

PRIMARY RESEARCH ARTICLE

The global decline of freshwater megafauna

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Abstract

Freshwater ecosystems are among the most diverse and dynamic ecosystems on Earth. At the same time, they are among the most threatened ecosystems but remain underrepresented in biodiversity research and conservation efforts. The rate of decline of vertebrate populations is much higher in freshwaters than in terrestrial or marine realms. Freshwater megafauna (i.e., freshwater animals that can reach a body mass ≥ 30 kg) are intrinsically prone to extinction due to their large body size, complex habitat requirements and slow life-history strategies such as long life span and late maturity. However, population trends and distribution changes of freshwater megafauna, at continental or global scales, remain unclear. In the present study, we compiled population data of 126 freshwater megafauna species globally from the Living Planet Database and available literature, and distribution data of 44 species inhabiting Europe and the United States from literature and databases of the International Union for Conservation of Nature and NatureServe. We quantified changes in population abundance and distribution range of freshwater megafauna species. Globally, freshwater megafauna populations declined by 88% from 1970 to 2012, with the highest declines in the Indomalaya and Palearctic realms (–99% and –97%, respectively). Among taxonomic groups, mega-fishes exhibited the greatest global decline (–94%). In addition, freshwater megafauna experienced major range contractions. For example, distribution ranges of 42% of all freshwater megafauna species in Europe contracted by more than 40% of historical areas. We highlight the various sources of uncertainty in tracking changes in populations and distributions of freshwater megafauna, such as the lack of monitoring data and taxonomic and spatial biases. The detected trends emphasize the critical plight of freshwater megafauna globally and highlight the broader need for concerted, targeted and timely conservation of freshwater biodiversity.

KEYWORDS

biodiversity, conservation, distribution, extinction, population, range contraction, size, vertebrate

1 | INTRODUCTION

Biodiversity loss is one of the biggest challenges facing our planet, leading to the erosion of ecosystem functions and services and

threatening human well-being (Diaz, Fargione, Chapin, & Tilman, 2006; Oliver et al., 2015). Surface freshwaters, including rivers and lakes, cover approximately 1% of Earth's surface, yet harbor around one third of all vertebrates and nearly half of all fish species

globally (Balian, Segers, Leveque, & Martens, 2008; Carrete-Vega & Wiens, 2012). Concurrently, freshwaters are exposed to multiple persistent and emerging threats (Dudgeon et al., 2006; Reid et al., 2019). Consequently, they are among the most threatened ecosystems globally, with their degradation likely to continue—or even accelerate—into the near future. For example, approximately 3,700 additional large hydropower dams are planned or under construction, increasing the fragmentation of rivers worldwide (Grill et al., 2015, 2019; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). Accelerating hydropower development and overexploitation, particularly in highly diverse river basins such as the Mekong, Congo, and Amazon may cause the extinction of hundreds of freshwater species (Castello et al., 2013; Winemiller et al., 2016). Current conservation actions fall short in safeguarding freshwater habitats and biodiversity, as freshwater ecosystems are rarely targeted in conservation management strategies and actions (Abell, Lehner, Thieme, & Linke, 2017; Darwall et al., 2018; Harrison et al., 2018). Consequently, a third of all classified freshwater species are threatened with extinction according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Collen et al., 2014). Furthermore, the rate of decline of freshwater vertebrate populations is twice as high as in terrestrial or marine ecosystems (McRae, Deinet, & Freeman, 2017).

Large-bodied animals are particularly susceptible to extinction owing to their intrinsic characteristics such as complex habitat requirements, low reproductive output, and late maturity (Cardillo et al., 2005; Olden, Hogan, & Vander Zanden, 2007; Winemiller, Humphries, & Pusey, 2015; Zuo, Smith, & Charnov, 2013). The term *megafauna* is widely used to describe large-bodied animals, despite inconsistent definitions existing between ecosystems and taxonomic groups (Ripple et al., 2019). Here, we use the term operationally, but for our analyses we restrict the use of the term to freshwater megafauna (i.e., 207 freshwater animal species with reported maximum body mass ≥ 30 kg), as introduced by He et al. (2017) and Carrizo et al. (2017). In freshwaters, 34 megafauna species have been assessed as Critically Endangered, and 51 species as Endangered or Vulnerable (IUCN, 2018). The baiji (*Lipotes vexillifer*) and Chinese paddlefish (*Psephurus gladius*) have not been recorded for over a decade, and the long-term survival of many sturgeon species (e.g., the Adriatic sturgeon, *Acipenser naccarii*; Yangtze sturgeon, *Acipenser dabryanus*; and Chinese sturgeon, *Acipenser sinensis*) currently depends on artificial stocking enhancement (Bronzi, Rosenthal, & Gessner, 2011; Xie, 2017).

