Received: 30 August 2017 | Revised: 13 February 2018 | Accepted: 26 April 2018
DOI: 10.1111/ddi.12780

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Freshwater megafauna diversity: Patterns, status and threats

Fengzhi He[1,2,3] | Vanessa Bremerich[1] | Christiane Zarfl[4] | Jonas Geldmann[5] | Simone D. Langhans[1] | Jonathan N. W. David[6] | William Darwall[7] | Klement Tockner[1,2,8] | Sonja C. Jähnig[1]

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
[2]Institute of Biology, Freie Universität Berlin, Berlin, Germany
[3]School of Geography, Queen Mary University of London, London, UK
[4]Center for Applied Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany
[5]Department of Zoology, Conservation Science Group, University of Cambridge, Cambridge, UK
[6]School of Geography and the Environment, University of Oxford, Oxford, UK
[7]Freshwater Biodiversity Unit, IUCN Global Species Programme, Cambridge, UK
[8]Austrian Science Fund (FWF), Vienna, Austria

Correspondence
Fengzhi He, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany.
Email: fengzhi.he@igb-berlin.de

Present addresses
Simone D. Langhans, Department of Zoology, University of Otago, Dunedin, New Zealand and Basque Centre for Climate Change (BC3), Leioa, Spain.

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: “GLANCE” project (01 LN1320A); European Union’s Horizon 2020 Programme for Research, Technological Development and Demonstration, Grant/Award Number: AQUACROSS (642317); Villum Fonden, Grant/Award Number: VKR023371; Education, Audiovisual and Culture Executive Agency (Erasmus Mundus Joint Doctorate programme “SMART”); EU Marie Sklodowska-Curie programme, Grant/Award Number: H2020-MSCA-IF-2015-706784, H2020-MSCA-IF-2016-748625; Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg (Junior Professorship Program)

Editor: Gwen Iacona

Abstract

Aim: Freshwater megafauna remain underrepresented in research and conservation, despite a disproportionately high risk of extinction due to multiple human threats. Therefore, our aims are threefold; (i) identify global patterns of freshwater megafauna richness and endemism, (ii) assess the conservation status of freshwater megafauna and (iii) demonstrate spatial and temporal patterns of human pressure throughout their distribution ranges.

Location: Global.

Methods: We identified 207 extant freshwater megafauna species, based on a 30 kg weight threshold, and mapped their distributions using HydroBASINS subcatchments (level 8). Information on conservation status and population trends for each species was extracted from the IUCN Red List website. We investigated human impacts on freshwater megafauna in space and time by examining spatial congruence between their distributions and human pressures, described by the Incident Biodiversity Threat Index and Temporal Human Pressure Index.

Results: Freshwater megafauna occur in 76% of the world’s main river basins (level 3 HydroBASINS), with species richness peaking in the Amazon, Congo, Orinoco, Mekong and Ganges-Brahmaputra basins. Freshwater megafauna are more threatened than their smaller counterparts within the specific taxonomic groups (i.e., fishes, mammals, reptiles and amphibians). Out of the 93 freshwater megafauna species with known population trends, 71% are in decline. Meanwhile, IUCN Red List assessments reported insufficient or outdated data for 43% of all freshwater megafauna species. Since the early 1990s, human pressure has increased throughout 63% of their distribution ranges, with particularly intense impacts occurring in the Mekong and Ganges-Brahmaputra basins.

Main conclusions: Freshwater megafauna species are threatened globally, with intense and increasing human pressures occurring in many of their biodiversity hotspots. We call for research and conservation actions for freshwater megafauna, as they are highly sensitive to present and future pressures including a massive boom in hydropower dam construction in their biodiversity hotspots.

KEYWORDS

conservation, flagship species, freshwater biodiversity hotspot, human impact, size, umbrella species

1 | INTRODUCTION

Megafauna species have long fascinated humans due to their spectacular appearance (Donlan et al., 2006). Despite this, over the past 50,000 years, approximately two-thirds of megafauna species have become extinct globally, mainly due to direct anthropogenic impacts and climate change (Barnosky, Koch, Feranec, Wing, & Shabel, 2004). Furthermore, many remaining megafauna species are experiencing range contractions and population declines (Malhi et al., 2016; Wolf & Ripple, 2017). This decline and loss of megafauna species and populations can have profound effects on local ecosystems, leading to altered habitat conditions for co-occurring species, disruption of biogeochemical processes and loss of key ecosystem services (Estes, Heithaus, McCauley, Rasher, & Worm, 2016; Estes et al., 2011; Naiman, Bilby, Schindler, & Helfield, 2002; Smith, Doughty, Malhi, Svenning, & Terborgh, 2016). To date, research and conservation activities have predominantly focused on marine and terrestrial megafauna, neglecting those in freshwaters (Cooke et al., 2013; He et al., 2017).

Freshwaters support a disproportionally large amount of biodiversity (approximately 9.5% of all animal species and 35% of all vertebrate species, despite covering less than 1% of the earth's surface; excluding wetlands) (Balian, Segers, Lévêque, & Martens, 2008) and provide a wide range of important services for humans, including food supply, water purification, flood regulation, carbon sequestration, transportation etc. (Aylward et al., 2005). However, freshwater biodiversity is experiencing unprecedented and growing pressure from human activities (Dudgeon et al., 2006; Vörösmarty et al., 2010). At the same time, the rate of decline of vertebrate populations is much higher in freshwaters (81%) than in terrestrial (38%) and marine (36%) realms (WWF, 2016). Indeed, one in three freshwater species is under threat (Collen et al., 2014).

Large-bodied freshwater species, despite many being well-known and iconic, are threatened worldwide (e.g., 16 of the 25 sturgeon species are Critically Endangered; IUCN, 2016) due to intrinsic factors such as K-selected life-history characteristics and extrinsic pressures. Given the multiple threats they are facing, and their susceptibility to extinction, these large-bodied freshwater animals are in urgent need of conservation actions (Hogan, 2011; Winemiller, Humphries, & Pusey, 2015). Establishing effective conservation strategies for freshwater megafauna requires knowledge of their distribution patterns, population trends and underlying threats. However, there remain key knowledge gaps in the conservation status and population trends of freshwater megafauna species (Carrizo et al., 2017), and the relationship between global diversity patterns of freshwater megafauna and multiple human pressures.

A comprehensive understanding of global freshwater megafauna diversity patterns and their conservation status is also required to assess their risk of extinction. Spatial congruence analyses between species distribution and human pressures may highlight potential conflicts between human activities and freshwater megafauna diversity, which will enable identification of basins where high biodiversity and intense human pressure coincide (Janse et al., 2015; Kehoe et al., 2015). Such information will facilitate the development of proactive and sustainable conservation strategies such as spatial conservation prioritization (Linke, Pressey, Bailey, & Norris, 2007).

