Diversity and risk patterns of freshwater megafauna: A global perspective

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Summary

Freshwaters are amongst the most diverse and dynamic ecosystems globally and provide vital ecosystem services for human well-being. At the same time, they are subject to intense and increasing threats due to the rapid growth of human population and the subsequent rise in demand for energy and food. However, freshwaters remain underrepresented in both biodiversity research and conservation actions. Consequently, populations of vertebrates in freshwaters have declined by 83% from 1970 to 2014 - the rate of decline being much higher than that recorded in either terrestrial or marine ecosystems. In addition, one third of all classified freshwater species are threatened with extinction according to the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List). Freshwater megafauna, i.e. freshwater animals ≥ 30 kg, are particularly susceptible to extinction owing to their intrinsic characteristics such as large habitat requirements, long lifespan, and late maturity. Despite the fact that many freshwater megafauna species such as sturgeons, river dolphins, crocodilians and giant turtles are teetering on the edge of extinction, a synthesis of global freshwater megafauna is lacking. In particular, changes in population abundance and distribution ranges of freshwater megafauna at large scales (e.g. continental and global scales) remain unclear. In addition, relationships between extinction risks of freshwater megafauna species and their life-history traits, and how human threats impact on such relationships are as yet insufficiently explored.

This thesis aims to gain a comprehensive picture of global freshwater megafauna, with emphasis on their distribution, conservation status, main threats, population trends, and extinction risks. The body-mass threshold of 30 kg was chosen to include most of the large freshwater animals with the potential of acting as flagship or umbrellas species. Based on this definition, I compiled a list of 207 extant freshwater megafauna species (i.e. 130 fishes, 44 reptiles, 31 mammals and 2 amphibians) and established a freshwater-megafauna database containing information on their distribution, life-history traits, population change, conservation status and intensity of human threats within their distribution ranges. I found that freshwater megafauna are threatened globally, with 54% of all classified species considered as threatened on the IUCN Red List.

There are intense and growing anthropogenic threats in many diversity hotspots of freshwater megafauna such as the Amazon, Congo, Mekong and Ganges-Brahmaputra river basins. The main threats to freshwater megafauna include overexploitation, dam construction, habitat degradation, pollution and biological invasions. These threats can cause reduced fitness, disrupted reproduction and increased mortality of freshwater megafauna, leading to population decline and range contraction. Indeed, global populations of freshwater megafauna declined by 88% from 1970 to 2012. Decline rates of populations in Indomalaya (-99%) and Palearctic (-97%) realms, and in mega-fish (-94%) were even higher. In addition, distribution ranges of 42% of all freshwater megafauna species in Europe contracted by more than 40% of historical areas. I found that the extinction risk of freshwater megafauna is jointly determined by external threats and traits associated with species' recovery potential (i.e. lifespan, age at maturity, and fecundity). This underscores the importance of maintaining species' recovery potential, particularly for those freshwater megafauna species with the smallest population sizes. On the basis of such relationships, 16 out of 49 unclassified freshwater megafauna species were predicted as threatened.

This thesis emphasizes the critical plight of freshwater megafauna globally. The loss of freshwater megafauna will pose, and most likely has already had profound impacts on other species and ecological processes in freshwaters and surrounding ecosystems. It also highlights large gaps in life-history data, monitoring and conservation actions for the world's largest freshwater animals, which reflects a currently poorly recognized global need, i.e. the conservation for freshwater biodiversity. This urges for more research to gain a comprehensive understanding of these large animals and more activities in science communication and outreach to inform the public and policymakers of the crisis in freshwater biodiversity and engage them in freshwater conservation. Based on the results of this thesis, freshwater megafauna are able to indicate the ecological integrity of ecosystems they inhabit and hold the potential to act as flagship and umbrella species. A megafauna-based approach could be a promising strategy to promote freshwater biodiversity conservation benefiting a broad range of co-occurring species. This should be considered when developing conservation strategies and establishing protected areas to halt biodiversity loss in freshwaters.

Zusammenfassung

Süßwasserökosysteme zählen zu den vielfältigsten und dynamischsten Ökosystemen weltweit. Sie bieten unverzichtbare Ökosystemdienstleistungen und sind essenziell für das menschliche Wohlergehen. Gleichzeitig sind sie aufgrund des rapiden Bevölkerungswachstums und der daraus resultierenden steigenden Nachfrage nach Energie und Nahrungsmitteln zunehmend intensiven Bedrohungen ausgesetzt. Trotzdem sind Süßwasserökosysteme in der Biodiversitätsforschung unterrepräsentiert und werden bei Schutzmaßnahmen vernachlässigt. Infolgedessen sind Populationen von Süßwasser-Vertebraten- zwischen 1970 und 2014 um 83% zurückgegangen. Die verzeichnete Abnahmerate ist weit höher als in terrestrischen oder marinen Ökosystemen. Darüber hinaus ist ein Drittel aller in der Roten Liste der bedrohten Arten der Weltnaturschutzunion (Roten Liste der IUCN) klassifizierten Süßwasserarten vom Aussterben bedroht. Süßwasser-Megafauna-Arten, d.h. Süßwassertiere $\geq$ 30 kg, sind aufgrund ihrer inhärenten Eigenschaften wie großer Lebensraumanforderung, langer Lebensdauer und später Geschlechtsreife besonders gefährdet. Obwohl viele Süßwasser-Megafauna-Arten wie Störe, Flussdelfine, Krokodile und Riesenschildkröten vom Aussterben bedroht sind, fehlt bisher eine umfassende Studie zur globalen Süßwasser-Megafauna. Insbesondere bleiben Änderungen der Populationsgröße und ihrer Verbreitungsgebiete in größeren, z. B. kontinentalen und globalen Maßstäben unklar. Darüber hinaus sind die Zusammenhänge zwischen ihrer Biologie, und dem Aussterberisiko der Süßwasser-Megafauna sowie den Auswirkungen menschlicher Einflüsse auf diese Beziehung wenig erforscht.

Ziel dieser Arbeit ist es, ein umfassendes Bild der globalen Süßwasser-Megafauna zu gewinnen, wobei die Schwerpunkte auf Verbreitung, Erhaltungszustand, Hauptbedrohungen, Populationstrends und Aussterberisiko liegen. Die Schwelle einer Körpermasse von mindestens 30 kg wurde gewählt, um die meisten Megafauna-Arten, die Flaggschiff- oder Schirmarten für ihr Ökosystem sein könnten, mit zu erfassen. Basierend auf dieser Definition wurde eine Liste von 207 rezenten Süßwasser-Megafauna-Arten (130 Fische, 44 Reptilien, 31 Säugetiere, 2 Amphibien) erstellt und eine Süßwasser-Megafauna-Datenbank aufgebaut. Hierin wurden Informationen zu Verbreitung, Biologie, Populationsveränderung und Erhaltungszustand der Süßwasser-Megafauna-Arten sowie der Intensität menschlicher Bedrohungen innerhalb ihrer Verbreitungsgebiete erfasst. Dabei stellte sich

heraus, dass die Süßwasser-Megafauna weltweit bedroht ist. Gemäß der Roten Liste der IUCN gelten 54 % aller klassifizierten Arten als gefährdet.

In vielen Hotspots der Süßwasser-Megafauna, wie dem Amazonas-, Kongo-, Mekong- und Ganges-Brahmaputra-Einzugsgebiet, gibt es intensive und zunehmende anthropogene Bedrohungen. Zu den Hauptbedrohungen für die Süßwasser-Megafauna zählen Übernutzung, Staudammbau, Habitatverlust, Umweltverschmutzung und biologische Invasionen. Diese Bedrohungen können zu verminderter Fitness, gestörter Fortpflanzung und erhöhter Mortalität der Süßwasser-Megafauna führen, was zu einem Populationsrückgang und einer Verkleinerung ihrer Verbreitungsgebiete führt. Tatsächlich sind weltweite Populationen der Süßwasser-Megafauna von 1970 bis 2012 um 88% zurückgegangen. Der Populationsrückgang in Indo-Malaysia (-99%) und der Paläarktis (-97%) sowie bei Megafischen (-94%) ist sogar noch ausgeprägter. Darüber hinaus sind die Verbreitungsgebiete von 42% aller Süßwasser-Megafauna-Arten in Europa um mehr als 40% im Vergleich zu den historischen Gebieten geschrumpft. Das Aussterberisiko der Süßwasser-Megafauna wird sowohl von äußeren Bedrohungen als auch gleichzeitig von Merkmalen des Erholungspotenzials der Arten, das heißt Lebensdauer, Alter bei Geschlechtsreife und Fruchtbarkeit, bestimmt. Dies unterstreicht die Bedeutung des Erhalts des Erholungspotenzials insbesondere von Süßwasser-Megafauna-Arten mit kleinen Populationsgrößen. Auf der Basis dieser ermittelten Beziehungen wurden 16 von 49 bisher nicht klassifizierten Süßwasser-Megafauna-Arten als gefährdet prognostiziert.

Dieser Arbeit zeigt die kritische Lage der Süßwasser-Megafauna weltweit auf. Ihr Verlust wird tief greifende Auswirkungen auf andere Arten und ökologische Prozesse im Süßwasser und angrenzenden Ökosystemen haben, bzw. höchstwahrscheinlich bereits gehabt haben. Darüber hinaus werden große Wissenslücken in Bezug auf Biologie, Lebenszyklus und weitere Merkmale dieser Arten aufgezeigt. Monitoring- und Erhaltungsmaßnahmen für die weltweit größten Süßwassertiere sind unzureichend. Dies zeigt einen bisher zu wenig beachteten globalen Handlungsbedarf für den Schutz der gesamten Süßwasser-Biodiversität auf. Weitergehende Forschung auf diesem Gebiet ist nötig, um ein umfassendes Verständnis über diese großen Tiere zu erlangen. Ferner sind verstärkte Aktivitäten in der Wissenschaftskommunikation und Öffentlichkeitsarbeit erforderlich, um die

Öffentlichkeit und politische Entscheidungsträger über die Krise der Süßwasserbiodiversität zu informieren und diese in Schutzmaßnamen einzubinden.

Auf der Grundlage dieser Resultate dieser Arbeit sind Süßwasser-Megafauna-Arten in der Lage, die ökologische Integrität der von ihnen bewohnten Ökosysteme aufzuzeigen, und besitzen das Potenzial, als Flaggschiff- und Schirmarten zu fungieren. Ein auf Megafauna-Arten fokussierenderr Ansatz könnte eine vielversprechende Strategie sein, um den Erhalt der gesamten Biodiversität im Süßwasser zu fördern und ein breites Spektrum gemeinsam vorkommender Süßwasser-Arten zu schützen. Bei der Entwicklung von Schutzstrategien und der Einrichtung von Schutzgebieten sollte dieser Ansatz berücksichtigt werden, um den Verlust der biologischen Vielfalt im Süßwasser zu aufzuhalten.

Thesis outline

This thesis is a cumulative work, consisting of seven manuscripts (Manuscripts 1 to 7) that have either been published, submitted for publication or are ready for submission to peer-reviewed journals. Manuscripts 1 and 6 are embedded as part of the general introduction (Chapter 1) and general discussion (Chapter 6), respectively while Manuscripts 2 to 5 form individual chapters of the thesis (Chapters 2 to 5). Manuscript 7 forms Appendix G. The general introduction (Chapter 1) provides background, context and general research aims for the thesis, as well as aims of individual chapters. The general discussion (Chapter 6) makes conceptual linkages between the results of individual chapters. In the general discussion, I put the results in a broader context, discuss potential implications and limitations of the thesis results and provide suggestions for future research.

Chapter 1 (General introduction)

The sections 1.2 and 1.3 have been modified from the Manuscript 1:

He, F., Jähnig, S.C., Wetzig A. & Langhans, S.D. The untapped potential of cover images to promote underrepresented biodiversity (to be submitted).

Author contributions: F.H., S.C.J. and S.D.L. conceived the idea. F.H., A.W. and S.D.L. collected the data. F.H. performed the analysis. F.H. and S.D.L. wrote the first draft, with substantial contributions from all coauthors.

Chapter 2 (Manuscript 2)

He, F., Bremerich, V., Zarfl, C., Geldmann, J., Langhans, S.D., David, J.N.W., Darwall, W., Tockner, K. & Jähnig, S.C. (2018) Freshwater megafauna diversity: Patterns, status and threats. *Diversity and Distributions* **24**:1395-1404. https://doi.org/10.1111/ddi.12780

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 substantial input from V.B.; F.H. led the writing and all authors contributed substantially to the drafts of the manuscript.

Chapter 3 (Manuscript 3)

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

Author contributions: F.H., C.Z. and S.C.J. conceived the ideas; F.H. wrote the first draft, all coauthors contributed substantially to revisions.

Chapter 4 (Manuscript 4)

He, F., Zarfl, C., Bremerich, V., David, J.N.W., Hogan, Z., Kalinkat G., Tockner, K. & Jähnig, S.C. The global decline of freshwater megafauna. (under review)

Manuscript submitted to *Global Change Biology* on April 12th, 2019

Author contributions: F.H., C.Z. and S.C.J. conceived the ideas; F.H., collected the data, and J.N.W.D. contributed part of the time series data; F.H. analysed the data with substantial input from V.B.; F.H. led the writing and all authors contributed substantially to the drafts of the manuscript.

Chapter 5 (Manuscript 5)

He, F., Langhans, S.D., Zarfl, C., Wanke, R., Tockner, K. & Jähnig, S.C. Extinction risks of freshwater megafauna: The combined effects of life-history traits and anthropogenic threats. (to be submitted)

Author contributions: F.H., S.D.L, C.Z. and S.C.J. conceived the ideas; F.H. and R.W. collected the data; F.H. analysed the data; F.H. wrote the first draft, with substantial contributions from all coauthors.

Chapter 6 (General discussion)

The sections 6.2 and 6.5.1 have been modified from the Manuscript 6:

He, F. & Jähnig, S.C. Put freshwater megafauna on the table before they are eaten to extinction (to be submitted).

Author contributions: F.H. conceived the idea, collected the data and led the writing, with substantial contributions from S. C. J.

Appendix G (Manuscript 7)

Carrizo, S. F., Jähnig, S. C., Bremerich, V., Freyhof, J., Harrison, I., He, F., Langhans, S.D., Zarfl, C., Tockner, K. & Darwall, W. (2017). Freshwater megafauna: Flagships for freshwater biodiversity under threat. *Bioscience*, **67**(10), 919-927. https://doi.org/10.1093/biosci/bix099

S.F.C. ran the analyses and wrote several versions of the manuscript, V.B. and F.H. contributed to distribution mapping and documentation, all coauthors contributed to ideas behind the paper and reviewed versions of the manuscript.

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1. General introduction

The sections 1.2 and 1.3 have been modified from the following submitted manuscript:

He, F., Jähnig, S.C., Wetzig A. & Langhans, S.D. The untapped potential of cover images to promote underrepresented biodiversity (to be submitted).

1.1 Freshwater biodiversity crisis

Freshwaters are amongst the most diverse, dynamic and complex ecosystems on Earth. Although freshwaters such as rivers and lakes make up 0.01% of the all water on Earth and cover less than 1% of Earth's surface area (3% with wetlands included; (Lehner & Doll, 2004), they provide habitats for approximately 10% of all described animal species, 35% of all vertebrate species and 50% all of fishes (Balian *et al.*, 2008; Carrete-Vega & Wiens, 2012). Additionally, freshwater ecosystems support the livelihoods of and provide vital ecosystem services for humans, including food, water filtration, flood regulation, carbon sequestration and transportation (Aylward *et al.*, 2005). Throughout history, human civilizations have been intimately associated with freshwaters dating back to cradles of civilization (Macklin & Lewin, 2015).

During the last century, the human population has increased rapidly, with a subsequent growing demand for water, urban and agricultural lands, energy and food (Fig. 1.1; Steffen et al. 2015) posing tremendous pressures on freshwater ecosystems. Since the beginning of the 20th century, 64% to 71% of global wetlands have disappeared (Davidson, 2014). Permanent surface water on Earth has also experienced an area contraction of approximately 90,000 km^2 from 1984 to 2015 (Pekel *et al.*, 2016). The disappearance of rivers, lakes and wetlands leads to habitat loss of freshwater species. More than 30,000 large (higher than 15 m) and 80,000 small dams have been built or are under construction and cause impoundment, disrupted connectivity and sediment transport, and altered flow and thermal regimes in rivers (Grill *et al.*, 2015; Steffen *et al.*, 2015; Couto & Olden, 2018). Dams block migratory routes of species, resulting in lost access to feeding and spawning grounds and disrupted reproduction, as well as droughts in downstream areas (Liermann *et al.*, 2012; Winemiller *et al.*, 2016; Couto & Olden, 2018). The total capture of global inland fishes have increased more than 5 times compared to 70 years ago due to advancements in techniques and equipment (Welcomme *et al.*, 2010). Overexploitation has caused local depletion or even species extinction in freshwater biodiversity hotspots such as the Amazon and Mekong river basins (Hogan, 2011; Castello *et al.*, 2013; Castello *et al.*, 2015). Due to expanding urban and agricultural areas, pollutants flushed into freshwaters have also increased dramatically (e.g. 30% increase of dissolved inorganic N and P from 1970 to 2010; Seitzinger *et al.*, 2010), leading to degradation in water quality and harmful algal blooms. Moreover, increasing water traffic, together with habitat degradation, has contributed to the spread of invasive species (Leuven *et al.*, 2009; Keller *et al.*, 2011). These persistent threats have caused declines in distribution ranges and population abundances of freshwater species or even species extinctions, in turn, leading to erosion in ecosystem services and threatening human wellbeing (Dudgeon *et al.*, 2006). In addition to these persistent threats, rapidly emerging threats including climate change, the ongoing boom in constructing hydropower dams, light and noise pollution, and newer contaminants (e.g. active pharmaceutical ingredients, illicit drugs, endocrine disrupters, nanomaterials and microplastics) have imposed further pressure on freshwater habitats and drive even more freshwater species towards extinction (Reid *et al.*, 2018).

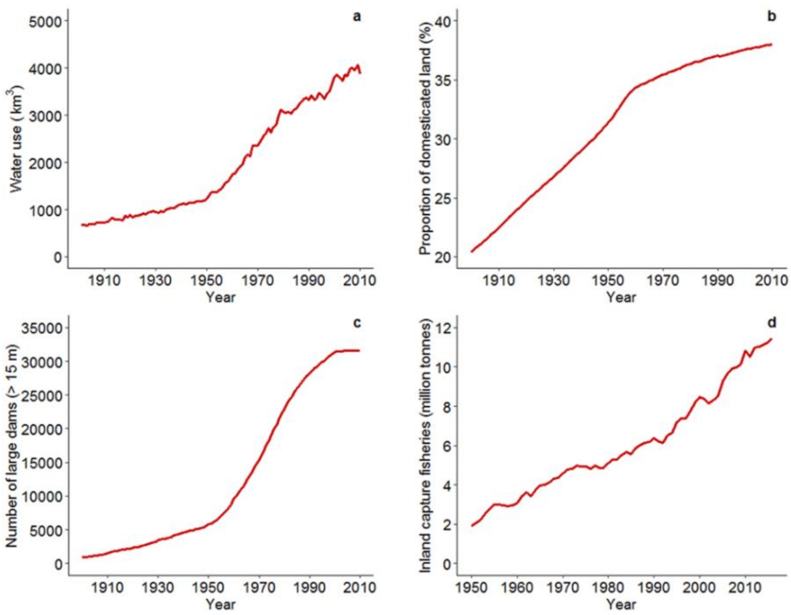

Fig. 1.1 Changes in global a) human-related water use, b) proportion of domesticated land compared within total land area, c) number of large dams with minimum 15 m height above foundation, and d) production of inland capture fisheries globally. Data for a, b and c were derived from Steffen *et al.* (2015), data ford were from the Fishery Statistical Collections of the Food and Agriculture Organization of the United Nations (FAO, 2018).