Unless a catastrophic event occurs, it may take years to decades for a species to become completely extinct. This is particularly the case for freshwater megafauna characterized by long life span (e.g., over 50 years for many sturgeons, crocodylians, and giant turtles). Individuals may remain in rivers and lakes for several decades after natural reproduction has ceased (i.e., functional extinction; Jarić, Gessner, & Solow, 2016). Due to the time lag between species decline and extinction, the window of opportunity for conservation and restoration could be missed. Population decline and range contraction are preludes to species extinction, since they respond rapidly to

short-term environmental changes (Ceballos & Ehrlich, 2002; Collen et al., 2009; Wolf & Ripple, 2017). Therefore, they are sensitive indicators of biodiversity loss and ecosystem degradation, often more so than species extinction (Channell & Lomolino, 2000; Collen et al., 2011). Monitoring population trends and distribution changes obtained from observations can inform managers about the status and trends of individual species, thereby facilitating the development of proactive conservation strategies and related management actions. In addition, analyses of range contractions provide spatially explicit information for conservation management, including the planning and establishment of protected areas as well as of restoration targets (Wolf & Ripple, 2017).

Population declines and range contractions have been well documented for terrestrial and marine megafauna (Myers & Worm, 2003; Wolf & Ripple, 2017; Worm & Tittensor, 2011). However, monitoring of freshwater megafauna species remains limited, particularly at continental or global scales. Therefore, our aims are twofold: (a) to quantify changes in population abundance of freshwater megafauna globally and (b) to determine changes in distribution range (i.e., contemporary distribution range compared to historical distribution range in ca 1,500 AD) of freshwater megafauna in regions where adequate data are available (i.e., Europe and the United States). We hypothesize that freshwater megafauna populations exhibit a larger decline than overall freshwater vertebrates, primarily because they are characterized by extinction-prone traits and subject to intense anthropogenic threats (Carrizo et al., 2017; He et al., 2017, 2018). Compared to other taxonomic groups, mega-fish species are generally more vulnerable to dam construction as dams block their migratory routes and their access to spawning and feeding grounds (Carrizo et al., 2017; He et al., 2017). Thus, we expect the rate of decline in mega-fish populations to be the largest among all taxonomic groups. Moreover, freshwater megafauna species usually have large habitat requirements, therefore, often require cross-boundary conservation efforts. Both Europe and the United States have established many environmental conservation programs and frameworks (e.g., Nature 2000, Water Framework Directive in Europe, Endangered Species Act, Magnuson-Stevens Fishery Conservation and Management Act in the United States). However, in Europe, the implementation of conservation programs and frameworks at river basin scale is often challenging due to political boundaries. In addition, Europe has a denser human population and a longer history of exploiting freshwater megafauna species when compared with the United States. Hence, we hypothesize that the range contractions of freshwater megafauna species are greater in Europe than in the United States.

2 | MATERIALS AND METHODS

2.1 | Population abundance

The underlying list of freshwater megafauna species (i.e., 207 freshwater animal species that can reach a body mass ≥ 30 kg) was taken from He et al. (2018). We compiled global population data for 126 freshwater megafauna species (i.e., 81 fishes, 22 mammals, 21

reptiles, and 2 amphibians), totaling 639 individual time series (see Table S1) and covering 72 countries or regions (Figure S1). Population data for 72 freshwater megafauna species were available from the Living Planet Index database (www.livingplanetindex.org), a continuously updated global database of vertebrate populations. Population data for a further 54 species were collated from published papers and reports. Despite an intensive search, no comprehensive data for the remaining 81 species were available. Population data were only included in the analysis if they fulfilled the following criteria (Collen et al., 2009): (a) population data were collected or estimated applying the same method throughout the time period; (b) data were available for at least 2 years after 1970; (c) the geographic area (e.g., sampling location or catchment) of the specific population was recorded; and (d) the data source was referenced.

Excluding the two amphibian species (i.e., the Chinese giant salamander, *Andrias davidianus*; and Japanese giant salamander, *Andrias japonicus*), population data coverage was highest for mammals (i.e., time series data for 73% of mammalian freshwater megafauna were available), followed by fishes (62%) and reptiles (48%). On average, mammals, fishes, and reptiles all had five time series per species. However, for fishes, the number of time series per species reduced to 3 when salmonids and sturgeons (23 species combined) were excluded. Geographically, the highest number of time series data for freshwater megafauna were available for Norway (107), the United States (92), and Canada (61), primarily due to the high data density of salmonids (Figure S1). In contrast, time series data in freshwater megafauna-rich regions, such as Southeast Asia (21), South America (47), and Africa (50), were scarce.

