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Review article

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Hydropower impacts on riverine biodiversity

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Abstract

Hydropower is a rapidly developing and globally important source of renewable electricity. Globally, over 60% of rivers longer than 500 km are already fragmented and thousands of dams are proposed on rivers in biodiversity hotspots. In this Review, we discuss the impacts of hydropower on aquatic and semi-aquatic species in riverine ecosystems and how these impacts accumulate spatially and temporally across basins. Dams act as physical barriers that disrupt longitudinal connectivity and upstream–downstream movement of species. Impoundment creates still-water habitats upstream of dams and leads to declines in lotic-adapted species. Intermittent water releases modify the natural flow, sediment and thermal regimes in downstream channels, altering water quality, substrate structure and environmental cues that are vital for species to complete their life cycles, resulting in reduced reproduction success. Moreover, retention effects of reservoirs and flow regulation alter river–floodplain exchanges of water, sediment and nutrients, modifying the habitats on which riverine species depend. Improvements to flow regulation, fishway design and sediment redistribution can mitigate these ecological impacts. Future research should support reforms to dam operations and design adaptations to balance renewable electricity development and biodiversity conservation through systematic basin-scale planning, long-term monitoring, adaptive management and involving multiple actors in decision-making.

Sections

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Introduction

Global development of hydropower plants (HPs) has been rapid since the mid-twentieth century[1], with over 82,000 estimated to have been built worldwide[2]. Currently, hydropower accounts for approximately 15% of global electricity production and over 50% of renewable electricity generation[3]. Growing demand for energy and the renewable energy transition further promote hydropower development[4]. Indeed, more than 3,400 HPs, each with an installed capacity greater than one megawatt, are planned or under construction worldwide[5], and over 4,600 sites have been identified as potentially profitable hydropower locations[6].

HPs provide a source of renewable energy, but the fragmentation and flow regulation impacts have environmental consequences, including for biodiversity[2,7,8]. The International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List) assessments consider dams to be a threat to almost 4,000 aquatic, semi-aquatic and terrestrial species. Many established and proposed sites of hydropower development are in hotspots of freshwater biodiversity, including the Amazon, Congo, Ganges and Mekong basins[5–7]. This vulnerability arises through various means, from altered river connectivity and exchange, both upstream and downstream, and between rivers, groundwater and floodplains (Fig. 1). Loss of connectivity impedes the movement of riverine species, and dams cause injuries and mortality from turbines and hydropeaking[9–11]. HPs also modify channel morphology[12], natural regimes of flow, sediment and water temperature[13–16], and biogeochemical cycling[17]. For example, the total capacity of existing reservoirs exceeds 7,000 km^3, accounting for 18% of global annual river discharge[18], and leading to retention of 25–30% of global sediment flux[19]. These alterations cause further changes in biotic communities and decline of riverine species[8,20,21] (Fig. 1). Globally, 1,864 monitored populations of freshwater migratory fish have declined by an average of 81% between 1970 and 2020, with dam-induced habitat loss and degradation posing a major threat[22].

The effects of HPs on biodiversity highlight the need for efficient and effective river management operating across river-reach and basin scales to account for network structure and connectivity in fluvial systems[23]. For example, the efficacy of protecting river sections is highly dependent on the ecological status of upstream areas given the downstream transport of water, sediments, nutrients and pollutants[24,25]. Similarly, headwaters are influenced by upstream–downstream connectivity owing to the influence of migratory animals on upstream ecological processes and biogeochemical cycling[26]. To date, the majority of research has focused on the impact of HP developments on certain taxonomic groups[27–30], within specific

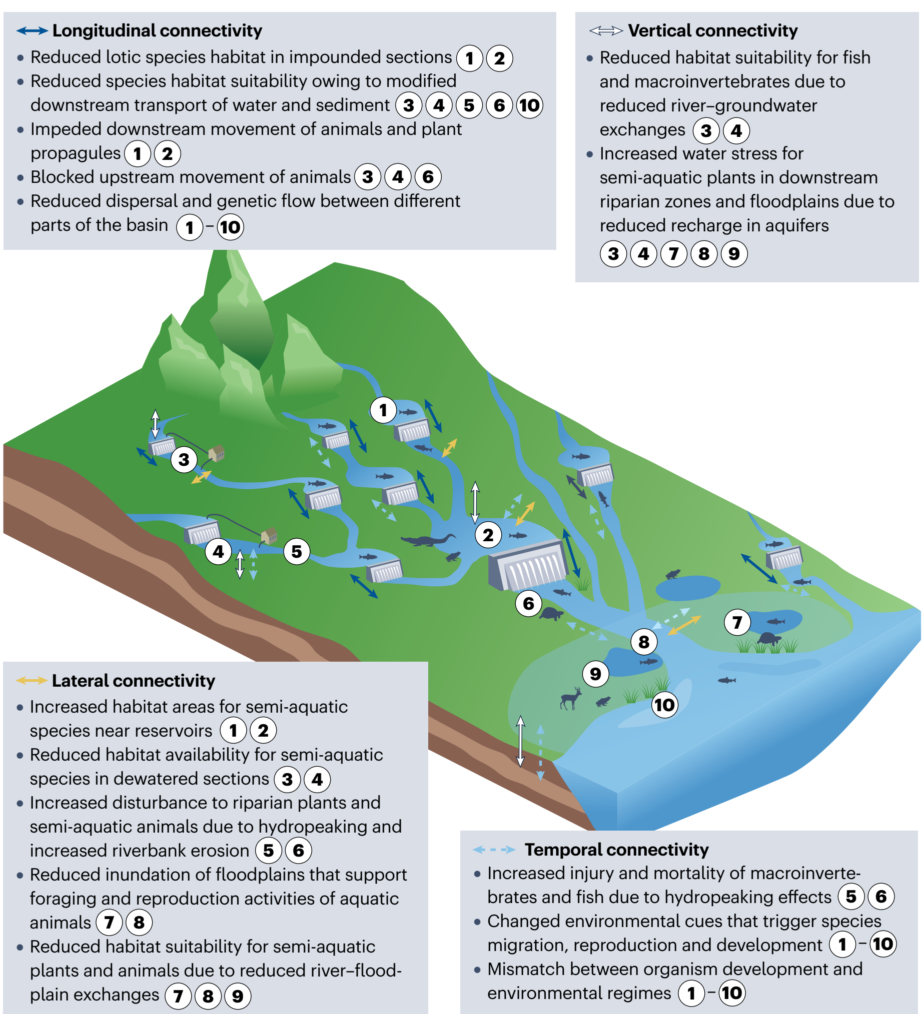


Fig. 1 | Impacts of hydropower plants on river connectivity and riverine species. Hydropower plants (HPs) impact multiple dimensions of connectivity across river basins. Longitudinal connectivity (dark blue arrows) is compromised by dams that fragment upstream–downstream connection of river channels. Lateral connectivity (yellow arrows) is impacted by modified exchanges between river, floodplain and riparian zone. Vertical connectivity (white arrows) is impacted by altered river–groundwater and river–atmosphere interactions[151,195]. In addition, HPs modify natural regimes of flow, temperature and sediment, altering the temporal dynamics of longitudinal, lateral and vertical connectivity (temporal connectivity, blue dashed arrows)[196]. These alterations have profound impacts on riverine species (Box 1). Circled numbers indicate examples of specific sections and areas in the river system. Only a selection of some of the most evident impacts of HPs on species in representative river sections are shown. HPs profoundly modify environmental conditions and alter different dimensions of river connectivity essential for riverine species to complete their life cycles.

