Freshwater megafauna shape ecosystems and facilitate restoration

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ABSTRACT

Freshwater megafauna, such as sturgeons, giant catfishes, river dolphins, hippopotami, crocodylians, large turtles, and giant salamanders, have experienced severe population declines and range contractions worldwide. Although there is an increasing number of studies investigating the causes of megafauna losses in fresh waters, little attention has been paid to synthesising the impacts of megafauna on the abiotic environment and other organisms in freshwater ecosystems, and hence the consequences of losing these species. This limited understanding may impede the development of policies and actions for their conservation and restoration. In this review, we synthesise how megafauna shape ecological processes in freshwater ecosystems and discuss their potential for enhancing ecosystem restoration. Through activities such as movement, burrowing, and dam and nest building, megafauna have a profound influence on the extent of water bodies, flow dynamics, and the physical structure of shorelines and substrata, increasing habitat heterogeneity. They enhance nutrient cycling within fresh waters, and cross-ecosystem flows of material, through foraging and reproduction activities. Freshwater megafauna are highly connected to other freshwater organisms *via* direct consumption of species at different trophic levels, indirect trophic cascades, and through their influence on habitat structure. The literature documenting the ecological impacts of freshwater megafauna is not evenly distributed among species, regions, and types of ecological impacts, with a lack of quantitative evidence for large fish, crocodylians, and turtles in the Global South and their impacts on nutrient flows and food-web structure. In addition, population decline, range contraction, and the loss of large individuals have reduced the extent and magnitude of megafaunal impacts in freshwater ecosystems, rendering *a posteriori* evaluation more difficult. We propose that reinstating freshwater megafauna populations holds the potential for restoring key ecological processes such as disturbances, trophic cascades, and species dispersal, which will, in turn, promote overall biodiversity and enhance nature's contributions to people. Challenges for restoration actions include the shifting baseline syndrome, potential human–megafauna competition for habitats and resources, damage to property, and risk to human life. The current lack of historical baselines for natural distributions and population sizes of freshwater megafauna, their life history, trophic interactions with other freshwater species, and interactions with humans necessitates further investigation. Addressing these knowledge gaps will improve our understanding of the ecological roles of freshwater megafauna and support their full potential for facilitating the development of effective conservation and restoration strategies to achieve the coexistence of humans and megafauna.

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Key words: body size, conservation, ecosystem function, dispersal, keystone species, large animal, nature's contributions to people, reintroduction, top predator, trophic complexity.

CONTENTS

I. INTRODUCTION

Megafauna were once highly diverse and abundant on Earth (Estes *et al.*, 2016; He *et al.*, 2019; Malhi *et al.*, 2016). However, many megafauna species have become extinct due to overhunting and habitat loss (Stuart, 2015). For example, in the Late Pleistocene, there were at least 50 mammalian megaherbivores on land with a body mass of over 1000 kg (Malhi *et al.*, 2016). Only 10 of these still remain (i.e. giraffe, hippopotamus, elephants, and rhinoceroses), with strongly reduced distributions and population density (Faurby & Svenning, 2015; Owen-Smith, 1988). As a result, the biosphere has undergone major trophic downgrading (Dirzo *et al.*, 2014; Estes *et al.*, 2011).

Compared to the massive megafauna extinction in terrestrial ecosystems in the Late Pleistocene and Early Holocene, megafauna in aquatic systems were probably less affected until a few hundred years ago, when intensive commercial harvesting and large-scale habitat modification began to alter marine and freshwater ecosystems in major ways (Estes *et al.*, 2016; He *et al.*, 2018). Intensive exploitation has contributed to the extinctions of several marine megafauna species (Estes *et al.*, 2016; IUCN, 2022), including the Caribbean monk seal (*Neomonachus tropicalis*), Japanese sea lion (*Zalophus japonicas*), and Steller's sea cow (*Hydrodamalis gigas*). Similarly, in freshwater ecosystems overexploitation and

habitat destruction (e.g. dam construction, wetland conversion) has contributed to the extinction of Baiji (*Lipotes vexillifer*), Schomburgk's deer (*Rucervus schomburgki*), and Chinese paddlefish (*Psephurus gladius*) in the 20th and 21st century (Turvey *et al.*, 2010b; Zhang *et al.*, 2020). Sharp population declines of various freshwater megafauna have been documented across the world (He *et al.*, 2019; Winemiller, Humphries & Pusey, 2015), highlighting that trophic downgrading is ongoing and freshwater ecosystems are not being spared.

While the decline of megafauna and its causes are well documented (Barnosky *et al.*, 2004; Ripple *et al.*, 2019), less scientific attention has been paid to their ecological roles and consequences of their decline (Malhi *et al.*, 2016; Estes *et al.*, 2016; Hammerschlag *et al.*, 2019). By virtue of their size, megafauna can modify the physical structure of the ecosystems they inhabit (Naiman & Rogers, 1997; Malhi *et al.*, 2016; Larsen, Larsen & Lane, 2021; Owen-Smith, 1988). For example, elephants break trees and create open space in forests, transforming forests into grasslands (Owen-Smith, 1988). Beavers fell trees and build dams, creating complex mosaics of streams, wetlands, and glades (Larsen *et al.*, 2021). Big cats, bears, otters, crocodylians, dolphins, and large sharks are apex predators and influence local and regional trophic dynamics from the top of the food web (Hammerschlag *et al.*, 2019; Ripple *et al.*, 2014).

Megafauna are often especially mobile and typically move between habitats while consuming large amounts of resources, thus functioning as important links among ecosystems and contributing to flows of nutrients and energy (Bakker *et al.*, 2016; Doughty *et al.*, 2016; Subalusky *et al.*, 2015). Therefore, megafauna profoundly shape ecological processes such as biogeochemical cycles, carbon sequestration, wildfire regimes, and disease transmission, and where megafauna are lost or their populations are severely reduced, major ecological change can be expected (Estes *et al.*, 2011; Doughty *et al.*, 2016; Malhi *et al.*, 2022; Doughty *et al.*, 2020).

Several reviews have emphasised the influence of megafauna on the structure and functioning of ecosystems (Malhi *et al.*, 2016; Estes *et al.*, 2016; Bakker *et al.*, 2016; Hammerschlag *et al.*, 2019). These reviews have mainly focused on megafauna in terrestrial (e.g. Malhi *et al.*, 2016) or marine (e.g. Estes *et al.*, 2016) ecosystems. The few studies that have considered freshwater megafauna included them as examples of large herbivores (Bakker *et al.*, 2016) or apex predators (Hammerschlag *et al.*, 2019) in aquatic ecosystems. Overall, the ecological impacts of megafauna in fresh waters remain largely unexplored, which is problematic considering that restoring megafauna could be a powerful tool for restoring ecological functions and supporting resilient and self-sustaining ecosystems (Lorimer *et al.*, 2015; Svenning *et al.*, 2016). The restoration of freshwater systems should be a priority for several reasons. Freshwater ecosystems provide essential contributions to human well-being, such as water and food supplies, flood regulation, and carbon sequestration (Lynch *et al.*, 2023). Fresh waters are disproportionately affected by multiple and often intense anthropogenic threats, and have experienced severe biodiversity decline (He *et al.*, 2019; Carrizo *et al.*, 2017). Despite the implementation of restoration efforts in many regions (e.g. Europe), recovery trends have come to a halt and ecological conditions in fresh waters remain poor (Haase *et al.*, 2023). Moreover, freshwater ecosystems are often underrepresented in conservation and restoration actions, receiving insufficient protection to safeguard their biodiversity and to meet the targets of the Kunming–Montreal Global Biodiversity Framework (Carrizo *et al.*, 2017; Flitcroft *et al.*, 2023; He *et al.*, 2021a; Mammola *et al.*, 2020).

In addition to their underappreciated ecological significance, freshwater megafauna have also received less conservation effort compared to their counterparts in terrestrial and marine ecosystems (He *et al.*, 2021a). Freshwater megafauna are not less threatened than marine and terrestrial species; the bias most likely reflects the overall underrepresentation of fresh waters in conservation science and practice (Carrizo *et al.*, 2017; He *et al.*, 2021a; Mammola *et al.*, 2020). Indeed, 57% of all assessed freshwater megafauna are evaluated as Vulnerable, Endangered, or Critically Endangered in the International Union for Conservation of Nature *Red List of Threatened Species* (hereinafter referred to as IUCN *Red List*; IUCN, 2022). Declines in their population abundance, distributional range, and functional diversity have been documented or projected (Griffith *et al.*, 2023; He *et al.*, 2019). Thus,

bold conservation and restoration actions are needed to halt their decline and support their recovery. Freshwater megafauna can serve as flagship and umbrella species, and hence conservation and restoration actions that target them are likely to benefit a broad range of freshwater species (Carrizo *et al.*, 2017; Campos-Silva *et al.*, 2018; Kalinkat *et al.*, 2017).

Herein, we provide a global synthesis of the ecological roles of freshwater megafauna (e.g. sturgeons, catfishes, river dolphins, beavers, otters, crocodylians, and turtles), covering different ecosystems (e.g. rivers, lakes, wetlands), to guide conservation actions towards these large animals. We demonstrate how megafauna shape the structure and functioning of freshwater ecosystems, with an emphasis on their impacts on hydromorphology, biogeochemical cycling, and other freshwater species (Fig. 1). We conclude with a forward-looking perspective on the opportunities that megafauna-based restoration actions may offer for conserving freshwater biodiversity and for restoring ecosystem functions and nature's contributions to people (NCP).

II. FRESHWATER MEGAFAUNA: DEFINITION AND DISTRIBUTION

The term *megafauna* has been widely used in ecology, conservation, and palaeontology (Moleón *et al.*, 2020). It has been used to refer to distinct groups of species, from marine benthic invertebrates (>*ca.* 1 cm) to large vertebrates with a threshold body mass ranging from 10 to 1000 kg (Moleón *et al.*, 2020). Here, we use a threshold of 30 kg (maximum reported body mass) to define freshwater megafauna, which includes large freshwater animals that may act as flagship or umbrella species for freshwater conservation (Carrizo *et al.*, 2017; He *et al.*, 2017). Using this 30-kg threshold, we identify a diverse group of freshwater megafauna, including 134 fishes, 47 reptiles, 33 mammals, and two amphibians (see examples in Fig. 2 and full species list in Table S1 in the online Supporting Information). We only included large animals that fully live in fresh waters (e.g. fish, river dolphins, manatees, giant salamanders) or use rivers, lakes, and wetlands as their main habitats for feeding or resting in their entire life cycle or part of it (e.g. crocodylians, turtles, hippopotamus, beavers, and tapirs). Freshwater megafauna occur in most of the world's main hydrological basins (Fig. 3), with the Amazon Basin harbouring the highest freshwater megafauna diversity (38 species), followed by the Orinoco (25), Congo (23), Mekong (22), Ganges–Brahmaputra (22), and Mississippi (21) basins.