To compare changes in the inventories of freshwater megafauna populations against overall freshwater vertebrate populations reported in the Living Planet Report by World Wildlife Fund (WWF, 2018), we followed the approach given in the Living Planet Report. Similarly, 1970 was considered as the reference year and 2012 was chosen to represent the contemporary state, due to time delays in data publications and updates (McRae et al., 2017; WWF, 2018). Population trends were calculated using the *rlpi* package (McRae et al., 2017) in R (R Core Team, 2016). The calculation procedure is summarized below (see McRae et al., 2017 for further details). For time series including fewer than six data points, the chain method was utilized to estimate the change in the population inventory (Loh et al., 2005), while generalized additive models were applied to the remaining time series having six or more data points. To avoid taxonomic or geographical biases, each taxonomic group and biogeographic realm were weighted proportionally according to their contribution to the overall freshwater megafauna diversity (McRae et al., 2017). For example, fishes represented 49.5% of all freshwater megafauna species in the Neotropical realm. As such, this value was used to weight the contribution of fish species to the overall population trend of freshwater megafauna species in the Neotropical realm. The 95% confidence intervals (CIs) were generated by bootstrapping (1,000 times). Changes in the population inventory were calculated for different biogeographic realms and taxonomic groups including fishes, reptiles, and mammals.

2.2 | Distribution range

Based on previously established databases (Carrizo et al., 2017; He et al., 2018), we identified all freshwater megafauna species that currently occur in Europe or the United States. For both regions, contemporary and historic distribution ranges for all 44 species were available. The distribution range data were derived from literature and the IUCN and NatureServe databases (IUCN, 2018; NatureServe, 2018) which were developed as part of the comprehensive assessments of biodiversity by IUCN and NatureServe (see www.iucnredlist.org/resources and explorer.natureserve.org/eodist.htm for detailed methodology). Only the native distribution range (i.e., Origin status coded as "Native" by IUCN or NatureServe) was considered in the analysis. The classification systems for occurrence status are slightly different between IUCN and NatureServe. For IUCN-derived data, areas with Presence status coded as "Extant" or "Probably Extant" were considered to represent the current distribution ranges of species. For data derived from NatureServe, areas with Occurrence status coded as "Current" were included for current distributions. For historical distributions (i.e., where species were formerly known or very likely to occur in an area), the reference year was set to ca 1,500 AD following IUCN Red List (IUCN, 2018). For the United States, NatureServe includes records of species occurrences from the time of European settlement, which is also after 1,500 AD (NatureServe, 2018). Choosing ca 1,500 AD as the reference year could be arbitrary. However, distribution data of freshwater megafauna prior to the 16th century are largely unavailable. Thus, areas with Presence status coded as "Possibly Extinct" or "Extinct" by IUCN, or with Occurrence status coded as "Historical" by NatureServe were included to represent historical distributions of species. All distribution data were converted into HydroBASINS (level 8; Lehner & Grill, 2013) following Carrizo et al. (2017), representing spatial information at the sub-catchment scale. The historical and current distributions of freshwater megafauna in Europe and the United States (excluding Alaska, Hawaii, and other overseas territories due to data deficiency) were mapped using QGIS (QGIS Development Team, 2017) and species richness in each HydroBASINS level 8 sub-catchment was calculated. If part of a sub-catchment (e.g., Lakes Superior, Huron, Erie, and Ontario) fell within the country border, the whole sub-catchment was kept in the analysis. Finally, the change in distribution area for each species was calculated with relation to its historical distribution area using the following equation:

$$\text{Fraction of range contraction} = \frac{\text{Historical distribution area} - \text{Current distribution area}}{\text{Historical distribution area}}$$

3 | RESULTS

Temporally, global freshwater megafauna populations declined by 88% from 1970 to 2012 (CIs: -80% to -92%; Figure 1a). Mega-fishes exhibited the largest decline (-94%; CIs: -85% to -97%; Figure 1b), followed by mega-reptiles (-72%; CIs: -94% to +13%; Figure S2b), while mega-mammal populations increased by 29% (CIs: -20% to