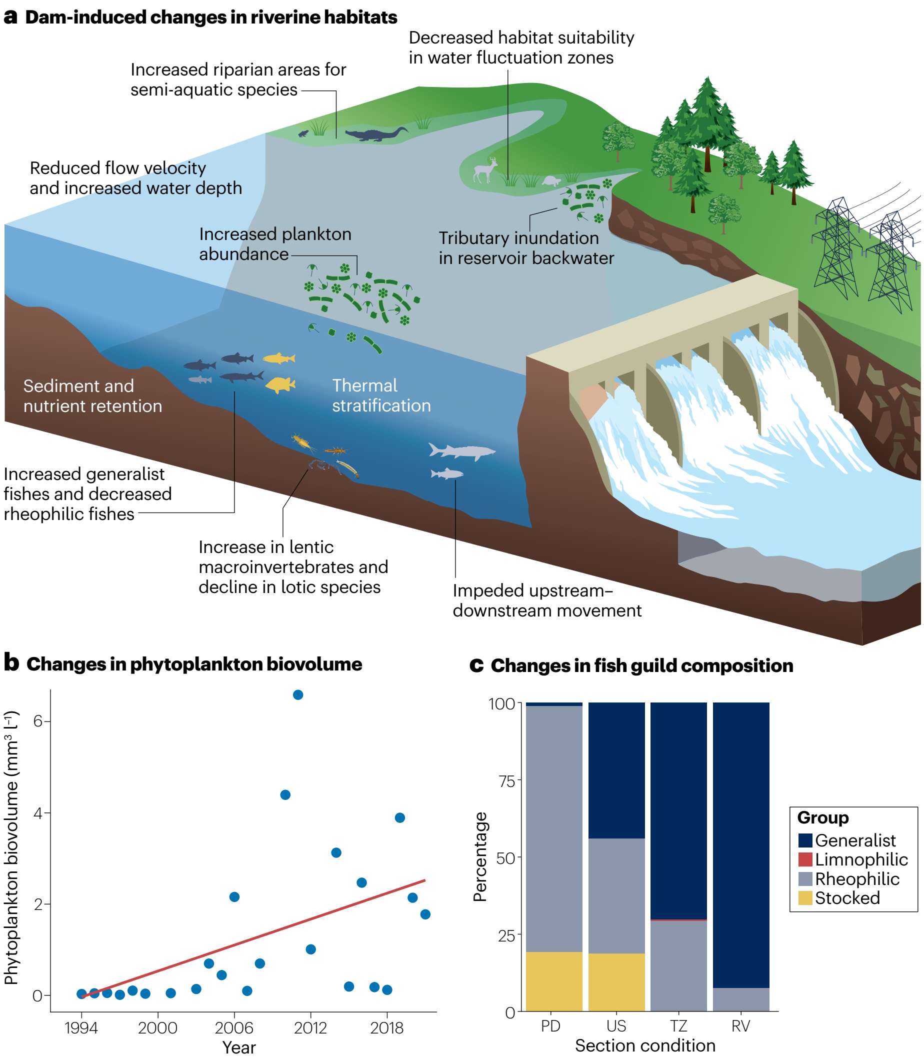


Fig. 2 | Impacts of a large hydropower plant on the river section upstream of the dam. **a**, Upstream riverine impacts. **b**, Temporal trend in phytoplankton biovolume at 1 m depth at forebay station (LPCR0024), Lake Powell, USA[197]. Blue dots represent data points, whereas the red line represents the trend of phytoplankton biovolume over time. **c**, Comparison of fish guild compositions[198] at River Malše, Czech Republic, before dam construction (PD), >5 km upstream of the Římov Reservoir (US), the transition zone between running-water section and the reservoir (TZ), and the reservoir (RV). Dams often impound rivers and create novel standing-water habitats, leading to fundamental changes in biotic communities in the impounded sections.

types of river system[31,32], and limited numbers[33,34] and types of HP[8,23,35]. The cumulative impacts of a range of designs of HP installations at the basin scale and over long timescales have rarely been considered in environmental policies[2,23].

In this Review, we explore the diverse and pervasive impacts of HPs on biodiversity across river networks. We discuss the upstream and downstream impacts of different types of HP on riverine ecosystems, highlighting the consequences for aquatic and semi-aquatic species. We consider how impacts vary and accumulate across spatial and temporal scales, from specific river sections to the entire river basin and from short-term water release events to long-term impacts on annual flow regime and genetic biodiversity. We explore potential measures for mitigating HP impacts on riverine biodiversity and ensuring sustainable development and management of HPs to meet growing energy demands and protect current and future riverine ecosystems.

Upstream impacts

All HPs, even small ones, represent obstacles to the movement of sediment, nutrients and species. Achieving sustainable HP development relies on accounting for network structure and connectivity across fluvial systems[23], including longitudinal dimensions (upstream–downstream transport of water, sediment and nutrients and movement of species[36]), lateral dimensions (exchanges between rivers and adjacent floodplain habitats, including lakes and wetlands[36,37]), vertical dimensions (exchanges between rivers and underlying sediments and groundwater, and the overlying atmosphere) and temporal dimensions (variation of environmental conditions over time, including the natural regimes of flow, water temperature, sediment, nutrients and organic matter[38]) (Fig. 1). Dams impact longitudinal connectivity of river systems and drive biodiversity changes upstream of dams[8,21]. These ecological impacts vary and critically depend on whether the dam creates an impounded reservoir section. The upstream impacts for HPs with and without reservoirs are now discussed.

Hydropower plants with a reservoir

Impounded river sections, including parts fragmented by dams and tributaries influenced by backwater, often change from lotic to lentic environments (Fig. 2a). The change in flow prolongs hydraulic residence time, increasing sediment retention and deposition and leading to elevated nutrient concentrations in impounded reservoirs. Together with thermal stratification (often occurring in large deep reservoirs), these conditions favour phytoplankton growth and formation of algal blooms[20,39]. For example, phytoplankton abundance in the Manwan Reservoir on the Upper Mekong River, China, increased by over tenfold after inundation[40], and algal blooms occurred in over 26 tributary bays between 2004 and 2015 in the Three Gorges Reservoir Region, Yangtze River[41]. Over time, remobilization of nutrients retained in sediments could further exacerbate algal bloom occurrences[17] (Fig. 2b).

The response of aquatic macrophytes varies depending on their location relative to the dam and the environmental changes that they experience. Altered substrates, increased water depth and frequent water-level fluctuations impede the growth of some submerged aquatic macrophytes[8]. Conversely, expansion of nearshore areas with increased inputs of nutrients and organic matter to the river system can benefit other submerged and floating species. These benefits are particularly apparent in reservoirs with stable water levels[42], as evidenced by enhanced growth of floating macrophytes such as water hyacinth (*Eichornia crassipes*) and giant salvinia (*Salvinia molesta*) in tropical reservoirs. Nevertheless, these species benefits have knock-on effects, as demonstrated by animal die-offs arising from oxygen depletion associated with accumulation of macrophyte biomass, which can cover the water surface and adversely affect the photosynthesis of submerged macrophytes and phytoplankton[42,43].

Aquatic animals have more varied responses to impoundments than phytoplankton and aquatic macrophytes. Impoundments tend to stimulate and sustain zooplankton growth owing to increased food supply from phytoplankton biomass and to prolonged hydraulic residence time[44]. For example, zooplankton species richness increased by 54% after impoundment in the João Borges Reservoir, Brazil[45]. Benthic macroinvertebrates feeding on macrophytes and organic matter also flourish in nearshore areas of reservoirs following dam closure[42], as what occurred in the Cow Green Reservoir, UK, where macroinvertebrate biomass increased from 0.12 g m^{-2} to 7.44 g m^{-2} after the reservoir was filled[46]. However, in deep reservoir areas, initially rapid accumulation of sediment and organic matter can lead to hypoxic stress and impair macroinvertebrate growth[47]. These new deepwater habitats are then colonized and dominated by hypoxia-tolerant and fine sediment-tolerant, burrowing lentic species, such as chironomids and oligochaetes[48]. By contrast, rheophilic species, which require flowing water and stony substrates, typically disappear[47].

Fish species are also impacted by impoundment. Fish diversity can temporarily increase after dam closure owing to newly submerged habitats and increased terrestrial inputs of nutrients and organic material. These changes support growth in trophic groups including detritivorous, omnivorous, insectivorous species and predators adapted to lentic environments[30,31,47]. Subsequent declines in native fish diversity often occur owing to the extirpation of rheophilic fish and periodic strategists[31,49,50] (Fig. 2c). Declines in native fish are probably more rapid in the tropics than in temperate or boreal reservoirs, as many species living in tropical rivers lack the morphological and ecological traits required to occupy lentic habitats[51]. A global synthesis of the responses of 539 fish species to dams found species were particularly vulnerable to impoundment if they had certain characteristics, including long-distance migrations, lotic or cold-water adaptations, floating eggs or inferior mouths (often benthic species)[52]. Impoundments also favour active introduction and establishment by lentic-adapted, pelagic or omnivorous alien species[51,53,54]. For example, the number of native fish species decreased from 50 to 23 in the Capivara Reservoir, Brazil, between 1990 to 2010, whereas the number of alien fish increased from 3 to 11 species[55].

Land inundation causes loss of habitat for terrestrial species[56], but the impacts on semi-aquatic animal and plant species are more complex[20,28]. Newly flooded areas are typically colonized by riparian vegetation, particularly in the upper reservoir where there are low levels of inundation but enhanced sediment deposition[57]. For example, the total area of riparian forest in the lower White River, USA, increased by 49% between the fluvial section and the area frequently inundated by reservoir backwater over the 70 years following dam closure and filling of the reservoir[58]. Conversely, frequent water-level fluctuations caused by hydropeaking can disturb riparian plants, as what occurred in the Three Gorges Reservoir, China, where riparian vascular plant diversity decreased by 43%, with a 64% decline in woody plants and 52% decline in perennial herbs between 2001 and 2009 (ref. 59).

Although impoundment increases habitat area for semi-aquatic animals, these habitats might be of poor quality[28,60]. For example, after closure of the Balbina Dam, Brazil, the open-water area increased by 63 times and the reservoir perimeter increased by 9 times, but the population size of the giant otter (*Pteronura brasiliensis*) only doubled in 25 years owing to reductions in food supply and suitable denning habitats[61]. Similarly, above the Cachoeira Caldeirão Dam, Brazil, the average density of yellow-spotted river turtle (*Podocnemis unifilis*) nesting sites declined from 0.48 to 0.15 per km after the reservoir was filled[62]. Therefore, reservoirs transform lotic environments into standing-water habitats, which often leads to the decline of species morphologically and ecologically adapted to flowing water but, conversely, benefits generalist species.

Hydropower plants without a reservoir

Some HP systems operate without a reservoir, including ultralow-head run-of-river and diversion-weir schemes (Box 1). Evidence of ecological impacts in these locations is relatively sparse[2,8]. However, even in the absence of a reservoir, dams increase water depth, decrease flow velocity and enhance sediment deposition, leading to slow-moving upstream river sections[63,64]. These changes probably have limited influence on phytoplankton and zooplankton owing to the short hydraulic residence time[8,65], but the changes could strongly impact organisms sensitive to habitat changes at the riverbed.