Consequently, 258 freshwater species have been assessed as Extinct or Extinct in the Wild according to the International Union for Conservation of Nature's Red List of Threatened Species (hereafter referred as IUCN Red List) (IUCN, 2018). Moreover, 6183 freshwater species have been listed as Critically Endangered, Endangered or Vulnerable, which are considered as threatened with extinction (IUCN, 2018). From 1970 to 2012, populations of vertebrates in freshwaters have declined by 81% (McRae *et al.*, 2017), which is twice as much as in marine or terrestrial ecosystems (Fig. 1.2); and the rate has further increased to 83% by 2014 (WWF, 2018).

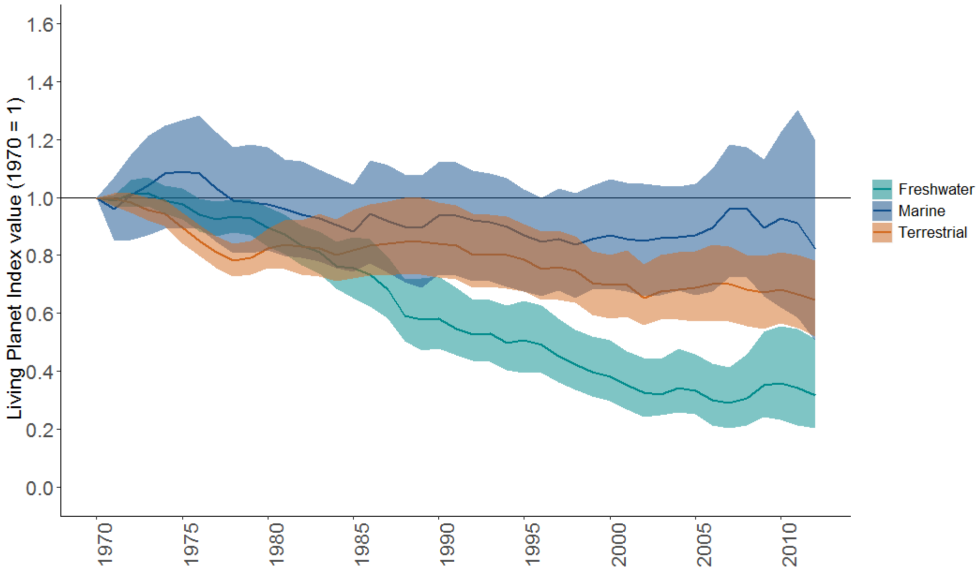

Fig. 1.2 The Living Planet Index (LPI) values for freshwater, terrestrial and marine ecosystems from 1970 to 2012, with 95% confidence intervals shown in shaded areas (adapted from McRae et al., 2017). Note that the data published online (https://github.com/Zoological-Society-of-London/rlpi) by the LPI team excluded around 3000 populations (approximate 2400 of them are marine populations) which are confidential. These data have been used in McRae et al., (2017) and the Living Planet Report (WWF, 2018), but not in this figure. Therefore, results shown in the figure are slightly different from McRae et al., (2017) and the Living Planet Report (WWF, 2018), particularly for marine ecosystems.

1.2 Overlooked freshwater biodiversity in current conservation schemes

Although freshwater ecosystems support a vast amount of biodiversity and are subject to intense threats (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010; Harrison *et al.*, 2018; Reid *et al.*, 2018), they still remain largely underrepresented in biodiversity and conservation research (Jucker *et al.*, 2018; Tydecks *et al.*, 2018). For example, only 18% of all the biodiversity studies published from 1945 to 2014 have focused on freshwater ecosystems (Tydecks *et al.*, 2018). Among all articles published in leading journals (i.e. journals with a 2016 Impact Factor ≥4.0) in ecology and biodiversity conservation from 2006 to 2016, only 5% focused on freshwaters (Mazor *et al.*, 2018).

Gaps in conservation actions could be even worse than those in research (Clark & May, 2002). According to the IUCN Red List, almost all the terrestrial birds and 85% of terrestrial mammals have been assessed, whilst 45% of all freshwater fishes remained unassessed (IUCN, 2018). This stands in contrast to the fact that proportions of extinct and threatened species in freshwater ecosystems are higher than those in terrestrial or marine ecosystems (Costello, 2015). Almost 90% of all seasonal freshwater wetlands are not covered by protected areas (Reis *et al.*, 2017). Most of the world's largest rivers have less than 10% of their basins targeted by integrated protection (Abell *et al.*, 2017). Although Bastin *et al.* (2019) suggested 15% of inland surface waters are within the boundaries of protected areas, freshwaters are often not considered in the management goals as rivers and lakes are usually used to delineate boundaries of protected areas rather than being integrated into conservation targets (Darwall *et al.*, 2011). The current protected areas are mostly based on terrestrial or marine ecosystems (Acreman & Duenas-Lopez, 2019). Critical habitats for freshwater species such as movement corridors of migratory fishes are rarely considered in the goals of protected areas (Bower *et al.*, 2015). Moreover, dam construction and pollution from agricultural and mining activities in upstream areas are beyond management goals of protected areas (Adams *et al.*, 2015; Abell *et al.*, 2017) but posing negative impacts on freshwater ecosystems within protected areas. Consequently, current protected areas fall short of providing efficient protection for freshwater biodiversity (Hermoso *et al.*, 2016; Juffe-Bignoli *et al.*, 2016).

It is suggested that biodiversity research and conservation actions to safeguard freshwater biodiversity are generally inadequate as a consequence of lower popularity (Monroe *et al.*, 2009). Indeed, freshwaters lack promotion by megafauna (Cooke *et al.*, 2013). Unlike terrestrial and marine ecosystems, represented by popular megafauna such as the polar bear, elephants, rhinos, whales, and dolphins, freshwater megafauna remain inconspicuous in the public eye. For example, no freshwater megafauna is considered amongst the ten most charismatic animals by the public (Courchamp *et al.*, 2018). A collection of information on covers of conservation journals from 1996 to 2016 (Table S1.1) revealed that freshwaters have been featured less on covers of conservation journals in comparison to terrestrial and marine ecosystems (Fig. 1.3). Since 2007, freshwater ecosystems have been portrayed on the fewest journal covers. Terrestrial megafauna regularly appear on conservation journal covers and marine megafauna are often shown, however no freshwater megafauna is among the 15 most featured species.

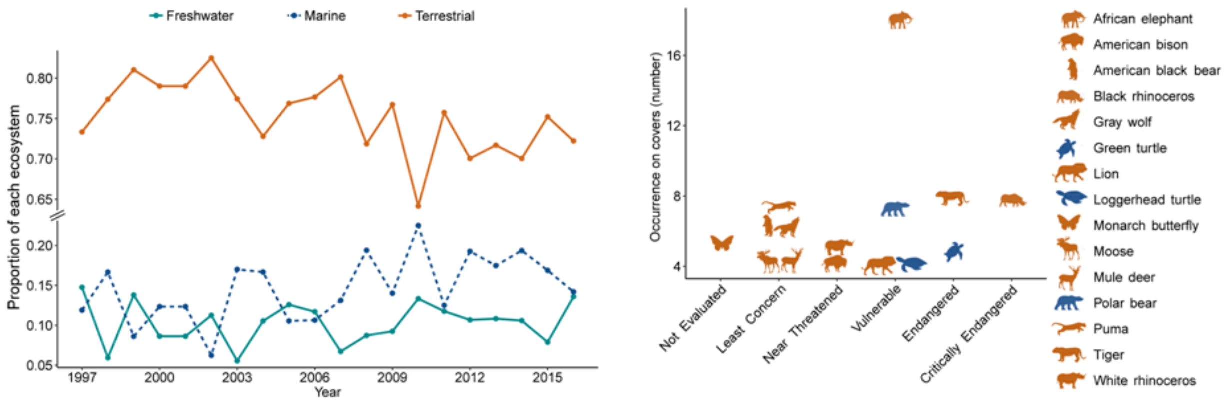

Fig. 1.3 Proportion of cover images displaying freshwater, marine, and terrestrial ecosystems (left) and the 15 most featured species and their IUCN conservation status (right) on covers of conservation journals between 1997 and 2016. Brown-colored animals are from terrestrial ecosystems, while blue-colored animals are associated with both marine and terrestrial ecosystems.

1.3 Megafauna: ecological roles, extinction risks and their potential in advancing biodiversity conservation

The term *megafauna* has been widely used in ecology, conservation and paleontology, including distinct groups of species such as marine benthic invertebrates (> ca. 1 cm) that are visible in photos (Kaufmann & Smith, 1997), large amphibians, reptiles, birds and mammals with body mass over various thresholds (e.g. 10 kg, McClenachan *et al.*, 2016; 15 kg, Ripple *et al.*, 2016; 40 kg, Ripple *et al.*, 2019; 44 kg, Barnosky *et al.*, 2004; 100 kg, Ripple et al. 2019; 1000 kg, Guimarães *et al.*, 2008). Apart from epibenthic research, most studies have used the term *megafauna* to refer to large vertebrates, which stands in line with the description (i.e. "*the hugest, and fiercest, and strangest*") by the British naturalist Alfred Russel Wallace (Wallace, 1876). Hence, megafauna species are considered as disproportionately large vertebrates within their taxonomic groups in the following discussion.

Megafauna often function as keystone species in ecosystems they inhabit and play important ecological roles: 1) Megafauna such as ground sloths and elephants have strong impact on vegetation structure as they can easily knock down woody plants and break closed-canopy vegetation (Bakker *et al.*, 2016a). Hippos and beavers destruct river banks and build dams, in turn, creating and maintaining habitats for smaller species (Bakker *et al.*, 2016b). 2) They also play vital roles in biogeochemical cycling. Whales transfer nutrients vertically by releasing feces near the surface while feeding at deeper areas (Roman & McCarthy, 2010). Anadromous fishes such as salmons and sturgeons move a large amount of nutrients every year from marine ecosystem to freshwater and terrestrial ecosystems (Doughty *et al.*, 2016); 3) Megafauna such as elephants, tapirs and migratory fishes disperse plant seeds, small animals and microbes over long distances (Fragoso *et al.*, 2003; Anderson *et al.*, 2011; Campos-Arceiz & Blake, 2011), therefore, influencing their spatial distributions. 4) Big cats, crocodilians and piscivore fishes are often top predators and exert profound influence on other biota cascading down through the food chain and ultimately affecting ecosystem processes and functioning (Malhi *et al.*, 2016; Hammerschlag *et al.*, 2019).

According to ecological theory, megafauna are particular vulnerable to extinction as they are often are k-strategist species and cannot recover rapidly after disturbance (McKinney, 1997; Olden *et al.*, 2007; Hutchings *et al.*, 2012; Ripple *et al.*, 2017). Indeed, two-thirds of terrestrial megafauna genera and half of all species have become extinct in the last 50,000 years (Barnosky, 2008; Malhi *et al.*, 2016). The remaining megafauna are also facing multiple threats including habitat loss and overexploitation (Estes *et al.*, 2016; Ripple *et al.*, 2016; Ripple *et al.*, 2019). They are particularly vulnerable to overexploitation as their meat, skin, eggs as well as other body parts (e.g. horn, tusk) are regarded as a luxury, e.g. as food, traditional medicine and ornament (Ripple *et al.*, 2016). During the last century, megafauna species such as the Schomburgk's deer (*Rucervus schomburgki*), Japanese sea lion (*Zalophus japonicus*) and Caribbean monk seal (Neomonachus tropicalis) have disappeared from Earth. In addition, two freshwater megafauna species (i.e. the baiji, *Lipotes vexillifer*, and Chinese paddlefish, *Psephurus gladius*) have become functionally extinct and probably no longer exists on Earth (Xie, 2017) while there are only three known individuals of the Yangtze giant softshell turtle (*Rafetus swinhoei*) remaining globally[1].

Owing to the fascination of humans with large animals, megafauna have been used to raise environmental awareness and attract media attention for over a half century (Leader-Williams & Dublin, 2000). The giant panda (*Ailuropoda melanoleuca*) has been used as the logo of the World Wide Fund for Nature (WWF) since 1961. In addition, big cats, rhinos, elephants, polar bear (*Ursus*

1 http://bit.ly/mega-introduction1 (Date of access: 2019-04-15)

maritimus), sharks, whales, dolphins and giant sea turtles have been successfully used as flagship species to establish emotional connections between the public and nature (Caro & O'Doherty, 1999; Walpole & Leader-Williams, 2002; Wilson & Tisdell, 2003; Cisneros-Montemayor *et al.*, 2013) and raise public awareness of environmental issues (Capietto *et al.*, 2014; Lewison *et al.*, 2014; Nelms *et al.*, 2016; Germanov *et al.*, 2018), in turn, boosting support for biodiversity conservation (Zacharias & Roff, 2001; Hooker & Gerber, 2004). Owing to their large habitat requirements and association with high level of biodiversity (Sergio *et al.*, 2006), megafauna-based protected areas can benefit smaller co-occurring species (Li & Pimm, 2016; Thornton *et al.*, 2016).

Although there is an increasing amount of studies focusing on terrestrial and marine megafauna, the concept of "freshwater megafauna" has been rarely mentioned in published scientific papers. For example, a search in Web of Science was conducted with the topics "megafauna" and ecosystem ("freshwater", "marine" or "terrestrial") in December 2015. Only nine articles were returned for the search on freshwater ecosystems, much fewer than those featuring marine (231) and terrestrial (67) ecosystems. However, there are many freshwater animals with spectacular appearances which are qualified as megafauna with the body-mass thresholds used to define megafauna in previous studies (Barnosky *et al.*, 2004; Estes *et al.*, 2016; McClenachan *et al.*, 2016; Ripple *et al.*, 2016) or the description by Alfred Russel Wallace (1876; "*the hugest, and fiercest, and strangest*"; Box 1.1). Freshwater megafauna species including river dolphins, sturgeons, hippos, crocodilians and giant salamanders are regarded as charismatic species (Fig. 1.4) and have the potential to act as flagship species to promote biodiversity conservation in freshwaters (Cooke *et al.*, 2013; Kalinkat *et al.*, 2017). Additionally, freshwater megafauna have the potential to serve as umbrella species. For example, migratory species including sturgeons and giant catfishes move hundreds of miles from downstream to upstream of rivers (Pikitch *et al.*, 2005; Hogan, 2011). Hence, protecting their migration corridors can maintain the river connectivity and benefit other co-occurring freshwater species.

Box 1.1 Freshwater megafauna species according to the description by Alfred Russel Wallace (1876)

Fig. 1.4 Selected charismatic freshwater megafauna species. Arapaima (*Arapaima giga*, top left) by Jeff Kubina (CC BY-SA 2.0). Beluga (*Huso huso*, top right) by Jeff Whitlock (CC BY-NC-SA 3.0). Chinese giant *salamander* (*Andrias davidianus*, middle left) b*y* Theodore Papenfuss (CC BY-NC 3.0). American Alligator (*Alligator mississippiensis*, middle right) by Clément Bardot (CC BY-SA 4.0). Hippopotamus (*Hippopotamus amphibious*, bottom left) by Brian Snelson (CC BY 2.0). Yangtze finless porpoise (*Neophocaena asiaeorientalis* ssp. *asiaeorientalis*, bottom right) by Huigong Yu.

The hugest: The beluga (*Huso huso*), green anaconda (*Eunectes murinus*), European sturgeon (*Acipenser sturio*) and white sturgeon (*Acipenser transmontanus*) grow over six meters long while the common hippopotamus (*Hippopotamus amphibius*) can weight over 2000 kg.

The fiercest: The Nile crocodile (*Crocodylus niloticus*) and black caiman (*Melanosuchus niger*) can exceed five meters long and have a powerful bite allowing them to take any animals unfortunate enough to encounter them.

The strangest: The electric eel (*Electrophorus electricus*) is able to produce electric discharges over 600 volts (Traeger et al., 2015) while the Chinese giant salamander (*Andrias davidianus*) emits a sound strikingly resembles to a human child's cry (Cunningham et al., 2015).

1.4 Research gaps, aims and thesis structure

Despite that the concept of "freshwater megafauna" has been mentioned in several studies (Mazzotti *et al.*, 2009; David, 2010; Turvey *et al.*, 2010; Turvey *et al.*, 2012), a synthesis of global freshwater megafauna is lacking. For example, Turvey et al. (2010) and Cooker et al. (2013) have called for more studies to promote charismatic freshwater megafauna, while David (2010) also emphasized the potential of freshwater megafauna acting as flagship species in his master thesis. However, no follow-up studies have been conducted and several gaps remain to gain a comprehensive understanding of the diversity and risk patterns of freshwater megafauna at global scale. The most prominent gaps are: 1) The definition of freshwater megafauna remains unclear in published literature. Therefore, a clear definition for megafauna in freshwaters followed by a compilation of a comprehensive list of contemporary freshwater megafauna species is still missing. 2) Global distributions of freshwater megafauna are yet to be mapped in high resolution. David (2010) has illustrated species richness of selected freshwater megafauna within each freshwater ecoregion. However, such a resolution (e.g. the whole Yangtze River basin has been divided into three units while the Danube has been divided into two) is not sufficient enough to support spatial prioritization of conservation management, which is often conducted in small catchment units (Linke *et al.*, 2007; Hermoso *et al.*, 2011). 3) The type, intensity and location of human pressure on freshwater megafauna are largely unknown, which could hamper identifying the areas of potential conflicts between freshwater megafauna diversity and human activities and prioritizing areas in need of conservation. 4) Although population decline and range contraction for individual freshwater megafauna species have been reported (Pikitch *et al.*, 2005; Hogan, 2011), a synthesis of changes in population abundance and distribution ranges of freshwater megafauna species at large scales (e.g. continental and global scales) is missing. Such research is important to inform the decision makers and the public about the dire situation of the world's largest freshwater animals, as well as the overall condition of global freshwater ecosystems. 5) Large freshwater animals have been suggested being particularly vulnerable to extinction due to their slow life-history strategies and high level of exploitation pressure (Olden *et al.*, 2007). The relationships between extinction risk of freshwater megafauna and their life-history traits, and the impact of human threats on such relationships remain unexplored. Understanding such relationships can enable us to identify species with high vulnerability to extinction, which is particularly needed for freshwater megafauna, as many of them have not been classified on the IUCN Red List.

This thesis aims to gain a comprehensive picture of the global freshwater megafauna, with emphasis on their distribution, conservation status, main threats, population changes and extinction risks (Fig. 1.5). To achieve the aim, the first step was to define and identify freshwater megafauna species. The threshold of 30 kg was chosen to include most of the large freshwater animals with the potential of acting as flagship or umbrellas species. Based on this definition, I compiled a list of 207 extant freshwater megafauna species. The data on freshwater megafauna are scattered over the literature. I collated the data and established a freshwater-megafauna database containing information on their distribution, life-history traits, population change, conservation status and intensity of human threats within their distribution range.