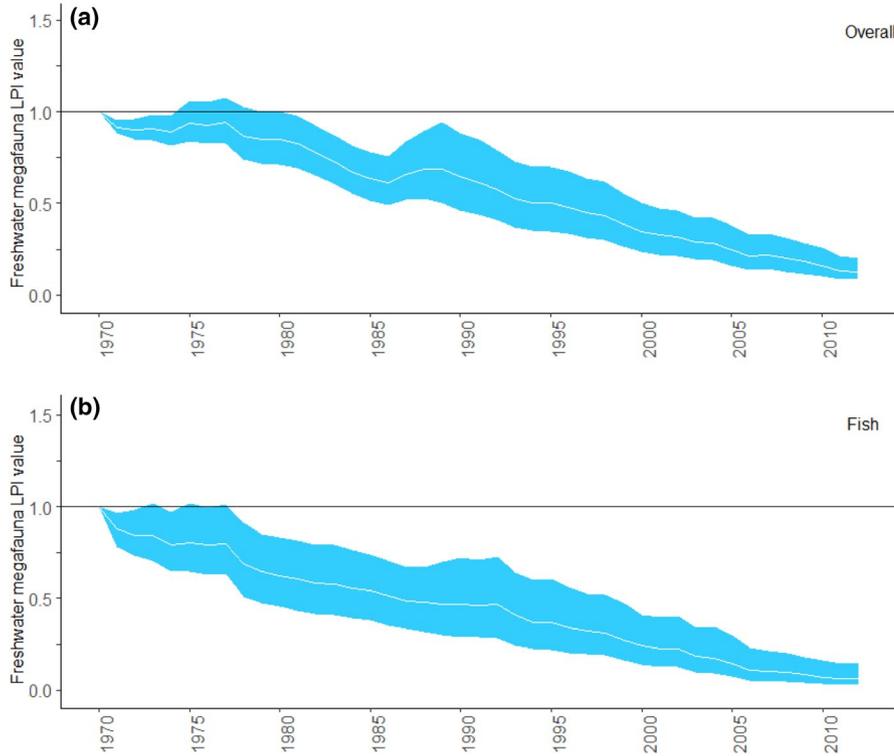


FIGURE 1 Changes in the population inventory of (a) global freshwater megafauna (126 species; 639 time series) and (b) mega-fish species (81 species; 404 time series) from 1970 to 2012. The value of the Living Planet Index (LPI) was set to 1 in the reference year 1970

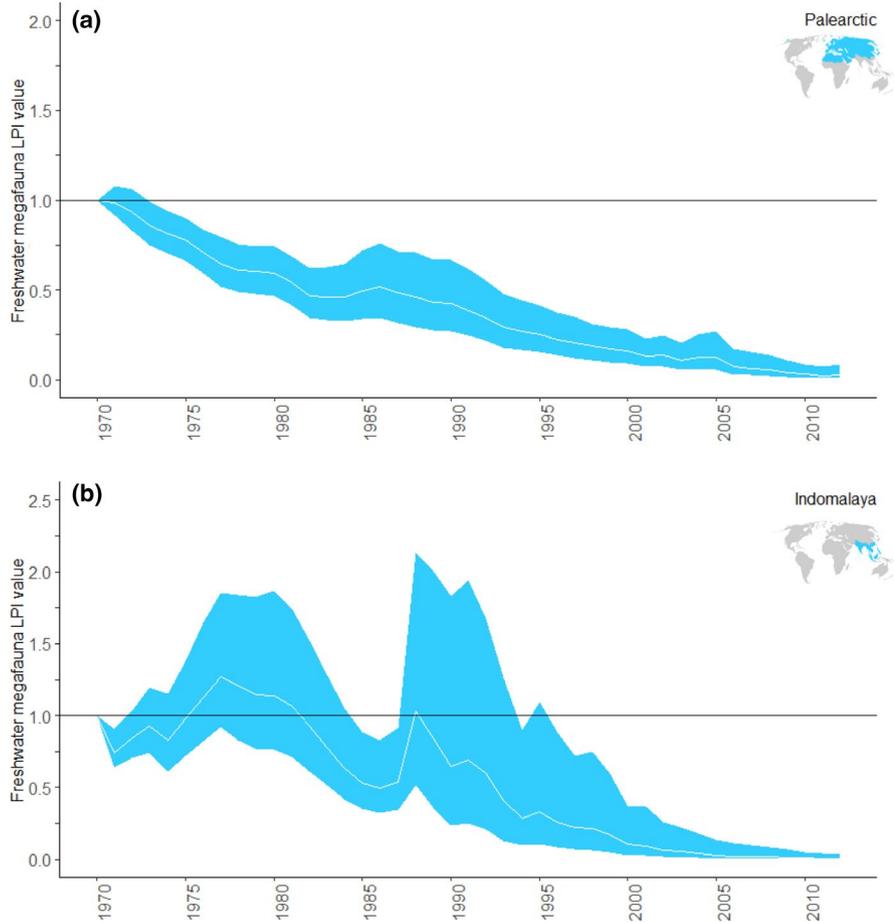


FIGURE 2 Changes in the population inventory of freshwater megafauna in (a) Palearctic (37 species; 239 time series) and (b) Indomalaya (25 species; 63 time series) realms from 1970 to 2012. The value of the Living Planet Index (LPI) was set to 1 in the reference year 1970

+125%; Figure S2a). However, CIs were very wide for mega-reptile and mega-mammal populations, primarily due to the limited number of species and population time series data available.

Spatially, freshwater megafauna populations exhibited the largest declines in the Indomalaya (−99%; CIs: −100% to −97%; Figure 2b) and Palearctic realms (−97%; CIs: −91% to −99%; Figure 2a). The sharp decline of Indomalayan populations began in the late 1980s, while Palearctic populations exhibited a continuous decline since 1970. Compared to those in the Indomalaya and Palearctic realms, freshwater megafauna populations exhibited smaller yet distinct

declines in the Afrotropical (−81%; CIs: −92% to −55%; Figure S3a) and Nearctic (−57%; CIs: −80% to −13%; Figure S3c) realms, with a stabilizing trend in both realms since the early 2000s. Population declines also occurred in the Neotropical (−64%) and Australasia realms (−3%); however, CIs are distinct (CIs: −20% to −67%, and −77% to +270%, respectively; Figure S3).