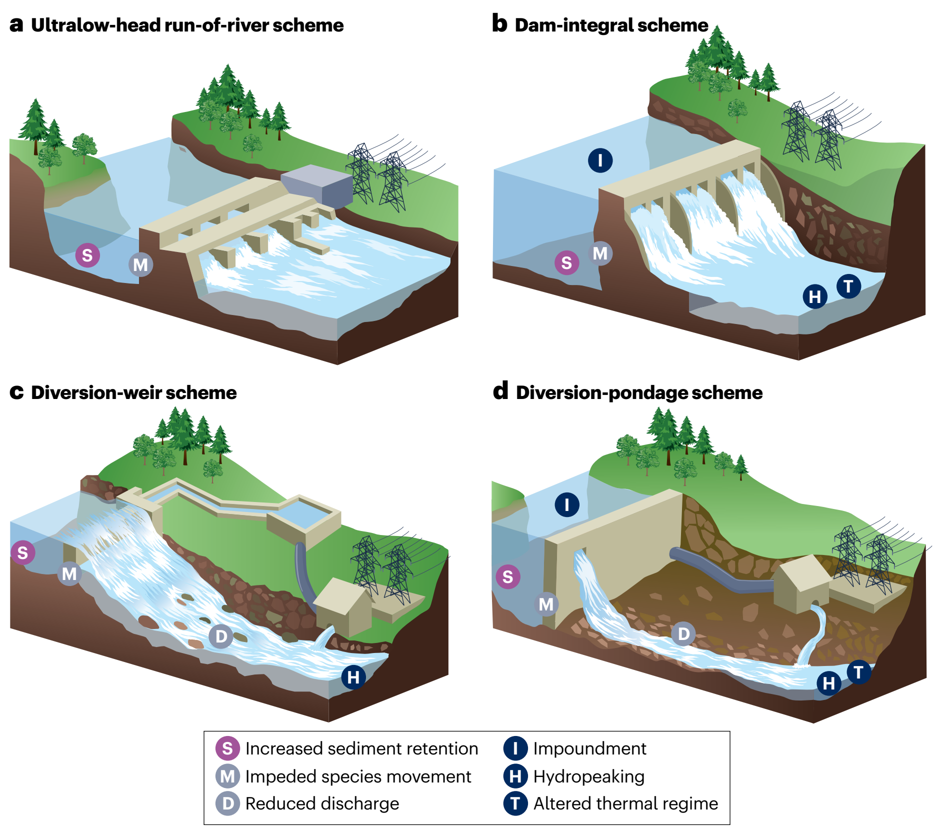
Increased fine sediment deposition in slow-moving sections covers coarse substrates and makes the riverbed less penetrable, impeding growth of benthic algae and macrophytes[8]. For example, macrophyte species richness declined by 75% in an upstream section above the small hydropower plant (SHP) on Ślęza River, Poland, compared to an unmodified section[66]. These types of changes also lead to declines in lotic species, such as macroinvertebrates (Plecoptera, Trichoptera, certain Ephemeroptera taxa) and rheophilic fish species[2,63,67]. In Southern Germany, for instance, species richness in sections upstream of dams has declined by 17% for benthic algae, 28% for macroinvertebrates and 23% for fish[64]. However, HP-induced alterations do not always negatively affect species, as illustrated by lentic macroinvertebrate species, such as Diptera and Oligochaeta, that thrive in slow-moving river sections[64]. Additionally, in cold winter regions, sections with elevated water depth and temperature can serve as refugia for fish, therefore, enhancing their survival[67].

Hydropower impacts on upstream sections of dams highly depend on the size and operation mode of HPs (Box 1) and vary greatly between regions with different topographic and hydrological conditions. HPs with large reservoirs typically have more profoundly upstream impacts on biotic communities than those without reservoirs, but all HPs adversely affect the movement of species.

Box 1 | Main operation modes of HPs

Hydropower plants (HPs) can be categorized into four main operation modes based on the presence of reservoir and diversion infrastructure[2]. Figure adapted with permission from ref. 2, The Ecological Society of America.

- **Ultralow-head run-of-river** schemes (see the figure, part **a**) generate energy without storing or diverting water[2]. Dams are often low (≤3 m), and water storage and retention above dams is minimal[8]. Dams still reduce the longitudinal connectivity of rivers, represent barriers to upstream–downstream species movement and impede downstream sediment transport.
- **Dam-integral** schemes (see the figure, part **b**) have the powerhouse built within the dam, creating a sizable reservoir[2]. The river reach above the dam is converted to a lentic environment. Water is released to the river channel immediately below the dam. Compared to the ultralow-head run-of-river scheme, the dam-integral scheme typically has a much longer hydraulic residence time and a stronger influence on riverine habitats, including impoundment and retention of sediment and nutrients in reservoirs and modified regimes of flow, sediment and temperature in downstream sections[201]. For example, intermittent water releases often generate hydropeaking effects in downstream sections.
- **Diversion-weir** schemes (see the figure, part **c**) divert water from the upstream section of the weir through a diversion channel or a penstock to downstream powerhouse[2]. The weir functions as a dam that reduces the flow velocity and increases water depth in the upstream section. For some HPs, water can spill over weirs. In other cases, all upstream discharge is diverted to the downstream powerhouse or a reservoir in a different catchment[80,202]. Therefore, a residual-flow section between the weir and the powerhouse is created with reduced discharge[23]. Water release from the powerhouse usually generates hydropeaking effects in downstream river sections[185].
- **Diversion-pondage** schemes (see the figure, part **d**) include both water storage and diversion. Water is diverted from the reservoir to the downstream powerhouse[2]. The diversion-pondage scheme causes profound changes in both the upstream and downstream sections. Its upstream impacts are similar to those of the dam-integral scheme, but it creates residual-flow reach similar to the diversion-weir scheme[203]. Hydropeaking impacts on downstream sections are more commonly documented for the diversion-pondage scheme than the diversion-weir scheme[8].



Upstream–downstream movements of species

HPs fragment the longitudinal connectivity of river systems and block the migration and dispersal of species along river channels. The life cycle of migratory fish is particularly affected by dam-induced river fragmentation[30]. Globally, of the 383 fish species with documented population declines caused by dams, 44% are migratory[52]. Upstream movements of other organisms, including river dolphins, turtles and freshwater shrimp, are also impeded by dams, although understanding of population-level effects is limited[28,68].

Design features have been implemented into HPs to help address the issue of obstructed upstream species movements. Various fishways are designed to enable fish to pass over or around dams[30]. However, where fishways have been installed, their efficiency often remains low, particularly for non-salmonids[69]. For example, the overall attraction efficiency of 73 investigated fishways worldwide is 62% for non-salmonids and 71% for salmonids, whereas the overall passage efficiency is only 46% and 78%, respectively[70]. As dams are often too high to overcome and the efficiency of fishways remains low, many migratory fish species have been extirpated upstream of dams, including, for example, sturgeons upstream of the Iron Gate Dam on the Danube River, Europe[21].

Hydropower impacts on downstream species movements are less well understood than upstream movements[71]. Some species move downstream through turbines or spillways, but they are at high risk of injury or mortality. For example, across 122 HPs, average fish mortality was 22% with substantial differences between turbine types (43% for cross-flow turbines and 1% for water-wheel turbines) but no clear influence of HP size[9]. Dams also impede downstream movement of other riverine organisms, such as plants, invertebrates and amphibians[72,73]. Retention of drifting plant propagules in reservoirs reduces downstream transport of seeds and increases seed mortality[74]. For instance, seed concentrations in waters downstream of the Gross Dam in Colorado, USA, are 70% lower than in waters upstream of the reservoir[73]. In Canada, HPs also retain coastal tailed frog (*Ascaphus truei*) larvae upstream of dams, resulting in a 60% decrease in downstream larval density[72].

Impacts of reduced species movement on biodiversity dynamics in river ecosystems are far reaching. Reduced dispersal of species between habitats leads to species extirpation if they are retained in less suitable habitats[23]. For example, in Romania, brown trout (*Salmo trutta fario*) and bullhead (*Cottus gobio*) have been extirpated in 24% and 43% of upstream and downstream river sections of 21 investigated HPs, respectively[75]. HPs also reduce gene flow between isolated populations of riverine fish, mammal and reptile species[23,28,76]. In Australia, for example, genetic differentiation between platypus (*Ornithorhynchus anatinus*) populations above and below the Darmouth Dam in the Mitta Mitta River was 12 times higher than that of populations in the adjacent undammed Ovens River[77]. Thus, dam-induced restrictions to upstream–downstream movement of species not only impact reproductive success, particularly for migratory species, but the resulting fragmentation of populations also impacts the long-term stability and viability of species in both upstream and downstream sections of the dam.

Downstream impacts of hydropower plants

Just as dams impact upstream habitats, HPs also impact downstream sections by altering the timing, duration and volume of water and sediment transported to downstream sections (Fig. 1). Changes in flow, temperature and sediment regimes impair species morphologically or ecologically adapted to natural flood pulses. The effects are highly variable and depend on the operation mode (Box 1) and size of HPs, regional environmental conditions and proximity to the hydropower infrastructure (dam and powerhouse). The varying downstream impacts of diversion and non-diversion hydropower schemes are discussed in this section.

Downstream of diversion dams

Diversion-weir and diversion-pondage schemes (Box 1) create residual-flow sections below dams, ranging from a few hundred metres to several kilometres[23]. The degree of discharge reduction could be up to 100% and depends on the size and operation mode of HPs[2,8]. Some HPs abstract water throughout the year and their impacts on downstream sections are most severe during low-flow seasons, as dam spillovers can occur during high-flow seasons[2,65]. Dam-induced low-flow or even no-flow conditions are a major stressor to macrophytes, macroinvertebrates, fish and riparian vegetation[2,8]. For example, in the Xiangxi Basin, China, average macroinvertebrate taxa richness and density decreased in residual-flow sections by 21% and 42%, respectively, compared to upstream sections (Fig. 3a), with a substantial reduction in lotic filter-collectors[78].

In mountain regions where several catchments are in sufficiently close proximity, river flow can be diverted across catchments to enhance water supply to HPs. For example, in the European Alps, water from multiple rivers has been diverted to a HP located in a different catchment without returning the abstracted water to its river of origin but still flushing the remaining sediments downstream of the diversion dam[79]. Water abstraction and sediment flushing mostly occur during high-flow periods in summer, resulting in severe degradation of downstream habitats for macroinvertebrates and riparian plants during summer, which impacts the natural seasonal dynamics of riverine biodiversity[79,80].