Building on a previous selection of ambassador freshwater megafauna species (Carrizo et al., 2017), we complement the species list to include all known extant freshwater megafauna species, identify hotspots of freshwater megafauna richness and endemism, and assess the global conservation status of these large-bodied animals. We then demonstrate spatial and temporal patterns of human pressures throughout their distribution ranges. Based on our analyses, we emphasise the future challenges of freshwater megafauna conservation and provide suggestions for conservation actions in different basins.

2 | METHODS

2.1 | Species distribution mapping

We compiled a comprehensive list of 207 extant freshwater megafauna species based on a pre-established 30 kg weight threshold

(Carrizo et al., 2017; He et al., 2017). The species list includes 130 fishes, 44 reptiles, 31 mammals and 2 amphibians (Table S1). As part of the assessments of species extinction risk for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter IUCN Red List), geographic distributions have been mapped for many species. Distribution maps for 155 of the 207 species were obtained from the IUCN Red List website (www.iucnredlist.org) (IUCN, 2016) and related databases and expert sources (e.g., the IUCN Species Survival Commission Specialist Groups). The standard spatial layer for IUCN distribution maps is the HydroBASINS dataset (version 1b with inserted lakes), which delineates catchments into 12 increasingly fine spatial resolutions using a hierarchically-nested approach at the global scale (Lehner & Grill, 2013). For freshwater biodiversity conservation, using HydroBASINS to map their distribution is essential, as management units for freshwaters are often delineated at the subcatchment scale (Hermoso, Linke, Prenda, & Possingham, 2011). Where a species distribution was not mapped to HydroBASINS by IUCN, we converted the existing range map to the subcatchment (level 8) of the HydroBASINS spatial layer. For species with no available map from the IUCN and related database (n = 52), we collected species distribution range descriptions from other databases (e.g., Fish Base, http://www.fishbase.org; NatureServe, http://www.natureserve.org), and from published literature (Table S2), to generate HydroBASINS distribution maps. For each species assessed and mapped for the IUCN Red List, "Presence" and "Origin" classifications were provided. "Presence" was coded as Extant, Probably Extant, Possibly Extant, Possibly Extinct, Extinct (post 1500), or Presence Uncertain, while "Origin" was coded as Native, Reintroduced, Introduced, Vagrant, or Origin Uncertain (IUCN, 2016). When creating new distribution maps, we followed the same approach as Carrizo et al., (2017). Only the native and currently extant (i.e., Extant, Probably Extant) ranges of a species were considered in this study. We derived species richness and threatened richness maps at the subcatchment (level 8) resolution of HydroBASINS. We also calculated freshwater megafauna richness within major basins such as the Amazon, Congo and Yangtze (level 3 HydroBASINS). Species restricted to a single, large level 3 basin were classified as basin-endemic species.

2.2 | Population trends and conservation status

We obtained population trends and conservation status for 170 freshwater megafauna species from the IUCN Red List website (IUCN, 2016). For the 37 species not assessed for the IUCN Red List, we considered their population trends as unknown. In addition, we also obtained the IUCN Red List Categories of all species classified as being freshwater dependent (25,965 species) from the underlying database, the IUCN Species Information Service, on 5th May 2016. Following the IUCN Red List classification, species listed as Critically Endangered, Endangered and Vulnerable were considered threatened. For the purposes of this study, we assumed that species listed as Data Deficient have the same proportion of threatened species as those with sufficient data. Therefore, the fraction of threatened species was calculated using the following equation:

$$\%\ \text{threatened} = (\text{Critically Endangered} + \text{Endangered} + \text{Vulnerable}) / (\text{total assessed} - \text{Extinct} - \text{Extinct in the Wild} - \text{Data Deficient})$$

2.3 | Human pressure on freshwater megafauna

The global spatial distribution and intensity of human impacts on freshwater megafauna were derived from the Incident Biodiversity Threat Index (IBTI), which combines multiple human stressors on freshwater ecosystems, including catchment disturbance, pollution, river fragmentation, exploitation pressure and invasive species (Vörösmarty et al., 2010). However, the IBTI and its layers represent a snapshot index of threats at a single point in time. In contrast, the Temporal Human Pressure Index (THPI) enables tracking of the temporal change in human pressures throughout freshwater megafauna distribution ranges. It presents levels of change between 1990 and 2010 for variables such as human population density, stable nightlight and land use transformation (Geldmann, Joppa, & Burgess, 2014). Although the initial purpose of the THPI was to track changes in the terrestrial environment, this index provides valuable information on the pressures facing freshwater ecosystems (e.g., habitat degradation, pollution), as rivers and lakes invariably receive the accumulated impacts of terrestrial based human activities throughout their catchments, occupying the lowest elevations in a landscape. In addition to the main IBTI and THPI indices, we analysed two sublayers of the IBTI separately, that is, dam density and fishing pressure, which are major threats to many freshwater megafauna species (He et al., 2017) but are not represented by threat layers included in the THPI.

The mean values for each HydroBASINS level 8 subcatchment of both IBTI and THPI were calculated using the zonal statistics tool in QGIS (Quantum GIS Development Team, 2015). Subcatchments with an IBTI value >0.75 were considered to have high levels of human pressure according to Vörösmarty et al. (2010), while those with a mean THPI value >0 were considered as having increased human pressure (Geldmann et al., 2014). Concordance maps were plotted to show the spatial relationship between freshwater megafauna diversity and human pressure. The colour axes were defined using the freshwater megafauna species richness and the value of human pressure indices. The IBTI, dam density and fishing pressure layers are available online (http://riverthreat.net/data.html) and the THPI data were provided by Geldmann et al. (2014).

3 | RESULTS

3.1 | Distribution and status of freshwater megafauna

Freshwater megafauna species occur in 76% of the world's main river basins (level 3 HydroBASINS) (Figure 1a; Figures S1 and S2). The