Changes in distribution ranges were assessed for all 44 freshwater megafauna species in Europe and the United States (Figure 3). For example, the once very common European sturgeon (*Acipenser sturio*) has been extirpated from all major European rivers, except the

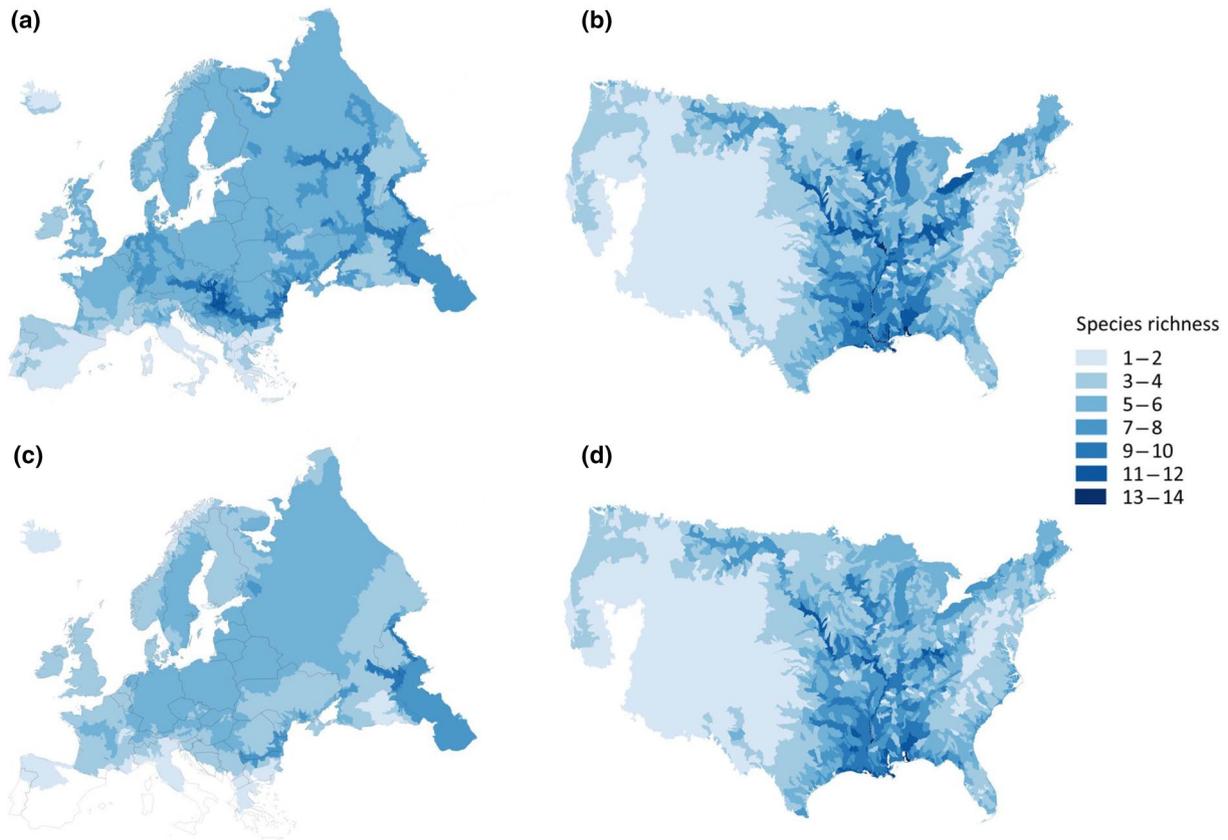


FIGURE 3 Species richness of freshwater megafauna for historical, i.e., ca 1,500 AD (a, b) and present day (c, d) in Europe (left) and the United States (right, excluding Alaska, Hawaii, and other overseas territories)

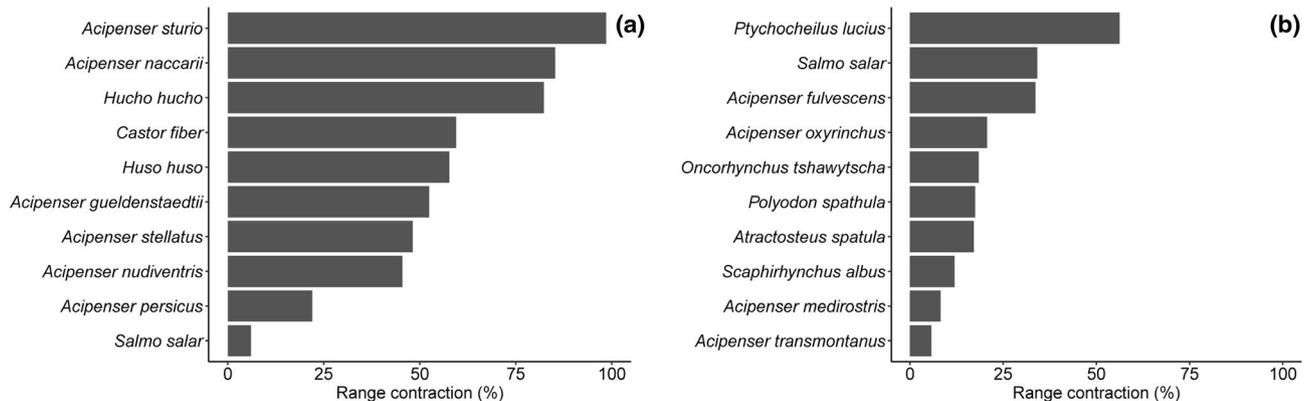


FIGURE 4 Ten freshwater megafauna species with the biggest range contractions in (a) Europe and (b) the United States

