior mouths	Decreased in abundances in upper Tocantins and Paraná rivers in Brazil, and in the Upper Mekong River in China (although abundances of benthic species may increase during the filling phase of the reservoirs)	[71,39]
	High dispersal ability (regional or long-distance migrators)	Traits associated with increased swimming performance (e.g. large muscle mass, long and deep caudal peduncle and large caudal and pectoral fin ratio areas)	Migratory species, including large fish with high market value, declined in several Neotropical rivers (e.g. Paraná, Tocantins and Madeira rivers); dams disrupted the migration routes of *Clupanodon thrissa* and *Cirrhinus molitorella* causing collapse of the fishery in the Zhujiang [Pearl] River, China. The Gezhouba Dam, China, also disrupted migrations of anadromous and semi-migratory fishes	[75,46,18,85,19, 40•,39]
Trophic strategies	Feeding specialists (invertivores, herbivores), large-sized carnivorous and herbivorous	Invertivores ingest variable fractions of microcrustaceans from the benthos or water column, shrimps, and mollusks, and aquatic and terrestrial insects and other arthropods. Herbivores feed predominantly on plant material (seeds, fruits or leaves) or filamentous algae. Large herbivorous and carnivorous fishes usually have high market value and are targeted by fisheries	Invertivores* and herbivores were the dominant trophic guilds before Xiaowan Dam construction but declined in abundances after completion of the dam; both guilds decreased in abundance after dam construction in the Paraná and Ivinhema rivers, Paraná Basin, Brazil; large apex predators and large herbivores decreased in abundance after dam construction in the Paraná River *Ref. [40•] found positive association between invertivorous fishes and reservoir size when insectivores were included in this category	[69,19,38•,40•]
More tolerant				
Life history strategies	Equilibrium	Moderate to long generation time, variable body size, low batch fecundity, large egg size and high investment per offspring (e.g. parental care), high juvenile survivorship	Increases in abundance of cichlids with strong sexual selection, nest building and parental care in several Neotropical rivers	[19,38•]
	Opportunistic	Short generation time, small body size, low batch fecundity, early maturation, low investment per offspring, low juvenile survivorship (e.g. no parental care)	Increases in abundance of small characids and other opportunistic species that colonized shallow shores in several Neotropical rivers	[19,40•]

Table 2 (*Continued*)

Functional groups		Functional Traits	Examples	References
Habitat use strategies	Pelagic	Pelagic maneuverable species usually have laterally compressed bodies and superior mouth position, whereas burst swimmers have fusiform bodies and terminal mouth position. Both groups have morphological traits associated with efficient swimming performance based on a hydrodynamic body and feeding within the water column.	Dominant habitat use strategy after the Xiaowan Dam construction in the Lancang-Mekong River, China. Increase in abundance after Peixe Angical Dam construction, Tocantins River, Brazil and Kariba Lake, Africa	[71,69]
Migratory behavior	Low dispersal ability (sedentary or only short distance migrators)	Deep body, large head and long pectoral fin. Less hydrodynamic than pelagic maneuverable fishes but efficient in making lateral and vertical turns. This group comprise species that spend much of their life-cycles within floodplain habitats typically moving relatively short-distances.	Increases in abundance in several upstream dams in the Madeira, Paraná, Tocantins, Sao Francisco, Iguaçu and Paranapanema rivers in Brazil, and several rivers in China. Dams planned for the mainstream of the Mekong River were estimated pose lower threat to floodplain-resident species (i.e. 'blackfish')	[7,38•,19,39,40•,70,85]
Trophic strategies	Omnivores	Ingest combinations of plant material, detritus, and invertebrates	Dominant trophic guild after construction of the Xiaowan Dam in the Lancang-Mekong River, China, and Peixe Angical Dam in the Tocantins River, Brazil (e.g. *Trachelyopterus galeatus*)	[69,39,38•]
	Piscivores adapted to lacustrine environments	Ingest adult, juvenile, or larval fish, either whole or in pieces, including scales and fins	Greater abundance of *Plagioscion squamosissimus, P. surinamensis, Raphiodon vulpinus* and *Hydrolicus scomberoides* in the upper-middle reaches of the Tucurui Reservoir, Tocantins River, and of *Cichla ocellaris, C. temensis, Serrasalmus rhombeus* and *Pygocentrus nattereri* in the lower reaches of the reservoir. *Plagioscion squamosissimus* was more abundant after construction of Santo Antonio and Jirau dams in the Madeira River. These and other piscivores also increased in abundances in reservoirs in the São Francisco, Iguaçu and Paranapanema rivers, Brazil, and Sinnamary River, French Guiana	[46,86,7,40•]
	Exclusively insectivores	Feed primarily on insects	Greater abundance reservoirs in the Paraná and Ivinhema rivers, Parana Basin, Brazil	[38•]
Variable response				
Trophic strategies	Detritivorous and algivorous fishes	Subterminal or ventrally positioned mouth, fleshy lips and fine dentition used for ingesting fine particulate organic matter, including microalgae and other components of biofilms detritus derived from algae or macrophyte tissues, and sometimes may ingest filamentous algae	Abundance of detritivorous catfishes and prochilodontids increased after construction of dams in certain reaches of the Upper Paraná River, Brazil; abundance of these forms decreased after construction of the Peixe Angical Dam in the Tocantins River, Brazil. Variation in response is likely associated with differences in habitats and community structure before impoundment (e.g. clear versus white water, rapids versus non-turbulent reaches) and differences in time periods of studies (short-term versus long-term responses)	[19,39,38•]