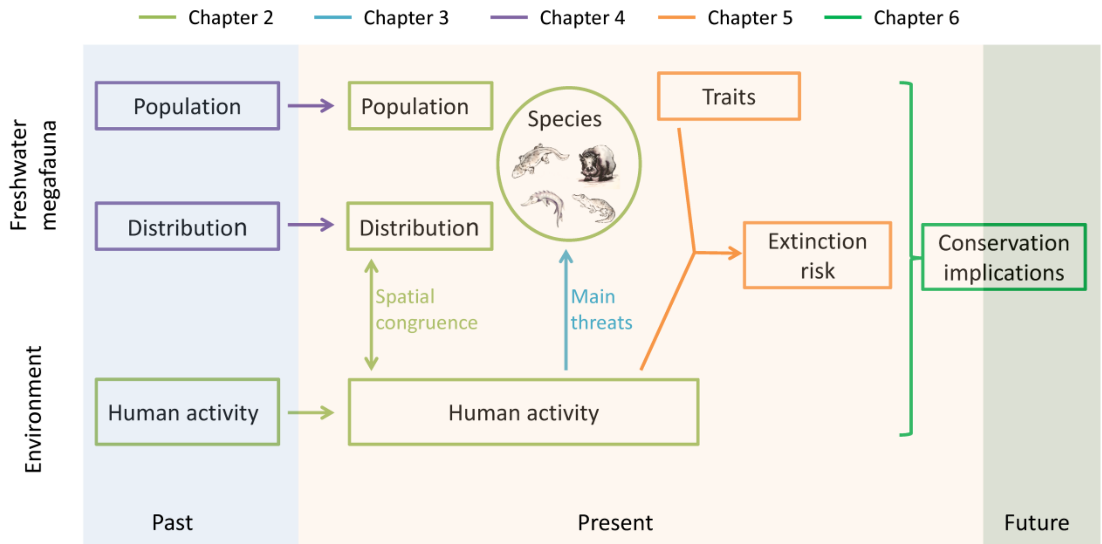

Fig. 1.5 Conceptual overview of linkages between chapters. Note that the spatial congruence between freshwater megafauna diversity and human pressures in the past has not been explored as it is difficult to find a historical time point when data on megafauna distribution and human pressures are both available.

Five research questions are embedded within this thesis: **1)** Where are regions of freshwater megafauna diversity hotspots? **2)** Where are regions of potential conflict between human activities and freshwater megafauna diversity? **3)** What are the main threats to freshwater megafauna? **4)** How did populations of global freshwater megafauna change over the last four decades? **5)** Which factors predispose freshwater megafauna to extinction?

Chapter 2 aims to answer the **first and the second research questions**. In this chapter, I collated distribution data of each freshwater megafauna species and then converted the information into HydroBASINS level 8 sub-catchments, in which global freshwater catchments are divided into 228,465 individual sub-catchments (Lehner & Grill, 2013). Global distributions of overall freshwater megafauna, threatened species, and species with different population trends (i.e. increasing and stable, decreasing, and unknown) were shown. Diversity hotspots of overall freshwater megafauna and threatened freshwater megafauna were also identified. Considering the fact that freshwater megafauna require complex habitats and often are top predators, I hypothesize that diversity hotspots of freshwater megafauna would largely overlap with diversity hotspots of overall freshwater species. In addition, I demonstrated the spatial congruence between freshwater megafauna diversity and human pressures. Moreover, I calculated temporal changes in human pressure from 1990 to 2010 within the distribution ranges of freshwater megafauna.

Chapter 3 focuses on **the third research question**. I did a comprehensive literature review on the threats to freshwater megafauna and categorized these threats into five groups. The impacts of these threats on freshwater megafauna were summarized and demonstrated with examples from different taxonomic groups and geographical regions. In addition, I compared the identified main threats to freshwater megafauna and to overall freshwater biodiversity summarized as by Dudgeon *et al.* (2006).

Chapter 4 explores **the fourth question**. I did an intensive search on time series data of freshwater megafauna populations in published literature, reports and online databases. Following the Living Planet Report, chain methods and general additive models were used to track the population change of global freshwater megafauna from 1970 to 2012. According to ecological theories, freshwater megafauna are characterized with extinction-prone traits such as large body size, long lifespan and late maturity (McKinney, 1997; Hutchings *et al.*, 2012). Therefore, I hypothesize that freshwater megafauna have declined more than their smaller counterparts. Population trends of freshwater megafauna in different biogeographic regions and taxonomic groups were also calculated. In addition, I collated historical (around the year 1500) and current distribution information for all freshwater megafauna species in Europe and the USA. The change in distribution ranges of each species was calculated. Moreover, maps of historical and current distributions in Europe and the USA were shown.

Chapter 5 focuses on **the last research question**. In this chapter, I collated twelve life-history traits for each freshwater megafauna species from published literature and calculated the intensity of human pressure within each freshwater megafauna species' distribution range. Then I used a generalized linear mixed model to explore the relationship between conservation status of freshwater megafauna and the combined effect of life history traits. In addition, the influence of human threats on such relationship was also examined. The best models were selected based on the Akaike information criterion. Conservation status of 49 species that were not assessed by the IUCN Red List were predicted with the selected models. In addition, the global distribution map of threatened freshwater megafauna was plotted based on both IUCN Red List assessments and model predictions and then compared with the one based only on the IUCN Red List assessments, which allowed identification of neglected diversity hotspots of threatened freshwater megafauna.

In **Chapter 6**, I summarize the key findings of the previous chapters and placed the results of the thesis in a broader context. Then I discuss their potential implications in conservation for freshwater megafauna and identified future challenges and opportunities for freshwater megafauna conservation. In addition, I discuss the potential ecological consequences of megafauna loss in freshwaters. Moreover, I demonstrate the potential of megafauna-based strategies in advancing conservation for overall freshwater biodiversity. Finally, I explore the potential to use freshwater megafauna to emphasize the gaps and problems in freshwater conservations and strengthen links between the general public and freshwater life.

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2. Freshwater megafauna diversity: Patterns, status, and threats

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2.1 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 sub-catchments (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.

2.2 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 (Naiman, Bilby, Schindler, & Helfield, 2002; Estes et al., 2011; Estes, Heithaus, McCauley, Rasher, & Worm, 2016; 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 high proportion 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 (Aylward et al., 2005). However, freshwater biodiversity is experiencing unprecedented and growing pressure from human activities (Dudgeon et al., 2006; Vörösmarty et al., 2010). Consequently, 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 action (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 status and 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 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 (Kehoe et al., 2015; Janse 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 emphasize the future challenges of freshwater megafauna conservation and provide suggestions for conservation actions in different basins.

2.3 Methods

2.3.1 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 S2.1). 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 publications 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 species, using HydroBASINS to map their distribution is essential for freshwater biodiversity conservation, as management units for freshwaters are often delineated at the sub-catchment 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 sub-catchment (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 datasets (e.g. Fish Base and NatureServe,), and from published literature (Table S2.2), 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 sub-catchment (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 catchment were classified as basin-endemic species.

2.3.2 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:

% threatened = (Critically Endangered + Endangered + Vulnerable) / (total assessed - Extinct - Extinct in the Wild - Data Deficient).

2.3.3 Human pressure on freshwater megafauna

The global spatial distribution and intensity of human impacts on freshwater megafauna was 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), since 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 sub-layers of the IBTI separately, i.e. 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 sub-catchment of both IBTI and THPI were calculated using the zonal statistics tool in QGIS (QGIS Development Team, 2015). Sub-catchments 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). Subsequently, 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).

2.4 Results

2.4.1 Distribution and status of freshwater megafauna

Freshwater megafauna species occur in 76% of the world's main river basins (level 3 HydroBASINS) (Fig. 2.1a, S2.1, S2.2). The Amazon basin exhibits the highest freshwater megafauna richness (35 species), followed by the Congo (23), Orinoco (23), Mekong (22), and Ganges-Brahmaputra (22) basins (Fig. S2.1a; Table S2.3). 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 S2.5).

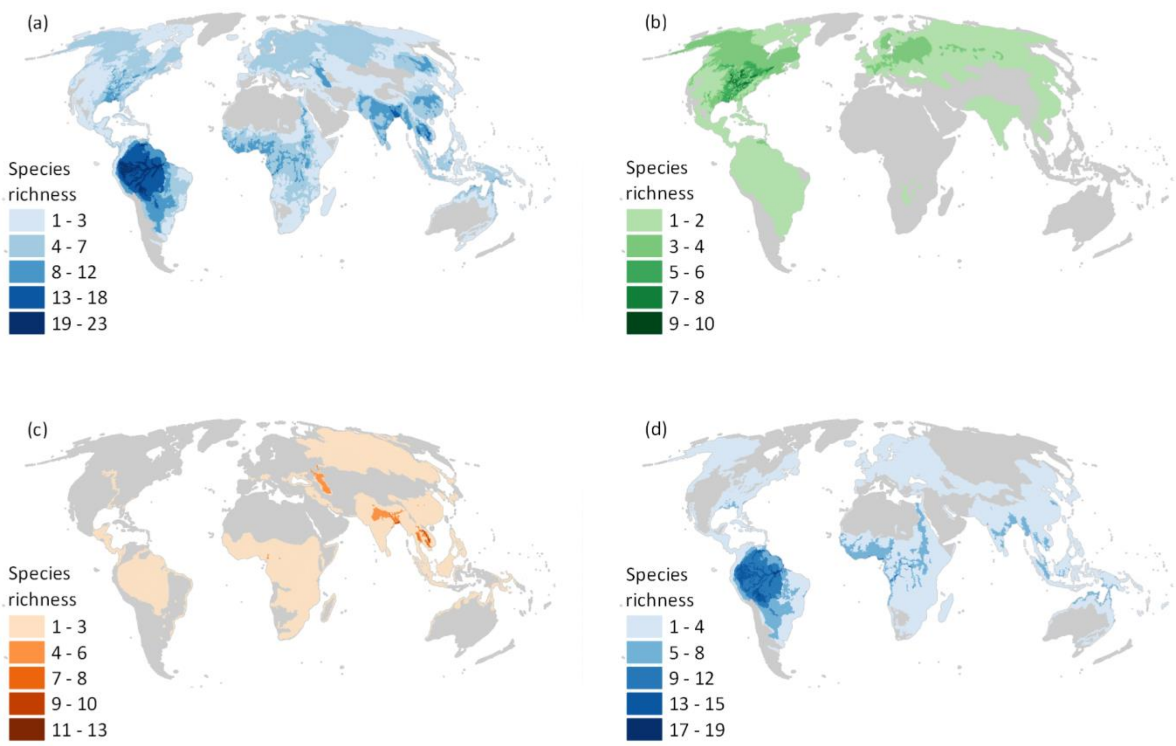

Fig. 2.1 Species richness of freshwater megafauna (a) overall (b) with increasing or stable, (c) declining, and (d) unknown population trends

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 (Fig. 2.1c). Sixty-two percent of freshwater megafauna species with stable or increasing population trends occur in North America (Fig. 2.1b). The greatest number of freshwater megafauna species with unknown population trends (33%) are found in South America (Fig. 2.1d).

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) (Fig. 2.2). The Mekong river basin exhibits the highest number of threatened species (15 species), followed by the Ganges-Brahmaputra basin (13) (Fig. S2.1b, S2.3a; Table S2.3). The proportion of threatened endemic freshwater megafauna species is substantial at 78% (Table S2.1). 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 ten years ago, Table S2.1).

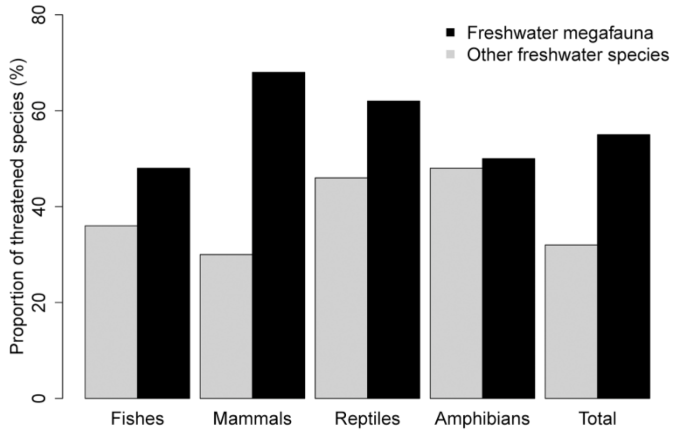

Fig. 2.2 Proportion of threatened freshwater megafauna (black) and other threatened freshwater species (grey) (total and within four taxonomic groups).

2.4.2 Human pressure on freshwater megafauna

Human pressure varies within the different basins (level 3 HydroBASINS; Table S2.4). 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 sub-catchments have IBTI values >0.75; Fig. 2.3a). In particular, the Mekong, Chao Phraya and Ganges-Brahmaputra basins are exposed to intense pressures from dam construction (Fig. 2.4a) and direct exploitation, such as fishing (Fig. 2.4b). In North America, freshwater megafauna species in the Mississippi river basin are also subjected 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 (Fig. 2.4b).

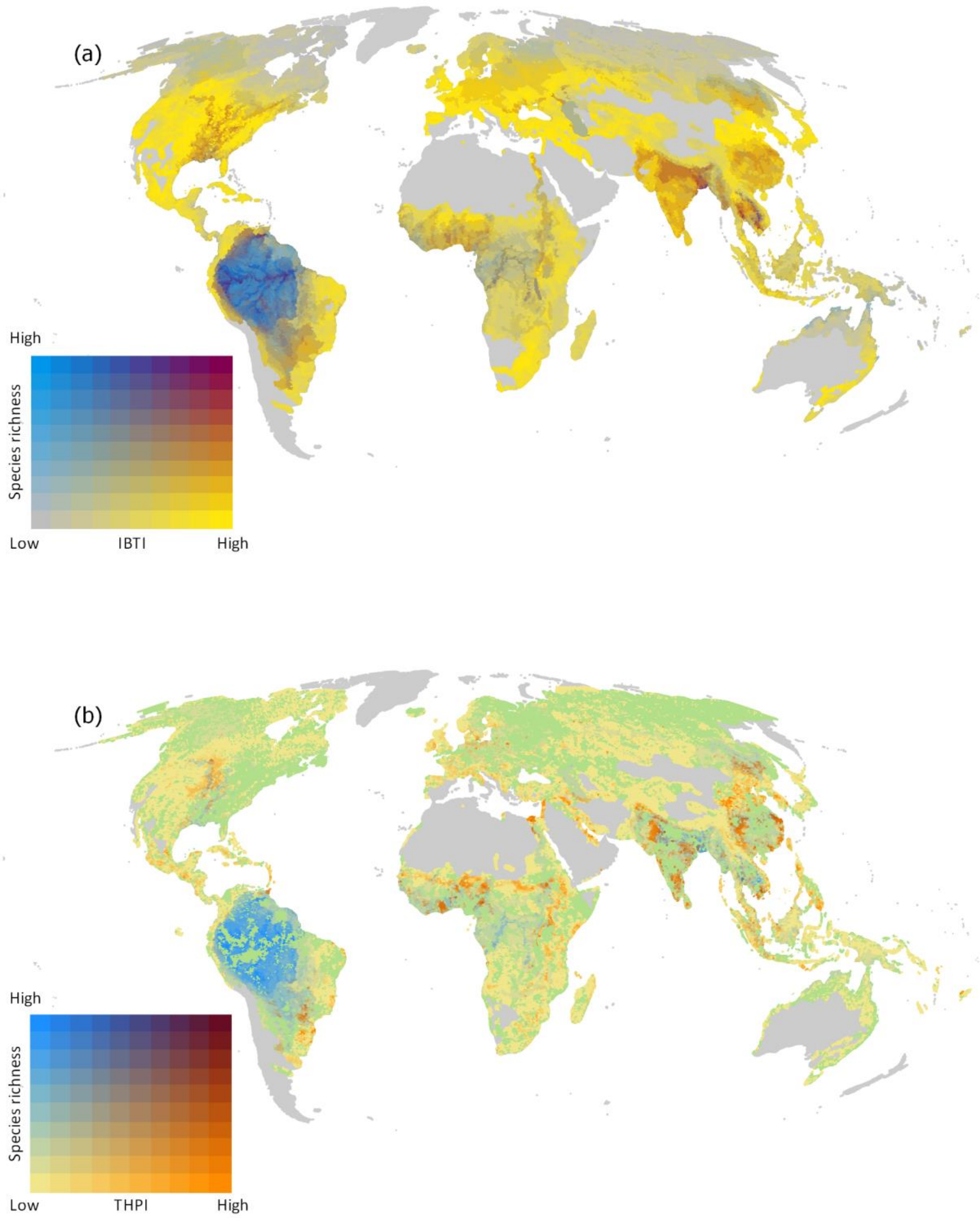

Fig. 2.3 Concordance map of freshwater megafauna species richness with (a) IBTI and (b) THPI. Green areas in (b) refer to regions with stable or decreased human pressure, while other colours indicate increased human pressure.

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 sub-catchments (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 (Fig. 2.3b). Conversely, 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 sub-catchments with THPI value <5).

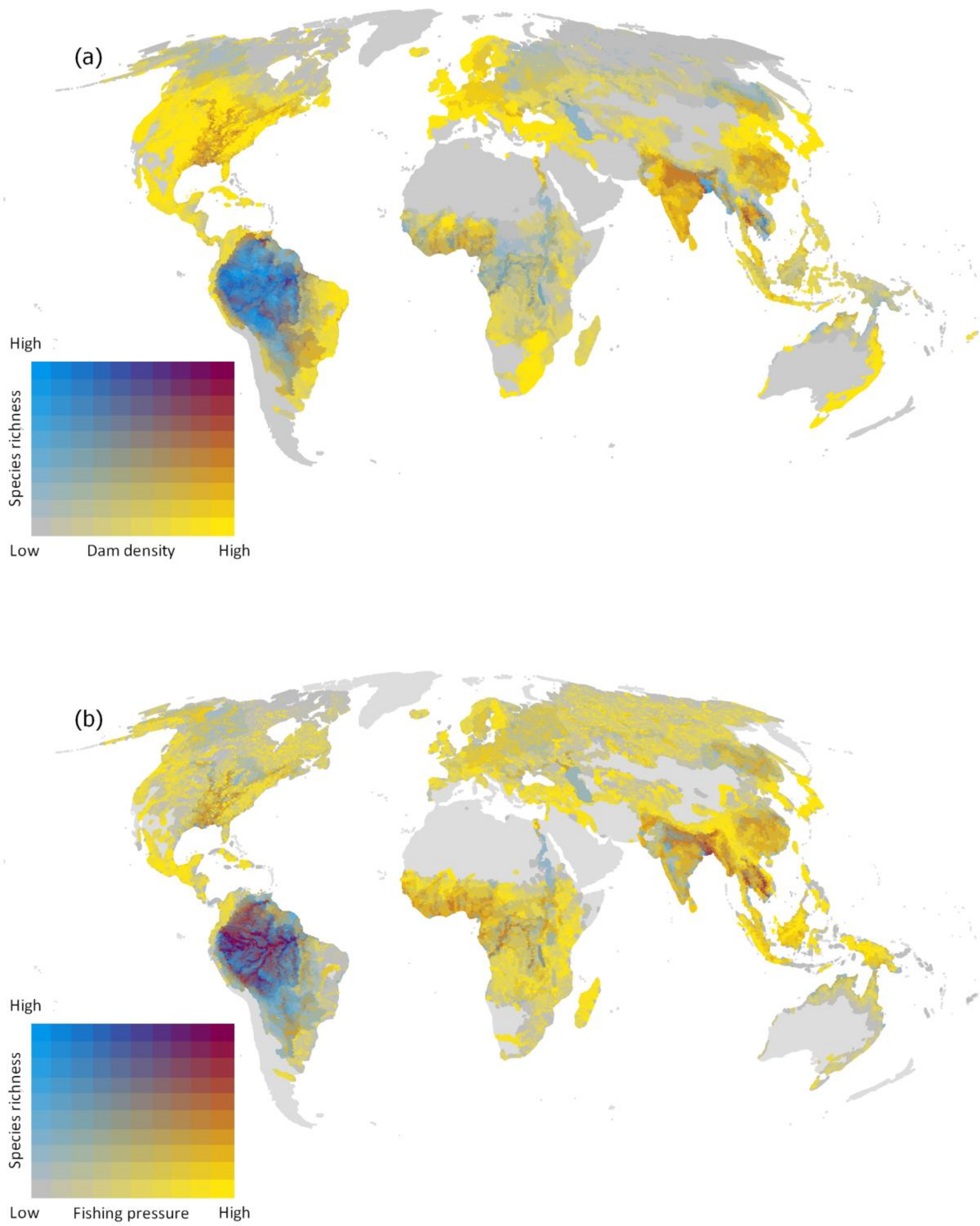

Fig. 2.4 Concordance map of freshwater megafauna species richness with (a) dam density and (b) fishing pressure.