Diversion dams also impact biomass and community composition of benthic algae through water stress. In some cases wherein water remains in residual-flow section, reduced shear stress, increased water temperature and reduced sediment input downstream of diversion dams favour diatoms with certain traits, such as high-profile diatoms and those with weak ability of attaching to the substrates[81]. Compared to unimpacted upstream sections, for instance, average taxa richness and functional richness of diatoms increased by 51% and 48% in residual-flow sections of 23 SHPs in the Xiangxi Basin (Fig. 3b), driven by increases in high-profile diatoms and other planktonic taxa in pool habitats downstream of dams created by overflow during high-flow seasons[82]. The changes in primary producers might affect food-web structure of the residual-flow section through trophic cascade.

Downstream of powerhouses in diversion schemes

In diversion-weir and diversion-pondage schemes, water is either released to the river from a powerhouse or it is subsequently diverted to another HP, as is common in mountain regions[8]. Hydropeaking effects associated with intermittent releases are the main stressor of riverine species in sections downstream of powerhouses, with the scale of impact again being strongly influenced by the HP operation mode, and regional topographic and climate characteristics.

The impact of hydropeaking from diversion schemes on aquatic plants and algae varies with distance from the HP. Intensified scouring during water release leads to the formation of deep pools below powerhouses in some mountain rivers. These pools form habitats that benefit high-profile and planktonic diatoms, which are less abundant in fast-flowing mountain rivers, and increase the overall taxonomic and functional richness of diatoms[82] (Fig. 3b). Conversely, scouring effects and, further downstream, subsequent deposition of scoured sediments might suppress the growth of benthic algae[83].

Hydropeaking effects also influence the distribution, feeding and reproductive success of downstream macroinvertebrates and fish through displacement, changes in sediment dynamics, and flow

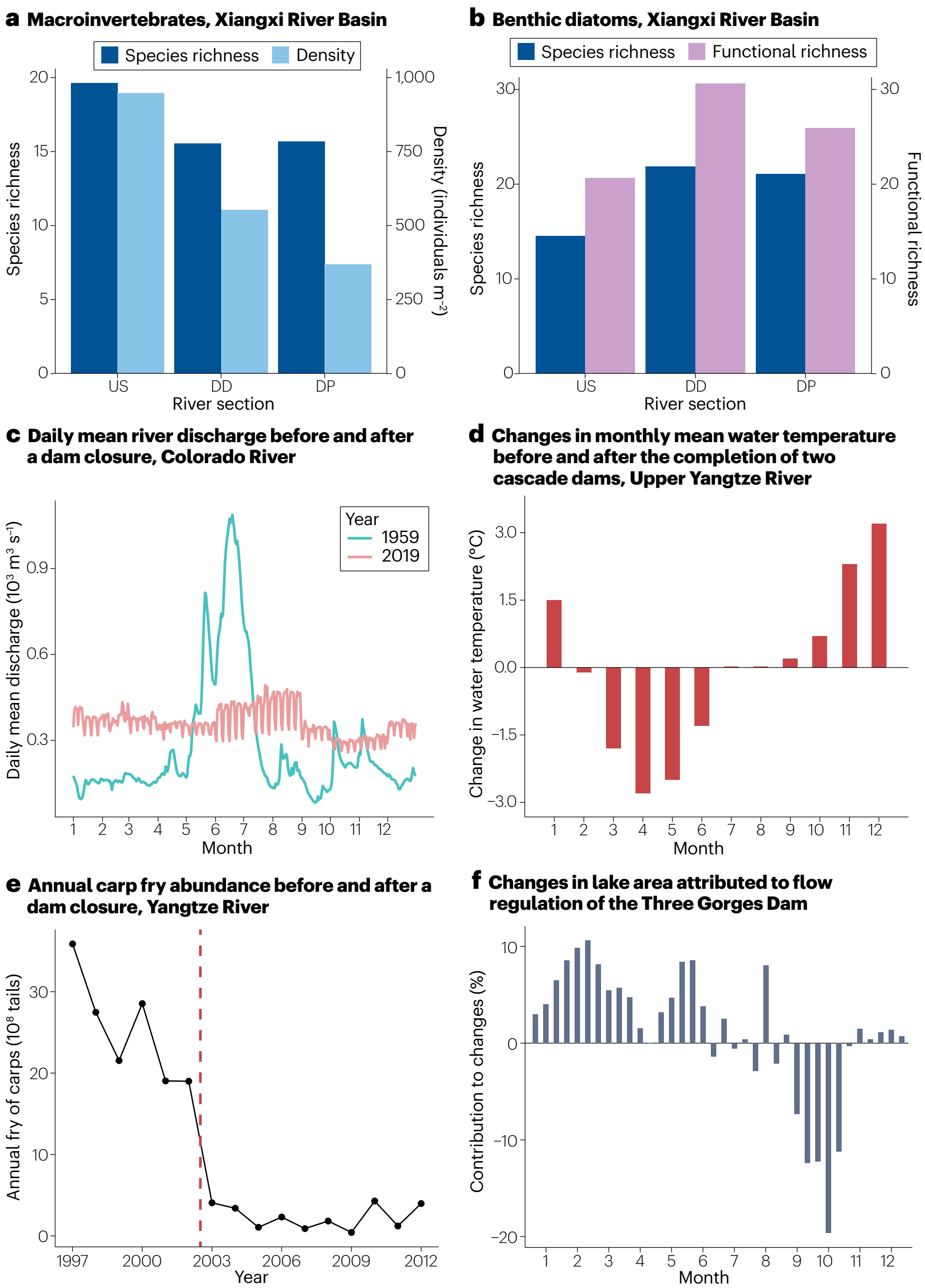


Fig. 3 | Downstream impacts of hydropower plants on riverine species. a, Species richness and macroinvertebrate density upstream of the diversion dam (US), downstream of the diversion dam (DD) and downstream of the powerhouses (DP) in the Xiangxi River Basin, China[78]. **b**, As in panel **a**, but for species richness and functional richness of benthic diatoms[82]. **c**, Daily mean discharge at Lees Ferry gauging station, Colorado River, USA, before (1959) and after (2019) the completion of the Glen Canyon Dam. Data were obtained from National Water Information System of US Geological Survey. **d**, Change in monthly mean water temperature at the Xiangjiaba gauging station before (between 2000 and 2011) and after (between 2013 and 2015) completion of the Xiluodu and Xiangjiaba dams, China[199]. **e**, The annual fry abundance of the four major domestic carp species at the Jianli gauging station, Yangtze River, China[99]. The red dashed line indicates the completion of the Three Gorges Dam. **f**, Contribution of flow regulation by the Three Gorges Dam to monthly changes in lake area naturally connected to the Yangtze River[126]. Lake area is calculated as 10-day mean values from 2000 to 2011 based on satellite-based delineations. Hydropower plants modify the natural flow, sediment and thermal regimes in downstream channels and reduce river–floodplain exchanges of water and sediment, altering habitats on which aquatic and semi-aquatic species depend.

fluctuations. Hydropeaking can increase the downstream drift of benthic macroinvertebrates by almost an order of magnitude in some mountain rivers[84]. Macroinvertebrates that use gills for respiration and scrapers feeding on biofilms on stony substrates are particularly vulnerable to enhanced sediment deposition associated with hydropeaking[85]. Strong flow fluctuations also increase stranding and drift of fish. Reductions in fish spawning and rearing success also occur in sections downstream of the powerhouse through, for example, altered migration behaviour, disrupted nesting and spawning activities, and dewatering of nesting sites during low-flow periods[30,86,87]. The effects of hydropeaking on macroinvertebrates and fish might accumulate over time, leading to changes in community composition and population decline or even extirpation of sensitive taxa.

Diversion scheme dams substantially alter flow and thermal regimes downstream of the powerhouse. In regions with large seasonal climate and hydrological variation, including some mountainous and high-latitude regions, some diversion schemes include large reservoirs to store abstracted water to ensure sufficient power generation during periods of low flow. For example, some HPs in the European Alps store water over summer for release and power generation in winter. Because the natural river discharge is high in summer and low in winter, this approach shifts the seasonal flow regime[88]. In addition, the thermal regime of rivers is profoundly impacted by hypolimnetic releases from large reservoirs, whereby low-oxygen deepwater of different temperature to surface waters is released and can lead to thermopeaking[89]. River sections and species downstream of powerhouses of HPs with hypolimnetic releases often experience cooling in summer and warming in winter[32,90]. Altered flow and thermal regimes lead to mismatches between organism development, such as hatching, growth and juvenile development, and environmental conditions, such as temperature, flow and food availability, leading to declines in growth and survival of macroinvertebrates and juvenile fish[32].

Downstream of non-diversion dams

Many large hydropower plants (LHPs) have powerhouses integrated into their dams and directly release water from reservoirs to downstream river sections. Although these systems do not form residual-flow sections, they still strongly modify natural flow, sediment and thermal regimes in downstream channels, altering water turbidity and nutrient loads and affecting community composition and food webs[17,91,92].

Reduced flow velocity and increased hydraulic residence time in reservoirs reduce the input of sediments and nutrients to downstream sections. Such reductions in nutrients, including nitrogen, phosphorus and silicon, can, in turn, decrease primary production and fish productivity[93]. The dynamics of nutrient retention in reservoirs and their impacts on downstream section can change over time[17]. The bioavailability of phosphorus and nitrogen in the downstream channel of old reservoirs might increase because of phosphorus release from accumulated sediment and transformation of nitrogen from nitrate to ammonium in reservoirs[94]. However, the release of dissolved silicon from reservoirs to downstream sections might remain limited as a large amount of dissolved silicon can be absorbed by diatoms and retained in reservoir sediments[95]. The alteration of silicon-to-nitrogen and silicon-to-phosphorus ratios can limit the growth of diatoms, which highly depend on dissolved silicon to develop their siliceous shells, leading to shifts in phytoplankton community composition in downstream channel[17,95]. For example, in the Upper Mekong River, these nutrient changes led to the relative abundance of diatoms dropping from 93% upstream of the cascade reservoirs (a series of reservoirs on the same river owing to multiple installations of dams) to 29% downstream, with green algae becoming the dominant phytoplankton group[94].