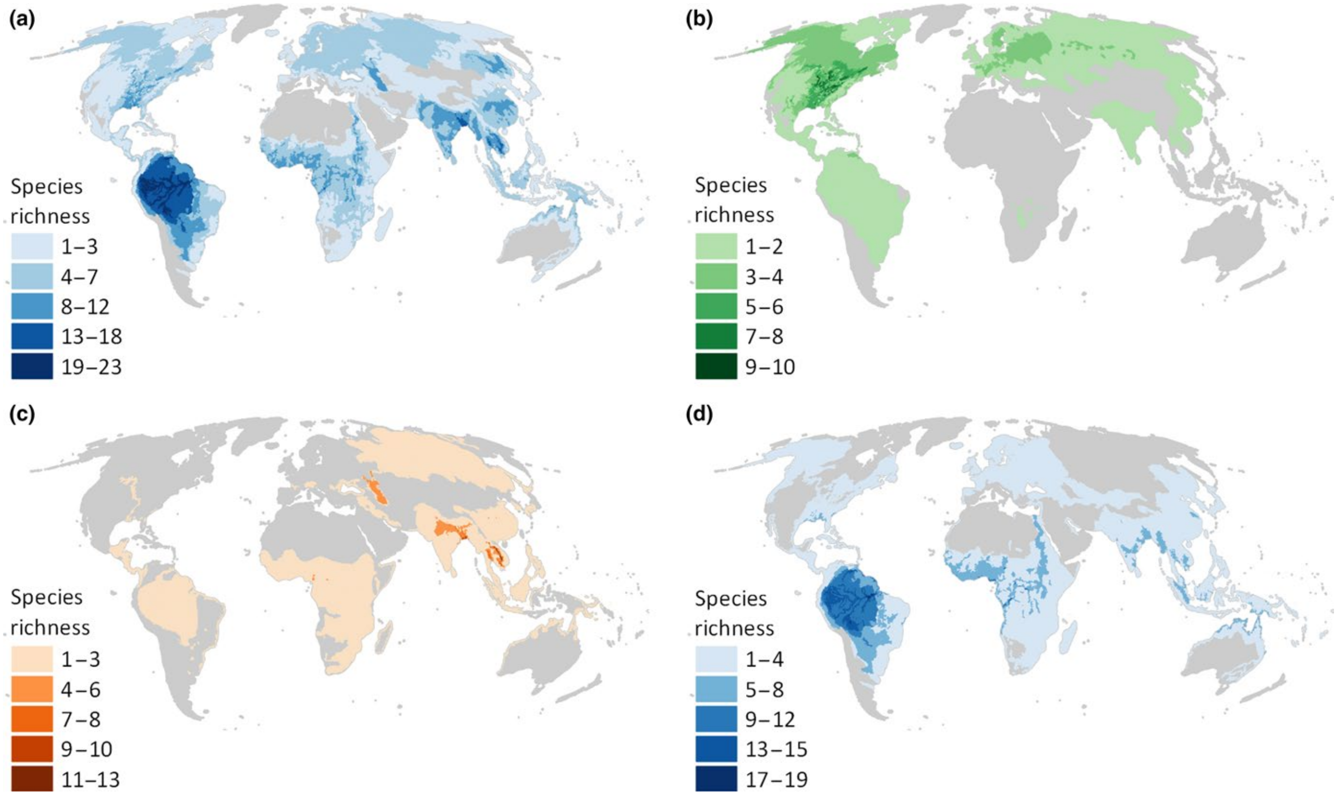

FIGURE 1 Species richness of freshwater megafauna (a) overall (b) with increasing or stable, (c) declining and (d) unknown population trends [Colour figure can be viewed at wileyonlinelibrary.com]

Amazon basin exhibits the highest freshwater megafauna richness (35 species), followed by the Congo (23), Orinoco (23), Mekong (22) and Ganges-Brahmaputra (22) basins (Figure S1a; Table S3). Forty-eight megafauna species (23% of all species) are endemic, i.e., they occur only in a single, large-scale basin (level 3 HydroBASINS). The Amazon (five endemic species), Congo (5), Mekong (4) and the Yangtze (4) contain the highest numbers of endemic freshwater megafauna species (Table S5).

Of the 93 (45%) freshwater megafauna species with known population trends, 71% species are in decline, particularly those occurring within the Caspian Sea region, Mekong, Chao Phraya and Ganges-Brahmaputra basins (Figure 1c). Sixty-two per cent of freshwater megafauna species with stable or increasing population trends occur in North America (Figure 1b). The greatest number of freshwater megafauna species with unknown population trends (33%) are found in South America (Figure 1d).

Compared to all freshwater species assessed for the IUCN Red List, freshwater megafauna have a higher proportion of threatened species than their smaller counterparts within specific taxonomic groups (i.e., fishes, mammals, reptiles, amphibians) (Figure 2). The Mekong river basin exhibits the highest number of threatened species (15 species), followed by the Ganges-Brahmaputra basin (13) (Figures S1b and S3a; Table S3). The proportion of threatened endemic freshwater megafauna species is substantial at 78% (Table S1). However, according to the IUCN Red List, 43% of freshwater megafauna species have insufficient data or data that require updating (i.e., they were last assessed more than 10 years ago, Table S1).

3.2 | Human pressure on freshwater megafauna

Human pressure varies within the different basins (level 3 HydroBASINS; Table S3 and S4). The spatial congruence analysis indicates that the megafauna species-rich basins of South and Southeast Asia are facing a high level of human pressure (i.e., many subcatchments have IBTI values >0.75; Figure 3a). In particular, the Mekong, Chao Phraya and Ganges-Brahmaputra basins are exposed to intense pressures from dam construction (Figure 4a) and direct exploitation, such as fishing (Figure 4b). In North America, freshwater megafauna species in the Mississippi river basin are also subject to intense human pressures. The IBTI indicates that total human pressure on freshwater megafauna is relatively low in the Congo and Amazon river basins (with the exception of the Andean Amazon). However, freshwater megafauna species are facing high exploitation pressure in the main stem of the Amazon and its major tributaries (Figure 4b).

According to the THPI, since the early 1990s, human pressure has increased throughout 63% of the global distribution ranges of freshwater megafauna. There are noticeable increases in human pressure within many subcatchments (i.e., THPI value >20) in monsoonal Asia (e.g., upper Yangtze, lower Pearl, Songhua, Red and Mahanadi basins), the Niger and Nile basins and in the upper reaches of the Paraná river (Figure 3b). On the contrary, human pressure has remained constant, or has decreased, in regions such as Siberia (with the exception of the Amur basin) and in the Amazon and the Congo basins (i.e., most subcatchments with THPI value <5).

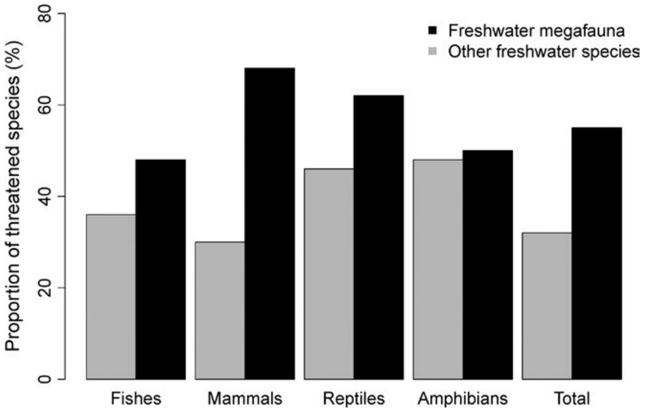

FIGURE 2 Proportion of threatened freshwater megafauna (black) and other threatened freshwater species (grey) (total and within four taxonomic groups)

4 | DISCUSSION

4.1 | Current status of freshwater megafauna

As observed previously (Carrizo et al., 2017), our study re-emphasises that freshwater megafauna diversity hotspots are located in tropical and subtropical regions. However, freshwater megafauna species are threatened globally and have higher extinction risks than their smaller counterparts. In addition, due to their relatively long generation times and complex life cycles (Stone, 2007), freshwater megafauna are more likely to face delayed extinctions (i.e., extinction debt), as previously demonstrated for other species with long generation times (Kuussaari et al., 2009). Thus, freshwater megafauna could still occupy rivers and lakes for many years after their reproduction has been disrupted; rendering them functionally extinct. Given the rapid degradation of freshwater ecosystems, in combination with long generation times and complex life cycles, many megafauna species will be at high risk of extinction in the future, as the rate of decline in many freshwater habitats may be too rapid for them to adapt (Winemiller et al., 2015). The proportion of threatened freshwater megafauna species is likely to be underestimated in this study, as it has been suggested that species classified as Data Deficient probably have a higher risk of extinction (Bland, Collen, Orme, & Bielby, 2015). This is certainly the case for those species inhabiting basins in rapidly developing regions of South America and monsoonal Asia.