2.5 Discussion

2.5.1 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 sub-tropical regions. However, freshwater megafauna species are threatened globally and have higher extinction risks than their smaller counterparts. Additionally, 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, since 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 are likely to 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 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 emphasizes the high levels of threat to freshwater megafauna species 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) is like that of terrestrial megafauna species (59%) (Table S2.6), 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 (Fig. S2.3b). 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).

2.5.2 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. urbanization, 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 sub-catchments 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 (Castello et al., 2013; Azevedo-Santos et al., 2016). In the Congo river basin, the situation is possibly worse, since 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 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) (Fig. 2.3; Table S2.3). 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 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 (Cheung & Dudgeon, 2006; Alves, da Silva Vieira, & Santana , 2008), 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 et al., 2013; Castello, Arantes, McGrath, Stewart, & Sousa, 2015). Unfortunately, the risk is further compounded, since rarity makes these species even more attractive to fishers and collectors, thus driving them into an extinction vortex (Courchamp et al., 2006).

Finally, 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 has 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 (Pikitch, Doukakis, Lauck, Chakrabarty, & Erickson, 2005; Hogan, 2011).

2.5.3 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 3700 major hydropower dams are planned or under construction globally, covering key biodiversity hotspots for freshwater megafauna (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015; Winemiller et al., 2016). 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) (Ziv, Baran, Nam, Rodríguez-Iturbe, Levin, 2012; Winemiller et al., 2016). 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 must be considered 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 programs 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 urengtly 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.

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3 Disappearing giants: A review of threats to freshwater megafauna

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3.1 Abstract

Charismatic megafauna species may act as both flagship and umbrella species. They influence local environments and biotas, determine related ecosystem processes and functions, and are associated with high levels of biodiversity. However, the intrinsic characteristics of megafauna species including long lifespan, large body size, sparseness and/or rarity, late maturity and low fecundity, as well as high market value, make them very prone to extinction. Up to now, scientific interest and conservation efforts have mainly focused on terrestrial and marine megafauna, while freshwater species have received comparatively little attention, despite evidence suggesting that freshwaters are losing species faster than marine or terrestrial realms. The high susceptibility of freshwater megafauna to multiple threats, coupled with immense human pressure on freshwater ecosystems, places freshwater megafauna amongst the most threatened species globally. The main threats include overexploitation, dam construction, habitat degradation, pollution and species invasion. These threats increase mortality, decrease productivity and reduce fitness, causing the decline of populations and the extinction of freshwater megafauna species. Given the essential ecological and biological roles of freshwater megafauna, further research should focus on their distribution patterns, extinction risks and population dynamics, thereby improving the knowledge base for conservation planning. Finally, freshwater megafauna-based conservation strategies may raise public awareness for freshwater conservation and therefore benefit a broader range of freshwater species and functions.

3.2 Introduction

Animals are classified according to various characteristics and traits, including size. The term megafauna refers to disproportionally large-bodied animals and is often associated with prehistoric large terrestrial vertebrates weighting more than 44 kg (ca. 100 pounds; Martin & Klein, 1989; Barnosky *et al.*, 2004). More recently, however, the concept of megafauna has been extended beyond a uniform weight threshold (Hansen & Galetti, 2009; Durant *et al.*, 2014; Ripple *et al.*, 2016), to cover both extinct and extant species in terrestrial, marine and freshwater ecosystems (Hooker & Gerber, 2004; Donlan *et al.*, 2005; Turvey *et al.*, 2010).

Megafauna species receive significant attention due to their charismatic nature and their susceptibility to extinction (Cardillo *et al.*, 2005; Sergio *et al.*, 2006; Turvey *et al.*, 2012). They are, therefore, often used as flagship and umbrella species, promoting public awareness (Leader-Williams & Dublin, 2000) and stimulating funding for environmental conservation (Walpole & Leader-Williams, 2002; Sergio *et al.*, 2008). For instance, the "big five" (i.e. buffalo, elephant, lion, leopard, and rhinoceros) are important flagship species for sub-Saharan Africa, having secured strong public attention and subsequent support (Caro & Riggio, 2014). Recently, research on megafauna has increased (Fig. 3.1), but with the scientific interest and conservation efforts mainly focusing on terrestrial and marine ecosystems. In contrast, freshwater megafauna remain underrepresented both in science and in public awareness (Cooke *et al.*, 2013). At the same time, freshwaters are among the most threatened ecosystems globally; with species populations declining much faster than in terrestrial and marine realms realms (Sala *et al.*, 2000; Jenkins, 2003; McLellan *et al.*, 2014). Furthermore, the concept of megafauna is rarely considered in freshwater research and conservation. Indeed, we still lack an official definition of freshwater megafauna. Carrizo et al. (unpublished data) defined freshwater megafauna as all animals with a body mass of at least 30 kg that spend an essential part of their life in freshwater or brackish ecosystems - their definition is adopted for this review. Based on a 30 kg threshold, freshwater megafauna species include representatives of fishes, reptiles, mammals and amphibians.

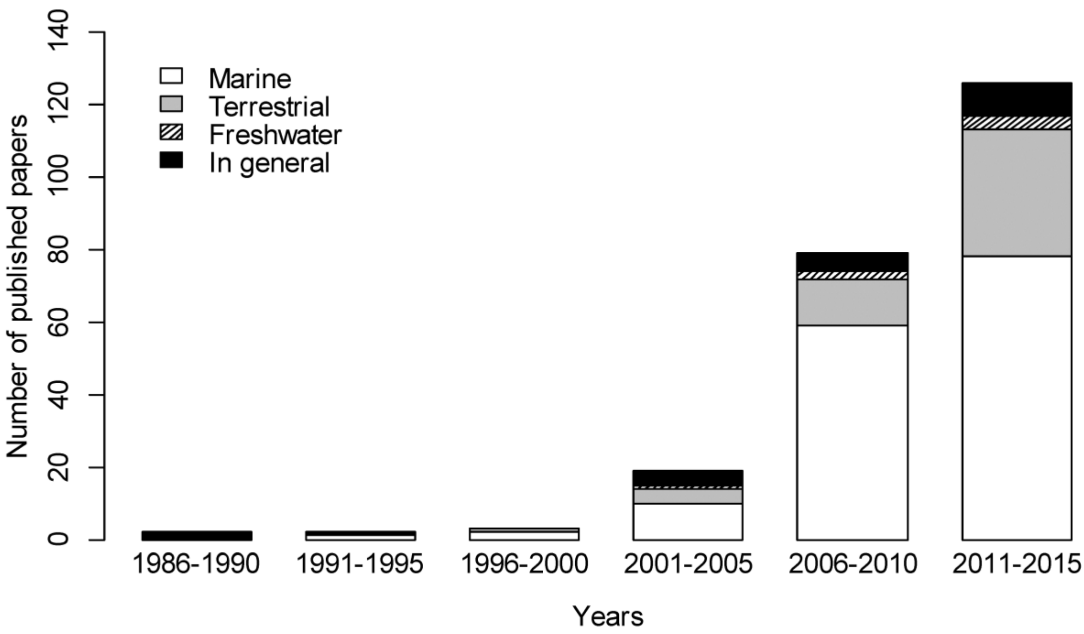

Fig. 3.1 Numbers of publications focused on megafauna in different ecosystems (for details on the underlying methodology see Appendix C).

Megafauna species shape ecosystems and their related processes, often representing key ecosystem engineers (McCarthy *et al.*, 1998; Moore, 2006; Mosepele *et al.*, 2009). For example, beavers (the American beaver, *Castor canadensis* and the Eurasian beaver, *Castor fiber*) alter stream morphology through dam building, thereby changing hydrological and biogeochemical processes, as well as affecting in-stream and riparian communities (Wright *et al.*, 2002; Nummi & Holopainen, 2014; Wohl, 2015). The American alligator (*Alligator mississippiensis*) modifies the Everglades landscape by creating and maintaining small ponds which, in turn, provide habitat and refugia for many additional plants and small animals (Campbell & Mazzotti, 2004). Freshwater megafauna may also increase the nutrient flow between freshwater, terrestrial and marine ecosystems. For instance, anadromous freshwater megafauna (e.g. the Atlantic salmon, *Salmo salar* and the Chinook salmon, *Oncorhynchus tshawytscha*) transfer large amounts of nutrients from the ocean to freshwaters and finally to terrestrial systems (Gende *et al.*, 2002; Doughty *et al.*, 2016), shaping productivity and food web dynamics in river and riparian systems.

Many freshwater megafauna species are top predators. Their extirpation would often lead to marked effects on local community structure through trophic cascades. For examples, the loss of large predatory fish might release small planktivorous species from predation, thus altering consumption pressures on zooplankton and phytoplankton (Estes *et al.*, 2011). Moreover, freshwater megafauna may create habitat for other species, such as through the creation of ponds and holes by hippopotamus or crocodilians so providing dry-season refugia for many fish species (Campbell & Mazzotti, 2004; Mosepele *et al.*, 2009). The decline of brown trout (*Salmo trutta*), mainly due to habitat fragmentation, threatens the freshwater pearl mussel (*Margaritifera margaritifera*), because it is an important host for the parasitic mussel larvae (Osterling & Soderberg, 2015). These few selected examples emphasize the potentially far-reaching ecological and biological consequences of freshwater megafauna loss.

A high proportion of the world's freshwater megafauna species are under threat (Pikitch *et al.*, 2005; Huang *et al.*, 2012; Gessner *et al.*, 2013). Indeed, 54% (i.e. 84 out of 155 assessed species) of freshwater megafauna are already listed as threatened (Critically Endangered, Endangered or Vulnerable; for details see Supporting Information), based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species™ (hereafter IUCN Red List; IUCN, 2015). Four species are Critically Endangered (Possibly Extinct), including the Chinese paddlefish (*Psephurus gladius*), the world's longest freshwater fish, which has not been seen since 2003 (Zhang *et al.*, 2016); the baiji (*Lipotes vexillifer*), which could represent the first human-caused extinction of a cetacean species (Turvey *et al.*, 2007); the Yangtze sturgeon (*Acipenser dabryanus*); and the Adriatic sturgeon (*Acipenser naccarii*). Today, both sturgeon species are strongly dependent on artificial stocking to maintain their populations in the wild (Bronzi *et al.*, 2013; Wu *et al.*, 2014). The Atlantic (or common) sturgeon (*Acipenser sturio*), once the most common sturgeon species across Europe, is now restricted to the Garonne River (France) and is experiencing an ongoing decline (Williot *et al.*, 2009).

Many freshwater megafauna species inhabit remote areas and their decline or loss will often go unnoticed due to poor monitoring. For instance, despite its large size, the freshwater whipray (*Himantura dalyensis*) still lacks information on many of the threats it faces and was only recently recognized as a separate species (Last & Manjaji-Matsumoto, 2008). Discussion on the taxonomy of *Arapaima* spp. is still ongoing (Stewart, 2013a; Stewart, 2013b), and the assessment of arapaima (*Arapaima gigas*) needs updating as it is still listed as Data Deficient on the IUCN Red List, in spite of increasing evidence that it is seriously threatened by overexploitation (Castello *et al.*, 2013; Cavole *et al.*, 2015). Although research on the conservation status has been conducted for individual species and taxonomic groups, such as sturgeons and paddlefishes, we lack a collective overview of the threat status for all freshwater megafauna at the global scale. Intending to fill this important information gap, this paper provides a comprehensive overview of the threats facing freshwater megafauna, and of the subsequent impacts. In addition, we highlight the urgent need for great focus on the conservation of freshwater biodiversity.

3.3 Threats to freshwater megafauna

The loss of freshwater megafauna is mainly driven by overexploitation, dam construction, habitat degradation, pollution and species invasion, along with the compounding impacts of climate change (Table 3.1). The interacting and combined impacts of these threats have led to a decline in population size and range reduction for many freshwater megafauna species (Choudhury *et al.*, 2007; Gesner *et al.*, 2010). Although there remains a lack of understanding of the influence of climate change on freshwater megafauna, global warming and drought are likely to increase habitat degradation, further increasing direct impacts of human activities. The freshwater whipray, for example, is considered highly susceptible to climate change effects due to its rarity and high degree of habitat specialization (Chin *et al.*, 2010). For the Caspian seal (*Pusa caspica*), warmer winters in the future might reduce the stability of ice breeding habitats and cause increased mortality among pups (Härkönen, 2008). In addition, global warming is likely to have severe impacts on crocodilians and turtles with temperature-dependent sex determination, altering sex ratios and affecting population demographics (Gibbons *et al.*, 2000).

Table 3.1 Major threats to freshwater megafauna

Threats	Impact	Examples
Overexploitation	Increased mortality due to intentional harvest or by-catch; depletion or extirpation of local populations	*Arapaima gigas* (Castello *et al.*, 2013; Cavole *et al.*, 2015), *Andrias davidianus* (Xie *et al.*, 2007; Tapley *et al.*, 2015), *Crocodylus rhombifer* (Targarona *et al.*, 2010)
Dam construction	Blocked migration pathways for migratory species; reduced access to spawning grounds; fragmented population; altered natural flow and thermal regime, thus influencing fitness and reproduction; drought and habitat loss at downstream locations	*Acipenser gueldenstaedtii* (Gesner *et al.*, 2010), *Acipenser sinensis* (Wu *et al.*, 2015), *Gavialis gangeticus* (Choudhury *et al.*, 2007), *Kobus leche* (IUCN SSC Antelope Specialist Group, 2008)
Habitat degradation	Loss and fragmentation of required habitats and spawning grounds; increased injury and death due to conflict with humans (e.g. settlement, agriculture, shipping)	*Crocodylus niloticus* (Ashton, 2010), *Hucho perryi* (Rand, 2006), *Pteronura brasiliensis* (Groenendijk *et al.*, 2015), *Trichechus manatus* (Nowacek *et al.*, 2004)
Pollution	Increased mortality due to acute toxicity and bioaccumulation; degraded water quality (e.g. eutrophication and sedimentation) resulting in chemical barriers to fish movement and reduced fitness; endocrine disruption leading to developmental and reproductive abnormalities	*Crocodylus moreletii* (Rainwater *et al.*, 2007), *Huso dauricus* (Shmigirilov *et al.*, 2007), *Pusa sibirica* (Tsydenova *et al.*, 2004)
Species invasion	Competitive exclusion of native species; introduced diseases; increased mortality through predation and toxicity of venomous species; modified food web structure; hybridization and introgression with native species	*Acipenser nudiventris* (Strauss *et al.*, 2012), *Clarias macrocephalus* (Na-Nakorn *et al.*, 2004), *Crocodylus johnstoni* (Letnic *et al.*, 2008), *Hypselobarbus mussullah* (Pinder *et al.*, 2015), *Tomistoma schlegelii* (Bezuijen *et al.*, 2014)
Climate change	Loss of suitable habitat due to changes in temperature, precipitation patterns, and extreme events (e.g. drought or flood); potential impact on development and growth in reptiles	*Alligator sinensis* (Zhang *et al.*, 2009), *Pusa caspica* (Härkönen, 2008)

Compared to other aquatic organisms, freshwater megafauna are typically more susceptible to hunting pressure and ecosystem degradation due to their long lifespan, large body size, late maturity and low fecundity (Olden *et al.*, 2007; Geist, 2011). They are exposed to a diverse array of threats before reaching maturity. Many freshwater megafauna species (e.g. the South American river turtle, *Podocnemis expansa*, and the false gharial, *Tomistoma schlegelii*) require at least ten years to reach sexual maturity (Mogollones *et al.*, 2010; Bezuijen *et al.*, 2014) while others (e.g. the beluga, *Huso huso* and the Siamese crocodile, *Crocodylus siamensis*) have generation times of 20 years or more (Pikitch *et al.*, 2005; Bezuijen *et al.*, 2012). Consequently, it may require many years to restore local populations to previous levels measures (Winemiller *et al.*, 2015). Unless actions are taken to change things, the current trajectory is for an increasing decline in the condition of freshwaters habitats, particularly in the species-rich Global South (Vorosmarty *et al.*, 2013; Zarfl *et al.*, 2015; Bunn, 2016).

3.3.1 Overexploitation

Overexploitation is a threat to many freshwater organisms, but it has often been accepted due to its long history throughout human civilization (Abell, 2002). Harvesting in an unsustainable way has led to major adverse impacts on freshwater species worldwide (Dudgeon *et al.*, 2006). Freshwater megafauna are particularly targeted as their meat, skin and eggs are often prized as high-value commodities, and they are often considered an "open access" free resource. For instance, sturgeons and paddlefishes have experienced a long history of intense overexploitation for caviar, pushing them to the brink of extinction (Pikitch *et al.*, 2005). The global population of Siamese crocodile has declined by more than 80% during the past 75 years due to hunting for its skin and the collection of eggs and living individuals (Bezuijen *et al.*, 2012). The Critically Endangered Chinese giant salamander (*Andrias davidianus*), the world's largest amphibian, is experiencing an ongoing population decline because of the capture of wild individuals for their highly prized meat (Xie *et al.*, 2007; Tapley *et al.*, 2015).

Although many freshwater megafauna species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), poaching remains a common phenomenon in many regions globally. For example, meat consumption has caused a sharp decline in the Cuban crocodile (*Crocodylus rhombifer*), a species listed in CITES Appendix (Ramos Targarona *et al.*, 2010). Relative to marine species, the capture of freshwater species is limited; however, it provides a critical source of animal protein for many local people, especially for poor communities in remote and rural areas (Allan *et al.*, 2005; Welcomme *et al.*, 2010). In Southeast Asia, which contributes more than a quarter of the total global inland capture fishery production (Welcomme *et al.*, 2015), giant carp (*Catlocarpio siamensis*), Mekong giant salmon carp (*Aaptosyax grypus*), giant pangasius (*Pangasius sanitwongsei*) and Mekong giant catfish (*Pangasianodon gigas*) are on the brink of extinction, mainly due to overharvesting and the construction of dams (see section below).