Garonne River (France). In the Danube and Volga rivers, sturgeon species, including the Russian sturgeon (*Acipenser gueldenstaedtii*), Persian sturgeon (*Acipenser persicus*), ship sturgeon (*Acipenser nudiventris*) and Stellate sturgeon (*Acipenser stellatus*), are restricted to downstream sections, primarily due to the construction of large dams. Compared to Europe, range contractions were less pronounced in the United States. However, species such as the lake sturgeon (*Acipenser fulvescens*), alligator gar (*Lepisosteus spatula*), and paddlefish (*Polyodon spathula*) have been extirpated in some parts of the Missouri and middle Mississippi river basins, as well as in the Great Lakes region.

Regarding individual species (Figure 4), the European sturgeon had the greatest proportional range contraction (−99%), followed by the Adriatic sturgeon (*A. naccarii*; −85%) and the Danube salmon (*Hucho hucho*; −82%). In Europe, eight species (42% of all species) lost more than 40% of their historical distribution range, compared to a single species (the Colorado pikeminnow, *Ptychocheilus lucius*) in the United States. Among the 20 species with the largest range contractions (i.e., 10 species each in Europe and the United States), the Eurasian beaver (*Castor fiber*) was the only non-fish species.

4 | DISCUSSION

To our knowledge, this is the first comprehensive study tracking changes in the population inventory of freshwater megafauna at the global scale. The results demonstrate that freshwater megafauna populations exhibit even larger declines (−88%) than those in overall freshwater vertebrates (−81%), which is twice of the decline reported in terrestrial (−38%) or marine (−36%) vertebrate populations (McRae et al., 2017). In addition to population declines, major range contractions of freshwater megafauna have been observed, which is more pronounced in Europe than in the United States.

4.1 | Uncertainty in population and distribution data of freshwater megafauna

Our results show a clear decline of freshwater megafauna across the globe. However, there are significant sources of uncertainty in tracking changes in population inventory and distribution range of freshwater megafauna. Primarily, this is due to a general paucity of long-term monitoring data available for these species. In addition, for existing data, a significant temporal, taxonomic, and spatial bias is evident.

Population data for the early 1970s are scarce (Figure S4). Moreover, the quantity of data in the recent decade is limited due to the time lag in data publication. In addition, populations of many freshwater megafauna species, such as sturgeons, had shown a declining trend before 1970 (Billard & Lecointre, 2001), which could have led to shifted baselines (Humphries & Winemiller, 2009; Pauly, 1995). Furthermore, IUCN Red List assessments suggest that many freshwater megafauna species, including the Mekong giant salmon carp (*Aptosyax grypax*), pangas catfish (*Pangasius pangasius*), and yellowcheek (*Elopichthys bambusa*), have experienced a severe population decline (IUCN, 2018). However, these species were not

included in the analysis due to a lack of available time series data. Consequently, an even sharper population drop would likely have been demonstrated if more species had been monitored and data made available.

The gaps in population data are particularly obvious for megareptiles and mega-fishes other than sturgeons and salmonids. Sturgeons and salmonids account for just 18% of all mega-fish species, yet contribute 60% of all time series for mega-fishes in this study. Furthermore, for 73% of all mega-mammals, one or more time series were available. Conversely, data for 52% of mega-reptiles were not available. This is consistent with the current monitoring prioritization (i.e., focus on mammals and economically valuable species; Ford, Cooke, Goheen, & Young, 2017).

Spatial gaps remain in monitoring freshwater megafauna populations. When taken together, Africa, Asia, and South America have contributed a mere 35% of all time series data, yet harbor 77% of all global freshwater megafauna species. This mirrors the current biodiversity and conservation research distribution (Tydecks, Jeschke, Wolf, Singer, & Tockner, 2018; Wilson et al., 2016). For mega-reptiles, such as crocodylians and giant turtles, six species in the Australasia and Nearctic realms contributed 54% of all time series, yet more than 80% of all mega-reptiles inhabit the Afrotropical, Indomalaya, and Neotropical realms. In these realms, mega-reptiles have experienced sharp population declines (Cheung & Dudgeon, 2006; He et al., 2017). Compared to those in the Afrotropical, Indomalaya, and Neotropical realms, mega-reptiles in both the Nearctic and Australasia realms are well protected and have relatively stable or even increasing populations. As such, inconsistencies in population trends among different species and biogeographic realms caused the broad CIs when tracking population trends in mega-reptiles, as well as in mega-mammals.