There are contrasting downstream impacts of non-diversion dams on benthic algae. Hydropeaking increases riverbed scouring in sections close to dams, limiting the growth of benthic algae that are intolerant to strong hydrological disturbance[11]. However, sediment retention upstream of dams reduces downstream turbidity and enhances water transparency, promoting benthic algal growth. For example, over 90% of suspended sediment was retained in Lake Powell, USA, leading to a 26-km clear-water stretch below the Glen Canyon Dam in the Colorado River and 33-fold higher biomass of benthic algae compared to a nearby turbid section[96].

Water releases from HPs substantially impact downstream flow and thermal regimes, affecting aquatic insect species. Flow regulation by LHPs with storage reservoirs not only reduces annual and seasonal variations in downstream flow but also strongly increases daily or sub-daily fluctuations[14] (Fig. 3c), with hypolimnetic releases modifying natural thermal regimes[15] (Fig. 3d). For example, downstream of the Glen Canyon Dam, USA, Ephemeroptera, Plecoptera and Trichoptera were nearly eliminated by the combined effects of regulated flow, reduced maximum water temperature in summer (by more than 10 °C) and narrowed annual temperature range (from 29.4 to 10.6 °C). Declines in these sensitive aquatic insects were owing to the loss of key environmental cues for their development, which means that they could not complete their life cycles[96]. In addition, many aquatic insects attach their eggs to partially submerged or shallow water substrates[97,98], which might be fully or partially submerged during water release but are subject to drying when water levels recede, leading to reduced egg viability[97].

Fish species that rely on natural flood pulses, including migratory species, rheophilic species or periodic strategists, are especially vulnerable to the hydropower impacts. For example, in river sections downstream of the Three Gorges Dam, the combined effects of changes in flow and thermal regimes delayed and shortened the spawning season for four major domestic carp species (*Ctenopharyngodon idella*, *Mylopharyngodon piceus*, *Hypophthalmichthys molitrix* and *Hypophthalmichthys nobilis*), contributing to their annual fry abundance declining by nearly 90%[99] (Fig. 3e). Native species with low cold-water tolerance have also experienced declines in downstream sections affected by hypolimnion release, as widely documented in regions such as Australia, China and the USA[15,100]. In addition, hydropower operations profoundly alter concentrations of dissolved gases in downstream channels, leading to either total dissolved gas supersaturation owing to high-dam discharge or low dissolved oxygen level owing to hypolimnetic release, both of which lead to greater fish mortality[30,101].

HPs also influence species reliant on riparian areas downstream of the dams. Hydropeaking disturbs riparian plants, hampering seed germination and plant growth, leading to increased mortality in species intolerant to scouring, prolonged submergence or water stress[102]. Species requiring long periods of light exposure to germinate, such as annual plants, and species lacking coleoptiles, efficient stomatal control, corticular photosynthesis or mycorrhizal symbioses are all particularly vulnerable to hydropeaking effects[103]. Conversely, frequent water-level fluctuations can also enhance transport of plant propagules from elevated riparian areas to rivers and subsequently flush them further downstream wherein they might be deposited in recently formed moist habitats[10].

Semi-aquatic animals, particularly those dependent on riparian area or sand bars for nesting such as turtles and crocodylians, are sensitive to downstream impacts of HPs. For instance, nesting sites of turtles might be consistently flooded during the nesting season or temporarily flooded after the deposition of turtle eggs owing to flow regulation. The former leads to egg deposition in suboptimal sites, enhancing the risk of predation and disturbance, and the latter increases the risk of hatching failure[28]. For example, *Batagur dhongoka* and *Batagur kachuga* turtles experienced 10% and 8% nest loss, respectively, in the Chambal River, India, because of submergence caused by water release[104]. Sediment retention in reservoirs and hydropeaking contribute to downstream channel incision and further degradation of important turtle and crocodylian habitats, such as sand beaches[28,105]. Thus, hydropeaking effects and increased channel incision are particularly detrimental to the reproductive success of semi-aquatic animals in river sections downstream of the dams. HPs can profoundly impact habitat conditions in river channel and riparian areas downstream of the dams, leading to declines of species that are adapted to natural regimes of flow, water temperature and sediment in river ecosystems. In the case of LHPs with large storage reservoirs, their impacts can extend for hundreds of kilometres and influence floodplains further downstream.

Downstream floodplains

HP operations profoundly impact lateral connections between rivers and floodplains, including lakes (Fig. 1). River channels and their

Glossary

Aquatic macrophytes
Plants that are submerged or can float at the water surface.

Attraction efficiency
The percentage of fish detected at the entrance of or inside the fishway in relation to all monitored fish.

Benthic macroinvertebrates
Invertebrates, such as aquatic insects, snails, worms and mussels, that attach to substrates or aquatic macrophytes or burrow into riverbed sediments.

Denil fishways
Fish passages with a series of symmetrical, closely spaced baffles that can redirect water flow and create low-velocity zones at the bottom to allow fish to ascend.

Detritivorous, omnivorous, insectivorous
Classification of animals according to their nutrient uptake by consumption of dead organic material, both plant and animal matter, or insects, respectively.

Equilibrium strategists
Fish species often of small to medium body size with intermediate maturation, small clutch size but high parental care.

Filter-collectors
Macroinvertebrates that feed on floating particles by filtering them from running water.

High-profile diatoms
Tall-stature diatoms that can form long colonies, have good access to nutrients and light, but are exposed to disturbances from fast flow and grazers.

Hydraulic residence time
The average time a water molecule is in a reservoir based on the ratio of reservoir volume to average flow rate.

Hydropeaking
Rapid changes in downstream water level and flow owing to intermittent water releases from hydropower plants.

Hypolimnetic releases
Release of deepwater that is of different temperature than surface waters and has low oxygen concentrations.

Opportunistic strategists
Fish species often of small size with early maturation and low juvenile survivorship.

Passage efficiency
The percentage of fish detected at or beyond the fishway exit in relation to fish detected at the entrance of or inside the fishway.

Periodic strategist
Fish species that are characterized by large body size, late maturity, high fecundity but low juvenile survivorship, and typically depend on highly seasonal environments.

Phytoplankton
Pelagic algae and bacteria that obtain energy via photosynthesis.

Pool-weir fishways
Fish passages with a series of interconnected pools separated by low weirs.

Rheophilic fish
Fish species that prefer to live in a fast-flowing environment.

Semi-aquatic species
Animals and plants that use both aquatic and terrestrial habitats.

Thermal stratification
Lakes and reservoirs have distinct thermal layers at different depths owing to density changes in dependence of temperature.

Thermopeaking
Sudden changes in water temperature in river sections downstream of powerhouses receiving water from high-elevation reservoirs.

Total dissolved gas supersaturation
The level of dissolved gases in water exceeds the solubility threshold under the local atmospheric pressure and temperature.

Zooplankton
Weak active swimming animals that inhabit the water column and obtain energy through consuming other organisms.

floodplains naturally form complex and interlinked systems that support some of the most diverse ecosystems in the world[37]. For example, approximately 630,000 km^2 of the Amazon Basin was historically flooded during the high-flow season, representing over 10% of the total basin area[106]. Thus, lateral exchanges of water, sediment and nutrients exhibited distinct seasonal fluctuations that were amplified during flood events[37,107]. However, hydropower operations have modified these fluctuations and have truncated flood events, which has impacted aquatic and semi-aquatic species reliant on floodplain habitats.

Many aquatic animals migrate between river channels and adjacent floodplains for foraging and/or reproduction[108,109], making them sensitive to changes in lateral connectivity. For example, at least 137 fish species migrate laterally in the Amazon Basin[110]. Flow regulation by HPs and sluice gates reduces lateral connectivity between downstream floodplains and the river channel and modifies environmental cues triggering fish migration, reducing the area of flooded habitats suitable for foraging and reproduction activities and leading to decreased biodiversity. In the Yangtze floodplain, for example, fish species richness in lakes disconnected from the Yangtze is 38% lower than in lakes connected to the river[111]. Aquatic mammals, such as river dolphins and manatees, that forage in floodplains are also subject to hydropower influence[43,112]. Amazonian manatees feed on macrophytes in shallow floodplain lakes during the high-flow season and migrate to deep refuges when the water level drops[113]. HPs alter the annual flow periodicity and regimes of water-level change in floodplains. Thus, hydropower operations might negatively impact manatee migration and lead to increased mortality owing to stranding in shallow waterbodies[114].

Hydropower operations influence floodplain vegetation as many species are adapted to periodical flooding conditions[115]. Water releases of HPs in low-flow season lead to prolonged inundation and anoxic conditions in lower-elevation areas of floodplains, increasing plant mortality[10]. For example, flow regulation by the Balbina Dam on the Uatumã River, Brazil, together with the effects of El Niño events, increased the inundation period of floodplain and contributed to forest mortality in 12% of the downstream floodplain areas[116]. A further 18% of these floodplain forests is also threatened by habitat alteration caused by the HP (consistent inundation owing to water release from the dam) and is probably undergoing slow mortality[116].