Representing another form of exploitation, recreational fishing is a popular activity worldwide contributing approximately 12% of the global fish harvest (Cooke & Cowx, 2004). Large freshwater fishes have been regarded as trophies since historical times, and popular use of terms such as “monster fish” and “river monsters” has increased the fascination for large freshwater fish. Recreational exploitation does of course add increasing pressure on freshwater megafauna and may have led to the decline of species such as Siberian taimen (*Hucho taimen*) and largetooth sawfish (*Pristis pristis*; Jensen et al., 2009; Fernandez-Carvalho et al., 2014). On the other hand, popular media coverage on large fish and recreational fishing could help create an incentive and greater awareness to protect freshwater life (Granek *et al.*, 2008).

Given the intrinsic sparseness of freshwater megafauna and their declining population size, the opportunities for encountering mates for reproduction are more limited (Bronzi *et al.*, 2011). Moreover, the sparseness and/or rarity of these species can make them more attractive and valuable for exploitation and poaching (Courchamp *et al.*, 2006). It is also worth noting that the incidental capture as by-catch is a potentially significant threat for many freshwater megafauna species. For example, Turvey *et al.* (2007) suggested that unsustainable by-catch in local fisheries was the primary factor responsible for possible extinction of the baiji. Similarly, the Yangtze finless porpoise (*Neophocaena asiaeorientalis* ssp. *asiaeorientalis*) is subject to incidental by-catch in gillnets (Zhao *et al.*, 2008). In the Caspian Sea region, by-catch in legal and illegal fisheries may cause the death of several thousand Caspian seals each year, representing a significant level of mortality for this threatened species in addition to intentional harvesting (Härkönen, 2008).

3.3.2 Dam construction

For centuries, people have built dams along rivers for flood regulation, water supply, irrigation, navigation, recreation, and hydropower generation (World Commission on Dams, 2000). Driven by rapid human population growth and increasing energy demand, the number of dams has increased strongly during the past six decades (Lehner *et al.*, 2011). Fragmentation and modified flow regime, both caused by dams, are among the most important anthropogenic impacts to the functioning of freshwater ecosystems (Poff & Hart 2002; Fan *et al*., 2006). For example, dams create physical obstructions to fish migration routes. Although various types of fish passages have been designed to improve connectivity along rivers, their efficiency often remains low, especially for species other than salmonids for which they were originally designed (Noonan *et al.*, 2012).

Many freshwater megafauna species undertake long-distance migrations between breeding and feeding areas, therefore they are highly susceptible to blockage by dams. For example, during the past 60 years, the Russian sturgeon (*Acipenser gueldenstaedtii*) has lost access to 70% of its spawning sites in the Caspian basin and to almost all spawning grounds in the Black Sea basin due to dam construction (Gessner *et al.*, 2010). In addition, dams affect the thermal regime (Olden, 2015) and may cause increased pollutants (Feist *et al.*, 2005), which could affect the growth and reproduction of freshwater megafauna. Angilletta *et al.* (2008) suggested that a modified thermal regime might have negative impacts on spawning activity and embryo development of Chinook salmon. The spawning activity of the Chinese sturgeon (*Acipenser sinensis*), for example, has been delayed and reduced by an increased water temperature downstream of the Three Gorges and the Gezhouba Dams (Yangtze River) (Wu *et al.*, 2015; Zhuang *et al.*, 2016).

In addition to adverse impacts on fishes, dams have led to increased mortality levels and genetic isolation of African manatee (*Trichechus senegalensis*) populations (Keith Diagne, 2015). Most rivers inhabited by gharial (*Gavialis gangeticus*) have been dammed for irrigation and other purposes. Subsequent seasonal droughts in previously perennial rivers may affect gharial individuals that are not able to cross land in search of alternative water sources or dig tunnels to avoid periods of drought (Choudhury *et al.*, 2007). Dam construction and other river engineering projects (e.g. channel straightening, levee construction and dredging) may fundamentally affect floodplain inundation and lateral connectivity, leading to habitat loss of many freshwater megafauna species. For instance, droughts and altered flooding regimes due to damming have led to an estimated 50% decline in the population of Kafue Lechwe (*Kobus leche* ssp. *kafuensis*) on the Kafue Flats (Zambia; IUCN SSC Antelope Specialist Group, 2008).

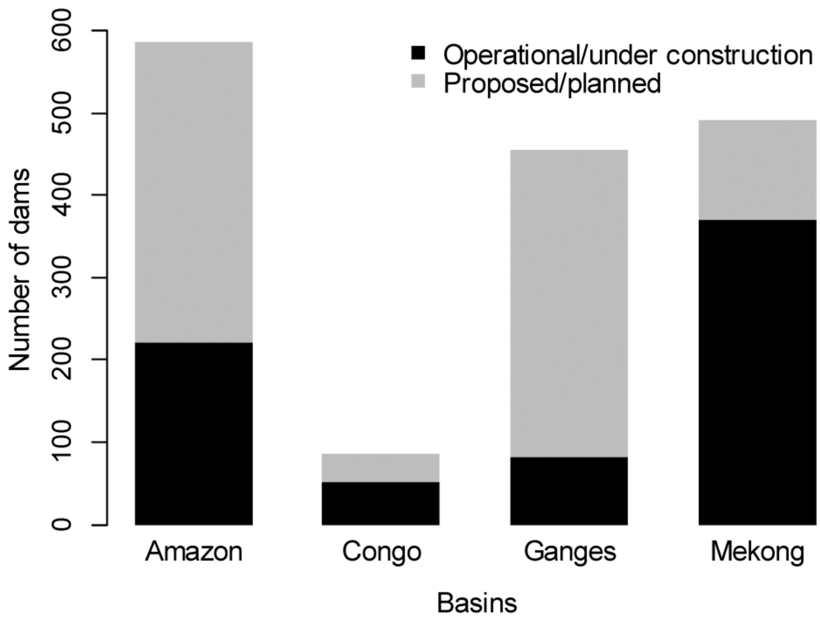

Fig. 3.2 Numbers of hydropower dams in four selected megafauna-rich basins (Lehner et al., 2011; Zarfl et al., 2015; Winemiller et al., 2016).

Many hydropower dams are planned or are under constructions in the Amazon, Mekong, Congo and Ganges River basins (Fig. 3.2; Box 3.1; Lehner *et al.*, 2011; Zarfl *et al.*, 2015; Winemiller *et al.*, 2016), which drain among the most species-rich river basins in the world. The boom in dam construction may threaten many freshwater megafauna species, including the Irrawaddy dolphin (*Orcaella brevirostris*), boto (*Inia geoffrensis*), Amazonian manatee (*Trichechus inunguis*), Ganges river dolphin (*Platanista gangetica* ssp. *gangetica*) and giant otter (*Pteronura brasiliensis*). It is also reported that already threatened tapirs (e.g. Baird's tapir, *Tapirus bairdii*) were illegally hunted to feed construction workers during the construction of Chalillo Dam in Belize (Castellanos *et al.*, 2008), representing one of many additional impacts of dam construction including creation of infrastructure such as roads, and settlements and land-use change.

Box 3.1 A global boom in hydropower and its subsequent impacts

Hydropower is a well-established technology for electricity production, accounting for about 80% of renewable energy production globally. Hydropower dam construction is currently accelerating worldwide, meeting increasing energy demands, in some case mitigating climate change consequences and closing the so-called electricity access gap. There are spatially explicit data available for 3700 hydropower dams (> 1 MW) worldwide that are either under construction or planned, which will more than double hydropower capacity within the next decades (Zarfl *et al*., 2015). In addition to electricity production, hydropower dams may serve as flood control infrastructure, and their respective reservoirs provide recreational services, food through aquaculture, as well as water for irrigation and industrial/domestic supply. However, hydropower development can also have severe social, economic and ecological consequences. Depending on the location and size of a reservoir, human populations may have to be relocated. Transboundary conflicts may arise from alterations in water availability downstream of dams. Land use change, river fragmentation, and alteration of flow, sediment and thermal regimes cause habitat loss, restrict the movement of aquatic organisms, and alter biodiversity and ecosystem processes (Winemiller *et al.*, 2016). However, knowledge on the expected social, economic, and ecological ramifications is limited and remains under-valued by practitioners. There is an urgent need to integrate the economic, environmental and social dimensions of future hydropower dams, thereby supporting decision making for dam construction and subsequent operation aims to reduce potential impacts and maximize benefits for both, humans and nature alike. Finally, we must be aware that the majority of dams are constructed for irrigation, drinking water and flood control – not for hydropower production; however, comprehensive data on those dams are missing.

3.3.3 Habitat degradation

Habitat degradation in freshwater ecosystems is caused by diverse human activities, creating direct (e.g. disturbance due to sand extraction and river straightening) and indirect impacts posed by environmental changes within the catchment (e.g. subsequent influence of deforestation and agricultural activities) (Dudgeon *et al.*, 2006). For example, sand and pebble extraction along the

Manipur River (Myanmar/India) has led to a rapid decline in populations of *Hemibagrus microphthalmus* (Ng, 2010). Similarly, gold mining as well as sand and gravel extraction from river beds in Mongolia, have caused serious degradation of Siberian taimen habitats, leading to the decline of mature individuals (Hogan & Jensen, 2013) .

The dependence of freshwater megafauna on freshwater habitats imparts on them a high chance of encountering human settlements and activities, aggravated by their large range requirements of intact and hydrologically connected habitats (Stone, 2007), increasing their susceptibility to anthropogenic disturbance. The global increase of shipping activities represents a serious threat to sturgeons, freshwater cetaceans and manatees due to their frequent encounters with vessels. Indeed, collisions with shipping vessels have increased substantially, causing the death of many Yangtze finless porpoise (Turvey *et al.*, 2013) and approximately 30% of documented Florida manatee (*Trichechus manatus* ssp. *latirostris*) mortalities each year (Nowacek *et al.*, 2004).

In South America, giant otter populations have declined sharply following expansion of human settlements, habitat degradation due to gold mining and deforestation, and hunting (Groenendijk *et al.*, 2015). Many crocodilians, including mugger (*Crocodylus palustris*), slender-snouted Crocodile (*Mecistops cataphractus*) and Nile crocodile (*Crocodylus niloticus*), are threatened by habitat destruction caused by anthropogenic activities. In addition, they are regularly killed by local people as they are regarded as a threat to humans and domestic livestock (Santiapillai & de Silva, 2001; Dunham *et al.*, 2010). With rapid human population growth, urbanization, agricultural and industrial expansion, there is an increasing likelihood of conflict due to encroachment by humans into the natural habitats of freshwater megafauna (Choudhury & de Silva, 2013). In Africa, for example, the historical habitats of African clawless otter (*Aonyx capensis*) have been significantly degraded by deforestation, bush clearing, overgrazing, water abstraction and the draining of wetlands (Nel & Somers, 2002). The pygmy hippopotamus (*Choeropsis liberiensis* ssp. *liberiensis*), which is endemic to the Upper Guinea forest of west Africa, is seriously threatened by habitat destruction as its historical forest habitat has been cut for the creation of human settlements, farms and plantations (Christie *et al.*, 2007; Norris *et al.*, 2010). Increasing mining activities and associated infrastructure development will put further stress on this threatened species (Ransom *et al.*, 2015). Similarly, the

Sakhalin taimen (*Hucho perryi*) has suffered from major habitat changes in Russia due to logging, road construction and rapidly expanding oil and gas developments, while its habitats in Japan are under threat from river channelization, agricultural and urban expansion (Rand, 2006).

3.3.4 Pollution

A wide range of chemical compounds are applied globally for purposes such as pest control and fertilizers in agriculture, industrial manufacturing, and as everyday products ranging from detergents to antibiotics. A substantial proportion of these pollutants ends up in freshwater ecosystems through diverse pathways including direct discharge, surface runoff and atmospheric deposition (Scholz & McIntyre, 2015). The toxic effects of some chemical pollutants can cause mortality in freshwater megafauna species such as the death of an estimated 4000 Caspian Seals along the coast of Kazakhstan due to pollution from agricultural and industrial sewage (Nasrollahzadeh, 2010). Other notable examples include the mortality of five Yangtze finless porpoises in the Dongting Lake (China) within a single week due to the toxic effect of a pesticide (i.e. Hostathion) and, possibly, long-term exposure to heavy metals (e.g. mercury and chromium) (Wang *et al.*, 2013). This represents a significant loss as the current population in the Dongting Lake is only around 90 individuals with an estimated 500 more individuals living in the main channel of the Yangtze River (Mei *et al.*, 2014).

Compared to most aquatic organisms, freshwater megafauna species are at higher risk of chronic effects and bioaccumulation of chemicals due to their long lifespan and high trophic level. Both, the Amur sturgeon *(Acipenser schrenckii)* and the kaluga sturgeon (*Huso dauricus*) are exposed to the cumulative effects of environmental pollution from oil exploitation, agricultural activities and mining operations in the Amur River basin (Chen, 2007; Shmigirilov *et al.*, 2007). Though pollutants might not be directly lethal to freshwater megafauna, they may reduce fitness and fecundity and make them more susceptible to disease. As a top predator in Lake Baikal, the Baikal seal (*Pusa sibirica*) is exposed to bioaccumulation of contaminants (e.g. polychlorinated biphenyls), which induce a suppression of its immune system and may have contributed to an outbreak of morbillivirus, which indirectly led to a mass mortality event in the late 1980s (Tsydenova *et al.*, 2004).

On the global scale, toxicants released by human activities have been identified as a major threat to freshwater ecosystems by The Millennium Ecosystem Assessment (Millennium Ecosystem

Assessment, 2005). Organic pollutants and heavy metals have been considered as the greatest threat to freshwater organisms. These pollutants enter freshwaters through waste water treatment plants, industrial discharge, mining drainage and runoff from agricultural soils and urban surfaces (Peters *et al.*, 2013). They have been found in fine sediments (Farkas *et al.*, 2007), causing the extirpation of benthic fauna (Kasymov, 1994), which is an important food resource for some freshwater megafauna species (e.g. sturgeons). Pollutants carried by sediments can also lead to an increased mortality of sturgeons due to their direct toxic effects (Bickham *et al.*, 1998). In North America, elevated concentrations of organic pollutants and heavy metals have been detected in the tissue and egg samples of gulf sturgeon (*Acipenser oxyrinchus*) (St. Pierre & Parauka, 2006). An increasing amount of research has reported that organic pollutants (e.g. organochlorine) and heavy metals from pesticide and industrial waste were detected in tissue and eggs of numerous crocodilians, including American alligator (Lind *et al.*, 2004), salt-water crocodile (*Crocodylus porosus*; Yoshikane *et al.*, 2006), American crocodile (*Crocodylus acutus*; Charruau *et al.*, 2013), Morelet's crocodile (*Crocodylus moreletii*; Rainwater *et al.*, 2007) and Nile crocodile (Bouwman *et al.*, 2014), which could lead to further population declines of these already threatened species. In addition, endocrine disrupting organic pollutants are reported to alter the hormonal balance of aquatic animals, inducing developmental and reproductive abnormalities (Guillette *et al.*, 2000; Milnes *et al.*, 2005; Abdel-moneim *et al.*, 2015) and ultimately leading to a population decline. For example, estrogenic pollution from industrial, agricultural and waste water treatment plant effluents contributed to the occurrence of intersex sharptooth catfish (*Clarias gariepinus*) individuals in South Africa (Barnhoorn *et al.*, 2004; Kruger *et al.*, 2013).

3.3.5 Species invasion

The introduction of non-indigenous species often produces predatory or competitive impacts on native species, therefore influencing local animal assemblages and ecosystem processes (Lockwood *et al.*, 2013). Species invasion is regarded as a major threat to global biodiversity, although its relative contribution to species decline and extinction is debatable as native species and their habitats are usually also subject to various other anthropogenic threats simultaneously (Allendorf & Lundquist, 2003; Gurevitch & Padilla, 2004). Due to their large body size, adult freshwater megafauna individuals are not likely to become the prey of invasive species, however, they are at risk during hatching and juvenile periods. Bezuijen *et al.* (2014) showed that introduction of the wild pig (*Sus scrofa*) posed a serious stress to the false gharial in Sumatra due to predation of eggs. Invasive species can directly increase the mortality of native freshwater megafauna populations. For example, the invasion of cane toads (*Bufo marinus*) has led to the massive mortality of Australian freshwater crocodiles (*Crocodylus johnstoni*) as they consume the toads which contain powerful toxins in their parotid glands (Letnic *et al.*, 2008). Less directly, lake trout (*Salvelinus namaycush*) populations in Ontario lakes declined following introductions of the smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris)* that led to a decline in their key food source, native littoral prey fishes through fishes (Vander Zanden *et al.*, 1999). Introduced Comb Jellyfish (*Mnemiopsis leidyi*) posed a serious risk to kilka (*Clupeonella cultriventris*), the main prey of Caspian Seal in the central and the southern Caspian Sea, by depleting kilka's food base (e.g. zooplankton) and also through predation on their eggs and larvae (Ivanov *et al.*, 2000; Dmitrieva *et al.*, 2015). In most cases, invasive species affect freshwater megafauna through competition for resources or through induced profound changes to local food webs, however, hybridization with invasive species is also a significant threat. For example, the hybrid of broadhead catfish (*Clarias macrocephalus*) and the introduced african catfish (*Clarias gariepinus*) is capable of breeding with both species, which can result in genetic introgression, thus leading to the local extinction of native broadhead catfish (Na-Nakorn *et al.*, 2004). In addition, the hybrids grow faster than the native broadhead catfish and are highly tolerant towards degraded water quality, giving them a competitive advantage (Welcomme & Vidthayanon, 2003).

In the last few decades, managed relocation, of species to areas outside of the native ranges has become a common practice for reducing their risk of extinction (Ludwig, 2006); however, it can also lead to unintended negative effects. For instance, the hump backed mahseer (*Hypselobarbus mussullah*), an endemic species in the Western Ghats of India, has been pushed to the edge of extinction due to the successful establishment and spread of the non-native blue-finned mahseer (*Tor khudree*), which was introduced for conservation purposes (Pinder *et al.*, 2015). Likewise, the invasive monogenean gill fluke, carried by Stellate sturgeon (*Acipenser stellatus*) and was inadvertently introduced from the Caspian Sea and played a significant role in the extirpation of ship sturgeon (*Acipenser nudiventris*) in the Aral Sea (Strauss *et al.*, 2012).

3.4 Outlook: Filling the freshwater megafauna information gap

Freshwater megafauna, but also freshwater ecosystems in general, are globally at risk from overexploitation, dam construction, habitat degradation, pollution and species invasion. At the same time, freshwaters contain a disproportionately high biodiversity and provide vital goods and services to humans. Conversely, freshwater ecosystems are underrepresented in conservation research and management actions (Abell, 2002; Lawler *et al.*, 2006; Monroe *et al.*, 2009; Allan *et al.*, 2010).

Though there is a general consensus that freshwater biodiversity is declining rapidly, the effective coverage of freshwaters by protected areas remains low, especially for large rivers (Abell *et al.*, 2017). The lack of public awareness towards biodiversity in freshwaters could largely stem from the invisibility of freshwater species hidden in turbid waters (Barrett & Ansell, 2003). Subsequently this may lead to a shift in the baselines, where many people forget the previous existence and abundance of such species as they are rarely encountered, further impeding awareness and knowledge of these species (Turvey *et al.*, 2010). Highlighting freshwater megafauna is potential flagship and umbrella species is recommended here as a potentially powerful tool to help raise public awareness and support freshwater conservation. Freshwater megafauna species such as river dolphins, hippopotamuses, sturgeons and paddlefishes are considered to have significant potential as both flagship and umbrella species (Kalinkat *et al.*, 2017) (Table 3.2). Furthermore, conservation strategies based on freshwater megafauna may provide major benefits for a wide range of lesser known but cohabiting species as well as of key ecosystems processes and functions. Darwall *et al.* (2011) cautioned, however, that those taxonomic groups for which there is better knowledge (most often terrestrial species) should not be utilized as surrogates for the distributions of less known freshwater taxa where it has been shown that there is low congruence between terrestrial and freshwater species distributions. Research focusing on charismatic species in freshwaters could improve their surrogacy effectiveness (i.e. benefit a larger set of less charismatic species via their umbrella effects) (Di Minin & Moilanen, 2014).