III. INFLUENCE ON THE FRESHWATER ENVIRONMENT

(1) Hydromorphology

Megafauna play a crucial role in creating and maintaining freshwater habitats. Their physical power enables some
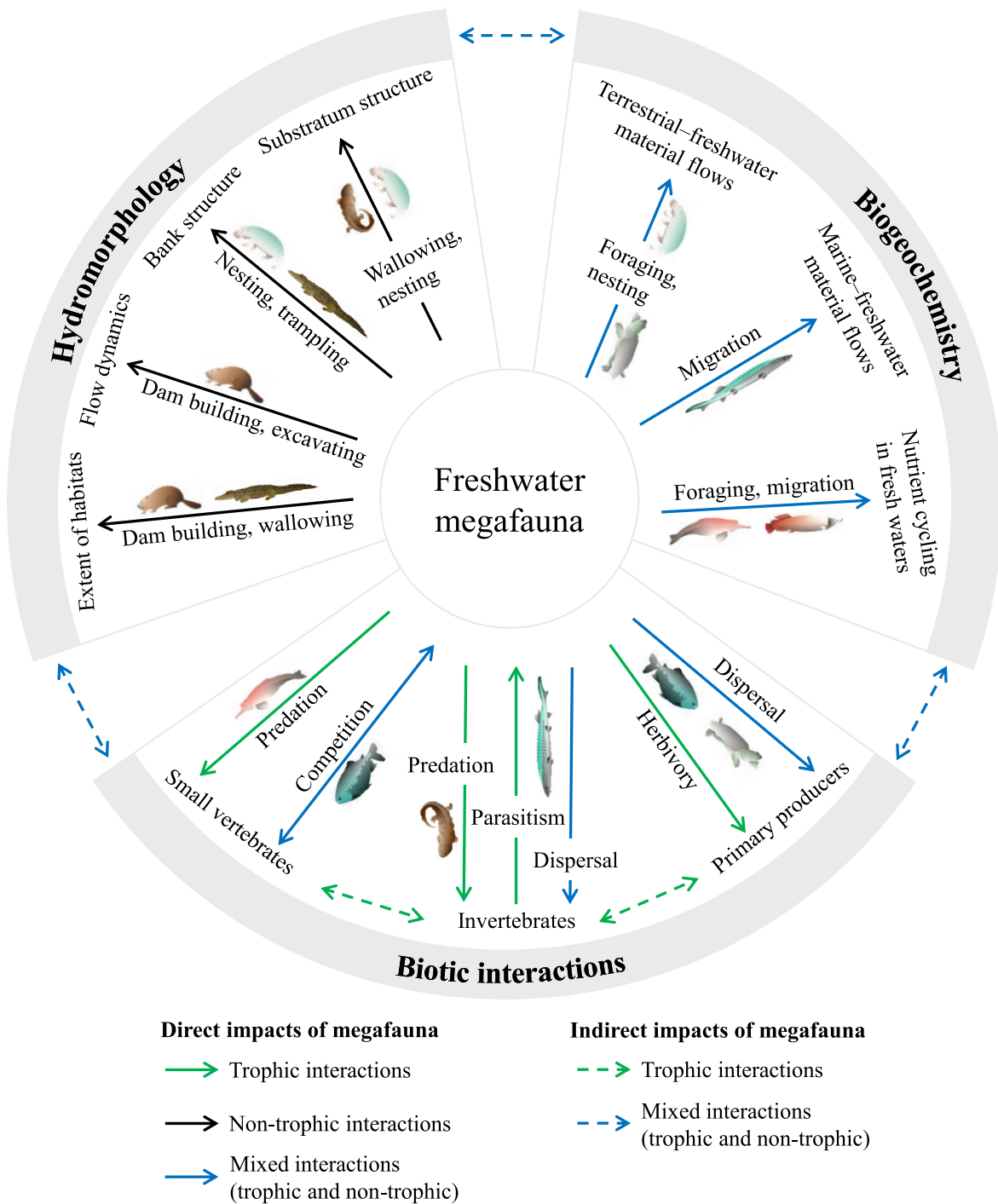
Fig. 1. Impacts of megafauna on hydromorphology, biogeochemical cycling, and other species in freshwater ecosystems.

megafauna to increase the extent of water bodies and the volume of water storage. The Eurasian beaver (*Castor fiber*) and the North American beaver (*C. canadensis*), which occur in various freshwater habitats, are prominent examples. They build dams that raise water levels and transform riparian zones and surrounding land into open-water areas and wetlands. The surface area of open water can increase by more than an order of magnitude compared to conditions prior to beaver modification (Jones *et al.*, 2020; Puttock *et al.*, 2017). Beavers also excavate canals to increase access
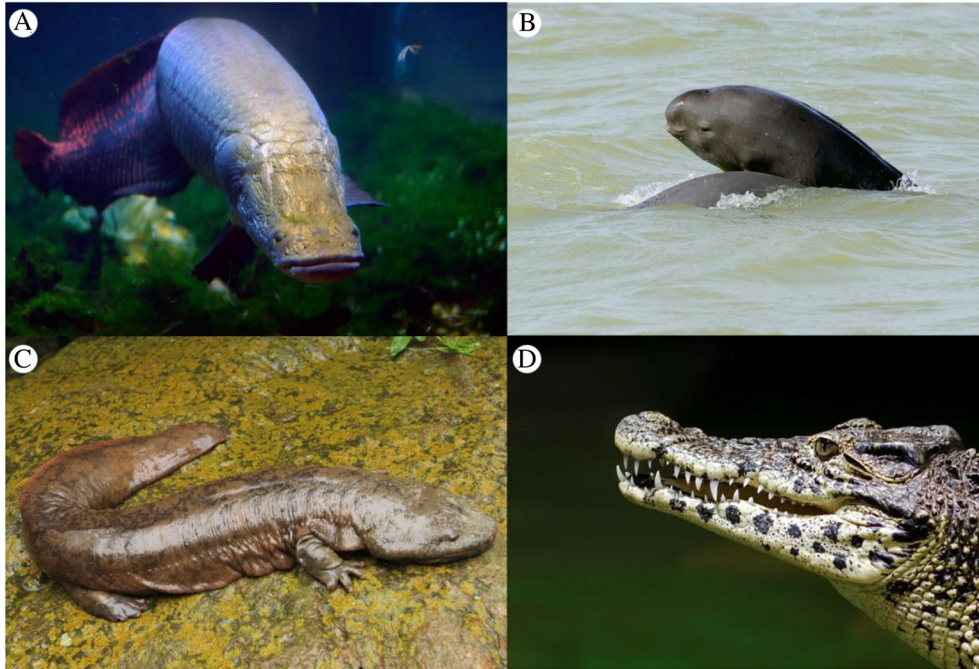
Fig. 2. Examples of freshwater megafauna: (A) a fish, arapaima (*Arapaima gigas*; photograph: Jeff Kubina); (B) a mammal, Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*; photograph: Huigong Yu); (C) an amphibian, Chinese giant salamander (*Andrias davidianus*, photograph: Theodore Papenfuss); and (D) a reptile, Cuban Crocodile (*Crocodylus rhombifer*; photograph: Mark Fox). See Appendix S1 for image sources.

Species richness
- 1–5
- 6–10
- 11–15
- 16–20
- 21–25
- 26–38
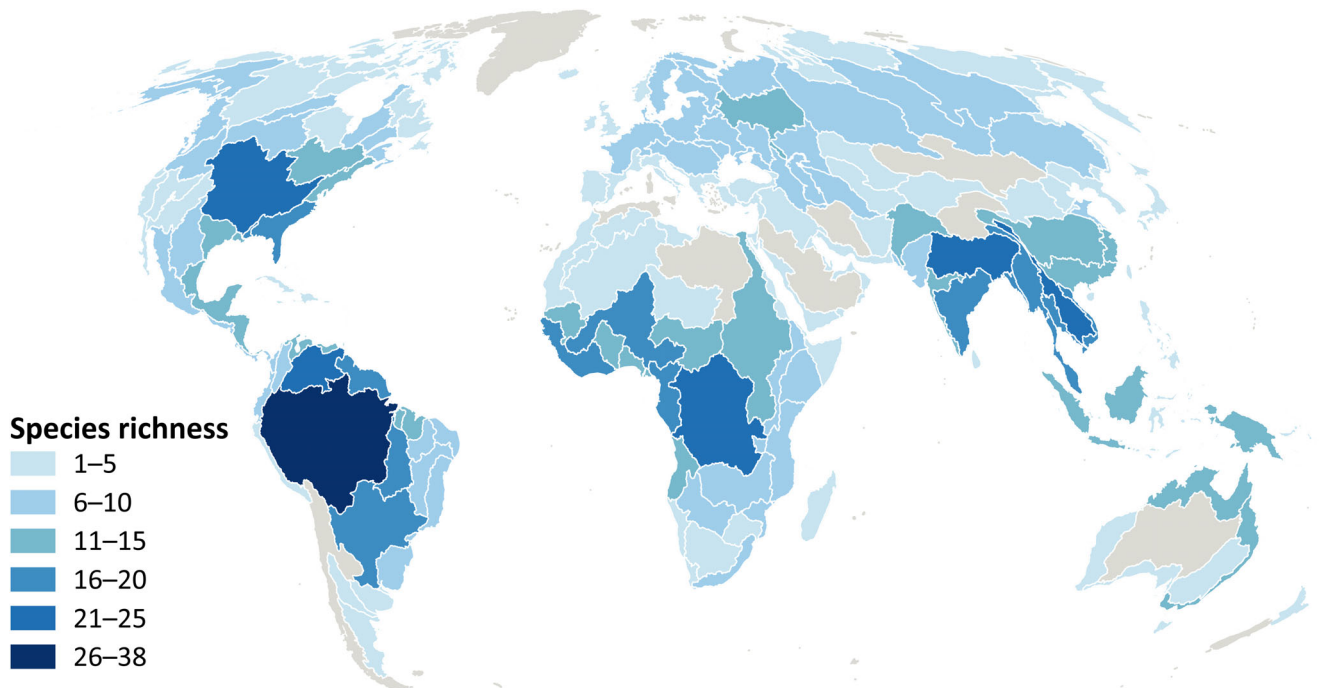
Fig. 3. Number of extant freshwater megafauna species within main river basins. Regions in grey are not inhabited by extant freshwater megafauna.

to new resources (e.g. food and building materials) and facilitate the transport of logs and branches. The length of these canals varies, with some of them exceeding 100 m (Grudzinski, Cummins & Vang, 2020). In some cases, these canals reach high densities and form a beaver-modified dendritic network. For example, over 1700 beaver canals, with a

total length of ∼40 km, were observed at the Miquelon Lake Provincial Park (Alberta, Canada), covering an area of 13 km² and increasing the wetland perimeter to five times its original length (Hood & Larson, 2015).