Moreover, the 48 endemic megafauna species are particularly susceptible to extinction due to their restricted distributions. For example, those species endemic to the Yangtze basin (Baiji, *Lipotes vexillifer*; Chinese Paddlefish, *Psephurus gladius*; Yangtze Sturgeon, *Acipenser dabryanus*; Yangtze Finless Porpoise, *Neophocaena asiaeorientalis* ssp. *asiaeorientalis*) are Critically Endangered or even Critically Endangered (Possibly Extinct) due to serious habitat fragmentation resulting from construction of the Gezhouba, Three Gorges, Xiangjiaba and Xiluodu dams, in addition to continuous habitat degradation within the basin (IUCN, 2016).

Our study emphasises the high levels of threat to freshwater megafauna and reveals the lack of basic information available on the status of many of these species. Although the proportion of freshwater megafauna species threatened with extinction (54% of all species) resembles that of terrestrial megafauna species (59%) (Table S6), all terrestrial megafauna species (i.e., carnivores ≥15 kg, herbivores ≥100 kg) have been assessed and reassessed for the IUCN Red List (IUCN, 2016; Ripple et al., 2016). In contrast, a quarter of freshwater megafauna species still lack sufficient information to evaluate their conservation status, particularly amongst species occurring in South America (Figure S3b). The majority of species with insufficient information or outdated assessments are reptiles and fishes, which suggests a bias in surveying towards better-known mammals (Ford, Cooke, Goheen, & Young, 2017).

4.2 | Human pressure throughout distribution ranges of freshwater megafauna

Freshwater megafauna are particularly impacted by water abstraction and habitat degradation resulting from rapid development (e.g., urbanisation, agriculture expansion), associated with human population growth and increasing energy demand. This is especially evident in monsoonal Asia, where economic growth usually overrides environmental conservation, resulting in increased river fragmentation, wetland drainage and pollution (Dudgeon, 2000; Hughes, 2017). Moreover, this region is also predicted to suffer high levels of future habitat conversion (e.g., urban and agricultural expansion) (Oakleaf et al., 2015), posing further stress on freshwater megafauna and their habitats.

Although the THPI shows that human impact in both the Amazon and Congo basins has not noticeably increased between 1990 and 2010 (i.e., most subcatchments within the basin have THPI values <5), threats to freshwater megafauna species are likely to be underestimated in these basins, due to a dearth of pressure data (Geldmann et al., 2014; Joppa et al., 2016). For example, 44.2% of the Amazon river basin is already protected (Abell, Lehner, Thieme, & Linke, 2016), yet freshwater megafauna species are still subject to habitat destruction, pollutants released from agriculture, mining and oil spills; particularly in the Andean Amazon region (Azevedo-Santos et al., 2016; Castello et al., 2013). In the Congo river basin, the situation is possibly worse, as the protected area coverage is lower (Abell et al., 2016), and the basin is experiencing ongoing habitat conversion due to deforestation and expansion of agricultural activities (Ernst et al., 2013; Zhou et al., 2014). The current protected area system is largely designed for terrestrial ecosystems and, therefore, provides limited protection for freshwaters and their species (Pimm et al., 2014). Even where there is a spatial overlap between freshwater megafauna and protected areas (Carrizo et al., 2017), little to no targeted management is provided

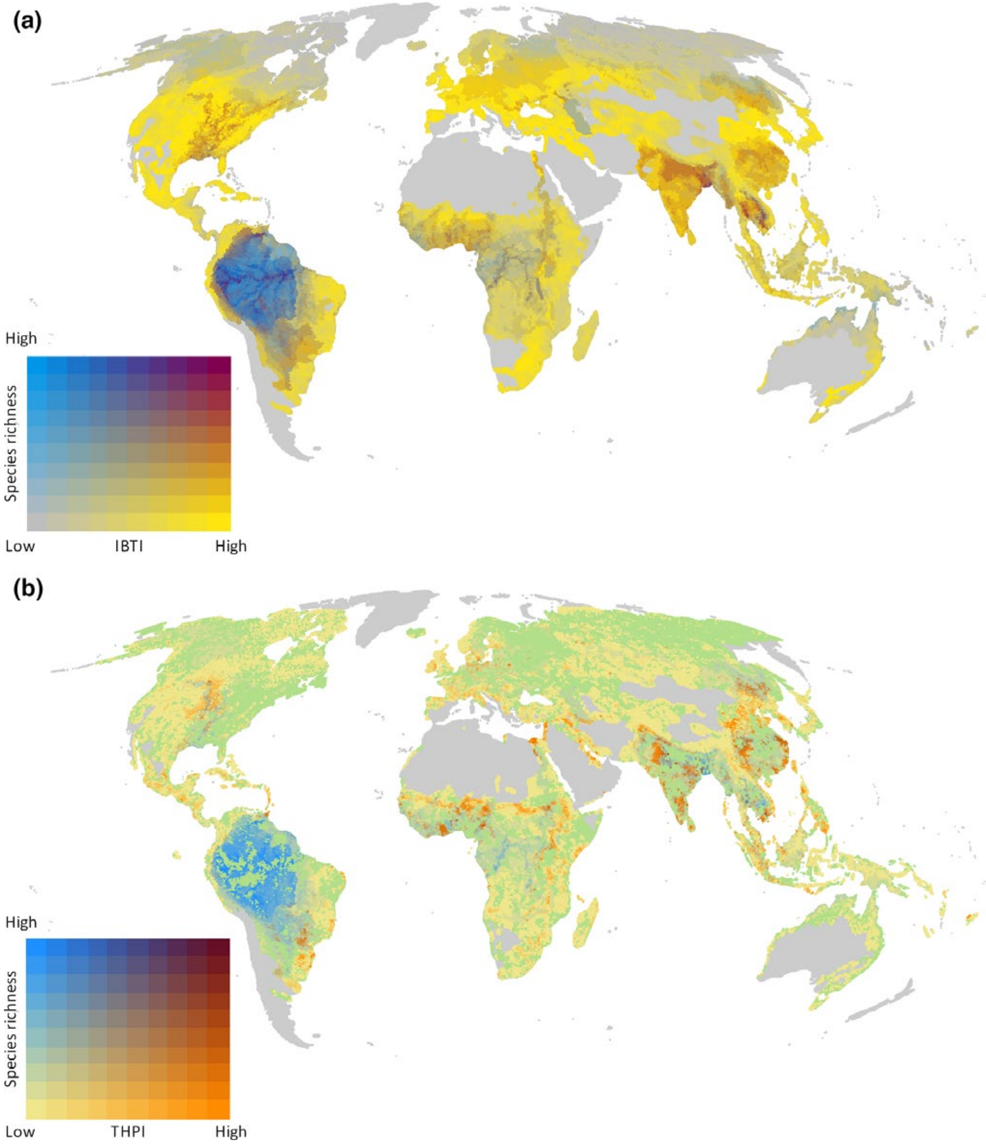

FIGURE 3 Concordance map of freshwater megafauna species richness with (a) IBTI and (b) THPI. Green areas in (b) refer to regions with stable or decreased human pressure, while other colours indicate increased human pressure [Colour figure can be viewed at wileyonlinelibrary.com]