Table 3.2 Focal species concepts (Caro, 2003; Hooker & Gerber, 2004; Darwall et al., 2011), with examples from freshwater megafauna

Type	Description	Examples
Flagship	Charismatic species that could act as ambassadors for broad-scale conservation, used to raise conservation funding, and to attract public attention.	River dolphins, giant salamanders, hippopotamus, sturgeons and paddlefishes
Keystone	Species that play critical and unique ecological roles to local ecosystems, and have disproportionate importance relative to their abundance.	Beavers, crocodilians, Hippopotamus
Umbrella	Species with large habitat requirements for which conservation action potentially benefits other sympatric species.	River dolphins, hippopotamus, sturgeons and paddlefishes

To conclude, our knowledge of large-scale distribution and risk patterns of freshwater megafauna is still lacking for large parts of the world. Future research should focus on these large animals in order to fill knowledge gap by: (i) collating information on their spatial distributions; (ii) exploring the potential of freshwater megafauna to act as flagship and umbrella species; (iii) compiling data to quantify the seriousness of each type of threat and their impacts to each taxonomic group; (iv) identifying potential regions of conflict between the requirements of freshwater megafauna biodiversity and human activities; (v) examining correlations between biological and ecological traits of freshwater megafauna and extinction risk; and (vi) tracking the global population dynamics of freshwater megafauna. Such a comprehensive understanding of freshwater megafauna will assist in the development of more effective conservation strategies and better consideration within development planning, in order to protect these species and to raise public awareness and support for overall freshwater biodiversity conservation.

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4. The global decline of freshwater megafauna

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4.1 Abstract

Freshwater ecosystems are amongst the most diverse and dynamic ecosystems on Earth. At the same time, they are amongst 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 and marine realms. Large freshwater vertebrates (i.e. freshwater megafauna) are intrinsically prone to extinction due to their large body size, complex habitat requirements and slow life-history strategies such as long lifespan and late maturity. However, population trends and distribution changes of freshwater megafauna, at continental or global scales, remain unclear. In the present study, we quantified changes in population abundance and distribution ranges 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 population trends of freshwater megafauna, such as the lack of monitoring data and taxonomic and spatial biases. The detected trends emphasize the critical plight of many freshwater megafauna globally and highlight the broader need for concerted, targeted and timely conservation of freshwater biodiversity.

4.2 Introduction

Biodiversity loss is one of the biggest challenges facing our planet, leading to the erosion of ecosystem services and threatening human well-being (Diaz *et al.*, 2006; Oliver *et al.*, 2015). Freshwaters cover approximately one percent of the Earth‘s surface, yet harbor around one third of all vertebrates, and half of all fish species globally (Balian *et al.*, 2008; Carrete-Vega & Wiens, 2012). At the same time, freshwaters are exposed to multiple persistent and emerging threats (Dudgeon *et al.*, 2006; Reid *et al.*, 2018). Consequently, freshwaters are amongst the most threatened ecosystems globally, with their degradation likely to continue – or even accelerate – in the near future. For example, approximately 3700 additional large hydropower dams are actually planned or under construction, increasing the fragmentation of rivers worldwide (Grill *et al.*, 2015; Zarfl *et al.*, 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 *et al.*, 2017; Darwall *et al.*, 2018; Harrison *et al.*, 2018). Consequently, a third of all freshwater species are threatened with extinction according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2018a). Furthermore, the rate of decline of freshwater vertebrate populations is twice as high as in terrestrial or marine ecosystems (McRae *et al.*, 2017).

Large-bodied animals are particularly susceptible to extinction owing to intrinsic characteristics such as large body size, large habitat requirement and late maturity (Cardillo *et al.*, 2005; Olden *et al.*, 2007; Zuo *et al.*, 2013; Winemiller *et al.*, 2015). 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 the freshwater megafauna definition (i.e. reported maximum body mass ≥ 30kg), as introduced by He et al (2017; 2018) and Carrizo et al (2018). 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. Adriatic sturgeon, *Acipenser naccarii*; Yangtze sturgeon, *Acipenser dabryanus* and Chinese sturgeon, *Acipenser sinensis*) currently depends on artificial stocking enhancement (Bronzi *et al.*, 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 lifespans (e.g. over 50 years for many sturgeons, crocodilians and giant turtles). Individuals may remain in rivers and lakes for several decades after natural reproduction has ceased (i.e. functional extinction) (Jaric *et al.*, 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 population abundance and habitat occupancy 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' extinctions (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 facilitate the development of proactive conservation strategies and related 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; Worm & Tittensor, 2011; Wolf & Ripple, 2017). However, monitoring of freshwater megafauna species remain limited, particularly at continental and global scales. Therefore, our aims are twofold: 1) to track changes in population abundance of freshwater megafauna globally and, 2) to determine distribution range contraction (i.e. contemporary distribution ranges compared to historical distribution ranges in 1500) of freshwater megafauna species in regions where adequate data are available (i.e. Europe and the USA). We hypothesize that freshwater megafauna populations exhibit a larger decline than overall freshwater vertebrates, primarily because they are characterized with extinction-prone traits and subject to intense anthropogenic threats (Carrizo *et al.*, 2017; He *et al.*, 2017; He *et al.*, 2018). Furthermore, freshwater megafauna species usually have large habitat requirements, therefore, often require cross-boundary conservation efforts. Both Europe and the USA have established several 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 USA). However, in Europe the implementation of conservation programs at the 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 USA. Hence, we hypothesize that the range contractions of freshwater megafauna species are greater in Europe than in the USA.

4.3 Methods

4.3.1 Population abundance

The underlying list of freshwater megafauna species (i.e. 207 freshwater animal species over 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, two amphibians), totaling 639 individual time series and covering 72 countries or regions (Fig. S4.1). Population data for 72 freshwater megafauna species were available from the Living Planet Index (LPI) database (www.livingplanetindex.org), a continuously updated global database of vertebrate populations. Population data for a further 54 species was collated from published papers and reports. Despite an intensive search, no suitable data for the remaining 81 species was available. Population data were only included in the analysis if they fulfilled the following criteria: 1) population data were collected or estimated applying the same method throughout the time period; 2) data were available for at least two years after 1970; 3) the geographic area (e.g. sampling location or catchment) of the specific population was recorded and; 4) the data source was referenced.

Excluding the two amphibian species (*Andrias japonicus* and *Andrias davidianus*), 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 had five time series per species. However, for fishes, the number of time series per species was reduced to three 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 USA (92), and Canada (61), primarily due to the high data density of salmonids (Fig. S4.1). In contrast, time series data in freshwater megafauna-rich regions, such as Southeast Asia (21), South America (47) and Africa (50), were scarce.

In order to compare changes in 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 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 in R (R Core Team, 2016). The calculation procedure is summarized below (see McRae *et al.* (2017) for further details). For time series spanning fewer than 6 years the chain method was utilized, whilst Generalized Additive Models were applied to the remaining time series spanning more than 6 years. To avoid taxonomic or geographical bias, 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 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 (hereafter referred as CI) were generated by bootstrapping (1000 times). Population changes were calculated for different biogeographic realms and taxonomic groups including fishes, reptiles and mammals.

4.3.2 Distribution range

Based on previously established databases (Carrizo *et al.*, 2017; He *et al.*, 2018), we identified all freshwater megafauna species that occur in Europe or the USA. For both regions, contemporary and historic distribution ranges for 44 species were available. The distribution range data were derived from IUCN and NatureServe databases (IUCN, 2018a; NatureServe, 2018), and were developed as part of the comprehensive assessment of biodiversity by both 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. Historical distributions, (i.e. where species were formerly known or very likely to occur in an area), the reference year was set to 1500AD following IUCN (IUCN, 2018a). For the USA, NatureServe includes records of species occurrences from the time of European settlement, which is also around 1500AD (NatureServe, 2018). Thus, areas with Presence status coded as "Possibly Extinct" and "Extinct" by IUCN, or with Occurrence status coded as "Historical" by Nature Serve were included to represent historical distributions of species. All distribution data was 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 USA (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. When only part of a sub-catchment (e.g. Lakes Superior, Huron, Erie, and Ontario) is within the country boarder, we still kept the whole sub-catchment 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: fraction of range contraction = (historical distribution area - current distribution area)/historical distribution area.

4.4 Results

Temporally, global freshwater megafauna populations declined by 88% from 1970 to 2012 (CI: -80% to -92%; Fig. 4.1). Mega-fishes exhibited the largest decline (-94%; CI: -85% to -97%), followed by mega-reptiles (-72%; CI: -94% to +13%), whilst mega-mammal populations increased by 29% (CI: -20% to +125%; Fig. S4.2). However, confidence intervals were very wide for mega-reptile and mega-mammal populations, primarily due to the limited number of species and population time series data available.

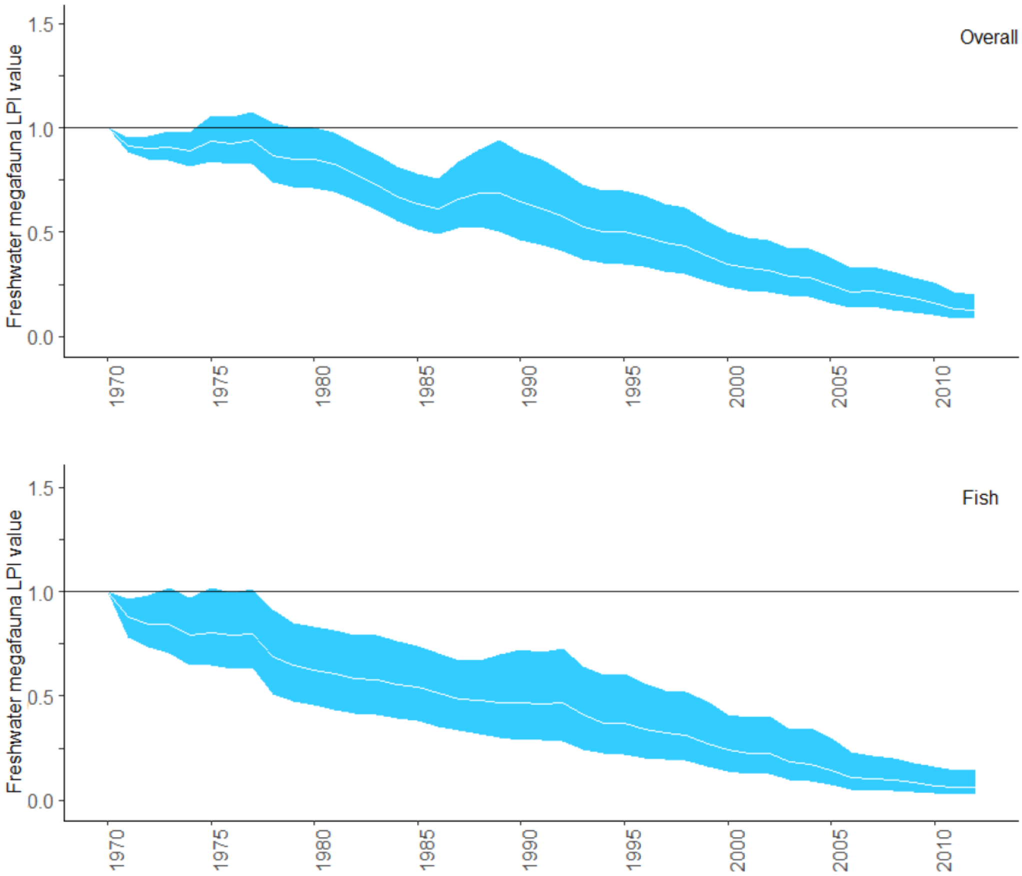
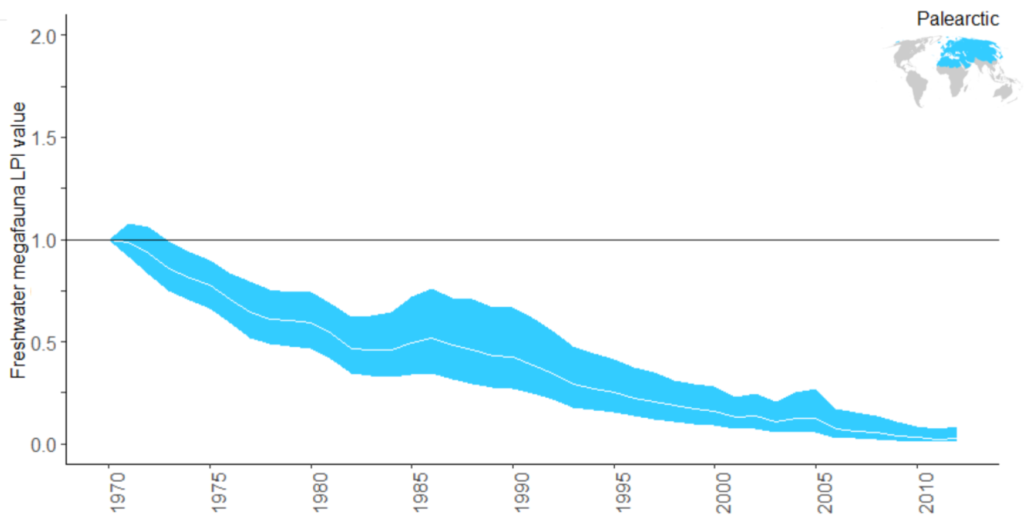


Fig. 4.1 Population change of global freshwater megafauna (126 species; 639 time series) and mega-fish species (81 species; 404 time series) from 1970 to 2012. The value of Living Planet index (LPI) was set to 1 in the reference year 1970.

Spatially, freshwater megafauna populations exhibited the largest decline in the Indomalaya (-99%; CI: -100% to -97%) and Palearctic realms (-97%; CI: -91% to -99%; Fig. 4.2). The sharp decline of Indomalayan populations began in the mid-1990s, while Palearctic populations exhibited a continuous decline since 1970. Furthermore, freshwater megafauna populations exhibited strong declines in the Afrotropical (-81%; CI: -92% to -55%) and Nearctic (-57%; CI: -80% to -13%) realms, with a stabilizing trend in both regions since the early 2000s (Fig. S4.3). Population declines occurred in the Neotropical (-64%) and Australasia realms (-3%) too; however, confidence intervals are distinct (CI: -20% to -67%, and -77% to +270%, respectively).



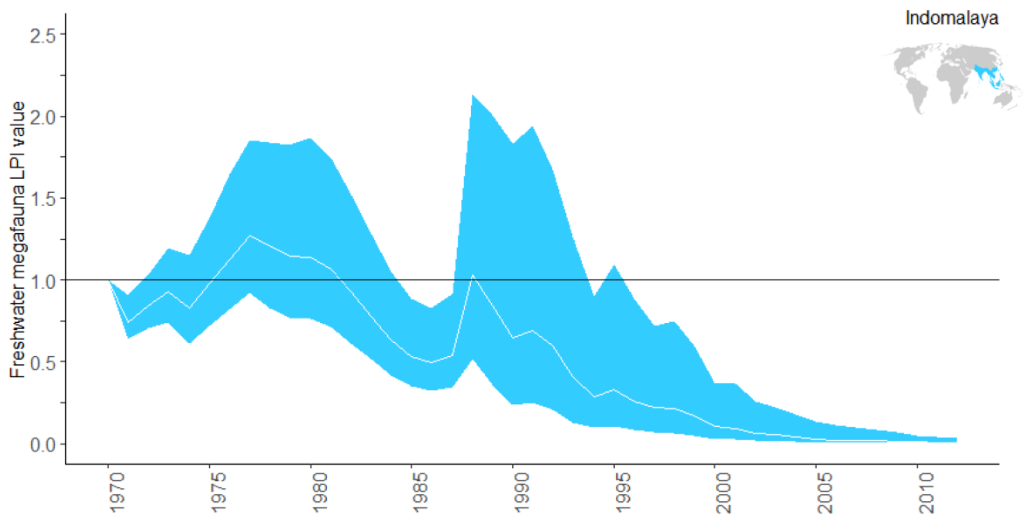


Fig. 4.2 Population change of freshwater megafauna in Palearctic (37 species; 239 time series) and Indomalaya (25 species; 63 time series) realms from 1970 to 2012. The value of Living Planet index (LPI) was set to 1 in the reference year 1970.

Changes in distribution ranges were assessed for all 44 freshwater megafauna species in Europe and the USA (Fig. 4.3). For example, the once very common European sturgeon (*Acipenser sturio*) has been extirpated from all major rivers, except the 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 the downstream sections, primarily due to the construction of large dams. In contrast, range contractions were less pronounced in the USA. However, species such as lake sturgeon (*Acipenser fulvescens*), alligator gar (*Lepisosteus spatula*) and paddlefish (*Polyodon* *spathula*) have been extirpated in some sections of the Missouri and middle Mississippi river basins, as well as in the Great Lakes region.

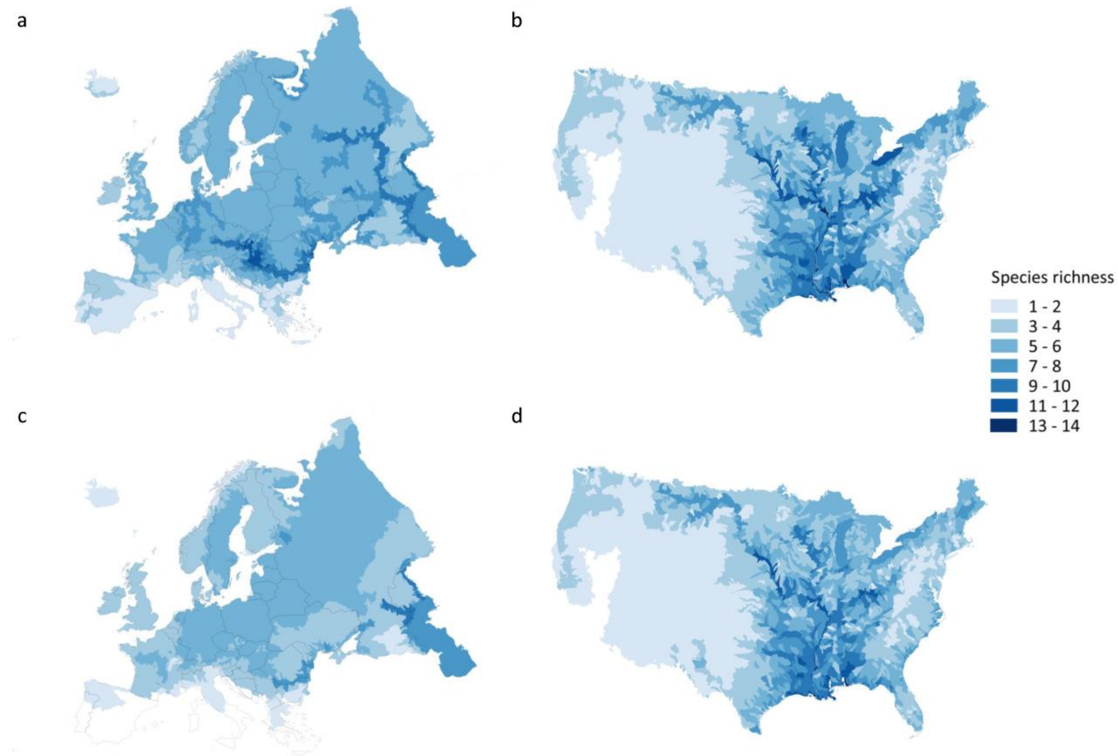


Fig. 4.3 Species richness of freshwater megafauna at historical, i.e. 1500, (a, b) and current time (c, d) in Europe (left) and USA (right, excluding Alaska, Hawaii and other overseas territories).