Other semi-aquatic megafauna, such as hippopotamus (*Hippopotamus amphibius*) and crocodylians, also create channels. Hippopotami live mainly in herds and often use the same paths (Naiman & Rogers, 1997). These paths may develop into new water channels due to flooding and repeated trampling (McCarthy, Ellery & Bloem, 1998; Voysey, de Bruyn & Davies, 2023). Hippopotami also increase the size of freshwater habitats through wallowing (Naiman & Rogers, 1997). Similar to hippopotamus, pygmy hippopotamus (*Choeropsis liberiensis*), wild water buffalos (*Bubalus arnee*), tapirs (*Tapirus* spp.), and crocodylians also wallow in river pools or puddles to cool themselves or to protect their skin from dehydration and insects (Magnusson & Taylor, 1982; Naiman & Rogers, 1997). Wallowing can increase the area and depth of natural puddles and pools over a long period. For instance, the holes created and maintained by American alligators (*Alligator mississippiensis*) in the Everglades can reach 15 m in diameter and 1 m in depth (Campbell & Mazzotti, 2004). These habitats created and maintained by large herbivores and predators are important for small aquatic and semi-aquatic species, particularly during dry seasons (Larsen *et al.*, 2021; Strickland *et al.*, 2023; Voysey *et al.*, 2023).

Beavers and hippopotami are also among the few species reported to alter flow dynamics. The impacts of beaver dams on the flow regime have been widely documented (Larsen *et al.*, 2021; Grudzinski *et al.*, 2022). During high-flow conditions, beaver dams and associated ponds form backwater channels, reducing flow velocities and flood peaks downstream of dams (Puttock *et al.*, 2021; Brazier *et al.*, 2021). During extreme flood events, dam breach or failure can occur, leading to severe downstream flooding (Westbrook, Ronnquist & Bedard-Haughn, 2020). In the dry season, the impact of beaver dams on stream flow in downstream reaches also varies among sites. Beaver dams may reduce discharge and flow velocity in downstream areas due to water storage and increased evaporation in beaver ponds, and increased hyporheic flow below dams (Grudzinski *et al.*, 2022; Meentemeyer & Butler, 1999). Conversely, the discharge below beaver dams can increase compared to conditions without beavers. Ponds and wetted areas associated with beaver dams often attenuate water and increase groundwater levels during the wet season (Majerova *et al.*, 2015; Hill & Duval, 2009). The stored water is released to downstream sections during the dry season, increasing the stream flow below dams.

Canals created by beavers and hippopotami also modify flow dynamics. For example, canals excavated by beavers may connect isolated aquatic habitats. Water is diverted from other streams to beaver ponds and canals to maintain the water level (Grudzinski *et al.*, 2020). In floodplains, hippo trails form direct water pathways that connect the main channel and distal reaches (Ellery *et al.*, 2003; Naiman & Rogers, 1997). Repeated trampling by hippopotami deepens the trails and removes aquatic vegetation, reducing

roughness and enabling efficient water movement (McCarthy *et al.*, 1998). Some trails even develop into new river channels (McCarthy *et al.*, 1998). These trails created and maintained by hippopotami may considerably influence water dispersal and local flow dynamics in floodplains (Ellery *et al.*, 2003; Mosepele *et al.*, 2009).

Many freshwater megafauna depend on both aquatic and terrestrial habitats. Their activities at the land–water interface often modify the structure of stream banks, shorelines of lakes and ponds, and riparian areas (Fig. 4). For example, hippopotami break the riverbanks when moving between foraging grounds on land and resting places in water (Naiman & Rogers, 1997). Beavers and otters excavate dens into stream banks as shelters for resting and raising their offspring (Buech, Rugg & Miller, 1989; Carter & Rosas, 1997). Burrowing activities of beavers and otters and their movement between land and water increase bank erosion. Meentemeyer *et al.* (1998) reported that beaver activities caused sediment erosion of ∼22 m³ from an 817-m-long stream bank over 5 years. Crocodylians excavate holes, burrows, and tunnels as refuges during the dry season or winter and as shelters to avoid predation (Somaweera *et al.*, 2020). The Chinese alligator (*Alligator sinensis*), for example, digs tunnels with complex structures including branches and enlarged chambers at the edge of ponds and swamps as hibernation shelters during cold winters (Thorbjarnarson & Wang, 2010). Besides excavating holes and tunnels as shelters, crocodylians and turtles also dig nests in areas close to water (Somaweera *et al.*, 2020; Moll & Moll, 2004). Depending on the local environment and abundance of crocodylians and turtles, nest density can reach high levels, strongly modifying riparian areas (Forero-Medina *et al.*, 2021). For example, nearly 500 nests were dug by Arrau turtle (*Podocnemis expansa*) within an area of less than 2000 m² along the Crixás-Açu River in Brazil (Ferreira Júnior & Castro, 2006). These semi-aquatic species reached high densities before heavy human influence (Wenger, Subalusky & Freeman, 2019). Hence, their impacts on the physical structure of stream banks, lake shores, and riparian vegetation in natural conditions were likely to have been extensive. Indeed, the geomorphological and vegetation characteristics of rivers and associated floodplains and wetlands with megafauna are often more heterogeneous than those where megafauna have been extirpated (Naiman & Rogers, 1997; Naiman, Johnston & Kelley, 1988; McCarthy *et al.*, 1998).

Sediment disturbance can be beneficial for freshwater ecosystems. Disturbance caused by animals can release nutrients, and create habitat heterogeneity which enhances biological diversity (Moore, 2006). Many megafauna species provide sediment-disturbing functionality to freshwater ecosystems, for example, hippopotami, tapirs, and wild water buffalos often wallow and plough through mud and sediment on the bottom of water bodies. When large semi-aquatic megafauna, such as marsh deer (*Blastocerus dichotomus*) and southern lechwe (*Kobus leche*), feed in floodplains and wetlands, their trampling imposes strong disturbances on the substratum. Although the two amphibian megafauna
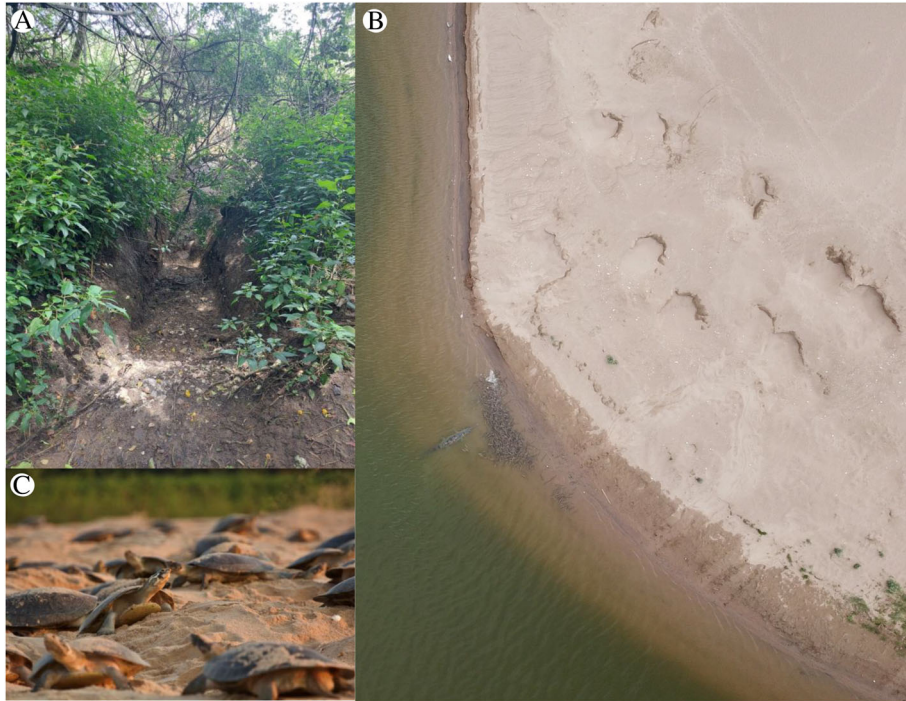
Fig. 4. Examples of how freshwater megafauna influence riparian areas, including (A) a river bank broken by hippopotami (*Hippopotamus amphibius*) due to their repeated movement between feeding and resting sites (photograph: Celesté Maré), (B) multiple nest craters at a communal nesting site of gharial (*Gavialis gangeticus*) in lower Chambal River, India (photograph: Gharial Ecology Project), and (C) nesting activities of the Arrau turtle (*Podocnemis expansa*) in the beach of the Guaporé river, Brazil (photograph: Camila R. Ferrara). See Appendix S1 for image sources.

Chinese giant salamander (*Andrias davidianus*) and Japanese giant salamander (*A. japonicus*) do not tend to excavate nests from scratch, male giant salamanders modify existing dens by pushing sand and gravel out to create nest depressions (Luo *et al.*, 2018; Terry *et al.*, 2019). As the population density of giant salamanders can be quite high in suitable environments [e.g. 103 Japanese giant salamanders were observed in a river section of 1.2 km (Browne *et al.*, 2014; Kawamichi & Ueda, 1998)], their disturbance of substrata, particularly during the spawning season, can be substantial. Similar behaviour has been documented for the eastern freshwater cod (*Maccullochella ikei*), where males remove loose sand and particles when cleaning nests in the riverbed (Butler & Rowland, 2009), and Chinook salmon (*Oncorhynchus tshawytscha*), which create redds (a nest depression for incubating eggs) that can reach 50 cm in depth (Gallagher & Gallagher, 2005; Gottesfeld, Hassan & Tunnicliffe, 2008). While the influence of each individual of these species on a river is relatively small, their overall influence on substrata is likely strong, especially considering that these species were highly abundant prior to severe anthropogenic impacts (Humphries & Winemiller, 2009).

(2) Biogeochemical cycling

Freshwater ecosystems are linear or mosaic features embedded into the terrestrial landscape matrix and frequently connected to the ocean. Many megafauna are highly mobile, crossing ecosystem boundaries, thereby increasing the flow of biomass and nutrients from terrestrial and marine realms to fresh waters (Doughty *et al.*, 2016; Moss, 2015). For example, terrestrial plants are an important dietary component of large semi-aquatic herbivores, including capybara (*Hydrochoerus hydrochaeris*), hippopotamus, pygmy hippopotamus, wild water buffalo, and beavers. Capybaras have daily ingestion rates of 1–3% of their body mass, which typically exceeds 35 kg for adults (Kiani *et al.*, 2019), while an adult hippopotamus can consume 40 kg of grass per night (Grey & Harper, 2002). The grazing range of hippopotami expands to areas over 5 km away from rivers (Harrison, Kalindekafe & Banda, 2008). Hippopotami spend extensive periods of time resting in the water during the day and discharge faeces and urine in freshwater habitats. Subalusky *et al.* (2015) estimated that a hippopotamus, on average, defecates 8.7 kg of faeces per day into the Mara River, with a total daily flux of 36,200 kg of faeces from hippopotamus populations to the river, containing 3499 kg total carbon, 492 kg total nitrogen and 48 kg total phosphorus. They also transport ∼400 kg of biogenic silicon to the river each day, representing roughly 32% of the biogenic Si flux (Schoelynck *et al.*, 2019). Similarly, beavers not only consume terrestrial plants but also transport wood into fresh waters for dam building. Nummi *et al.* (2018) estimated that ∼8000 kg of trees were removed each year by a beaver colony, with

almost 90% of these trees used for dams. Their activities thus markedly increase nutrient and woody biomass input to fresh waters (Larsen *et al.*, 2021).