when developing action plans. In addition, hydrological connectivity within catchments leaves freshwater megafauna more susceptible to disturbances originating beyond the boundaries of the protected areas (e.g., dams and sources of pollution in upstream areas), further reducing their effectiveness (Pringle, 2001). A greater focus is needed on the design and management of protected areas to provide greater protection for freshwater species, as demonstrated to be effective in some cases (Britton et al., 2017).

While the THPI and IBTI identify many of the same areas as being subject to intense human pressures (e.g., Songhua river basin, lower Yangtze river basin, upper stretches of the Paraná river), there are marked differences between the two indicator values in other regions (e.g., Mekong and Ganges-Brahmaputra basins, Caspian Sea and Black Sea regions) (Figure 3; Table S3). This is likely due to the use of different pressures within the indices. For example, the THPI–initially designed to track changes in human pressures on terrestrial habitats, likely underestimates threats such as harvesting and dam construction (Geldmann et al., 2014), which represent major threats to many freshwater megafauna species (He et al., 2017) and are included in the IBTI. In addition to harvesting pressure and dam construction, freshwater megafauna are also subject to threats such as habitat degradation, pollution, invasive species and the potential impact of climate change (He et al., 2017). Some of these threats (e.g., habitat degradation and pollution) are often correlated with human population density and land-use intensity, which are included within the THPI. However, knowledge gaps on the impacts of these threats (e.g., impacts of climate change on freshwater megafauna), and limited data availability at the global scale (e.g., data on invasive species in freshwater ecosystems), prevented separate analysis of congruence between these threats and freshwater megafauna diversity.

In the Amazon, Mekong and Ganges-Brahmaputra basins, where 74 freshwater megafauna species exist, exploitation pressure

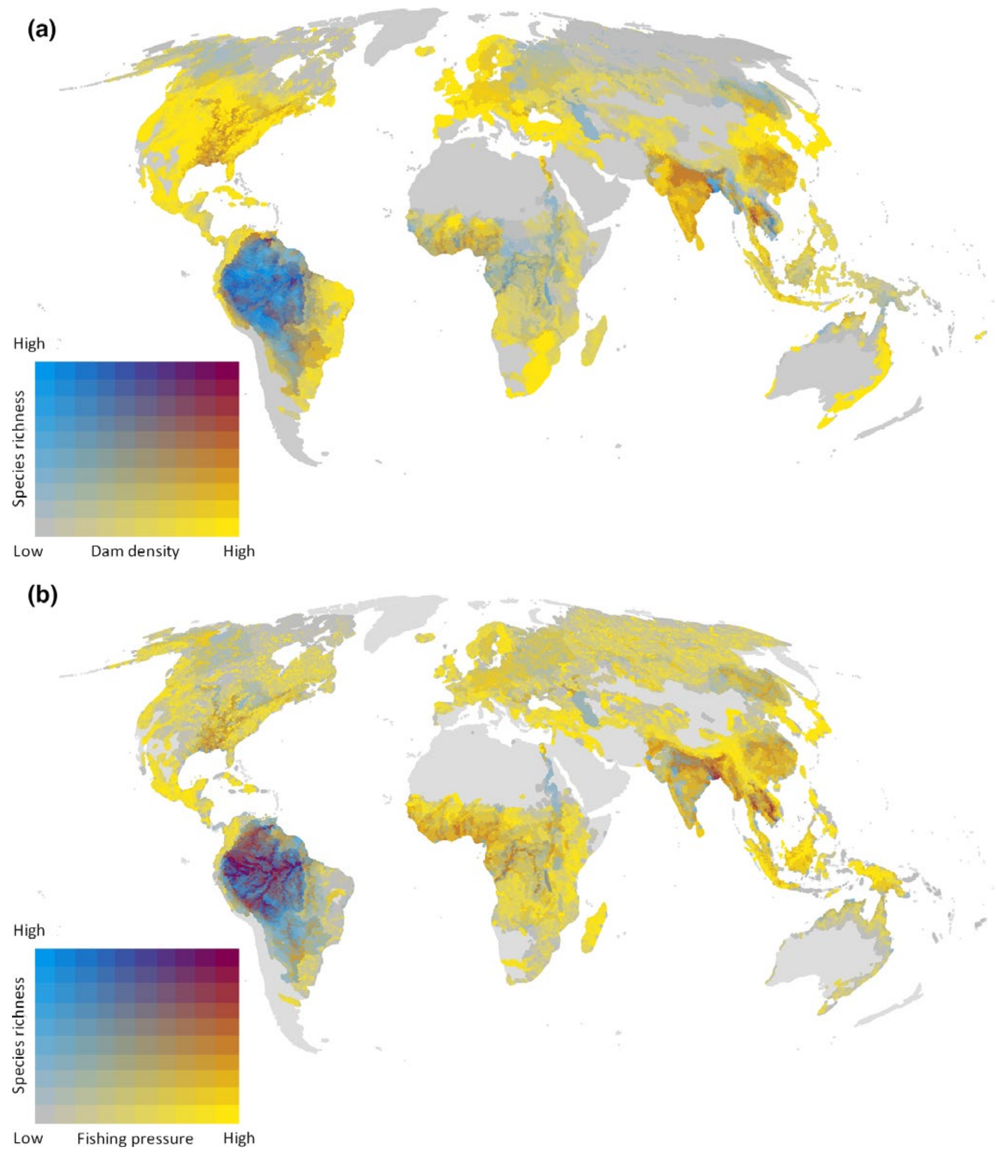

FIGURE 4 Concordance map of freshwater megafauna species richness with (a) dam density and (b) fishing pressure [Colour figure can be viewed at wileyonlinelibrary.com]

is intense (McIntyre, Liermann, & Revenga, 2016). Although 94 freshwater megafauna species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), they still face high levels of exploitation driven by a vast demand for consumption as food and for traditional medicine (Alves, da Silva Vieira, & Santana, 2008; Cheung & Dudgeon, 2006), alongside being caught as bycatch (Raby, Colotelo, Blouin-Demers, & Cooke, 2011). For instance, freshwater turtles are intensively exploited in Asia, with an estimated annual trade of 13,000 tonnes, including a number of threatened megafauna species (e.g., the New Guinea Giant Softshell Turtle, *Pelochelys bibroni*, Asian Giant Softshell Turtle, *Pelochelys cantorii*, Asian Narrow-headed Softshell Turtle, *Chitra chitra* and Indian Narrow-headed Softshell Turtle, *Chitra indica*) (Cheung & Dudgeon, 2006). In the Amazon river basin, unsustainable harvesting is common and has led to sharp population declines, and in some cases, local extinctions of freshwater megafauna species such as the Arapaima, *Arapaima* spp. and the Amazonian Manatee, *Trichechus inunguis* (Castello, Arantes, McGrath, Stewart, & Sousa, 2015; Castello et al., 2013). The risk is further compounded, as rarity makes these species even more attractive to fishers and collectors, thus driving them into an extinction vortex (Courchamp et al., 2006).