Regarding individual species (Fig. 4.4), the European sturgeon had the greatest proportional range contraction (-99%), followed by the Adriatic sturgeon (*Acipenser 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 (Colorado pikeminnow, *Ptychocheilus lucius*) in the USA. Amongst the twenty species with the largest range contractions (i.e. ten species each in Europe and the USA), the Eurasian beaver (*Castor fiber*) was the only non-fish species.

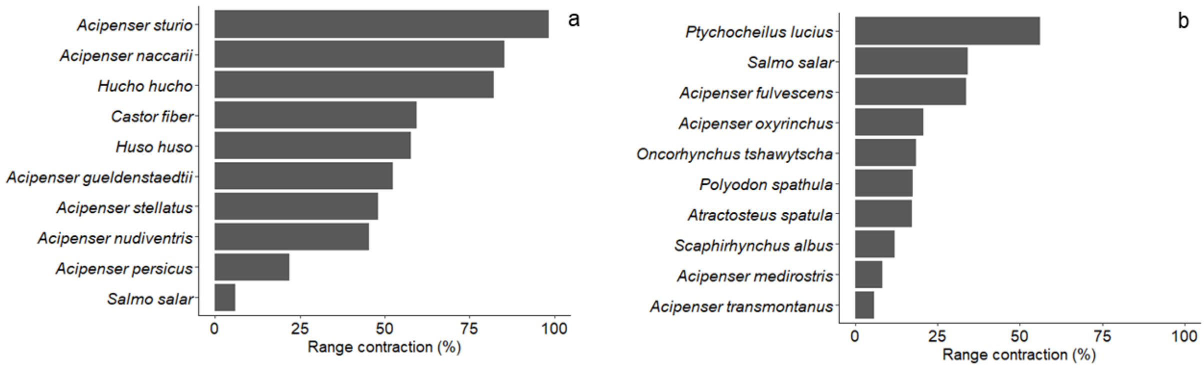


Fig. 4.4 Ten freshwater megafauna species with the biggest range contraction in (a) Europe and (b) USA. Note that only Castor fiber is mammal and all other species are fish.

4.5 Discussion

4.5.1 The loss of freshwater megafauna

To our knowledge, this is the first comprehensive study tracking population changes 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 the decline reported in terrestrial (-38%) and marine (-36%) vertebrate populations (McRae *et al.*, 2017). Amongst all the taxonomic groups, mega-fishes are in a particularly dire situation. Indeed, the Russian sturgeon (*Acipenser gueldenstaedtii*), Amur sturgeon (*Acipenser schrenckii*), Chinese sturgeon (*Acipenser sinensis*) and ship sturgeon (*Acipenser nudiventris*) have experienced population declines of over 90% during the past three generations (IUCN, 2018). In mega-fish-rich basins, such as the Mekong and Amazon, the situation is continuously deteriorating. For example, populations of the Mekong River mega-fishes have dropped close to zero (Hogan, 2011; Gray *et al.*, 2017; Ngor *et al.*, 2018). This includes the Mekong giant catfish (*Pangasianodon gigas*), giant Siamese carp (*Catlocarpio siamensis*) and giant pangasius (*Pangasius sanitwongsei*). Furthermore, the arapaima species (*Arapaima* spp.) have been locally extirpated from 19% of surveyed communities along the main stem of the Amazon River (Castello *et al.*, 2015).

Multiple anthropogenic threats have contributed to the decline of freshwater megafauna (He at al., 2017). Among them, overexploitation remains the key threat, since meat, eggs and skin from sturgeons, crocodiles and turtles are used as luxury foods and medicines (Cheung & Dudgeon, 2006; Bronzi & Rosenthal, 2014). In addition, conflicts between freshwater megafauna and humans have escalated due to their large habitat requirement and rapidly increasing human population and expanding anthropogenic activities (He *et al.*, 2018). This has led to increased mortality rates caused by direct killing (Dunham *et al.*, 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 (Hogan, 2011; Winemiller *et al.*, 2015; He *et al.*, 2017).

High levels of freshwater megafauna richness are usually associated with high levels of overall freshwater biodiversity (Carrizo *et al.*, 2017). Freshwater megafauna perform essential ecological roles and function as top predators or keystone species in their respective habitats (Moore, 2006; Bakker *et al.*, 2016b; He *et al.*, 2017; Hammerschlag *et al.*, 2019). 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). The depletion of freshwater megafauna may also lead to reduced landscape heterogeneity and a loss of habitat or refuges for small species (Moore, 2006), interrupted seed dispersal (Anderson *et al.*, 2009; Costa-Pereira *et al.*, 2018) and nutrient cycling among freshwater, marine and terrestrial ecosystems (Janetski *et al.*, 2009; Service *et al.*, 2019).

4.5.2 Uncertainty in population data of freshwater megafauna

There are significant sources of uncertainty in tracking population trends of freshwater megafauna. Primarily, this is due to a general paucity of long-term monitoring data available for these species. Furthermore, for existing data, a significant temporal, taxonomic and spatial bias is evident. For example, population data for the early 1970s is scarce (Fig. S4.4). 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). Furthermore, IUCN Red List assessments suggest that many freshwater megafauna species, including the Mekong giant salmon carp (*Aaptosyax grypus*), pangas catfish (*Pangasius* pangasius) and yellowcheek (*Elopichthys bambusa*), have experienced severe population decline

(IUCN, 2018). However, these species were not included in the analysis, due to a lack of viable time series data. Consequently, a more significant population drop would likely have been demonstrated in our analysis had more species been monitored and data made available. Indeed, amongst the 81 freshwater megafauna species without time series data, 27 are considered as threatened by the IUCN Red List. When taken together, these caveats suggest that the actual situation may be significantly worse than our results indicate.

The data gaps are particularly obvious for mega-reptiles and mega-fishes, other than sturgeons and salmonids. Sturgeons and salmonids account for just 18% of mega-fish species, yet contribute 60% of all time series for mega-fishes in this study. Furthermore, 73% of all mega-mammals had one or more time series available, whilst data for 52% of mega-reptiles were not available. This is consistent with the current monitoring prioritization (i.e. mammal and economically-valuable species centered; Ford et al., 2017). Indeed, our results suggest that global populations of freshwater mega-mammals have increased since 1970. Hippos and beavers (four species in total) are well targeted in conservation actions and contributed more than 40% of all time series for 31 mega-mammals. These numbers suggest that well-documented and charismatic species often benefit more from conservation efforts and thus display stable or increasing population sizes (but see Courchamp *et al.*, 2018).

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 (Wilson *et al.*, 2016; Tydecks *et al.*, 2018). For mega-reptiles, such as crocodilians 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 are often subject to intense threats, including overexploitation and habitat degradation, and 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 preserved and have relatively stable or increasing populations. As such, these inconsistencies in population trends amongst different species and biogeographic realms caused the broad CI when tracking population trends in mega-reptiles. Furthermore, there is insufficient data for the IUCN Red List to evaluate the current conservation status of a quarter of all freshwater megafauna species, most notably in South America (He et al., 2018). However, the pressures facing freshwater megafauna species in these underrepresented regions, (e.g. the Amazon, Congo and Mekong), are predicted to intensify due to emerging threats (i.e. the boom in hydropower dam construction) (Winemiller et al., 2016). Therefore, it is highly likely that the future facing freshwater megafauna in these regions is likely to get worse before it gets better.

4.5.3 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 monitoring management strategies are implemented. Owing to persistent conservation efforts, populations of 13 freshwater megafauna species (e.g. Green sturgeon, *Acipenser medirostris*, White sturgeon, *Acipenser transmontanus*, and the American beaver, *Castor canadensis*) in the USA are stable (He *et al.*, 2018). Conversely, in Europe, efficient conservation actions at a large scale are difficult to establish and fully implemented due to the political boundaries and variations in economic development and environmental awareness between countries (Kukkala *et al.*, 2016). Nevertheless, several freshwater megafauna species have been targeted for rewilding actions across several European countries. For example, the Eurasian beaver (*Castor fiber*) has been reintroduced into many areas of its previous distribution range including the Czech Republic, Estonia, Finland, Sweden and the UK (Halley, 2011). Furthermore, reintroduction programs of the European sturgeon have begun in countries including France, Germany and the Netherlands. Finally, in Asia, the population of the Irrawaddy river dolphin (*Orcaella brevirostris*) has recently shown the first increase in the last two decades (WWF Cambodia, 2018).

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 (He *et al.*, 2017; Courchamp *et al.*, 2018). Knowledge on migratory routes and spawning grounds of freshwater megafauna, such as giant catfishes, is still limited (Hogan 2011). This will hinder the establishment of effective conservation strategies to prevent the extinction of these species. Further to this point, 122 freshwater megafauna species are migratory, making them ideal candidates for inclusion in the ICARUS (International Cooperation for Animal Research Using Space) project (https://www.icarus.mpg.de/), a global initiative to monitor migratory routes and living conditions of species.

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 dolphin (*Orcaella brevirostris*) 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 actions balanced.

In addition, freshwater megafauna species can indicate the integrity of an ecosystem, since they have large and complex habitats 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.*, 2018), meaning megafauna-based strategies hold the potential to benefit both megafauna and sympatric, 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 concern due to its potential impact on the habitats of Yangtze Finless Porpoise (*Neophocaena asiaeorientalis asiaeorientalis*). 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 situations facing freshwater megafauna in the Indomalaya and Palearctic realms, and those of mega-fishes globally, are 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 (Monroe *et al.*, 2009; Ford *et al.*, 2017; Darwall *et al.*, 2018). This is highly likely to be true. Nevertheless, 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 focused 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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5. Extinction risks of freshwater megafauna: The combined effects of life-history traits and anthropogenic threats

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5.1 Abstract

Freshwater ecosystems are subject to intense and growing threats. Consequently, one third of all classified freshwater species are considered as threatened on the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List). Freshwater megafauna (i.e. freshwater animals ≥ 30 kg) are at even greater risk of extinction than their smaller counterparts, with 54% of all classified species being threatened as of the IUCN Red List. Identifying the underlying drivers can help facilitate more effective and proactive conservation actions. IUCN Red List assessments are an important basis for conservation actions, but remain incomplete for a quarter of all freshwater megafauna species. Here we collated 12 life-history traits for 207 freshwater megafauna species. We used generalized linear mixed models to examine the relationship between extinction risks (measured with conservation status on IUCN Red List) and the combined effect of multiple traits as well as the influence of anthropogenic threats on this relationship for 157 classified species. The models that best explained the extinction risks of freshwater megafauna included anthropogenic threats and traits related to species' recovery potential (i.e. lifespan, age at maturity, and fecundity). Applying these models to 49 species that remained unclassified by IUCN Red List predicted 16 of them to be threatened. On the basis of the model predictions, the Amazon and Yangtze river basins have become emerging global hotspots of threatened freshwater megafauna species, in addition to existing ones (i.e. Ganges and the Mekong river basins and the Caspian Sea region) according to the IUCN Red List assessments. Considering the multiple threats that freshwater megafauna are facing, their rapidly declining population and large gaps in their life-history data and assessments, more studies are called to focus on their life-history traits, which will form a solid scientific basis for proactive conservation actions. In addition, artificial population enhancement should be implemented for freshwater megafauna species with extremely small sizes of population and geographical range.

5.2 Introduction

Accelerated biodiversity loss is one of the biggest environmental issues humankind is facing (Ceballos *et al*., 2015). The current rates of species extinction are 100-1000 times faster than the background rate (Ceballos *et al*., 2015; De Vos *et al*., 2015). Species extinction can be caused by various factors. The vulnerability of individual species to extinction largely depends on their life-history traits (Pearson *et al*., 2014; Purvis *et al*., 2000; Reynolds *et al*. 2005; Wang *et al*., 2018). Hence, quantifying the relationship between species traits and extinction risks has been of increasing interest in both ecological and conservation research (Cardillo & Meijaard 2012; Gonzalez-Suarez *et al*. 2012; Murray *et al*. 2014).

Previous studies revealed that body size is one of the most important extinction-prone traits (Cardillo *et al.*, 2005; Wang *et al.*, 2018). Moreover, large body size is often associated with further extinction-prone traits such as long lifespan, late maturity and low population abundance. Consequently, it is argued that large-bodied animals (i.e. megafauna) are particularly susceptible to extinction (Payne *et al.*, 2016; Ripple *et al.*, 2017a; Ripple *et al.*, 2016). Indeed, 51% of terrestrial megafauna species have become extinct since the Late Pleistocene (Malhi *et al.*, 2016). Overall, 59% of the remaining terrestrial and aquatic megafauna is considered as threatened according to the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List; Ripple *et al.*, 2019). Recently, the hypothesis that large-bodied animals are more prone to extinction than small ones has been challenged. It has been demonstrated that small-bodied fish and amphibian species, for example, are at similar or even higher extinction risk than their larger counterparts (Kalinkat *et al.*, 2017; Kopf *et al.*, 2017; Olden *et al.*, 2007; Reynolds *et al.*, 2005; Ripple *et al.*, 2017b). At the same time, extinction risk is most likely determined by a combination of several traits rather than a single one (Lee & Jetz 2011; McKinney 1997; Pearson *et al.*, 2014).

Extinction risk depends on the interaction between intrinsic traits of species and extrinsic threats (Murray *et al.*, 2014). This is particularly the case in the era of the Anthropocene, with rapidly expanding human activities (Steffen *et al.*, 2015) and subsequent growing threats to biodiversity including habitat destruction, overexploitation, climate change and introduction of exotic species (Pereira et al., 2012; Pimm et al., 2014). Understanding how intrinsic traits and extrinsic threats shape species extinction risks can facilitate development of proactive conservation actions. In addition, it can also help predict conservation status of unclassified species or their susceptibilities to future threats such as climate change (Cardillo & Meijaard 2012; Murray *et al.*, 2014).

The conservation status assigned by IUCN Red List is widely used as a proxy of species' extinction risk (Gonzalez-Suarez *et al.*, 2012; Murray *et al.*, 2014). According to the IUCN Red List, one third of all classified freshwater species are considered as threatened with extinction (Collen et al., 2014). The situation of freshwater megafauna is even worse, with 54% of all classified being considered as threatened and 71% of all species with known population trends actually being in decline (He *et al.*, 2018). At the same time, 49 out of 207 species freshwater megafauna species remain unclassified (i.e. listed as Data Deficient or Not Evaluated) due to insufficient data on population size, distribution pattern, and underlying threats (IUCN 2018a).

In the light of an unprecedented freshwater megafauna crisis, we need to identify those species that are at greatest risk of extinction, and to prioritize conservation actions accordingly. Therefore, a big challenge is to fill the information gap in the conservation status of freshwater megafauna species. Given that most of the unclassified species occur in developing countries with sparse data on their current population size and distributions, completing IUCN Red List assessments for all of them is likely expensive as well as time consuming. A promising approach to bridge the information gap is to perform comparative extinction risk analyses, predicting conservation status based on the relationships between life-history traits, anthropogenic threats and extinction risk of species (Cardillo & Meijaard 2012; Murray *et al.*, 2014).

In the present study we examine these relationships with Generalized Linear Mixed Models. Previous studies have emphasized the importance of body size and species' recovery potential in determining extinction risk of vertebrates (Cardillo *et al.*, 2005; Hutchings *et al.*, 2012; Kopf *et al.*, 2017; Wang *et al.*, 2018). Hence, we hypothesize that body size and traits related species' recovery potential (e.g. fecundity and age of maturity) are the most influential traits in determining extinction risks of freshwater megafauna. In addition, freshwater megafauna are subject to intense anthropogenic threats including overexploitation, habitat degradation and dam construction (Carrizo et al., 2017; He et al., 2017; Ripple et al., 2019). Given their vulnerability to these threats (He et al., 2018), we further hypothesize that including interactions between life-history traits and anthropogenic threats will improve the model performance of explaining extinction risks of freshwater megafauna in comparison to purely trait-based models. On the basis of these relationships, we predict the conservation status of 49 unclassified freshwater megafauna species with the most parsimonious models.

5.3 Methods

5.3.1 Extinction risks

In this study, conservation status of freshwater megafauna on the IUCN Red List were used as a proxy of their extinction risks. We collected information on the IUCN Red List database (version 2018-1, accessed on June 12th 2018; IUCN, 2018a) for 207 freshwater megafauna species (He *et al.*, 2018). Following the IUCN Red List, we considered species that are listed as Critically Endangered, Endangered or Vulnerable as threatened species, while species listed as Least Concern or Near Threatened are considered as not-threatened species. Among the 158 species with sufficient information, 85 species were categorized as threatened and 72 species as not threatened. One species (i.e. Black Softshell Turtle, *Nilssonia nigricans*) was excluded from further analyses, as it was assessed as Extinct in the Wild. In addition, 49 species were listed as Not Evaluated or Data Deficient, i.e. the existing information so far is insufficient to evaluate their conservation status.

5.3.2 Life-history traits

For each freshwater megafauna species, we compiled information on 12 traits (Table S5.1) from published literature, reports, and online databases such as FishBase (Froese & Pauly 2018), IUCN Red List database (IUCN 2018a), and AnAge database (Tacutu *et al.*, 2018). In the final analysis, eight traits were included: maximum body mass, lifespan, migration, age at maturity (female), fecundity (i.e. average number of offspring), offspring type, habitat, and feeding habits. When trait data were not available for an individual species, information was adopted from phylogenetically and morphologically related species (i.e. “sister species” in the same genus and with similar body size). In addition, the “Life-history tool” in FishBase was used to estimate traits for fishes lacking adequate information. When trait information was unavailable for more than 30% of the species, the respective traits were excluded from the analysis (Fig. S5.1). This applied to the traits including generation length, spawning/postnatal periodicity and hatching/gestation time. Considering the various body shapes of freshwater megafauna, the maximum body length was also excluded. The information on body size, represented by maximum body length, can also be indicated by maximum body mass, which allows a better comparison of fish, reptile, mammal, and amphibian species. To avoid autocorrelation, size of geographic range was intentionally excluded, since it is used by IUCN as one of the key criteria to assign the conservation status (Kopf *et al.*, 2017).

5.3.3 Relationship between extinction risks and traits and anthropogenic threats

When traits were measured quantitatively (i.e. maximum body mass, lifespan, age at maturity), the correlation between conservation status of freshwater megafauna and their traits were examined applying logistic regressions, which allow the estimation of linear relationships between continuous data on traits and binomial data on conservation status (threatened or not threatened). When the traits (i.e. feeding habit, migration, and offspring type) were described with categorized data, the proportion of threatened species in each category was compared. Fecundity was quantified as the average number of offsprings of a species. However, information on the exact number of offsprings remains unknown for 28% of all species, especially for megafishes. To narrow the data gap, we categorized their fecundity into five levels (Table S5.1) according to the average number of offsprings and treated it as a categorized trait.