Large semi-aquatic predators and omnivores also contribute to nutrient flows between terrestrial and freshwater ecosystems, mainly by consuming terrestrial animals and plants (Cucherousset *et al.*, 2012; Subalusky *et al.*, 2015). Anacondas (*Eunectes* spp.) ambush various terrestrial animals, including reptiles, birds, and mammals (Thomas & Allain, 2021). Terrestrial animals such as agoutis, opossums, monkeys, armadillos, rats, and porcupines were documented in the diet of smooth-fronted caiman (*Paleosuchus trigonatus*) (Magnusson, da Silva & Lima, 1987) and American crocodile (*Crocodylus acutus*) (Balaguera-Reina *et al.*, 2018), while large herbivores, including wildebeest and zebra, fall prey to Nile crocodiles (*Crocodylus niloticus*) (Subalusky *et al.*, 2017). Fruits, seeds, and leaves of terrestrial plants are widely reported to be consumed by large freshwater turtles such as the alligator snapping turtle (*Macroclemys temminckii*) and Arrau turtle (Cunha, Bernhard & Vogt, 2020; Sloan, Buhlmann & Lovich, 1996). Conversely, crocodylians, turtles, and their eggs, as well as salmonids and catfish, move nutrients counter current (from water to land) by becoming the prey of terrestrial predators (Somaweera *et al.*, 2020; Eriksson *et al.*, 2022). This lateral movement occurs counter to the directions of most passive modes of transport (e.g. water moving downslope to accumulate in water bodies). Currently, there is limited research quantifying nutrient transfer by freshwater megafauna (except for hippopotami and beavers) between land and fresh water (Somaweera *et al.*, 2020). This lack of studies has impeded our understanding of cross-ecosystem interactions driven by megafauna.

Apart from receiving nutrients from land, fresh waters also receive subsidies from the ocean transported by freshwater megafauna (Rosenblatt & Heithaus, 2011; Gende *et al.*, 2002; Naiman *et al.*, 2002; Samways *et al.*, 2015). Doughty *et al.* (2016) estimated that anadromous fish species, including large salmonids and sturgeons, moved 140 million kg of phosphorus each year prior to severe anthropogenic impacts (e.g. dam construction and overexploitation). Such subsidies not only happened in large rivers such as the Danube, Volga, Ural, and Yangtze but also in smaller streams connected to the ocean. Kohler *et al.* (2013) reported that, on average, juvenile Chinook salmon only export 22% of the nitrogen and 30% of the phosphorus that their parents imported from the ocean to streams in Idaho. In California, Chinook salmon imported eight times more phosphorus from the ocean to coastal streams than their juveniles exported back to the ocean (Moore *et al.*, 2011). The nutrients transported by anadromous megafauna from the ocean to fresh waters may finally be transferred to riparian zones (Naiman *et al.*, 2002). Indeed, there is evidence that nutrients transported by anadromous fish increase riparian productivity and biodiversity (Wagner & Reynolds, 2019).

Large catfishes, carps, and some sturgeons are potamodromous and move between different river sections or between lakes and rivers, contributing to the redistribution of nutrients between different freshwater habitats. Compared to anadromous fish, the influence of potamodromous fish on nutrient translocation has received less attention. However, potamodromous fish play a critical role in nutrient redistribution within freshwater ecosystems (Flecker *et al.*, 2010). Large potamodromous catfishes such as dorado (*Brachyplatystoma rousseauxii*), gilded catfish (*Zungaro zungaro*), and redtail catfish (*Phractocephalus hemiliopterus*) feed in downstream river reaches and move upstream for spawning (Petrere *et al.*, 2004). The deposition of their eggs in upstream sections represents nutrient flows against gravity. A considerable portion of their eggs or hatched juveniles fall prey to resident predators, transferring nutrients to local assemblages and ecosystems. In addition, grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*), and black carp (*Mylopharyngodon piceus*) feed in lakes and migrate to rivers for spawning (Ru & Liu, 2013), redistributing large amounts of nutrients between lakes and connected rivers.

Although river dolphins, manatees, and crocodylians generally do not conduct long-distance migration to complete their life cycles, they can still roam over large areas and, through this, contribute to the redistribution of nutrients within fresh waters. River dolphins and crocodylians capture migratory fish and increase the nutrient input to local systems (Flecker *et al.*, 2010). River dolphins, manatees and some crocodylians have large habitat requirements and forage in multiple habitats that are distant from each other (Bakker *et al.*, 2016; Keith-Diagne *et al.*, 2021; Rosenblatt & Heithaus, 2011). By feeding in one location and discharging in another, freshwater megafauna boost nutrient exchange among habitats (Bakker *et al.*, 2016; Boulêtreau *et al.*, 2011). The feeding activities of megafauna also modify nutrient cycling within local systems. For example, herbivorous megafauna, such as manatees, marsh deer, lechwe, and grass carp, feed on aquatic plants and accelerate the decomposition of these plants (Bakker *et al.*, 2016). Crocodylians and large turtles prey on benthic invertebrates such as aquatic insects, molluscs, and crustaceans (Moll & Moll, 2004; Magnusson *et al.*, 1987; Somaweera *et al.*, 2020), thereby translocating nutrients from benthic habitats to the water column *via* excrement and resuspension of sediments (Vanni, 2002).

IV. INTERACTIONS WITH OTHER FRESHWATER SPECIES

(1) Aquatic plants and algae

The interactions between megafauna and primary producers have multiple facets, including direct interactions through feeding and physical disturbances and indirect interactions through smaller consumers. Aquatic plants are an important part of the diets of large mammalian herbivores such as manatees, marsh deer, lechwe, sitatunga (*Tragelaphus spekii*) and water buffalo (Guterres-Pazin *et al.*, 2014; Shrestha *et al.*, 2020; Ndawula *et al.*, 2011; Tomas & Salis, 2000;

Franceschini *et al.*, 2020). Their herbivory activities profoundly influence the composition and growth of aquatic vegetation. Manatees, for example, feed on over 30 plant species in both Africa and South America (Takoukam Kamla *et al.*, 2021; Guterres-Pazin *et al.*, 2014). The amount of aquatic plant biomass consumed daily by manatees ranges from 4 to 13% of their body mass, which may exceed 400 kg as adults (Best, 1981; Bengtson, 1983). Although aquatic plants are usually supplementary food to beavers, hippopotami, and capybaras, their feeding activities still cause considerable changes in community compositions of aquatic vegetation (Bakker *et al.*, 2016). For example, the herbivory effects of beavers led to a reduction in dominant macrophytes and a threefold increase in aquatic plant richness over a 10-year period in east Scotland (Law, Jones & Willby, 2014). Large fish (e.g. grass carp and rohu, *Labeo rohita*) and turtles (e.g. Arrau turtle, common snapping turtle, *Chelydra serpentine*, and Asiatic softshell turtle, *Amyda cartilaginea*) also regularly consume aquatic plants (Mandal *et al.*, 2010; Cunha *et al.*, 2020; Jensen & Das, 2008; Aresco & Gunzburger, 2007). For example, the foraging activities of grass carp directly alter the abundance and composition of aquatic vegetation (Dibble & Kovalenko, 2009). Therefore, they have been widely used for aquatic weed control (Pipalova, 2006). Other large fishes, such as silver carp, giant barb (*Catlocarpio siamensis*), and Mekong giant catfish (*Pangasianodon gigas*) feed on algae (Poulsen *et al.*, 2004; Medo *et al.*, 2020). Indeed, planktivorous megafauna such as silver carp are used for algae control in lakes and reservoirs (Zhang, Xie & Huang, 2008).

In many cases, freshwater megafauna also influence primary producers indirectly through trophic cascades. For example, American paddlefish (*Polyodon spathula*), smallmouth buffalo (*Ictiobus bubalus*), and bighead carp feed on zooplankton, thereby reducing grazing pressures by zooplankton on certain phytoplankton. In addition, river dolphins, crocodylians, otters, and various large fish species (e.g. *Arapaima* spp., *Brachyplatystoma* spp., *Esox* spp., *Maccullochella* spp.) are top predators (Hammerschlag *et al.*, 2019; Winemiller *et al.*, 2015) and prey on fish that feed on algae and zooplankton. Hence, megafauna can interact with primary producers indirectly through other species and thereby influence phytoplankton abundance and composition. The influence of megafauna foraging activities on phytoplankton abundance is often complicated and not unidirectional, depending on the abundance of megafauna and the community composition of phytoplankton and zooplankton. For example, silver carp can lead to decreased total chlorophyll-a concentrations in the water column due to direct consumption of phytoplankton or to increased total chlorophyll-a levels by suppressing zooplankton and promoting small-sized phytoplankton species (Zhang *et al.*, 2008; Shen *et al.*, 2021).

Megafauna species also impact primary producers through their influence on physicochemical conditions in fresh waters. Freshwater habitats created or enlarged by megafauna activities, including wetlands, ponds, and canals created by beavers and crocodylians, provide a suitable environment for various aquatic plants (Brazier *et al.*, 2021; Somaweera *et al.*, 2020). Hippopotami, beavers, turtles, and large anadromous fish species transport nutrients from land or ocean to fresh waters (Doughty *et al.*, 2016; Schoelynck *et al.*, 2019), which is likely to boost the growth of algae, macrophytes, and riparian plants (Naiman *et al.*, 1988; Hocking & Reynolds, 2011). In addition, foraging activities of benthivorous megafauna often release nutrients from sediments and benthic animals to water columns and enhance nutrient availability for phytoplankton (Vanni, 2002). Although megafaunal impacts on primary producers in freshwater ecosystems have been observed in various regions (Wood *et al.*, 2017; Bakker *et al.*, 2016), our knowledge of such interactions remains limited and the net effect unquantified, particularly of indirect interactions through smaller consumers.

(2) Invertebrates

The interactions between megafauna and invertebrates in fresh waters are similar to those with primary producers, including direct predation and indirect interactions through the food web. More freshwater megafauna, particularly megafish, consume invertebrates as a vital part of their diets compared to algae and aquatic plants. Despite the large size of freshwater megafauna in their adult stage, most of them prey on invertebrates during at least one of their life-cycle stages. Most sturgeon species are primarily benthic feeders with molluscs, crustaceans, and insect larvae as food throughout their whole life (Billard & Lecointre, 2000) with only three species (*Huso huso*, *H. dauricus*, *A. transmontanus*) becoming exclusive predators after reaching a certain size. Other megafish species, including goonch (*Bagarius yarrelli*), Jullien's golden carp (*Probarbus jullieni*), Chinese high-fin banded shark (*Myxocyprinus asiaticus*), black carp, and common carp (*Cyprinus carpio*) also prey on benthic invertebrates both in their juvenile and adult stages (Roberts, 1983; Poulsen *et al.*, 2004). In addition to benthic invertebrates, zooplankton is an important food resource for megafish species such as the American paddlefish, silver carp, and bighead carp (Billard & Lecointre, 2000; Zhang *et al.*, 2008).

While piscivorous megafish primarily prey on other fish species during their adult stage (Winemiller *et al.*, 2015), they often depend on invertebrates during their juvenile stage. Benthic invertebrates and zooplankton have been widely observed in the diets of juvenile arapaima (*Arapaima gigas*) (Oliveira, Poleto & Venere, 2005), Murray cod (*Maccullochella peelii*) (Kaminskas & Humphries, 2009), Siberian taimen (*Hucho taimen*) (Matveyev *et al.*, 1998), and Nile perch (*Lates niloticus*) (Cornelissen *et al.*, 2018). Adult individuals of these top predators also consume invertebrates in addition to fish (Matveyev *et al.*, 1998).