Flow regulation of HPs reduce natural hydrological disturbances and water availability in floodplain zones of higher elevation owing to lowered peak discharge downstream of dams. Consequently, upland terrestrial vegetation can encroach on floodplains and replace native floodplain vegetation[91,115]. In addition, flow regulation disrupts the synchrony between seasonal flood patterns and plant phenology, affecting species recruitment and causing shifts in floodplain vegetation composition[117,118]. Many floodplain plants rely on fish for seed

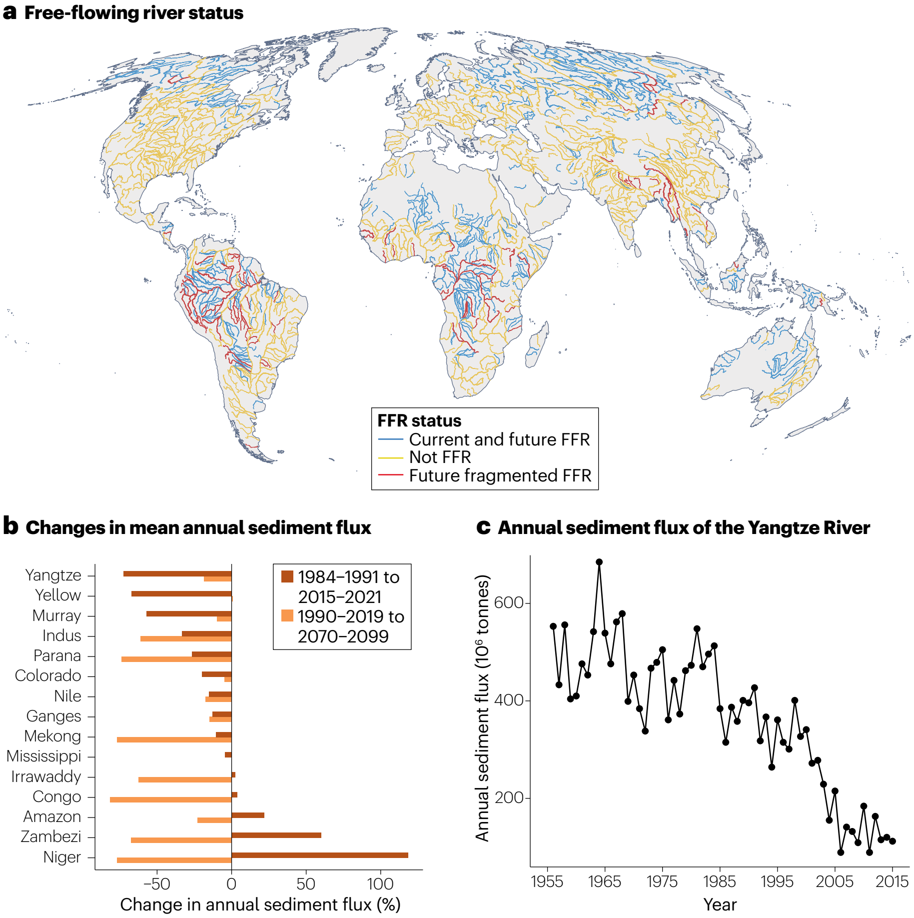


Fig. 4 | Cumulative impacts of hydropower plants on river connectivity and sediment flux. a, Free-flowing river (FFR) status of rivers longer than 500 km (refs. 16,177,200). The current estimation considers the impacts of infrastructure, including roads, urbanization and existing dams, and the future scenario includes additional impacts of proposed hydropower dams. **b**, Estimated change in mean annual sediment flux in 15 large rivers owing to observed human activities[13] (red) and proposed hydropower dams[136] (orange); estimated changes before 2021 are the difference between the periods of 2015–2021 and 1984–1991, and projected changes are the difference between the periods of 2070–2099 and 1990–2019. **c**, Annual sediment flux[13] of the Yangtze River, China, from 1956 to 2015. Hydropower impacts can accumulate along river network, leading to the loss of river connectivity and reduced sediment flux to river deltas.

dispersal[119]. Thus, altered flood pulses owing to flow regulation of HPs change the timing and spatial extent of fish migration between river channel and floodplain and further impede seed dispersal and recruitment of floodplain plants[115].

Although hydropower effects on semi-aquatic animals inhabiting floodplains are currently poorly understood[20], HPs are recognized to cause alteration of the extent and quality of semi-aquatic habitats. According to the IUCN Red List assessments, dams are considered a threat to 909 semi-aquatic vertebrate species, including mammals, waterbirds, amphibians and turtles. Hydropower operation reduces fluxes of water, sediment and floating materials and their subsequent redistribution or deposition in floodplains[120,121]. These changes negatively impact vital habitats for semi-aquatic animals, such as ponds, aquatic vegetation, vegetated islands and large wood deposits[122–124]. For example, flow regulation of the Three Gorges Dam, alongside climate variability and human water consumption, contributed to changes in the areas of the Poyang and Dongting lakes in the Lower Yangtze Basin[125,126]. The influence of flow regulation was particularly evident in autumn (Fig. 3f) and caused the dry season to arrive 15–25 days earlier in these lakes[126]. Consequently, wetland vegetation in both lakes experienced a major shift[127], leading to a mismatch between the arrival of migratory herbivorous waterbirds and food availability. For example, the growth of sedges (*Carex* spp.) was accelerated by early exposure to the recessional zone, with these sedges often being too tall to be exploited by the migratory geese when they arrive[128]. Connections between the river channel and floodplains are highly influenced by periodical flood events, and regulated dynamics of flow and sediment in downstream floodplains can cause rapid habitat degradation for aquatic and semi-aquatic species. In addition, HPs also lead to the progressive disappearance of some important habitats such as sand bars and threaten the long-term survival of species that depend on these habitats, reflecting the importance of monitoring the cumulative impacts of HPs.

Cumulative impacts of HPs

In many river basins, particularly large ones, hundreds of HPs have been constructed or are planned[5,129], leading to loss of free-flowing rivers (Fig. 4a). The direct and indirect impacts of individual HPs on riverine species can accumulate over space and time. Greater habitat fragmentation is a prominent direct impact of multiple HP installations and is particularly problematic for migratory fish[130,131]. Generally, the cumulative effects of how HPs influence flow, temperature and sediment regimes and, ultimately, biodiversity varies between the size and operate mode of different HPs.

Cascade HPs tend to increase turbine-associated mortality or severe injury of fish, which is already high for individual HPs at 22% (an average number based on assessments at 122 locations worldwide[9]). The cumulative effects of flow regulation and thermal alteration by cascading dams can affect the development and reproduction of riverine species in downstream sections of river networks[132]. For example, when all constructed and proposed HPs in the upper Yangtze Basin are operational, it is estimated that the occurrence of suitable spawning water temperature for Chinese sturgeon and four major domestic carp species would be delayed by 22 and 34 days, respectively, shortening their reproductive window[133].

The presence of multiple barriers along the migratory pathways of fish also sharply reduces their chances of reaching spawning grounds. For example, although the success rate of fish passing individual obstacles, including dams, fishways and lifts, ranged from 63% to 100% in the River Conon system, UK, only 18% of tagged Atlantic salmon (*Salmo salar*) eventually overcame all six obstacles to reach their spawning grounds[134]. Hence, local populations of migratory fish above cascading dams are either converted to residency or, more probably, extirpated[23]. Cascading dams also restrict species dispersal between isolated river sections, which increases the chance of inbreeding and a reduction in genetic diversity in both aquatic[135] and semi-aquatic animals[77]. Isolated populations with reduced genetic diversity have higher tendency to be affected by recessive traits and subject to local extinction[23,76].

The potential cumulative impacts of HPs in tropical regions are of particular concern as those ecosystems are rich in biodiversity but have been experiencing rapid hydropower development[7,121]. For example, 334 hydropower plants have been planned or are under construction in the Amazon and 98 in the Mekong River basin[5,7]. As a result, the mean range connectivity index of lotic fish that spend their whole life in freshwater ecosystems is projected to decline by 30% in the Amazon and 20% in the Mekong, owing to cumulative impacts the proposed dams on habitat fragmentation[130]. In the Amazon, at least 86 fish species conduct longitudinal and 137 fish species conduct lateral migration, using seasonal and predictable hydrological regimes as environmental cues[110]. Fragmentation and flow regulation by multiple dam installations could, therefore, block their migratory corridors and/or alter environmental cues, disrupting their life cycle. Sediment fluxes are projected to decline by 23% in the Amazon and by 77% in the Mekong basins between 1990–2019 and 2070–2099 (ref. 136) (Fig. 4b). The altered flow and sediment regimes will modify river–floodplain exchanges of water and sediment, profoundly affecting riparian plants and animals reliant on downstream floodplains and deltas for reproduction, foraging and refuge[119,121,137,138].

Alteration of annual and multi-annual flow periodicity can accumulate along river networks[14,139], which can have wider impacts than just those on species migration. HPs make flow regimes unpredictable for species at long timescales and lead to shifted community composition, as some native riverine species may not survive unexpected flood or drought events owing to their life-history strategies being shaped by natural flow periodicity[140,141]. For example, river sections downstream of dams typically have more equilibrium strategists and fewer opportunistic strategists compared to fish communities in free-flowing counterpart rivers[142]. Therefore, changes in flow regime owing to HPs can profoundly affect river community composition over time.

Similarly, the cumulative impacts of cascade SHPs, which are commonly installed in mountain regions where rivers are typically characterized by steep slopes and fast flow, can profoundly impact species living in mountain rivers, as they are highly adapted to fast flow and highly seasonal environment[8,23]. However, the impacts of SHPs have received less attention than those of LHPs and are often overlooked in environmental management and policy[2]. Water released from SHPs can be diverted directly to another SHP, thereby extending the length of residual-flow reaches and exacerbating dewatering impacts on riverine species[8,143]. Because SHPs account for over 90% of the global hydropower installation (SHP:LHP = 11:1) (ref. 2), their cumulative impacts on river ecosystems are probably comparable with or even greater than those of LHPs. The adverse effects of the cumulative biophysical impacts per unit of power generated in the Upper Salween River Basin, China, were compared for SHPs and LHPs. The findings have suggested that the impacts of SHPs were at least ten times greater than those of LHPs in terms of length of inundated or residual-flow reaches, habitat diversity, river connectivity at sub-catchment scale, and flow modification[144]. When considering both LHPs and SHPs, the average potential range loss (8.3%) of 1,497 lotic fish in Brazil is more than doubled in comparison to the estimated range loss (3.7%) due to LHPs alone[145].