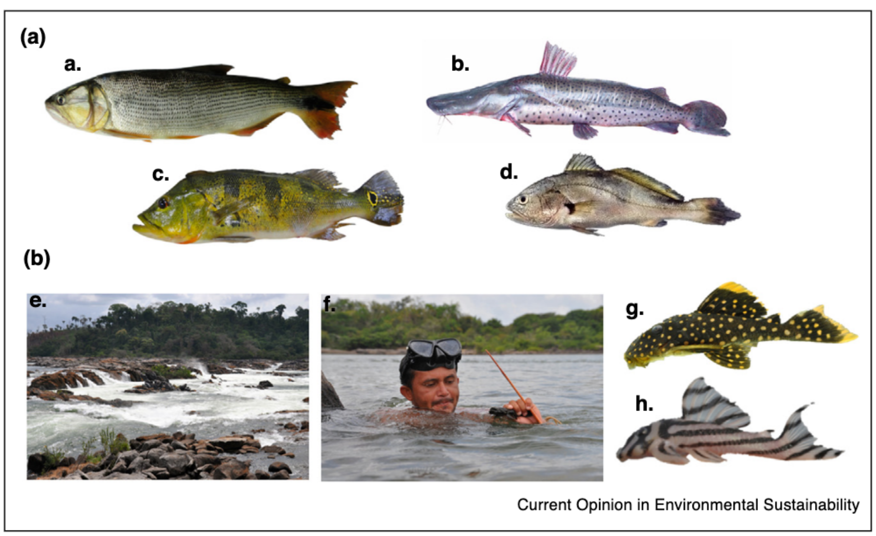
Although such populations can exhibit large inter-annual fluctuations in abundance tied to natural variation in recruitment and year-class abundance, high compensatory reserve and the storage effect provide a degree of demographic resilience to fisheries harvest. Traditionally, tropical river fisheries mimic natural drivers of mortality for periodic strategists by harvesting during the annual period of flood-water recession, thus fishing mortality has limited effects on population dynamics and long-term sustainability [54]. Equilibrium strategists that frequently dominate reservoir fish assemblages are expected to possess less compensatory reproductive potential [52,53], but should exhibit relatively strong density-dependent population dynamics and be able to sustain appropriate levels of harvest. Small opportunistic species have high demographic resilience owing to their rapid life cycles and population growth potential [53], and some that are ecological generalists may persist in systems impacted by dams and fishing.

Declines in functional diversity also may impact the resilience of fisheries via loss of functional redundancy and reduction of the portfolio effect [55]. High functional diversity in free-flowing rivers affords more fishing options in space (e.g. floodplain lakes, slow and swift-moving main channel habitats) and time (e.g. seasonally available migratory stocks, greater capture efficiency during low-water conditions). These options allow fishers to use a variety of gears to exploit diverse stocks and habitats, spreading fishing pressure across multiple production sources and maintaining yields despite inter-annual variation in any particular functional group [54,56]. For example, greater catches of periodic strategists following high recruitment years may temporarily reduce pressure on equilibrium strategists. Moreover, intraspecific functional diversity should influence how a stock responds to environmental variation and potentially could enhance sustainability of exploited stocks [55].

In addition to effects on fisheries yield, changes in functional diversity may impact the market value of catches if dam impacts cause desirable traits to be less prevalent within the fish assemblage. For example, large periodic strategists (e.g. pimelodid catfishes, *Salminus brasiliensis* and *Prochilodus lineatus* in the Paraná River, paddlefish, and sturgeons in the Yangtze River) impacted by river impoundments typically have high commercial value (Figure 2). Thus, the total market value of fisheries declines as these high-value species become rare because increased yields of low value species are insufficient to compensate for the lost value of culturally preferred species [e.g. 17]. While a positive relationship between fish size and market value probably is generalizable (though also dependent on cultural preferences such as for species with or without scales, fat content, etc.), more research is needed to predict how functional traits affecting population vulnerability to hydrologic alteration impact fisheries value.