Large turtles such as Leith's softshell turtle (*Nilssonia leithii*), Asian giant softshell turtle (*Pelochelys cantorii*), and common snapping turtle regularly prey on benthic invertebrates (Das *et al.*, 2014; Das, 2008; Punzo, 1975). Crabs, crayfish, and aquatic insects have been observed in the stomach of alligator

snapping turtles, Asiatic softshell turtles, and Indian narrow-headed softshell turtles (*Chitra indica*) (Elsey, 2006; Jensen & Das, 2008; Das & Singh, 2009). Although crocodylians are often categorised as apex predators and prey on large vertebrates, invertebrates represent a considerable proportion of the diets of many crocodylians (Somaweera *et al.*, 2020). For example, invertebrates, including crustaceans, insects, and molluscs are the most common prey items for dwarf crocodile (*Osteolaemus tetraspis*) populations that live in forest streams (Shirley *et al.*, 2017). Aquatic insects, crabs, shrimps, and molluscs are often consumed by American alligator, spectacled caiman (*Caiman crocodilus*), smooth-fronted caiman, and dwarf caiman (*Paleosuchus palpebrosus*) (Rosenblatt *et al.*, 2015; Magnusson *et al.*, 1987; Moldowan *et al.*, 2016). Similar to crocodylians and large turtles, the two extant giant salamanders also consume invertebrates such as crabs and crayfish (Browne *et al.*, 2014). Crabs comprise about 25 and 35% of the stomach content of Chinese giant salamanders (Song, 1994) and Japanese giant salamanders (Okada *et al.*, 2008), respectively. Freshwater crabs, molluscs, and insects are also the prey of otters, including African clawless otters (*Aonyx capensis*) and giant otters (*Pteronura brasiliensis*), in addition to fish (Andarge, Wube & Balakrishnan, 2017; Carter & Rosas, 1997).

Recently, Watanabe, Baranov & Miyazaki (2020) found that Baikal seals (*Pusa sibirica*) actively hunt freshwater pelagic amphipods (*Macrohectopus branickii*), which might contribute to ~20% of their daily energy requirements. It is an important illustration that we still do not have a comprehensive knowledge of the feeding habits of many freshwater megafauna. Their predation on invertebrates might not have been well documented, or even considered as an anomaly because these species are believed to prey predominantly on vertebrates, such as fish. Hence, the influence of megafauna on invertebrate abundance and community composition might be underestimated.

In addition to direct predation on invertebrates, megafauna may also consume species that themselves prey on invertebrates; hence, reducing predatory pressure on invertebrates. For example, the main prey fish of Baikal seals are *Comephorus* spp. and *Cottocomephorus* spp. (Silow *et al.*, 1995; Moore *et al.*, 2009), which themselves mainly feed on invertebrates including copepods and amphipods (Silow *et al.*, 1995; Miyasaka *et al.*, 2006). The persistence of some parasites (including invertebrates with parasitic larvae such as freshwater pearl mussels) is highly influenced by the abundance and distributions of freshwater megafauna hosts (Geist, Porkka & Kuehn, 2006; Modesto *et al.*, 2018; Tellez, 2014). In addition, megafauna modify the habitats of invertebrates and thereby affect their community composition. Foraging activity of grass carp reduces the extent of aquatic vegetation, which leads to habitat loss and decreased abundance of epiphytic invertebrates but may promote benthic invertebrates (Dibble & Kovalenko, 2009). At the landscape scale, habitat modification by beavers could potentially increase invertebrate diversity due to enhanced habitat heterogeneity (Law, McLean & Willby, 2016; Larsen *et al.*, 2021).

(3) Vertebrates

In fresh waters, megafauna mainly interact with other smaller vertebrates through carnivory (both predation and scavenging) and modifying their food resources and habitats. River dolphins, anacondas, crocodylians, and many large fish species are top predators that feed on other freshwater vertebrates (Hammerschlag *et al.*, 2019; Winemiller *et al.*, 2015). Fish is a vital food resource for freshwater cetaceans (i.e. *Inia geoffrensis*, *Lipotes vexillifer*, *Platanista gangetica*, *P. minor*, *Sotalia fluviatilis*, *Orcaella brevirostris*, *Neophocaena asiaeorientalis* ssp. *asiaeorientalis*) in the Ganges, Indus, Irrawaddy, Mekong, Yangtze, Amazon, and Orinoco rivers and their major tributaries and connected lakes (Huang *et al.*, 2012). Amazon river dolphins (*Inia geoffrensis*) feed on over 40 fish species, with a daily consumption of ~2.5% of their body mass (da Silva & Martin, 2018). Fish species are also the main component of the diet of large otter species (Quéméré *et al.*, 2021). The daily consumption of fish by giant otters is about 10% of their weight (Rosas-Ribeiro, Rosas & Zuanon, 2012). For adult females, average daily fish consumption ranges from 1.4 to 3.7 kg (Carter *et al.*, 1999). Large fish species, including pimelodids (e.g. *Brachyplastystoma* spp., *Pseudoplatystoma* spp., *Zungaro* spp.), gars (Lepisosteidae), freshwater cods (*Maccullochella* spp.), arapaima, yellowcheek (*Elopichthys bambusa*), and northern pike (*Esox lucius*) are also piscivorous (Winemiller *et al.*, 2015). These top predators can directly regulate fish populations through predation (Winemiller *et al.*, 2015; Hammerschlag *et al.*, 2019). Such impacts are well documented when these top predators are introduced to a new environment (Dunker *et al.*, 2018). After the introduction of the northern pike to a lake located in northwestern Ontario, Canada, the previously abundant yellow perch (*Perca flavescens*) experienced a drastic decline while another native fish, pearl dace (*Margariscus margarita*), was extirpated (Findlay *et al.*, 2005). The direct predation and competition caused by the introduced Nile perch have contributed to the extinction of many haplochromine fish species in Lake Victoria (Witte *et al.*, 2000).

Large reptiles such as crocodylians and turtles also consume vertebrates. The gharial (*Gavialis gangeticus*) is a specialised fish-eater, with a long, narrow snout with sharp interlocking teeth (Whitaker, 2007). Although other crocodylians are less specialised in fish hunting, fish is widely reported as a part of the diet of the Sunda gharial (*Tomistoma schlegelii*), the Australian freshwater crocodile (*Crocodylus johnsoni*), the spectacled caiman and the Nile crocodile (Bezuijen *et al.*, 1997; Somaweera *et al.*, 2020; Thorbjarnarson, 1993). Turtles are often regarded as slow-moving animals, but large turtles can ambush fish with a fast strike when prey is within a short distance of their head (Alcott, Long & Castro-Santos, 2020). For example, fish were found in the gastrointestinal tracts of 79.8% of all sampled alligator snapping turtles from Arkansas and Louisiana (Elsey, 2006). Akani, Capizzi & Luiselli (2001) observed fish in 60.7% of the stomach contents and 80.5% of the faeces of investigated African softshell turtle (*Trionyx triunguis*) in Nigeria.

These large semi-aquatic reptiles are often opportunistic predators, feeding on a variety of food sources. Hence, other aquatic and semi-aquatic vertebrates, including frogs, snakes, birds, and mammals, also fall prey to large turtles, crocodylians, and anacondas (Akani *et al.*, 2001; Miranda *et al.*, 2017; Somaweera *et al.*, 2020; Elsey, 2006). It is worth noting that the regulatory effects of large semi-aquatic reptiles on their vertebrate prey might not be as strong as that of other large predators such as sharks and big cats because of their opportunistic feeding habits (i.e. they prey both on vertebrates and invertebrates) and relatively low feeding frequency (Somaweera *et al.*, 2020).

Most carnivorous megafauna may also be regarded as scavengers. For example, many crocodylians and large turtles feed on carcasses in the water and in riparian areas (Elsey, 2006; Subalusky *et al.*, 2017). Megafish, including wels catfish (*Silurus glanis*), African catfish (*Clarias gariepinus*), and alligator gar (*Atractosteus spatula*), are considered scavengers as well (Goodyear, 1967; Adamek, Fašaić & Siddiqui, 1999; Hickley & Chare, 2004). Even largely herbivorous species such as hippopotami scavenge occasionally (Dudley *et al.*, 2016). However, the amount of prey that is scavenged by freshwater megafauna and its impacts on local food webs have probably been underestimated, as is the case for terrestrial carnivorous megafauna (Wilson & Wolkovich, 2011).

Apart from consuming living or dead animals, freshwater megafauna also influence the resources available to smaller vertebrates. Silver carp, bighead carp, and bigmouth buffalo (*Ictiobus cyprinellus*) share a similar diet with other planktivorous fish species (Pendleton *et al.*, 2017; Lazzaro, 1987). On the bottom of rivers and lakes, sturgeons, stingrays, and black carp prey on invertebrates and compete with other benthivorous fish (Miller, 2004; Nico, Williams & Herod, 2001; Shibuya, Araújo & Zuanon, 2009). Given their wide spectrum of food resources and large body size, freshwater megafauna are likely to have advantages over smaller vertebrates when competing for food resources. Moreover, megafaunal impacts on water chemistry and habitat structure can indirectly affect vertebrates. For instance, hippopotami modify water quality in river pools during the dry season, strongly influencing fish diversity and assemblage compositions (Stears *et al.*, 2018; Voysey *et al.*, 2023). Pools and wetlands created by beavers provide habitats for aquatic and semi-aquatic vertebrates, promoting diversity of vertebrates such as fish, amphibians, and waterbirds (Larsen *et al.*, 2021).

V. IMPACT OF LOSING MEGAFAUNA

In fresh waters, overexploitation, habitat modification (e.g. dam construction, wetland conversion), and species introduction have led to major reductions in the distribution and abundance of megafauna (Chen *et al.*, 2023; He *et al.*, 2017). Globally, monitored populations of freshwater megafauna declined by 88% from 1970 to 2012 (Fig. 5A; He *et al.*, 2019), and for many freshwater megafauna the

estimated number of mature individuals in the wild that are capable of reproduction is less than 1000 (Fig. 5B). As ecological impacts of megafauna on ecosystems are closely associated with population size (Galetti *et al.*, 2018; Malhi *et al.*, 2016), the decline of populations directly alters the magnitude of megafaunal impact on the environment. For example, overexploitation has severely reduced the population density of beavers in Europe and North America (Halley & Rosell, 2002; Butler & Malanson, 2005). Although populations of beavers in North America and Europe have greatly increased after the regulation of hunting and implementation of reintroduction programs, their population abundance is still far lower than historical levels (Halley, Saveljev & Rosell, 2021; Wohl, 2021). Therefore, their influence on flow regime, sediment fluxes, nutrient cycling, and vegetation is drastically weakened compared to historical times. The extirpation of freshwater megafauna often leads to the disappearance of habitats (e.g. canals, burrows, and wallowing ponds) created and maintained by their activities, exerting adverse impacts on species that depend on these habitats. Such impacts might be further amplified by climate change [e.g. increased frequency and extent of drought and wildfires (Fairfax & Whittle, 2020; Gomez Isaza, Cramp & Franklin, 2022)]. Many megafish species, including sturgeons, salmonids, and large catfishes migrate long distances from the ocean or the lower river reaches to upstream areas. Due to construction of dams and other obstacles, the number of large migratory fish reaching their historical spawning areas has drastically declined compared to the past (Humphries & Winemiller, 2009; Hogan, 2011). In many cases, large migratory fish are completely extirpated upstream from dams (He *et al.*, 2019). The nutrient transport associated with their migrations, which provides important nutrient subsidies to upstream regions (Flecker *et al.*, 2010; Gende *et al.*, 2002), is also disrupted (Doughty *et al.*, 2016). In some cases, the direction of such nutrient flows can even be reversed where reduced adult fish densities lead to low spawning numbers, causing reductions in competition among smolts and as a consequence, relatively more nutrients being moved downstream by the young fish than were moved upstream by the adult fish (Scheuerell *et al.*, 2005).