Cumulative upstream sediment retention together with flow regulation can contribute to coastal erosion, salinity intrusion and reduced biodiversity in river deltas[105]. Sediment retention by dams is the main driver of widely observed declines in sediment fluxes of rivers located in the global hydrologic north (defined as north of ~20° N), reducing the sediment inputs to river deltas[13] (Fig. 4b). For example, the annual sediment flux to the Yangtze Delta declined by 79.7% between 1956 and 2015 (ref. 13) (Fig. 4c). Owing to increasing anthropogenic impacts, including proposed HPs, in the tropics, the projected declines in sediment flux between 1990–2019 and 2070–2099 are evident in rivers such as the Amazon (−23%) and Mekong (−77%)[136] (Fig. 4b). The reduction of fluvial sediment inputs might decrease the stability of sandy beaches in coastal areas, leading to retreat of coastal shorelines[146]. In addition, altered fluvial inputs of freshwater and sediment to the coastal regions caused by HPs, together with sea level rise, can increase the risk of salinity intrusion into the river estuaries[147]. HP-induced shoreline retreat and alteration in salinity of river estuaries can adversely impact species that depend on these important habitats[148]. Hence, the impacts of individual HPs can accumulate along the river network and over time, threatening the long-term survival of species living in different parts of river basin if these impacts are not mitigated by conservation and restoration actions.

Mitigating the impacts of hydropower

Various measures can be implemented at different stages of HP development to help mitigate their negative impact on biodiversity. Such measures include protecting free-flowing rivers, considering alternative renewable energy resources, strategic planning of HP locations, optimizing installation and operation of HPs, and removal of dams with high biodiversity impacts but little contribution to regional energy production[149–152].

Additional measures not directly associated with HP installation and operation, such as restoring habitats or stocking populations of targeted species, can also improve the survival and recovery of impacted riverine species (Table 1). For example, over 100 different mitigation approaches were identified across 5,130 records associated with 309 licences issued by the US Federal Energy Regulatory Commission between 1998 and 2013 (ref. 153). Among these records, 29% of measures focused on hydrology, 18% on biodiversity, 11% on fishway, 10% on habitat and 10% on water quality. The strategies and challenges in improving the management of operational HPs or HPs under construction are now discussed, highlighting the need for basin-scale strategic planning.

Restoring environmental regimes and habitats

A wide range of approaches have been developed to reduce hydropower impacts by managing the volume, timing and variation of river flow[154,155]. For example, increasing water release during dry seasons can help sustain downstream riverine habitats[156], and managed high-flow

Table 1 | Measures to mitigate the ecological impacts of existing hydropower plants

Mitigation category	Strategy	Environmental effects	Effects on riverine species	Research needs
Flow	Environmental flow releases from hydropower plants to mimic the natural flow dynamics[8,38]	Shorter hydraulic residence times; more water mixing; restored natural flow dynamics below dams	Reduced algal blooms; restored environmental cues for species; restored riparian vegetation and lateral movements of water, sediments and species	Potential of additional hydropower from environmental flow releases; optimization of flow to meet ecosystem needs in terms of coupled natural flow, thermal and sediment regimes
Water quality	Reducing hydraulic residence time; enhancing water mixing; water release from multiple depths; designs to avoid extreme levels of dissolved gas[15,17,101]	Reduced nutrient concentrations; reduced thermal stratification in reservoirs; reduced downstream changes in temperature and dissolved gas level	Reduced algal blooms; enhanced possibility for species to complete their life cycles; reduced fish mortality caused by extreme levels of dissolved gas	Synchronizing mitigation efforts to ensure that water quality conditions meet the ecological needs of riverine species in both space and time
Sediment	Sediment bypass tunnels; sediment sluicing; flushing; dredging; land-use management and sediment traps to reduce upstream sediment inputs[12,166]	Reduced sediment and nutrients in reservoirs; increased sediment and nutrient availability in downstream areas; erosion control of downstream channel; maintenance of floodplain habitats	Reduced algal blooms in reservoirs; improved substrate structure for benthic organisms and fish spawning in downstream channels; maintenance of habitats for semi-aquatic species	Coordinating actions at the basin level to improve sediment transport to river deltas and avoid upstream–downstream conflicts; including the influence of land-use change in hydropower plant sediment management
River morphology	Restoring habitat structure of river channels, riverbeds and riparian areas[153]	Increased habitat heterogeneity in river channels and riparian areas; enhanced habitat connectivity	Increased habitat availability of species; enhanced trophic complexity and species dispersal	Integrating habitat restoration related to hydropower plant impacts with land-use and protected area management
Species movement	Installing effective movement passages; performing catch–transport–release; improving turbine design[69,168,169,194]	Potential contribution to flow release and sediment transport	Improved upstream–downstream movement of some species; reduced injuries and mortality caused by dams and turbines	Improving passage and turbine design to support movement and reduce species mortality during downstream movement; determining the evolutionary effects of selective movement passages
Species population	Captive holding facilities and conservation hatcheries to propagate and release species of concern into the wild[76,165]	Abiotic environment is usually not targeted	Enhanced wild population size; preserved genetic diversity and variation in life history traits through conservation programmes of wild-caught eggs or larvae	Good management practices to enhance survival, genetic diversity and natural reproduction of stocked populations; developing robust protocols to mitigate risks of bringing fish into captivity

pulses in regulated rivers can provide cues for fish migration, spawning and juvenile drift[87]. Reducing the number of hydropeaking events and adjusting the timing of events to take account of species life histories can lower mortality associated with rapid water-level fluctuations, such as fish strandings[157] or the eggs of aquatic insects in nearshore habitats being exposed to dry conditions[97]. Managing downstream water levels through flow regulation in this way can strongly reduce the negative impacts of changes in flow regime owing to HPs on aquatic species.

Environmental flows have also been managed to support riparian vegetation by promoting germination and establishment of native riparian plants[158], to recharge alluvial aquifers to support existing vegetation[159], and to wash salts from riverbanks to favour mesic native plants over salt-tolerant invasive plants[160]. There has been an increasing focus on holistic approaches to design environmental flows, rather than a focus on improving individual organism performance, wherein the goal is to retain specific process-based components of the hydrograph, or functional flows, to support ecosystem processes such as food-web dynamics and nutrient cycling in riverine ecosystems[38,91,107]. Thus, environmental flow releases can benefit downstream ecosystems impacted by HPs and can help improve river management practices[161,162].

Optimized operations could improve water quality in reservoirs and downstream channels, which can reduce the chance of harmful algal blooms forming. Regulating water release can create hydrodynamic conditions that inhibit excessive growth of phytoplankton in reservoirs, for instance by reducing hydraulic residence time and enhancing flow velocity and water mixing during periods when algal blooms tend to occur[163]. Selective withdrawal using multi-level intake structures can also help avoid algal blooms. For instance, in the long term, drawing cold hypolimnetic water could help prevent algal blooms by reducing internal nutrient loads and altering thermal stratification in reservoirs, and direct flushing out of warm water and phytoplankton from the surface layer could be used as an emergency measure[39].

Selective withdrawal provides the flexibility to mimic seasonal thermal regimes of natural flows and help mitigate thermal alteration in downstream channels. For example, the Flaming Gorge Dam in Utah, USA, used this approach to increase summer water temperature for native fish species that prefer warm water, and selective withdraw also provides opportunities to decrease summer water temperatures to mitigate the effects of climate warming and benefit native cold-water fishes in California such as Chinook salmon (*Oncorhynchus tshawytscha*)[15,164]. In alpine systems, thermopeaking owing to reservoir releases reduced water temperatures during heatwaves and provided suitable thermal habitats for brown trout[89]. Selective withdrawal systems show the potential of dam operations to be modified to better meet the water temperature preferences for riverine species and help provide some refuge to climate change-induced warming.

Various solutions have been proposed to avoid gas supersaturation or low dissolved oxygen concentration in released water. The former might cause gas bubble disease in fish and the latter can directly lead to increased fish mortality. Solutions include installing flow deflectors, baffle blocks and stepped cascades to minimize bubble transport to downstream water and help avoid gas supersaturation[101]. Dissolved oxygen concentrations can be raised using air injection facilities and aerating turbines to help increase water oxygenation and avoid downstream hypoxia[165].

Moving sediment that has accumulated above dams to downstream sections is more challenging that moving water retained behind dams; however, various techniques have been developed to reduce sediment accumulation in reservoirs. Sediment can be diverted around dams through a bypass, which involves high flows being discharged during flood events to reduce sediment trapping. Turbidity currents with high sediment concentrations can be vented through low-level outlets or accumulated sediments can be remobilized and flushed downstream[166]. Mechanical dredging can also be implemented to remove sediment from the dam reservoir and relocate it downstream. Many of these management techniques can be combined with environmental flow releases designed to reduce downstream impacts on riverine species. For example, a series of controlled floods released from Glen Canyon Dam, USA, simultaneously restored natural flow dynamics and mobilized sediment, creating habitats for endangered native fishes in the Colorado River[167].

Improving species movements

Various types of fishways have been developed to facilitate species movements past HPs[30,168]. These facilities can help fish individuals overcome dams during their upstream movements and reduce entrainment and mortality at hydropower turbines when moving downstream[169]. However, most fishways are predominantly designed and installed for migratory fish species in temperate regions, particularly salmonids, and their efficiency varies tremendously among species and locations, often being low for non-salmonids[170]. For example, pool-weir fishways have an attraction efficiency of 79% and a passage efficiency of 83% for salmonids, which is higher than other fishways based on a global assessment of 76 fishways; however, the efficacy of pool-weir fishway with non-salmonids is much lower with only 38% attraction efficiency and 35% passage efficiency[70]. For non-salmonids, Denil fishways have the highest attraction efficiency (65%) and passage efficiency (64%). Thus, there is not yet a single fishway design that appears to provide good attraction and passage efficiency across a range of fish species and that could become a standardized part of HP design.