At last, one of the greatest rising threats to freshwater species, and megafauna in particular, is dam construction. Dams have been built along most large rivers (Nilsson, Reidy, Dynesius, & Revenga, 2005), blocking migratory routes of many mega-fishes (Hogan, 2011), often resulting in their inability to reach critical spawning and feeding grounds. Dams also modify upstream and downstream habitat conditions through alterations to the natural flow, sediment and thermal regimes, further changing river morphology and habitat conditions. The combined impacts of overexploitation and fragmentation by dams have pushed sturgeons in the Yangtze river, Caspian Sea and Black Sea regions, as well as many large catfishes in South and Southeast Asia, to the verge of extinction (Hogan, 2011; Pikitch, Doukakis, Lauck, Chakrabarty, & Erickson, 2005).

4.3 | Future challenges for freshwater megafauna conservation

Despite the general recognition that freshwater megafauna species are facing a disproportionately high level of extinction risk, information on their life histories, population dynamics and even taxonomy (e.g., *Arapaima* spp.) remains insufficient for many species, and conservation actions are scarce (Carrizo et al., 2017). Such knowledge gaps may constrain development of efficient management strategies and implementation of conservation actions (Humphries & Winemiller, 2009), with potentially devastating impacts on the future survival of many megafauna species. In addition, human pressure on freshwaters is likely to grow precipitously (Bunn, 2016), considering the rapidly growing economy, increase in human population and subsequent water and energy demands, urban expansion, agricultural intensification and the manifold interactions with climate change (Vörösmarty, Green, Salisbury, & Lammers, 2000).

Furthermore, over 3,700 major hydropower dams are planned or under construction globally, covering key biodiversity hotspots for freshwater megafauna (Winemiller et al., 2016; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). With dams widely considered a source of green energy, this boom in hydropower could be further accelerated by the recent Paris climate agreement (Hermoso, 2017). Thus, the location and operation of new dams requires careful consideration and balancing of multiple, often potentially conflicting interests (e.g., biodiversity conservation vs. energy provision) (Winemiller et al., 2016; Ziv, Baran, Nam, Rodríguez-Iturbe, & Levin, 2012). Altered flow regimes and truncated connectivity may not only impact migratory fishes, but also mammals and reptiles in downstream areas (e.g., the Gahrial, *Gavialis gangeticus* and the Giant Otter, *Pteronura brasiliensis*). Effective fish passages should be designed that not only target jumping fish species such as salmonids, but also facilitate the movement of other large migratory fishes such as sturgeons and catfishes, when dams are constructed. Furthermore, maintaining environmental flows for downstream reaches will be essential to mitigate the negative impacts of dams on freshwater megafauna and other species (Poff & Zimmerman, 2010; Sabo et al., 2017).

Although freshwater megafauna species face severe threats, there is still an opportunity to prevent their extinction if timely conservation actions, based on political will, credible research and evidence are undertaken. North America provides a good example, where populations of most freshwater megafauna are stable or increasing despite high levels of human pressure (Haxton, Sulak, & Hildebrand, 2016; IUCN, 2016). This success results from extensive monitoring, well-developed research and conservation actions, and public and political will to ensure the persistence of these species.

Our study suggests that the highly threatened, yet poorly known, freshwater megafauna are in urgent need of conservation action, given the rapidly increasing pressures of global development. Impacts on these remarkable species also represent a symptom of the unrecognised impacts on the many other freshwater species that share their habitats. To facilitate the planning and prioritization of conservation actions, we identified basins where high levels of freshwater megafauna diversity and severe persistent pressures coincide (e.g., the Mekong and Ganges-Brahmaputra basins). Integrated catchment management planning must incorporate consideration of the ecological requirements of freshwater megafauna, the connectivity of freshwater systems, environmental flows, alongside outreach and education programmes for local communities in these priority basins. We also highlight hotspots of freshwater megafauna diversity with relatively low human pressure and large information gaps (e.g., the Amazon and the Orinoco basins), where assessments of the status of freshwater megafauna and research on improved design of protected areas for freshwater ecosystems should be a priority. In addition, management strategies accounting for the life-history traits of targeted species (e.g., regulations on catch and sale during breeding/spawning seasons) are urgently required. As dams proliferate globally it is critical that their design and placement better avoids or mitigates impacts on freshwater species, particularly for the megafauna highlighted in this study. Despite their large size and impressive nature, freshwater megafauna remain poorly known and continue to decline at an alarming rate throughout many of their ranges. To ensure the persistence of these iconic species for future generations we should urgently balance the needs of global development with those of freshwater megafauna.

ACKNOWLEDGEMENTS

This work has been carried out within the SMART Joint Doctorate (Science for the MAnagement of Rivers and their Tidal systems), funded with the support of the Erasmus Mundus programme of the European Union. We gratefully acknowledge the contribution of Savrina F. Carrizo in a previous freshwater megafauna project, particularly establishing the distribution mapping procedures and data collection. We thank two anonymous referees and the editor Gwen Iacona for their constructive comments on the manuscript. We also thank Annett Wetzig for assistance in collecting species distribution information. J.G. was funded by Villum fonden (VKR023371). J.G. and S.D.L. acknowledge the EU Marie Sklodowska-Curie programme (H2020-MSCA-IF-2015-706784; H2020-MSCA-IF-2016-748625). S.C.J. was funded through the "GLANCE" project (Global Change Effects in River Ecosystems; 01 LN1320A; German Federal Ministry of Education and Research, BMBF). S.C.J., V.B. and S.D.L. acknowledge funding through the "AQUACROSS" project (Knowledge, Assessment, and Management for AQUAtic Biodiversity and Ecosystem Services aCROSS EU policies; 642317) supported by the European Union's Horizon 2020 Programme for Research, Technological Development and Demonstration. C.Z. acknowledges funding through the Junior Professorship Program of the Ministry for Science, Research and Culture (MWK), Baden-Württemberg, Germany.