Nowadays, individuals of freshwater megafauna species often do not reach their potential maximum body size because large individuals are preferentially targeted in harvest (Humphries & Winemiller, 2009; Ripple *et al.*, 2019; Garcia *et al.*, 2012). The reduced abundance of large predators releases predation pressures on smaller planktivorous and algivorous fish, altering the trophic dynamics and ecological processes in rivers and lakes (Power *et al.*, 1996; Estes *et al.*, 2011). A clear body-size reduction in large freshwater fish species has been observed in many regions (Costa-Pereira *et al.*, 2018; Humphries & Winemiller, 2009). For example, both Mary River cod (*Maccullochella mariensis*) and eastern freshwater cod could exceed over 30 kg, but nowadays, it is uncommon to observe individuals over 10 kg (Simpson & Jackson, 2000; Lintermans *et al.*, 2005). Given that prey size is often associated with the size of predators
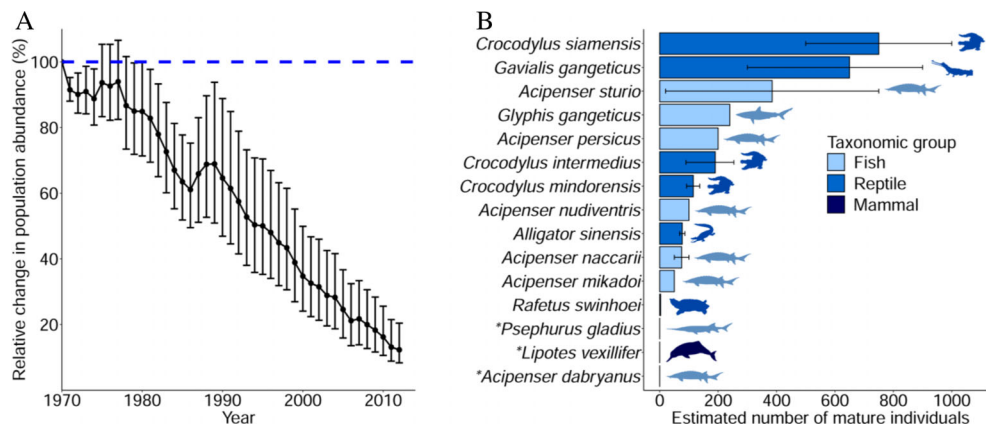
Fig. 5. (A) Estimated relative change in monitored population abundance of global freshwater megafauna from 1970 to 2012 (modified from He *et al.*, 2019). Error bars indicate 95% confidence intervals of the estimated values in each year. The changes in population abundance are relative to a benchmark value of 100% in 1970 shown by the blue dashed line. (B) The 15 freshwater megafauna with fewer than 1000 estimated mature individuals that are capable of reproduction based on IUCN *Red List* assessments (IUCN, 2022). Species believed to have no mature individuals in the wild that are capable of natural reproduction are marked with an asterisk. When only ranges of the estimated number of mature individuals were provided by IUCN *Red List* assessments, the median is shown with error bars indicating the upper and lower ranges.

(Gaeta *et al.*, 2018), the loss of large predators directly influences their regulation effects on their prey (Hammerschlag *et al.*, 2019). Dwindling abundances and the loss of large individuals are likely to reduce the complexity and stability of the food webs in the local ecosystem (Brose *et al.*, 2017). Additionally, megafauna downsizing will affect the seed dispersal of riparian plants because the fruit sizes dispersed by freshwater megafauna and the seed-dispersal distance are often positively correlated with the body size of megafauna (Anderson *et al.*, 2011; Costa-Pereira *et al.*, 2018).

VI. RELEVANCE FOR ECOSYSTEM RESTORATION

Major political and institutional frameworks for making ecosystem restoration a priority have emerged recently, including the United Nations UN Decade on Ecosystem Restoration 2021–2030 and the Kunming–Montreal Global Biodiversity Framework, which targets that at least 30% of degraded inland water areas should be under 'effective restoration' by 2030. Owing to their disproportionate impacts on ecosystems, the recovery of megafauna populations is a promising tool for ecosystem restoration, with co-benefits for biodiversity conservation and nature's contributions to people (NCP) (Lorimer *et al.*, 2015; Svenning *et al.*, 2016). In fresh waters, restoring megafauna populations can also enhance habitat heterogeneity and promote diversity, supporting the recovery of ecosystem functions and services (Larsen *et al.*, 2021; Strickland *et al.*, 2023; Voysey *et al.*, 2023). Some freshwater megafauna species, such as beavers (Halley & Rosell, 2002), sturgeons (McAdam *et al.*, 2018; Huang & Wang, 2018), crocodylians

(Somaweera *et al.*, 2020), large turtles (Campos-Silva *et al.*, 2018), and giant salamanders (Cunningham *et al.*, 2016) have been included in *in-situ* and *ex-situ* programmes to facilitate their population recovery and support ecosystem restoration. However, including freshwater megafauna in restoration actions also has uncertainties and risks.

(1) Potential for restoring ecological processes

As synthesised above, freshwater megafauna have profound ecological impacts. Reinstating freshwater megafauna holds the potential for restoring ecosystem functions in relation to three key ecological processes (Fig. 6): disturbances, trophic cascades, and dispersal of other species (Perino *et al.*, 2019). Restoring these ecological processes is, in turn, expected to benefit the conservation of a broad range of freshwater species.

Freshwaters are highly dynamic ecosystems characterised by various stochastic disturbances created by flow regimes and animal activities. Nowadays, stochastic disturbances are often suppressed by anthropogenic impacts (e.g. river regulation and fragmentation, defaunation), leading to decreased habitat complexity and a decline in biodiversity and ecosystem resilience (Rideout *et al.*, 2021). Reinstating megafauna holds the potential to increase disturbances and habitat heterogeneity in freshwater ecosystems through their activities (e.g. trampling, foraging, wallowing, excavating, dam or nest building), in turn, promoting overall freshwater biodiversity (Law *et al.*, 2014; Larsen *et al.*, 2021). It is expected that megafauna will enhance habitat heterogeneity in fresh waters, as has been documented for species such as beavers, hippopotamus, and some crocodylians (Bakker *et al.*, 2016; Somaweera *et al.*, 2020; Larsen *et al.*, 2021; Voysey *et al.*, 2023). However, it is important to recognise
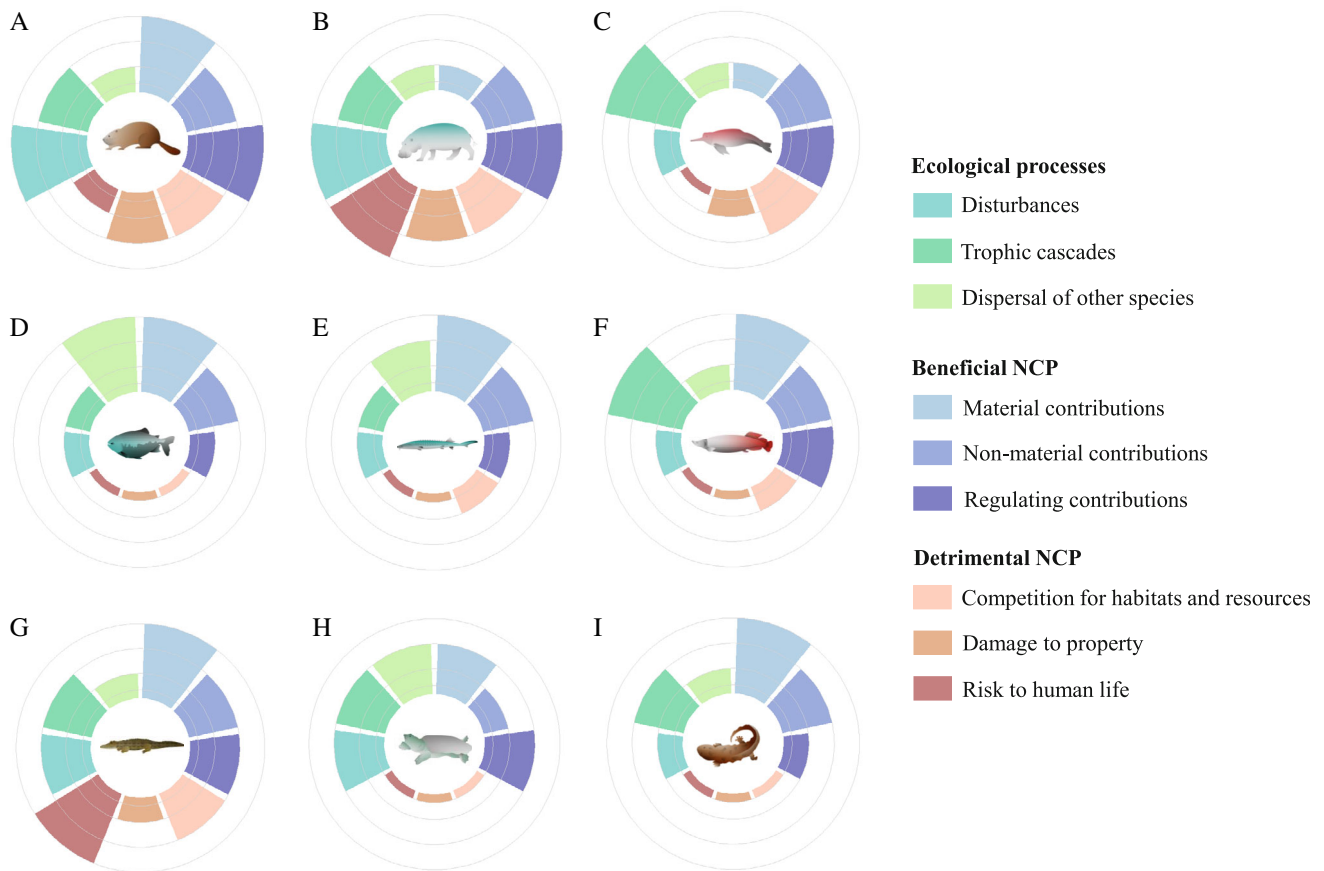
Fig. 6. Conceptual diagram showing potential impacts of reinstating freshwater megafauna populations on ecological processes and nature's contributions to people (NCP): (A) beavers, (B) hippopotamus, (C) freshwater cetaceans, (D) frugivorous fish such as the tambaqui, (E) sturgeons, (F) piscivorous fish such as the arapaima, (G) crocodylians, (H) large turtles, and (I) giant salamanders. The heights of the bars indicate the levels of their relative potential (i.e. low, medium, high, very high) in each category of ecological processes, beneficial NCP, and detrimental NCP. The definition and examples of each category are presented in Table S2.

that the impacts of many freshwater megafauna species on habitat heterogeneity have yet to be comprehensively investigated empirically (Strickland *et al.*, 2023). Future research needs explicitly to quantify megafauna disturbances and their net effects on ecosystem processes at different spatial and temporal scales.