Changes in functional diversity following dam construction can have a variety of impacts on food web dynamics. Loss of migratory species and altered abundances of fishes that feed at the base of aquatic food webs have potential consequences for ecosystem structure and processes [57]. These functional groups play important roles in linking food web elements vertically across trophic levels as well as spatially across habitat subunits [57]. For example, by acting as ecosystem engineers, detritivorous prochilodontid fishes influence sediment dynamics and benthic communities of Neotropical rivers [16,58]. Some prochilodontids feed in productive floodplain regions during the wet season and then migrate to nutrient-poor rivers where they provide nutritional subsidies to resident predators. Dams and other barriers to fish migration may

Figure 2



Examples of fish species and habitats in tropical rivers impacted by dams. **(a)** Examples of periodic-strategist fishes with high dispersal ability that dominated yields in the Upper Paraná River, Brazil, before the construction of Itaipu Dam: (a) *Salminus brasiliensis*, and (b) *Pseudoplatystoma corruscans* (photographs: Harumi Irene Suzuki and Angelo A. Agostinho). After impoundment, visually oriented pursuit predators (c) *Cichla* spp. and pelagic and sedentary piscivores (d) *Plagioscion* spp. increased in abundance in the reservoir. **(b)** Middle Xingu River, Brazil: (e) rapids, (f) traditional fishing technique (diver uses a wooden stick to pry rapids-dwelling fishes from rocks for export in ornamental fish trade, photograph: Mark Sabaj), and the catfishes (g) *Baryancistrus xanthellus* and (h) *Hypancistrus zebra* (adapted from Ref. [12]). These catfishes of the Neotropical family Loricariidae are well adapted to live within rapids (dorso-ventrally flattened bodies, dorsally positioned eyes, inferior mouths). *B. xanthellus* had high mortality after reservoir completion [84].

Figure 3

Traditional fishery in the Madeira River, Amazon, Brazil. Large migratory catfishes (photo in the right: *Brachyplatystoma rousseauxii*) with traits that enhance sustained swimming performance and endurance, such as large muscle mass, long and narrow caudal peduncle, and large caudal and pectoral fin ratio areas, are able to ascend the Teotônio Cataracts. During these migrations, fishers traditionally used harpoons (locally called *fisga*) to catch these fishes; however, the cataracts were flooded by the Santo Antônio dam in 2011, and this fishery was destroyed [63,64].
Photographs: Sant'Anna, I.R.A.

result in trophic cascades in local food webs; for example, when lentic-adapted piscivores, such as *Cichla* spp., dominate reservoir communities [59]. In reservoirs, greater importance of pelagic productivity and abundance of species with functional traits adapted for lentic environments may increase food-chain length and reduce ecological efficiency of fisheries production ([60], Table 1). Lower availability of allochthonous resources, such as fruits, seeds and leaves, following deforestation and reservoir creation, may impact commercially important herbivores (e.g. *Colossoma macropomum* in the Amazon) [61,62].

Loss of certain functional groups following hydrologic alteration impacts the very nature of fisheries, thereby determining which people receive benefits and affecting cultural heritage. Hydroelectric dams are typically built in locations that exploit potential kinetic energy where large volumes of water are forced into constrained channels or down elevation gradients (e.g. cataracts). When rapids are submerged under reservoirs and species adapted to swift-moving water are extirpated, traditional fishing practices in these areas may be lost in just one generation. For example, fishers traditionally used harpoons to catch large migratory catfishes (e.g. *Brachyplatystoma rousseauxii*) ascending falls on the Madeira River, Brazil, located where the Santo Antônio and Jirau dams were built [63,64] (Figure 3). Similarly, construction of the Belo Monte Dam on the Xingu River, Brazil, eliminated most of the rapids habitat where local fishers dived to capture valuable ornamental fishes (e.g. *Baryancistrus xanthellus*, *Hypancistrus zebra*) (Figure 2). This traditional knowledge was transmitted over multiple generations, but likely will be lost as sport fisheries and aquaculture replace artisanal fisheries within newly formed lacustrine environments. Functional changes in fish assemblages induce fishers to target different species using alternative fishing gears in new locations during different periods. In addition to losing traditional knowledge and customs, such as food taboos, fishers may be entirely excluded from fishing if they are unable to adapt to changes in the functional composition of the local fish assemblage.

Conclusions

Fish assemblages change in relatively predictable ways following river impoundment, and this can be traced to differential species responses based on their functional traits. Timing and magnitude of assemblage changes are dependent on several factors, such as specific characteristics of the fish fauna, river basin and dams. Changes in assemblage structure and functional trait distributions may negatively affect fishery yields, market values, and traditional fishing practices, placing regional income, food security and traditional knowledge at risk. These changes also adversely affect some ecosystem processes and services not discussed here (e.g. water quality, aesthetic and recreation value) [65,66]. Questions remain regarding how, and the extent to which, changes in taxonomic and functional composition of fish assemblages and fisheries are spatially distributed throughout river networks as well as the implications of this for social and ecological systems at multiple spatial and temporal scales. River flow disruption and fragmentation affect fish demographic parameters (e.g. survival, growth, reproduction) and population dynamics within impoundments and over entire drainage networks. Unfortunately, ecological and socio-economic impacts generally are assessed only in the immediate vicinity of a hydroelectric project rather than at the basin scale [2]. As a result, hydropower projects have failed to account for impacts to the livelihoods of more than 470 million people living downstream from dams who depend on river ecosystem services [67]. We propose that adoption of a functional-traits perspective can improve our ability to predict responses of fishes and fisheries to river impoundment across multiple scales and thereby help to address ecological and socioeconomic impacts.

Conflict of interest statement

Nothing declared.

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