DATA ACCESSIBILITY

The data generated by this study will be archived through the Freshwater Information Platform (http://www.freshwaterplatform.eu).

ORCID

Fengzhi He http://orcid.org/0000-0002-7594-8205

Jonas Geldmann http://orcid.org/0000-0002-1191-7610

Simone D. Langhans http://orcid.org/0000-0001-9581-3183

Sonja C. Jähnig http://orcid.org/0000-0002-6349-9561

REFERENCES

Abell, R., Lehner, B., Thieme, M., & Linke, S. (2016). Looking beyond the fenceline: Assessing protection gaps for the world's rivers. *Conservation Letters*, *10*, 384–394.

Alves, R., da Silva Vieira, W., & Santana, G. (2008). Reptiles used in traditional folk medicine: Conservation implications. *Biodiversity and Conservation*, *17*, 2037–2049. https://doi.org/10.1007/s10531-007-9305-0

Aylward, B., Bandyopadhyay, J., Belausteguigotia, J.C., Borkey, P., Cassar, A., Meadors, L., … Tognetti, S. (2005). Freshwater ecosystem services. *Ecosystems and human well-being: policy responses*, *3*, 213–256.

Azevedo-Santos, V., Garcia-Ayala, J., Fearnside, P., Esteves, F., Pelicice, F., Laurance, W., & Benine, R. (2016). Amazon aquatic biodiversity imperiled by oil spills. *Biodiversity and Conservation*, *25*, 2831–2834. https://doi.org/10.1007/s10531-016-1192-9

Balian, E., Segers, H., Lévêque, C., & Martens, K. (2008). The freshwater animal diversity assessment: An overview of the results. *Hydrobiologia*, *595*, 627–637.

Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L., & Shabel, A. B. (2004). Assessing the causes of Late Pleistocene extinctions on the continents. *Science*, *306*, 70–75. https://doi.org/10.1126/science.1101476

Bland, L. M., Collen, B., Orme, C. D. L., & Bielby, J. (2015). Predicting the conservation status of data-deficient species. *Conservation Biology*, *29*, 250–259. https://doi.org/10.1111/cobi.12372

Britton, A., Day, J., Doble, C., Ngatunga, B., Kemp, K., Carbone, C., & Murrell, D. (2017). Terrestrial-focused protected areas are effective for conservation of freshwater fish diversity in Lake Tanganyika. *Biological Conservation*, *212*, 120–129. https://doi.org/10.1016/j.biocon.2017.06.001

Bunn, S. E. (2016). Grand challenge for the future of freshwater ecosystems. *Frontiers in Environmental Science*, *4*, 21.

Carrizo, S. F., Jähnig, S. C., Bremerich, V., Freyhof, J., Harrison, I., He, F., … Darwall, W. (2017). Freshwater megafauna: Flagships for freshwater biodiversity under threat. *BioScience*, *10*, 919–927. https://doi.org/10.1093/biosci/bix099

Castello, L., Arantes, C. C., McGrath, D. G., Stewart, D. J., & Sousa, F. S. D. (2015). Understanding fishing-induced extinctions in the Amazon. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*, 587–598. https://doi.org/10.1002/aqc.2491

Castello, L., McGrath, D. G., Hess, L. L., Coe, M. T., Lefebvre, P. A., Petry, P., … Arantes, C.C. (2013). The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, *6*, 217–229. https://doi.org/10.1111/conl.12008

Cheung, S., & Dudgeon, D. (2006). Quantifying the Asian turtle crisis: Market surveys in southern China, 2000-2003. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *16*, 751–770. https://doi.org/10.1002/(ISSN)1099-0755

Collen, B., Whitton, F., Dyer, E., Baillie, J., Cumberlidge, N., Darwall, W., … Bohm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, *23*, 40–51. https://doi.org/10.1111/geb.12096

Cooke, S. J., Lapointe, N. W. R., Martins, E. G., Thiem, J. D., Raby, G. D., Taylor, M. K., … Cowx, I. G. (2013). Failure to engage the public in issues related to inland fishes and fisheries: Strategies for building public and political will to promote meaningful conservation. *Journal of Fish Biology*, *83*, 997–1018.

Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *Plos Biology*, *4*, 2405–2410.

Donlan, C. J., Berger, J., Bock, C. E., Bock, J. H., Burney, D. A., Estes, J. A., … Greene, H.W. (2006). Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *The American Naturalist*, *168*, 660–681. https://doi.org/10.2307/3873461

Dudgeon, D. (2000). Riverine biodiversity in Asia: A challenge for conservation biology. *Hydrobiologia*, *418*, 1–13. https://doi.org/10.1023/A:1003998519910

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Leveque, C., … Sullivan, C.A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182. https://doi.org/10.1017/S1464793105006950

Ernst, C., Mayaux, P., Verhegghen, A., Bodart, C., Christophe, M., & Defourny, P. (2013). National forest cover change in Congo Basin: Deforestation, reforestation, degradation and regeneration for the years 1990, 2000 and 2005. *Global Change Biology*, *19*, 1173–1187. https://doi.org/10.1111/gcb.12092

Estes, J., Heithaus, M., McCauley, D., Rasher, D., & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, *41*, 83–116. https://doi.org/10.1146/annurev-environ-110615-085622

Estes, J., Terborgh, J., Brashares, J., Power, M., Berger, J., Bond, W., … Wardle, D. (2011). Trophic downgrading of planet earth. *Science*, *333*, 301–306. https://doi.org/10.1126/science.1205106

Ford, A. T., Cooke, S. J., Goheen, J. R., & Young, T. P. (2017). Conserving megafauna or sacrificing biodiversity? *BioScience*, *67*, 193–196.

Geldmann, J., Joppa, L., & Burgess, N. (2014). Mapping change in human pressure globally on land and within protected areas. *Conservation Biology*, *28*, 1604–1616. https://doi.org/10.1111/cobi.12332

Haxton, T. J., Sulak, K., & Hildebrand, L. (2016). Status of scientific knowledge of North American sturgeon. *Journal of Applied Ichthyology*, *32*, 5–10. https://doi.org/10.1111/jai.13235

He, F., Zarfl, C., Bremerich, V., Henshaw, A., Darwall, W., Tockner, K., & Jähnig, S. C. (2017). Disappearing giants: A review of threats to freshwater megafauna. *Wiley Interdisciplinary Reviews: Water*, *4*, e1208. https://doi.org/10.1002/wat2.1208

Hermoso, V. (2017). Freshwater ecosystems could become the biggest losers of the Paris Agreement. *Global Change Biology*, *23*, 3433–3436. https://doi.org/10.1111/gcb.13655

Hermoso, V., Linke, S., Prenda, J., & Possingham, H. P. (2011). Addressing longitudinal connectivity in the systematic conservation planning of fresh waters. *Freshwater Biology*, *56*(1), 57–70. https://doi.org/10.1111/j.1365-2427.2009.02390.x

Hogan, Z. (2011). Ecology and conservation of large-bodied freshwater catfish: A global perspective. *American Fisheries Society Symposium*, *77*, 39–53.