In human-modified ecosystems, ecological processes are often affected by the extirpation, reduction, or alteration of the size structure of megafauna populations (Estes *et al.*, 2011; He *et al.*, 2019; Ripple *et al.*, 2019), and anthropogenic influences may reduce the top-down effects of large predators (Dorresteijn *et al.*, 2015). Such changes lead to simplified ecological networks and reduced ecosystem stability (Solé & Montoya, 2001; Brose *et al.*, 2017). However, it is challenging to assess comprehensively the impacts of freshwater megafauna on local trophic dynamics due to the generally small remaining populations. The abundance of freshwater megafauna in many industrialised countries is probably as low as it has been for decades (Humphries & Winemiller, 2009). Therefore, their potential roles in shaping local trophic cascades are likely underappreciated and

weakly understood (Winemiller *et al.*, 2015). Given their diverse connections with other freshwater biotas (e.g. *via* direct consumption of species at different trophic levels or indirect trophic cascading interactions; Winemiller *et al.*, 2015; Hammerschlag *et al.*, 2019), restoring populations and the size structure of megafauna, together with other restoration measures (e.g. reduced anthropogenic stressors and enhanced river connectivity), will promote trophic interactions and increase trophic complexity as envisioned in the concept of trophic rewilding (Svenning *et al.*, 2016), which so far has seen limited application to freshwater megafauna.

Many freshwater habitats today are highly fragmented due to wetland conversion, water abstraction, and construction of weirs, dams, and levees, impeding the movements of freshwater species (Grill *et al.*, 2019; Winemiller *et al.*, 2016). Restoration actions targeting freshwater megafauna may improve connectivity in freshwater ecosystems, promoting the dispersal of other smaller freshwater species. For example, conservation and restoration actions targeting large migratory fish species often include improving habitat connectivity as a critical element, providing benefits to other

smaller migratory species (Worthington *et al.*, 2022). In addition, freshwater megafauna themselves might provide connectivity and function as dispersal vectors of plants, microbes, and smaller animals. For example, tambaqui (*Colossoma macropomum*) and freshwater turtles such as common snapping turtle, alligator snapping turtle, and Arrau turtle engage in frugivory and seed dispersal of plants (Falcón, Moll & Hansen, 2020; Correa *et al.*, 2015; Anderson *et al.*, 2011) while crocodylians may also contribute to seed dispersal (Somaweera *et al.*, 2019). Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are the primary hosts for the larvae of freshwater pearl mussels (*Margaritifera margaritifera*) in Europe (Geist *et al.*, 2006), while several sturgeons (*Acipenser sturio*, *A. naccarii*, and *A. baerii*) are the hosts of Spengler's freshwater mussel (*M. auricularia*) (Soler *et al.*, 2019). Therefore, restoring freshwater megafauna and their habitats will also facilitate the dispersal of other species and help with their persistence and recovery (Modesto *et al.*, 2018).

(2) Potential for enhancing nature's contributions to people

Freshwater ecosystems support vital NCP, including the provision of food and water, flood regulation, water purification, and cultural inspiration (Díaz *et al.*, 2018; Lynch *et al.*, 2023). Freshwater megafauna underpin or amplify many of these contributions. For example, reinstating freshwater megafauna assemblages can enhance regulating NCP directly through the facilitation of dispersal and habitat creation and maintenance (Naiman & Rogers, 1997; Larsen *et al.*, 2021; Moore, 2006). Habitats created and maintained by freshwater megafauna (e.g. beaver ponds, alligator holes, hippopotamus pools) contribute to the regulation of freshwater quality and quantity and are important refugia during drought or wildfire (Palmer & Mazzotti, 2004; Fairfax & Whittle, 2020; Larsen *et al.*, 2021), and may mitigate the effects of climate change (Hammerschlag *et al.*, 2019; Malhi *et al.*, 2022).

Freshwater megafauna provide various material elements, including food, medicine, and ornaments for humans. The meat of many megafish species (e.g. arapaima, giant barb, Mekong giant catfish, and tambaqui) fetches high prices while eggs of sturgeons, crocodylians, and large turtles are also considered highly valuable (Ripple *et al.*, 2019). Freshwater megafauna are, or used to be, important sources of food and income for local human communities (Hogan, 2011; Winemiller *et al.*, 2015; Forero-Medina *et al.*, 2021). Hence, the restoration and sustainable management of freshwater megafauna populations would improve the livelihoods of local human communities. For example, successful community management in the Juruá River, Brazil, has led to an increased arapaima population and improved income for local communities (Campos-Silva & Peres, 2016; Campos-Silva *et al.*, 2021). Conservation and restoration actions targeting megafauna are likely to benefit a broad range of other species (Campos-Silva *et al.*, 2018), which in turn further increases the services and products provided by freshwater ecosystems.

Due to human fascination with large animals, reinstating freshwater megafauna is likely to enhance non-material NCP, including physical and psychological experiences (e.g. ecotourism, recreational fishing), artistic inspiration, and supporting identities. Various megafishes, including Siberian taimen, Wels catfish, northern pike, muskellunge (*Esox masquinongy*), Putitor mahseer (*Tor putitora*), and Murray cod are popular and highly prized by recreational anglers (Nyboer *et al.*, 2021). Many megafauna species, including river dolphins, hippopotamus, beavers, and crocodylians, are charismatic foci for ecotourism, which can provide economic benefits for local communities (Walter & Sen, 2018; Cohen, 2019; Auster, Barr & Brazier, 2020; Bonye, Yiridomoh & Dayour, 2022). Moreover, megafauna, including sturgeons, crocodylians, and large turtles, are often closely associated with the cultures and identities of indigenous peoples and local communities (Freitas *et al.*, 2020; Noble *et al.*, 2016). For example, Murray cod is part of the intangible cultural heritage of Australian aboriginal peoples, with a pivotal role in the creation story of the Murray River (Rowland, 2005). Similarly, in North America, the lake sturgeon (*Acipenser fulvescens*) was traditionally the first fresh meat of Menominee people each spring and has been associated with the story of the tribe's origins and religion (David, 1995). Therefore, restoration targeting freshwater megafauna holds great potential for enhancing non-material NCP and providing economic and cultural benefits. In turn, it can restore or enhance bonding between humans and freshwater megafauna, which may further increase the involvement of local communities in conservation and restoration and facilitate sustainable development.

(3) Challenges for restoration

Although reinstating megafauna populations can restore ecological processes and enhance beneficial NCP, the potential for conflict between megafauna and people exists. The restored megafauna population may inflict detrimental NCP (Pascual-Rico *et al.*, 2021), including competition between humans and megafauna for habitats and resources, property damage, and risk to human life. These detrimental NCP may impede the development of conservation and restoration actions if human–megafauna coexistence is not well managed (Ceauşu *et al.*, 2019).

Freshwater megafauna often rely on large habitat areas and the same resources as humans, which may lead to conflicts over the exploitation of freshwater resources (e.g. fish, water, and energy). For example, river dolphins, crocodylians, and giant otters feed on fish and might be perceived to cause depredation of fish stocks and therefore be killed by fishermen (Cook *et al.*, 2022; Loch, Marmontel & Simões-Lopes, 2009). Many megafishes need to migrate a long distance to reach spawning or feeding grounds (Winemiller *et al.*, 2016; Hogan, 2011; Worthington *et al.*, 2022). Conservation and restoration actions targeting

them require river connectivity to be maintained or restored, which directly conflicts with hydropower development, particularly in megafish-rich basins such as the Amazon and Mekong (Zarfl *et al.*, 2019; He *et al.*, 2021*b*). Growing energy demands and international agreements on energy transition promote hydropower development (Hermoso, 2017); therefore, it is politically and economically challenging to cancel planned hydropower dams or to remove large existing ones. Proposals for functional solutions especially for large dams include substitution habitats in bypasses that ensure the ecological function of a river while allowing hydropower but requiring a compromise in discharge utilisation (Zhang *et al.*, 2023).

Although freshwater megafauna provide economic benefits for local communities, restoring populations of some species might increase the risk of damage to human property. Crop damage by hippopotami has occurred in many parts of Africa, particularly near wetlands (Kanga *et al.*, 2012). Damage to fishing nets caused by crocodylians, river dolphins, and giant otters is also frequent (Marowa, Matanzima & Nhiwatiwa, 2021; Cook *et al.*, 2022). In addition, crocodylians may attack livestock (Dunham *et al.*, 2010; Pooley *et al.*, 2021). Such damage can lead to considerable economic loss and affect the livelihoods of local people. For example, there are concerns that beaver reintroduction in Europe and North America will cause damage to valued trees, flood agricultural land and hinder the movement of economically important fish such as salmonids (Coz & Young, 2020; Auster, Barr & Brazier, 2021). Furthermore, megafauna such as hippopotami and crocodylians can attack humans, leading to fatalities (Kanga *et al.*, 2012; Marowa *et al.*, 2021; Cook *et al.*, 2022; Dunham *et al.*, 2010; García-Grajales & Buenrostro-Silva, 2019). For example, 149 unprovoked attacks on humans by crocodylians, including 25 fatal ones, were reported in Mexico between 2000 and 2018 (García-Grajales & Buenrostro-Silva, 2019). In Mozambique, Nile crocodiles killed 134 and injured 36 people in 27 months, while hippopotami killed 12 people and resulted in 10 injury cases in the same period (Dunham *et al.*, 2010). Real or perceived risk to humans could therefore translate to objections against reinstating freshwater megafauna by local communities (Balaguera-Reina & Farfàn-Ardila, 2018).

In addition to detrimental NCP, shifting baselines is another challenge for reinstating freshwater megafauna in regions where they were extirpated a long time ago, as long-extirpated species might not be considered a restoration target (Humphries & Winemiller, 2009). Sturgeons and Atlantic salmon were perceived as native species in Europe by only 40% of respondents in a survey conducted in France, Germany, Norway, and Sweden in 2015 (Kochalski *et al.*, 2019). In China, older fishermen are more likely to recognise the Baiji and Chinese paddlefish than younger ones (Turvey *et al.*, 2010*a*). Younger generations get used to the degraded freshwater ecosystems, thereby continuously lowering their expectations of the natural environment and reducing their willingness to support the

restoration of long-extirpated freshwater megafauna (i.e. the shifting baseline syndrome).