The expansion of hydropower has been widely occurring in subtropical and tropical regions[5], where a diverse range of non-salmonid fish, such as catfishes, carps and characins, migrate long distances to complete their life cycles[7]. Without careful consideration of the characteristics of targeted species and the local environment context, some fishways could function as ecological traps and lead to negative outcomes[171]. Beyond fish, a host of other aquatic animals such as river dolphins and turtles also move long distances along river networks and require passage through dams[172]. Together, there is a pressing need to develop effective facilities to assist movement for different types of riverine species[171,173,174].

Strategic basin-scale planning of dam locations

HP planning and construction is usually considered on a project-by-project basis, without taking account of the wider basin connectivity, which can lead to profound cumulative environmental impacts. For example, in the 3S (Se Kong, Se San and Sre Pok) subbasin of the lower Mekong Basin, project-by-project development has resulted in only 54% of the hydropower potential being harnessed, but it has also resulted in over 90% of sand loads being trapped[175]. Strategic planning at the basin scale could have achieved 68% of hydropower potential with only 21% of the sand load being trapped[175]. Uncoordinated HP developments also have catastrophic impacts on riverine biodiversity, fisheries and food supply[176]. It is challenging and costly to retrospectively implement mitigation measures after HPs have been installed[149,177], and so it is critical that the basin scale context should be considered throughout planning and implementation of HP developments.

Early assessment of hydropower impacts and strategic planning of dam locations at a basin scale, or even regional scale, can help achieve power generation goals with fewer HPs and, thus, minimize negative impacts on riverine biodiversity[151,178]. For example, in Brazil, optimizing the location of future dams was estimated to potentially halve the total number of HPs required to meet projected national energy demand, substantially reducing the loss of habitat connectivity essential for migratory fishes[179]. Similarly, multi-objective optimization was used in the Amazon Basin to identify portfolios comprising different configurations of HPs that simultaneously meet energy production goals and minimize impacts on fish biodiversity and other components of riverine ecosystems, such as hydrological connectivity, flow regime, sediment transport and greenhouse gas emissions[180]. It is also important to consider the uncertainties and the effects of climate change on future flow regimes and species distributions when assessing potential HP developments to help avoid dam locations that tend to have less hydropower potential and more negative impacts on biodiversity in the future[178,181]. Although various mitigation measures can help reduce specific hydropower impacts, it is challenging to synchronize hydropower mitigation efforts to simultaneously meet the different requirements of species in terms of flow dynamics, water temperature and chemistry, and river morphology. Hence, these challenges should be carefully considered and addressed when planning for HPs to comprehensively assess the trade-offs between economic benefits and environmental impacts associated with hydropower development.

Summary and future perspectives

Global hydropower development has fundamentally changed riverine ecosystems from headwaters to deltas, strongly affecting numerous aquatic and semi-aquatic species. Hydropower dams directly impede upstream–downstream movements of species, preventing migratory species from completing their life cycle[30] and leading to increased injury or mortality when individuals pass through hydropower infrastructure[9]. Impoundment fundamentally alters environmental conditions upstream of the dam and causes declines in native species that are morphologically and ecologically adapted to lotic fluvial habitats[8,20,31]. In downstream channels and floodplains, species with life cycles adapted to natural hydrological dynamics in rivers are vulnerable to hydropower-induced alterations in flow, thermal and sediment regimes[30,119,182], particularly during key periods in their life cycles, such as during breeding and recruitment. Impacts posed by individual HPs can accumulate spatially and temporally across river networks and adjunct systems, leading to declines in taxonomic, functional and genetic diversity of native riverine species[8,49,76,85].

Considering the growing demand for energy and ongoing transition towards renewable energy[183], it is improbable that hydropower development will stop in the near future[4]. Given the profound impacts of HPs on riverine species, it is crucial to balance energy generation with sustained biodiversity and associated ecosystem services. We recommend applying the STREAM framework to help achieve the goal, which consists of Systematic planning for renewable energy infrastructure, Tracking hydropower impacts through long-term monitoring and research schemes, Responsive adaptive management strategies, Elimination of hydropower infrastructure where possible and necessary, Assessment of socioecological trade-offs, and Multi-actor decision-making.

Systematic planning for renewable energy infrastructure should be conducted at basin or regional scale to avoid loss of existing free-flowing rivers and to minimize cumulative negative ecological impacts on riverine ecosystems. The multifaceted and cumulative impacts of HPs and the challenges for mitigating these impacts highlight the need for strategic hydropower planning. There is a growing body of evidence of the advantages of strategic planning in reducing adverse ecological impacts of HPs[175,176,178,180]. In addition, strategic planning for sustainable energy production needs to systematically optimize dam locations, consider other available renewable energy sources, and account for the potential impacts of climate change[152,177]. For example, combining hydropower and intermittent renewable energy from solar and wind power holds the potential to minimize threats to riverine biodiversity and also meet energy production goals and peak energy demand[178,184].

Tracking hydropower impacts should be achieved through long-term monitoring and research schemes, with the operators of individual HPs being responsible for the associated costs. Baseline information before dam construction and regular monitoring data on abiotic and biotic elements of river ecosystems can improve understanding of the dependency of different species and functional groups on the four dimensions of river connectivity. Such coordinated efforts between research and industry will further help tackle the challenges in mitigating ecological impacts of HPs (Table 1). For example, information on the timing and habitat requirements of key life-cycle events of riverine species such as spawning, nesting and seedling seasons can help improve hydropower designs and operations to meet their ecological needs[38,97,185]. Knowledge of the sensitivity of different functional traits to hydropower-induced alterations can also offer mechanistic insights into how riverine species respond to hydropower impacts and enhance the transferability of research findings across geographic boundaries. Long-term monitoring of different HPs and components of river ecosystems across each basin should be integrated into a harmonized database to shed light on the cumulative impacts of HPs and improve management strategies at the basin scale (Table 1).

Responsive adaptive management strategies should be established for individual HPs and coordinated at the basin scale. These strategies will allow a continually updated operation plan based on long-term monitoring data to improve mitigation strategies over the lifespan of HPs. Measures for mitigating certain aspects of hydropower impacts sometimes trigger adverse effects on non-targeted species. For instance, releasing water from a lower outlet could help control algal blooms in reservoirs[163], enhance sediment transport[166] and avoid gas supersaturation in downstream channel[101]. Such an operation will profoundly modify downstream thermal regimes and adversely affect native species, such as fish and aquatic insects[15]. In addition, further construction of new HPs in upstream sections would require the operation of downstream existing HPs to be adjusted if a joint plan to minimize ecological impacts of cascade HPs were to be successful. Hence, it is important to implement a responsive adaptive strategy to meet the ecosystem requirements of riverine species that depend on coupled natural flow, thermal and sediment regimes[186].

Elimination of existing dams needs to be considered as a key measure to restore riverine ecosystems. Although there is an increasing trend in dam removal, particularly in North America and Europe[187,188], several key challenges remain. Such challenges include the potential risk of releasing large amounts of water, sediment and associated nutrients and pollutants to downstream sections[17], the uncertain ecological effects of dam removal, such as invasive species spread[189], and growing energy demands[4]. Subsidies associated with the renewable energy transition also represent an obstacle for removing inefficient and environmentally detrimental dams[190]. In addition, depending on the age of the dam and its potential co-use, associated infrastructure has been developed and land use could have changed over the years, which means that ecosystem recovery might be limited by other stressors[191]. Nevertheless, dam removal might still be the most direct and effective approach to restore different dimensions of river connectivity and eliminate hydropower impacts on biodiversity[76,151]. Therefore, decommissioning existing HPs should be considered a priority, wherein the negative ecological impacts of HPs outweigh their contribution to energy generation.

Assessment of socioecological trade-offs should be incorporated into the planning and management of HPs throughout their lifespan. It is crucial to consider the multifaceted interactions between hydropower impacts and other activities in the basin, such as water extraction, fisheries and management of protected areas[151]. For example, at least 278 existing LHPs and over 500 HPs that are under construction or proposed are located in protected areas[192]. Without carefully assessing potential trade-offs, HP installation and operation can jeopardize the effectiveness of protection and restoration measures that aim to facilitate the recovery of riverine biodiversity[193] and additionally cause catastrophic consequences on river fisheries, which provide important food sources and are economically valuable in many regions, including the Global South[7,31,176]. Hence, socioecological trade-offs associated with HPs must be thoroughly investigated in early planning phases and reassessed throughout their lifespan.

Multi-actor decision-making should be initiated to support sustainable hydropower development. HPs impact ecosystems and people, thus, minimizing the ecological impacts of hydropower is just one key element of many in the sustainable development[1]. For instance, a sustainable energy policy should focus on reducing consumption rather than on increasing production to avoid excessively increasing environmental pressures on rivers through building new HPs. Hydropower developments often only benefit certain groups of people and adversely impact the livelihoods of numerous local people. Open dialogue with local people can help optimize HP planning and management. Local knowledge of key habitats of species and timing of certain life-cycle events could better inform mitigation measures during the development and design phase of HPs. Decision-making should incorporate the interests of various actors, including across the natural and social sciences, engineering, basin management, government agencies and civil society. Collaboration at this scale supports the development of holistic management plans and offers opportunities to create synergies among different conservation and management actions across basins[24,151,177], which will help safeguard riverine biodiversity, provide energy to the society, and support livelihoods and well-being of people.

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