Hughes, A. C. (2017). Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere*, *8*, e01624. https://doi.org/10.1002/ecs2.1624

Humphries, P., & Winemiller, K. (2009). Historical impacts on river fauna, shifting baselines, and challenges for restoration. *BioScience*, *59*, 673–684. https://doi.org/10.1525/bio.2009.59.8.9

IUCN (2016) The IUCN red list of threatened species. Version 2016-3.

Janse, J. H., Kuiper, J. J., Weijters, M. J., Westerbeek, E. P., Jeuken, M. H. J. L., Bakkenes, M., … Verhoeven, J. T. A. (2015). GLOBIO-Aquatic, a global model of human impact on the biodiversity of inland aquatic ecosystems. *Environmental Science & Policy*, *48*, 99–114. https://doi.org/10.1016/j.envsci.2014.12.007

Joppa, L. N., O'Connor, B., Visconti, P., Smith, C., Geldmann, J., Mann, M. H., … Burgess, N. D. (2016). Filling in biodiversity threat gaps. *Science*, *352*, 416–418. https://doi.org/10.1126/science.aaf3565

Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Václavík, T., & Kreft, H. (2015). Global patterns of agricultural land-use intensity and vertebrate diversity. *Diversity and Distributions*, *21*, 1308–1318. https://doi.org/10.1111/ddi.12359

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., … Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, *24*, 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Lehner, B., & Grill, G. (2013). Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. *Hydrological Processes*, *27*, 2171–2186. https://doi.org/10.1002/hyp.9740

Linke, S., Pressey, R. L., Bailey, R. C., & Norris, R. H. (2007). Management options for river conservation planning: Condition and conservation re-visited. *Freshwater Biology*, *52*, 918–938. https://doi.org/10.1111/j.1365-2427.2006.01690.x

Malhi, Y., Doughty, C., Galetti, M., Smith, F., Svenning, J., & Terborgh, J. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 838–846. https://doi.org/10.1073/pnas.1502540113

McIntyre, P. B., Liermann, C. A. R., & Revenga, C. (2016). Linking freshwater fishery management to global food security and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 12880–12885. https://doi.org/10.1073/pnas.1521540113

Naiman, R. J., Bilby, R. E., Schindler, D. E., & Helfield, J. M. (2002). Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, *5*, 399–417. https://doi.org/10.1007/s10021-001-0083-3

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, *308*, 405–408. https://doi.org/10.1126/science.1107887

Oakleaf, J. R., Kennedy, C. M., Baruch-Mordo, S., West, P. C., Gerber, J. S., Jarvis, L., & Kiesecker, J. (2015). A world at risk: Aggregating development trends to forecast global habitat conversion. *PLoS ONE*, *10*, e0138334. https://doi.org/10.1371/journal.pone.0138334

Pikitch, E. K., Doukakis, P., Lauck, L., Chakrabarty, P., & Erickson, D. L. (2005). Status, trends and management of sturgeon and paddlefish fisheries. *Fish and Fisheries*, *6*, 233–265. https://doi.org/10.1111/j.1467-2979.2005.00190.x

Pimm, S., Jenkins, C., Abell, R., Brooks, T., Gittleman, J., Joppa, L., … Sexton, J. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*, 1246752. https://doi.org/10.1126/science.1246752

Poff, N. L., & Zimmerman, J. K. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Pringle, C. M. (2001). Hydrologic connectivity and the management of biological reserves: A global perspective. *Ecological Applications*, *11*, 981–998. https://doi.org/10.1890/1051-0761(2001)011[0981:HCATMO]2.0.CO;2

Quantum GIS Development Team (2015) Quantum GIS Geographic Information System (version 2.14). Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Raby, G. D., Colotelo, A. H., Blouin-Demers, G., & Cooke, S. J. (2011). Freshwater commercial bycatch: An understated conservation problem. *BioScience*, *61*, 271–280. https://doi.org/10.1525/bio.2011.61.4.7

Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., … Zhang, L. (2016). Saving the world's terrestrial megafauna. *BioScience*, *66*, 807–812. https://doi.org/10.1093/biosci/biw092

Sabo, J. L., Ruhi, A., Holtgrieve, G. W., Elliott, V., Arias, M. E., Ngor, P. B., … Nam, S. (2017). Designing river flows to improve food security futures in the Lower Mekong Basin. *Science*, *358*, eaao1053. https://doi.org/10.1126/science.aao1053

Smith, F. A., Doughty, C. E., Malhi, Y., Svenning, J. C., & Terborgh, J. (2016). Megafauna in the Earth system. *Ecography*, *39*, 99–108. https://doi.org/10.1111/ecog.02156

Stone, R. (2007). The last of the leviathans. *Science*, *316*, 1684–1688. https://doi.org/10.1126/science.316.5832.1684

Vörösmarty, C. J., Green, P., Salisbury, J., & Lammers, R. B. (2000). Global water resources: Vulnerability from climate change and population growth. *Science*, *289*, 284–288. https://doi.org/10.1126/science.289.5477.284

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., … Davies, P.M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*, 555–561. https://doi.org/10.1038/nature09440

Winemiller, K. O., Humphries, P., & Pusey, B. J. (2015). Protecting large apex predators. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of Freshwater Fishes* (pp. 361–398). Cambridge, UK: Cambridge University Press.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., … Saenz, L. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, *351*, 128–129. https://doi.org/10.1126/science.aac7082

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, *4*, 170052. https://doi.org/10.1098/rsos.170052

WWF (2016). *Living Planet Report 2016. Risk and resilience in a new era.* Gland, Switzerland: WWF International.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*, 161–170. https://doi.org/10.1007/s00027-014-0377-0

Zhou, L., Tian, Y., Myneni, R., Ciais, P., Saatchi, S., Liu, Y., … Hwang, T. (2014). Widespread decline of Congo rainforest greenness in the past decade. *Nature*, *509*, 86–90. https://doi.org/10.1038/nature13265

Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., & Levin, S. A. (2012). Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proceedings of the National Academy of Sciences*, *109*, 5609–5614. https://doi.org/10.1073/pnas.1201423109

BIOSKETCH

Fengzhi He is a PhD candidate at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Freie Universität Berlin, and Queen Mary University of London. He is interested in impacts of global changes on freshwater biodiversity, with a focus on biodiversity and risk patterns of freshwater megafauna.

Author contributions: F.H., C.Z. and S.C.J. conceived the ideas; F.H., V.B. and J.N.W.D. collected megafauna data, and J.G. contributed data on temporal human pressure index; F.H. analysed the data with input from V.B.; F.H. led the writing and all authors contributed substantially to the drafts of the manuscript.

SUPPORTING INFORMATION

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

How to cite this article: He F, Bremerich V, Zarfl C, et al. Freshwater megafauna diversity: Patterns, status and threats. *Divers Distrib*. 2018;24:1395–1404. https://doi.org/10.1111/ddi.12780