Similar uncertainty also exists for spatial distribution data of freshwater megafauna. For example, data on historical distributions of freshwater megafauna are mainly based on early literature or museum records (IUCN, 2018; NatureServe, 2018). Considering that many freshwater megafauna species live under water or in rural areas, some of their previous distribution areas are likely to be overlooked in these records, leading to an underestimation of historical distribution range. In addition, only native distribution ranges were considered in our study, as up-to-date information on non-native distribution ranges was often unavailable. Thus, shifts in spatial distribution of freshwater megafauna due to introduction or species invasion are not shown here (e.g., the wels catfish, *Silurus glanis*, an invasive mega-fish in many European catchments; Cucherousset et al., 2018). Moreover, information on historical distribution ranges of freshwater megafauna outside of Europe and the United States is largely unavailable, which has limited our ability to gain a comprehensive picture of global change in freshwater megafauna distribution.

4.2 | The loss of freshwater megafauna

Two main factors could have contributed to the severe decline of global freshwater megafauna: First, their complex habitat requirements, low fecundity, and slow life history make them less flexible toward

environmental changes and thus more prone to extinction. Second, they are subject to intense anthropogenic threats (He et al., 2017). Among these threats, overexploitation remains the key threat, since meat, eggs, and skin from sturgeons, crocodiles, and turtles are used as luxury food and medicines (Bronzi & Rosenthal, 2014; Cheung & Dudgeon, 2006; Ripple et al., 2019). In addition, conflicts between freshwater megafauna and humans have escalated due to their large habitat requirements and the rapidly increasing human population and expanding anthropogenic activities (He et al., 2018). This has led to increased mortality rates caused by direct killing (Dunham, Ghiurghi, Cumbi, & Urbano, 2010) or through accidents, such as vessel collisions (Nowacek et al., 2004; Wang, 2009). Furthermore, habitat loss and degradation associated with dams and pollution also contribute to population declines and range contractions of freshwater megafauna (He et al., 2017; Hogan, 2011; Winemiller et al., 2015).

Among all taxonomic groups, mega-fishes are in a particularly dire situation due to their high susceptibility to both overexploitation and dam construction (Carrizo et al., 2017; He et al., 2017). Indeed, the Russian sturgeon, Amur sturgeon (*Acipenser schrenckii*), Chinese sturgeon, and ship sturgeon have experienced population declines of over 90% during the past three generations (IUCN, 2018). In megafauna-rich basins, such as the Mekong and Amazon, the situation is continuously deteriorating. For example, populations of mega-fishes in the Mekong River basin have dropped close to zero (Gray, Phommachak, Vannachomchan, & Guegan, 2017; Hogan, 2011; Ngor et al., 2018). This includes the Mekong giant catfish (*Pangasianodon gigas*), giant Siamese carp (*Catlocarpio siamensis*), and giant pangasius (*Pangasius sanitwongsei*). Furthermore, Arapaima (*Arapaima* spp.) have been locally extirpated from 19% of surveyed fish communities along the main stem of the Amazon River (Castello, Arantes, McGrath, Stewart, & Sousa, 2015). Considerably more worrisome is the predicted intensification of existing pressures facing mega-fishes in basins such as the Amazon, Congo, and Mekong due to the boom in hydropower dam construction (Winemiller et al., 2016).

High levels of freshwater megafauna richness are usually associated with high levels of overall freshwater biodiversity (Carrizo et al., 2017). Freshwater megafauna species perform essential ecological roles and function as top predators or keystone species in their respective habitats (Bakker, Pages, Arthur, & Alcoverro, 2016; Hammerschlag et al., 2019; He et al., 2017; Moore, 2006). The extirpation of top predators, such as crocodilians and large piscivore fishes, causes the simplification of food webs, which in turn has severe impacts on ecological processes and functioning through trophic cascades (Hanson et al., 2015; Winemiller et al., 2015). This flow of causality ultimately results in the reduced resistance of whole communities and ecosystems to external threats (Brose et al., 2017). In addition, freshwater megafauna such as hippos, beavers, and crocodilians modify river morphology and riparian vegetation, creating and maintaining the complexity of local habitats. Many small animal and plant species will lose these habitats or refugia during drought periods if beaver dams or small pools maintained by crocodilians and hippos disappear (Moore, 2006). The depletion of freshwater megafauna may also lead to interrupted seed dispersal (Anderson, Rojas,

& Flecker, 2009; Costa-Pereira et al., 2018) and nutrient cycling between freshwater, marine, and terrestrial ecosystems (Janetski, Chaloner, Tiegs, & Lamberti, 2009; Service et al., 2019).