Given that many freshwater megafauna species have few mature individuals in the wild (Fig. 5B), *ex-situ* restoration programmes (e.g. captive breeding) have been implemented to support their population recovery and to reduce stress from unsustainable harvesting. For example, laboratory-reared juvenile and subadult sturgeons and salmonids have been released to rivers repeatedly in Europe, North America, and Asia to enhance wild populations (Fraser, 2008; McAdam *et al.*, 2018; Huang & Wang, 2018; Friedrich, Reinartz & Gessner, 2019). Captive breeding programmes have also been initiated for large reptiles (Marioni *et al.*, 2021) and amphibians (Cunningham *et al.*, 2016). These *ex-situ* programmes can help prevent species extinction when *in-situ* measures fail or take too long to restore the required habitats. However, they bring their own set of challenges. For instance, substantial financial investments are needed to establish and maintain breeding facilities, limiting the development of reintroduction programmes in many regions (Marioni *et al.*, 2021). Captive-reared individuals may have low genetic variability and limited capacity to adapt to changing environmental conditions, which could lead to reduced population fitness when wild populations are supplemented by these individuals (Fraser, 2008; Williams & Osentoski, 2007). Releasing captive-reared individuals into the wild may also introduce diseases and parasites, particularly in the case of translocation across river basins (Cunningham *et al.*, 2016; White *et al.*, 2023). Moreover, it is difficult to restore the population size of freshwater megafauna to historical levels if their habitats remain degraded, limiting the potential fully to recover their ecological impacts. Hence, a mix of *in-situ* and *ex-situ* measures is needed to restore the ecological functions supported by freshwater megafauna.

VII. FUTURE INVESTIGATIONS

In this review, we synthesised existing evidence documenting the impacts of megafauna on freshwater ecosystems and discussed the potential that their restoration will have for enhancing biodiversity conservation, ecological functionality, and NCP. Our review was based on information from articles published in English and Chinese, and may therefore overlook relevant studies published in other languages. Within the identified literature, evidence was unevenly distributed among species, regions, and types of ecological impact, pointing to research gaps and, thus, avenues for future research. For example, species such as the common hippopotamus, beavers, river dolphins, and large salmonids have received the most research attention, while many large fish species, turtles, and crocodylians, particularly in the Global South, remain understudied. Such gaps may impede ecological justification for their conservation and lead to underestimation of their potential in ecosystem conservation

and restoration efforts (Somaweera *et al.*, 2020; Svenning *et al.*, 2016). Further research is particularly needed in four domains.

(1) Historical baselines

Information on contemporary freshwater megafauna prior to intense anthropogenic influences could improve our understanding of their ecological roles and help us to set appropriate conservation and restoration goals (Humphries & Winemiller, 2009). Historical occurrence data of freshwater megafauna provides information on the extent of their ecological impacts in a natural environment. For example, historical records of migratory megafish species in upstream sections of rivers reveal where megafauna-driven subsidies occurred. Such information is often recorded in historical accounts and in natural-history museum collections, or preserved in the culture of indigenous peoples and local communities (Díaz *et al.*, 2015; Blanco-Garrido, Hermoso & Clavero, 2023). Digitising historical documents and increasing recognition of indigenous and local knowledge will advance biodiversity research by making these data easier to access. Furthermore, rapid developments in species distribution modelling will help researchers to reconstruct past environmental conditions of megafauna (Svenning *et al.*, 2011; Hallman *et al.*, 2021). As well as occurrence records, abundance data under natural conditions are needed to understand the magnitude of megafaunal impacts. For example, such data could provide essential information for calculating the amounts of nutrients migratory megafishes could transport from the ocean to inland areas or redistribute within fresh waters (Doughty *et al.*, 2016). Abundance data can also help researchers estimate the magnitude of disturbance posed by crocodylians and turtles in riparian habitats through nesting and foraging activities and the amounts of nutrients they transport across ecosystems due to hatching failure or egg predation. Information from historical accounts (e.g. records of observed abundance or the number of individuals harvested over a certain period) can assist in estimating their historical abundance (Forero-Medina *et al.*, 2021; Humphries & Winemiller, 2009). In addition, advancements in methods for estimating historical population sizes of species based on fossil records (Pilowsky *et al.*, 2022) or genomic data of existing individuals (Yuan *et al.*, 2018; Waldman *et al.*, 2019) will further improve our understanding of their population changes over time.

(2) Life history of freshwater megafauna

We still have limited knowledge of the life history of many freshwater megafauna, particularly of non-mammalian megafauna in the Global South. Life-history data, including information on diet, age of maturity, timing and location of reproduction, home range, and movement patterns, indicate the habitat requirements of freshwater megafauna and how they interact with the environment and other species. Detailed data on demographic structure are essential to understand population dynamics and elaborate accurate population viability analyses. Such information is imperative for developing effective conservation and restoration strategies. Information on migration corridors and the timing and location of megafish spawning will assist optimisation of dam locations (He *et al.*, 2021*b*; Zarfl *et al.*, 2019; Couto, Messager & Olden, 2021; Ziv *et al.*, 2012) and operation (Huang & Wang, 2018). Although many freshwater megafauna are challenging to monitor, emerging technologies in animal tracking (e.g. camera-trapping and Global Positioning System devices), laboratory techniques (e.g. stable isotope analyses and genetic approaches), and data processing can help us understand better the life history of freshwater megafauna and their responses to environmental change (Nathan *et al.*, 2022; Huang *et al.*, 2022). These technological advances also improve our understanding of the effectiveness of restoration efforts. For example, monitoring the movements of migratory megafish species in different life stages will help to assess the effects of fish passages on migration, reproduction, and population demography, which in turn will improve the design of fish passages (Cooke *et al.*, 2020; Elings *et al.*, 2024).

(3) Trophic interactions

Although researchers have emphasised the ecological importance of large herbivores and top predators in aquatic environments (Hammerschlag *et al.*, 2019; Bakker *et al.*, 2016), most observations of megafauna-linked trophic interactions are from the oceans. We still know very little about the trophic impacts of freshwater megafauna, particularly top predators, compared to their marine or terrestrial counterparts, limiting their integration into trophic rewilding efforts. Observing direct interactions between freshwater megafauna and other species in the field is challenging because many of them are cryptic, and their feeding activities often occur in aquatic environments with low levels of visibility. Diet data have been documented for many freshwater megafauna based on their stomach contents or faeces, which could lead to bias towards prey with hard structures that remain undigested in stomachs and might not accurately reflect their full diet or influence on local trophic dynamics (Somaweera *et al.*, 2020). The inclusion of emerging methodologies such as DNA barcoding approaches can improve our understanding of trophic interactions between megafauna and smaller species in freshwater environments (De Sousa, Silva & Xavier, 2019). In addition, controlled experiments to monitor how local trophic dynamics change when the presence and population abundance of freshwater megafauna are manipulated would be particularly beneficial for that purpose.

(4) Human–megafauna interactions

Human–nature interactions ultimately determine the implementation and outcomes of restoration actions. Ecologists and social scientists should collaborate to investigate

interactions between freshwater megafauna and human social systems to facilitate sustainable management strategies and improve human–freshwater megafauna coexistence in different environmental contexts (e.g. from natural to human-modified and urban freshwater systems). In regions such as the Amazon, Congo, and Mekong basins, freshwater megafauna are often closely associated with the livelihood and culture of indigenous peoples and local communities (Freitas *et al.*, 2020; Hogan, 2011; Noble *et al.*, 2016). Through collaboration with local communities and documenting their local ecological knowledge we can improve our understanding of beneficial NCP provided by freshwater megafauna (e.g. food and feed, supporting identities) and human–megafauna bonds. When planning for conservation and restoration actions, we need to assess the potential detrimental NCP associated with freshwater megafauna (e.g. competition for habitats and resources, damage to property, and risk to human life) and the frequencies of detrimental NCP, as well as when and where detrimental NCP occur (Ceauşu *et al.*, 2019). Such information will assist researchers in assessing how the benefits and costs of restoring freshwater megafauna populations will be shared by different groups. Although people often do not directly encounter wild freshwater megafauna in many parts of the world, including most urban areas in the Global South and most areas of the Global North, it is also important to investigate their perceptions of these large animals. It will provide insights into how to increase people's appreciation of freshwater megafauna and raise public awareness of freshwater biodiversity conservation. In turn this can benefit conservation and restoration actions, such as the establishment of new protected areas and reintroduction of freshwater megafauna, by influencing policymakers' decisions and increasing the potential for ecotourism.

Apart from influencing the population abundance of freshwater megafauna in their native ranges, humans also introduce these large animals to other regions for aquaculture, recreational fishing, biological control, or as pets (Chen *et al.*, 2023; White *et al.*, 2023). While the introduction of alien species does not inevitably have adverse impacts, some alien populations of freshwater megafauna have been shown to impact native species negatively through altering habitat structure and biotic interactions in the recipient ecosystems (Witte *et al.*, 2000; Chen *et al.*, 2023). Conversely, the novel (introduced) ranges of species such as Chinese giant salamander and large salmonids have become strongholds, while they have experienced population declines and range contraction in their native ranges (Browne *et al.*, 2014; Chen *et al.*, 2023). Thus, introduction of freshwater megafauna to non-native regions might be an option to prevent species extinction and restore ecosystem functions lost due to native megafauna extinctions, but their environmental and socio-economic impacts in the recipient ecosystems must first be thoroughly investigated (Chen *et al.*, 2023; Subalusky *et al.*, 2023). Such investigations could provide valuable information for conserving freshwater megafauna, managing introductions, and justifying their removal from non-native ecosystems.

VIII. CONCLUSIONS

(1) Our review compiled evidence documenting the ecological impacts of freshwater megafauna. These species shape freshwater ecological processes through their influences on habitat structure, flow dynamics, biogeochemical cycling, and biotic interactions.

(2) Declines in population abundance and loss of large individuals of freshwater megafauna, due to overexploitation and habitat destruction, have rapidly and profoundly reduced their ecological impacts in fresh waters.

(3) Restoring populations of freshwater megafauna is a promising approach for leveraging co-benefits between biodiversity conservation, ecological restoration, and NCP. We propose that reinstating freshwater megafauna populations holds the potential for restoring key ecological processes (e.g. disturbances, trophic cascades, and dispersal) and promoting overall freshwater biodiversity. It can also enhance NCP for local human communities, e.g. through provisioning aquatic resources, mitigating the effects of extreme weather events, and supporting cultural identities.

(4) Potential detrimental NCP associated with megafauna restoration, including competition for habitats and resources, damage to human property, and risk to human life, needs to be acknowledged and carefully addressed to improve human–freshwater megafauna coexistence.

(5) We still have a limited understanding of the roles of freshwater megafauna in shaping ecosystem functioning. Key research gaps relate to (*i*) historical baselines regarding distributions and abundance of freshwater megafauna, (*ii*) their life history, (*iii*) interactions with other freshwater species, and (*iv*) interactions with humans. Filling these gaps is important to understand the role of these species in freshwater ecosystems, their full potential for ecosystem restoration, and how the coexistence of humans and megafauna in different environments can be achieved.

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XI. SUPPORTING INFORMATION

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

Table S1. List of extant and recently extinct freshwater megafauna species.

Table S2. Definitions and examples of different levels of megafauna impacts on ecological processes and nature's contributions to people.

Appendix S1. Sources and licences for the images used in Figs 2 and 4.