4.3 | Implications for freshwater biodiversity conservation

Despite the plight of freshwater megafauna described in this study, opportunities to protect them still exist if timely and effective conservation strategies are implemented. Owing to persistent conservation efforts, populations of 13 freshwater megafauna species (e.g., the green sturgeon, *Acipenser medirostris*; white sturgeon, *Acipenser transmontanus*; and American beaver, *Castor canadensis*) in the United States are stable or increasing (He et al., 2018). Conversely, in Europe, efficient conservation actions on a large scale are difficult to establish and fully implement due to political boundaries and variations in economic development and environmental awareness among countries (Kukkala et al., 2016). Nevertheless, the Eurasian beaver has been reintroduced into many areas of its previous distribution range including the Czech Republic, Estonia, Finland, Sweden, and the UK (Halley, 2011). In Asia, the population of the Irrawaddy river dolphin (*Orcaella brevirostris*) has recently shown the first-time increase in the last two decades (WWF Cambodia, 2018). The population trends of global mega-mammals and freshwater megafauna in the United States confirm that targeted conservation actions can benefit freshwater megafauna and lead to increasing population size (He et al., 2018). In addition, the long life span of freshwater megafauna might provide a larger time window for implementing novel molecular techniques to save them from extinction.

However, current monitoring and targeted conservation actions for the vast majority of freshwater megafauna appear inadequate. Compared to megafauna in terrestrial or marine realms, they have received much less research, conservation efforts, and public attention (Courchamp et al., 2018; He & Jähnig, 2019; He et al., 2017). For example, IUCN Red List assessments are insufficient for a quarter of all freshwater megafauna species, most notably in South America (He et al., 2018). In addition, knowledge on migratory routes and spawning grounds of freshwater megafauna, such as giant catfishes in South and Southeast Asia, is still limited (Hogan, 2011). This will hinder the establishment of effective conservation strategies (e.g., optimization of dam locations) to prevent the extinction of these species, especially considering the increase in the prevalence of hydropower dams (Winemiller et al., 2016; Zarfl et al., 2015).

Considering the human fascination with megafauna species, freshwater megafauna could and should be leveraged to inform the public of the crisis in freshwaters and promote conservation for overall freshwater biodiversity (Carrizo et al., 2017). Several freshwater megafauna species (the Yangtze finless porpoise [*Neophocaena asiaeorientalis asiaeorientalis*] in China, the Irrawaddy river dolphin, and Mekong giant catfish in the Greater Mekong region) have already been listed as flagship species by the WWF. Possibly extinct species, such as the baiji, also have the potential to raise public awareness for conservation, particularly

given it is a well-known species and its extinction was caused by human activities (Kyne & Adams, 2017). Conversely, the concerns from terrestrial species conservation that giving priority to well-monitored megafauna could have negative impacts on small species because of limited conservation resources (Ford et al., 2017) should be carefully considered and balanced.

In addition, freshwater megafauna species can indicate the integrity of an ecosystem (Gómez-Salazar, Coll, & Whitehead, 2012; Mazzotti et al., 2009), since they have large and complex habitat requirements and are sensitive to environmental degradation. As such, megafauna-based conservation strategies could benefit a broad range of species sharing the same habitats (Carrizo et al., 2017). Indeed, they are associated with high freshwater biodiversity and share common threats with small freshwater species (Dudgeon et al., 2006; He et al., 2017; Reid et al., 2019), meaning megafauna-based strategies hold the potential to benefit both megafauna and smaller species (Ford et al., 2017; Kalinkat et al., 2017). For example, the proposed Poyang Lake Water Control Project in China has raised vast public concerns due to its potential impact on the habitats of Yangtze Finless Porpoise. Negative influence on other freshwater species such as waterfowl and small fishes will be averted if these public concerns would make the government change the current plan.

Our study highlights the drastic population declines and range contractions of freshwater megafauna. The situation facing freshwater megafauna in the Indomalaya and Palearctic realms, and those of mega-fishes globally, is particularly dire due to overexploitation and dam construction. It is often suggested that freshwater species suffer a lack of focus for conservation, as they are largely out of sight and out of mind (Darwall et al., 2018; Ford et al., 2017; Monroe, Baxter, Olden, & Angermeier, 2009). Despite this, our work shows that even the best known of our freshwater species are in danger of being lost. Their highly threatened, yet overlooked, status also reflects the calamitous situation facing all freshwater biodiversity. There remain large gaps in freshwater megafauna monitoring and assessment, which is the first challenge that must be tackled. To aid the establishment of proactive conservation strategies, future studies focusing on population monitoring, distributions (e.g., key habitats, migratory routes), and life-history traits of freshwater megafauna are called for. These are particularly necessary in megafauna-rich basins (e.g., the Amazon, Congo, Mekong, and Ganges river basins) and must account for rapidly increasing and emerging threats. In addition, a comprehensive and regularly updated database of freshwater megafauna species is sorely needed, alongside a global initiative to combine and consolidate knowledge and data on freshwater biodiversity (Darwall et al., 2018).

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