Logistic regressions were used to examine correlations between conservation status of freshwater megafauna and anthropogenic threats. The intensity of anthropogenic threats was measured with an average value of the Incident Biodiversity Threat Index (IBTI) within each species distribution range. The IBTI is a compound threat index, combining information on multiple threats to freshwater ecosystems, including pollution, catchment disturbance, river fragmentation, harvesting pressure, and species invasion (Vörösmarty *et al.*, 2010). Information on freshwater megafauna distribution and IBTI were converted into the HydroBASINS level 8 sub-catchment template (Lehner & Grill 2013). Details on the methods are described in He *et al*. (2018).

To identify which trait combinations best explain the conservation status of freshwater megafauna, we fitted a Generalized Linear Mixed Model (GLMM) also based on a logistic function. The traits of freshwater megafauna were used as fixed effects, while family was used as the random effect to control for the potential phylogenetic correlation. The 157 assessed species were included in the model. We examined the correlation coefficients among traits and checked the variance inflation factors (VIFs). Thresholds of 0.7 (Dormann *et al.*, 2013) for correlation coefficients, and three for

VIFs (Zuur *et al.*, 2010) were used to avoid collinearity among traits. Habitat was excluded due to a VIF larger than three.

Using the *glmulti* package (Calcagno & de Mazancourt 2010) in R (R Core Team 2016), the best model from different combinations of fixed factors and their interactions was selected based on the Akaike information criterion (AIC). The AIC considers both model performance (i.e. estimated residual variance) and complexity (i.e. the number of parameters; Aho *et al.*, 2014). For comparison between models, the one with a lower AIC value is considered as better fit. During the model selection, only two-way interactions (i.e. interactions between two fixed factors) were included. First, only life-history traits were included as fixed factors. Second, IBTI was added as a fixed factor into the model to examine the impact of anthropogenic threats on the linkage between conservation status and life-history traits. To evaluate the predictive performance of the two selected models, we conducted the ten-folds cross-validation analysis. To do so, the dataset was split into ten groups randomly. At each time, nine groups were taken out as training data. Then the model was fitted on the nine groups (training data) and evaluated on the one remaining group (test data). Eventually, each group was treated as test data once and as training data nine times. The cross-validated areas under the curve (AUC) resulting from the ten-folds cross-validations were calculated with the *cvAUC* package in R (LeDell *et al.*, 2015). With the two selected models, we predicted the conservation status (i.e. threatened or not threatened) of the 49 unclassified species which were listed as Not Evaluated or Data Deficient. The GLMM models predicted the probabilities (range from zero to one) of the unclassified species being threatened. Species with the predicted-threatened probabilities over 0.5 were considered as threatened under the medium scenario. To demonstrate potential variability in the conservation status of these unclassified species, two additional scenarios were explored, with thresholds of 0.3 and 0.7, reflecting a stricter or a milder categorization. For example, species with predicted-threatened probabilities over 0.3 were considered as threatened under the strict scenario while only species with predicted probabilities of being threatened over 0.7 were considered as threatened under the mild scenario. The maps of global distribution of threatened megafauna were plotted in QGIS (QGIS Development Team 2017).

5.4 Results

Freshwater megafauna are characterized by large body size (183 ± 388 kg; mean ± standard deviation), long life span (40 ± 25 years), and late maturity (6 ± 4 years). The probability of a species being threatened increases with maximum body mass (slope coefficient 1.56 [standard error 0.44], $p < 0.01$), lifespan (2.61 [0.65], $p < 0.01$) and age at maturity (2.09 [0.54], $p < 0.01$; Fig. 5.1). However, no significant relationship was detected between the probability of a species being threatened and average Incident Biodiversity Threat Index (IBTI) within their distribution ranges (1.98 [1.14], p = 0.08). Freshwater megafauna with high fecundity have a lower proportion of threatened species than those with low fecundity (Fig. 5.2). Migratory and viviparous megafauna exhibit a higher extinction risk than non-migratory and egg-laying species, respectively. Herbivorous megafauna have the highest proportion of threatened species, followed by omnivorous and carnivorous megafauna.

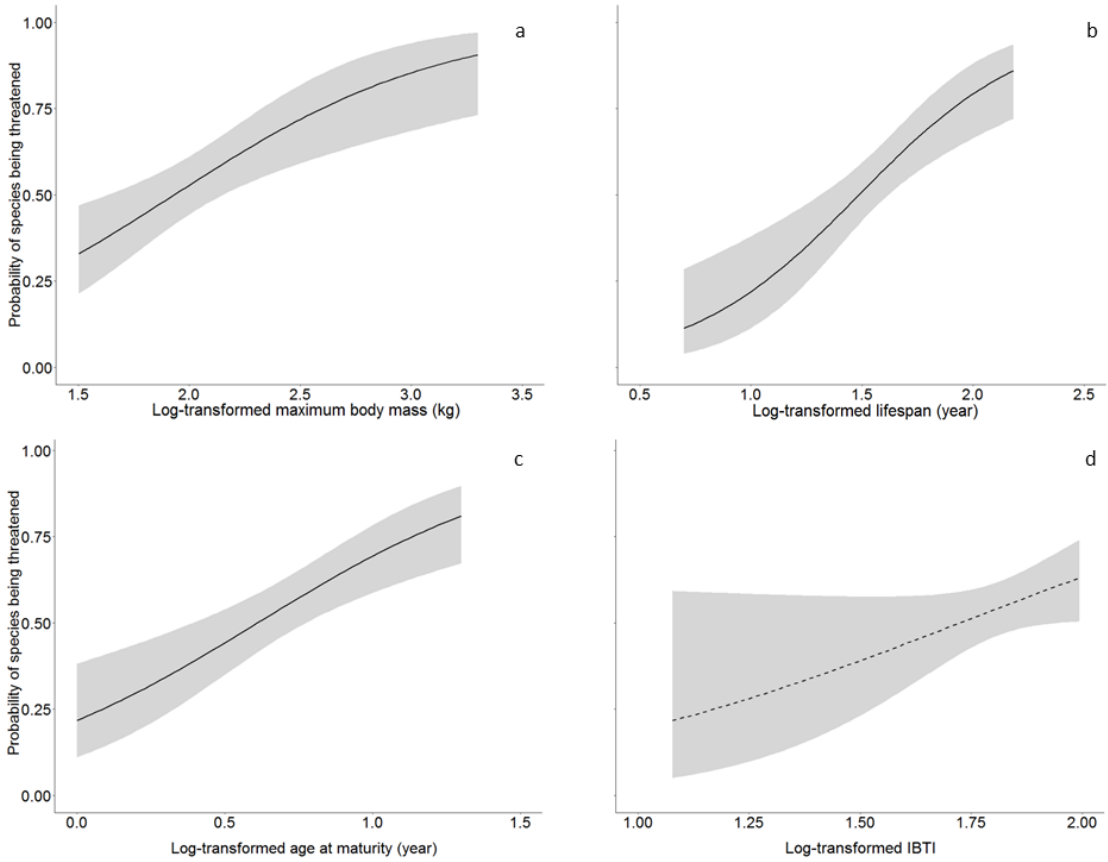

Fig. 5.1 Logistic relationships between probability of species being threatened, traits (a-c) and IBTI (d). Significant relationships (p < 0.05) are shown with solid lines, while the dashed line indicates a non-significant relationship. Shaded area: 95% confidence intervals.

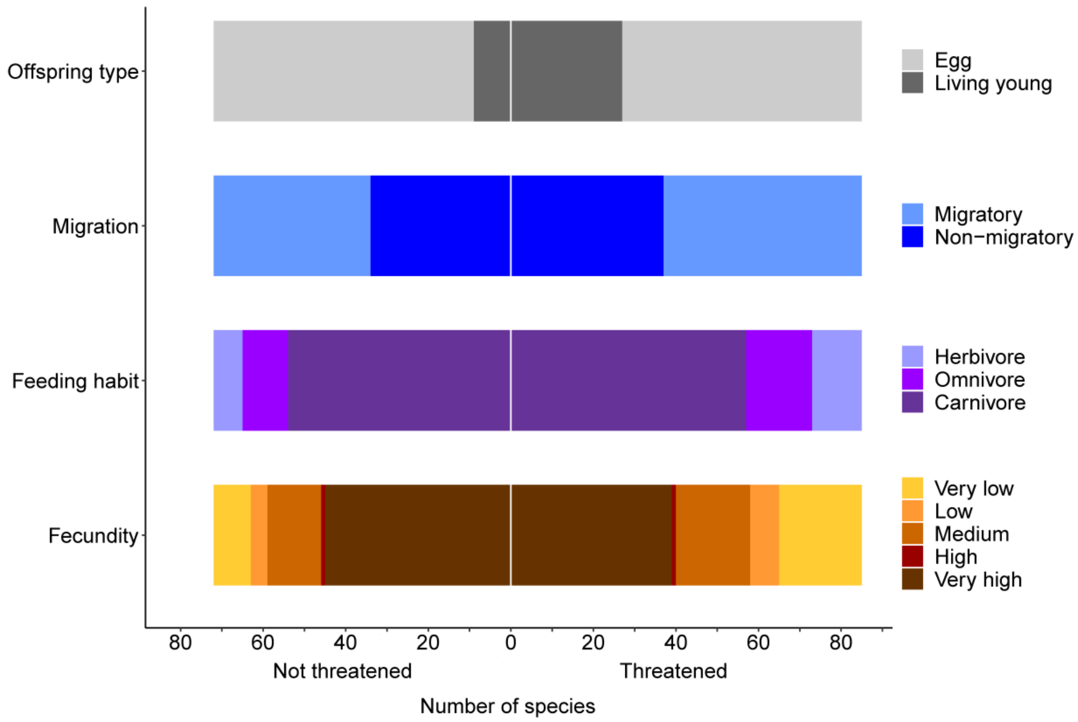

Fig. 5.2 Numbers of threatened and not-threatened species (different traits). The category of fecundity was determined with the average number of offspring (very low: 1-5; low: 6-20; medium: 21-200; high: 201-1000; very high: >1000)

When only life-history traits were considered in the GLMM, lifespan (9.45 [2.95], $p < 0.01$), age at maturity (18.79 [5.78], $p < 0.01$), fecundity (-0.57 [0.21], $p < 0.01$) and the interaction between maximum age and age of maturity (-10.89 [3.61], $p < 0.01$) were included in the best-fit model (Table 5.1). When both traits and anthropogenic threats were considered, lifespan (10.09 [3.08], $p < 0.01$), age at maturity (21.95 [6.36], $p < 0.01$), fecundity (-0.85 [0.26], $p < 0.01$) and the interaction between lifespan and age at maturity (-12.46 [3.88], $p < 0.01$) were still included in the best-fit model, in addition to the IBTI (5.71 [1.93], $p < 0.01$).

Table 5.1 The two most parsimonious models explaining the conservation status of freshwater megafauna. MatAge stands for age at maturity. The family-level taxonomy was used as the random effect to control the potential phylogenetic correlation

Model structure	AIC	AUC	R^2
Conservation status ~ Lifespan + MatAge + Fecundity + Lifespan:MatAge + (1 | Family)	176	0.73	0.61
Conservation status ~ Lifespan + MatAge + Fecundity + Lifespan:MatAge + IBTI + (1 | Family)	168	0.76	0.68

Both models predicted that the same 16 species, out of 49 species with insufficient information, are actually threatened, including nine fish, three reptile, and four mammal species (Table 5.2). Although the two selected models did not show much difference in the included traits and predictions, it is worth noting that a decreased AIC value (i.e. from 176 to 168) and increased AUC value (i.e. from 0.73 to 0.76) were observed when anthropogenic threats were considered in the GLMM. In addition, the variance explained by the model increased from 63% to 68% when anthropogenic threats are included. It indicated that model performance improved when both intrinsic traits and external threats are considered.

Table 5.2 Species which were predicted as threatened by both GLMM models under medium scenario (i.e. species with predicted-threatened probability over 0.5)

Binomial name	Common name	Group
Aspiorhynchus laticeps	big-head schizothoracin	fish
Elopichthys bambusa	yellowcheek carp	fish
Hypophthalmichthys nobilis	bighead carp	fish
Mylopharyngodon piceus	black carp	fish
Neoceratodus forsteri	Australian lungfish	fish
Paratrygon ajereba	Manzana ray	fish
Potamotrygon brachyura	short-tailed river stingray	fish
Potamotrygon motoro	Ocellate river stingray	fish
Salvelinus namaycush	lake trout	fish
Inia araguaiaensis	Araguaian river dolphin	mammal
Inia boliviensis	Bolivian river dolphin	mammal
Inia geoffrensis	Amazon river dolphin	mammal
Sotalia fluviatilis	tucuxi	mammal
Chitra vandijki	Burmese narrow-headed softshell turtle	reptile
Osteolaemus osborni	Osborn’s dwarf crocodile	reptile
Pelochelys signifera	Northern New Guinea softshell turtle	reptile

Among the 16 species predicted as threatened, seven species (44%) occur in South America, particularly in the Amazon River basin, and four species in China. The remaining five species occur in Africa, Australia, North America, and Southeast Asia. Accounting for all species predicted to be threatened, the Amazon and Yangtze River basins have become emerging global hotspots of threatened freshwater megafauna species (Fig. 5.3), in addition to existing ones (i.e. Ganges and the Mekong river basins and the Caspian Sea region) according to the IUCN Red List assessments. The Amazon River basin has been highlighted as the hotspot of threatened freshwater megafauna species by both models under all three scenarios (Fig. S5.2; Table S5.2).

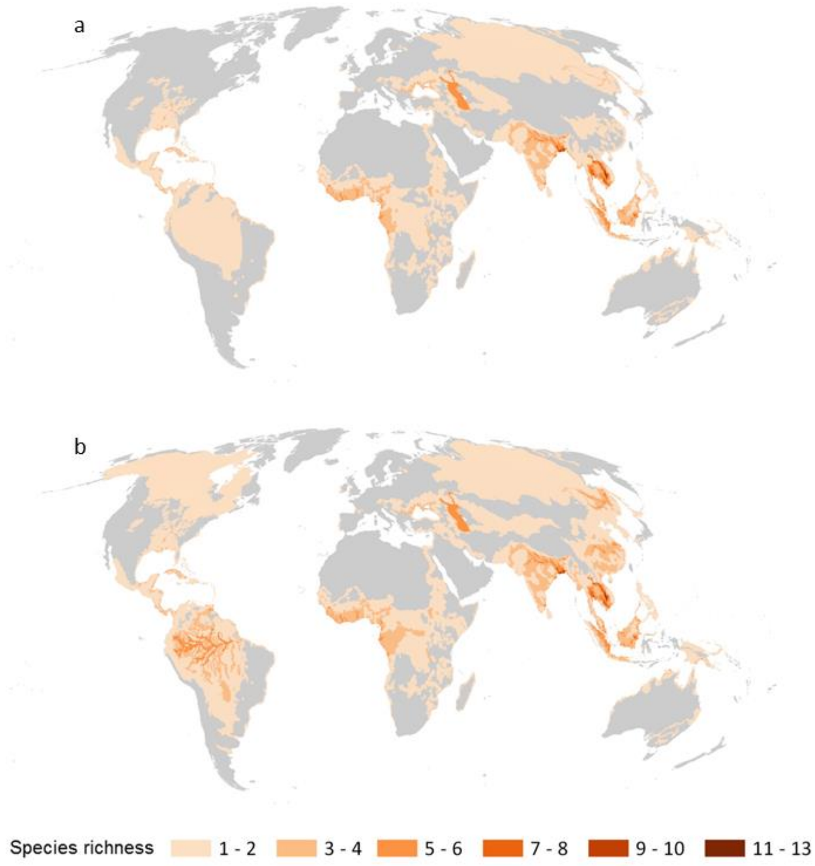

Fig. 5.3 Species richness of freshwater megafauna (a) considered as threatened according to IUCN Red List and (b) considered as threatened according to IUCN Red List and model predictions under medium scenario.

5.5 Discussion

5.5.1 Extinction risks of freshwater megafauna

Our study provides a comprehensive overview of life-history traits of freshwater megafauna. Freshwater megafauna are characterized by large body size, long lifespan and late maturity, which are usually suggested as extinction-prone traits (Hutchings *et al.*, 2012; McKinney 1997). These traits are characteristics for a slow life-history strategy (i.e K-selected strategy), with low maximum rate of population growth and low recovery potential after disturbance (McKinney 1997; Purvis *et al.*, 2000).

Human pressures on freshwater megafauna are intense and have increased during the past decades (He *et al.,* 2018). However, we did not find a significant relationship between anthropogenic threats and extinction risks of freshwater megafauna when effects of life history traits were not considered. This is not surprising, since species with distinct life histories respond differently to anthropogenic threats (Murray *et al.,* 2011). In Europe, for example, overexploitation, dam construction and habitat degradation have caused catastrophic effects on migratory species such as sturgeons (Pikitch *et al.*, 2005), while the non-migratory Wels catfish (*Silurus glanis*) has not suffered significantly from these impacts. Hence, it is necessary to consider combined effects of life-history traits and anthropogenic threats in extinction risk analyses (Murray *et al.*, 2014).

Although the logistic regression exhibited a significantly positive relationship between body size and extinction risks of freshwater megafauna, body size was not included in neither of the finally selected models. This is in contrast to studies indicating that body size is one of the most important traits correlated with extinction risks of vertebrates such as fishes (Kopf *et al.*, 2017; Olden *et al.*, 2007), mammals (Cardillo *et al.*, 2005; Purvis *et al.*, 2000), and birds (Wang *et al.*, 2018). Body size has been regarded as important factor in determining the extinction risk of a species due to its correlation with other factors such as distribution range, dispersal ability and habitat specialization, which strongly influence species resistance to extinction (McKinney 1997). For freshwater megafauna, body size is not strongly associated with these factors due to their large variety in taxonomy, preferred habitat types, and in distribution ranges. Large freshwater megafauna such as the New Guinea giant softshell turtle (*Pelochelys bibroni*) do not necessarily have a larger distribution range and higher dispersal ability than relatively small species such as the Atlantic salmon (*Salmo salar*). Instead, body size is often negatively associated with abundance, another important extinction-related factor, which is jointly determined by traits such as fecundity, age at maturity, and reproductive life span and external threats.

Abundance-related traits determine the recovery potential of species after disturbance caused by external threats. Given the multiple and intense threats that freshwater megafauna are exposed (Carrizo *et al*., 2017; He *et al.*, 2018), their ability to cope with various threats is particularly crucial for maintaining stable population size. For example, species with early maturity and high fecundity would have a higher chance to survive from intense harvesting pressure (Hutchings *et al.*, 2012). Freshwater megafauna such as sturgeons, freshwater sharks and rays, river dolphins, crocodilians and giant turtles only reach maturity after at an age of five to ten years. The chance is high that they get captured before reaching maturityreproduction. Compared to megamammals and megareptiles in freshwaters, megafish have much larger numbers of offspring. Consequently, megafish should therefore be more resistant against extinction. However, the is not always the case. Even if megafish make it to the age of maturity, their access to spawning grounds is often blocked by dams, or natural environmental conditions (flow and thermal regimes, and natural substrates) are altered due to hydropower dams and dredging in a way that heavily impacts spawning success (He *et al.*, 2017).

5.5.2 Predicting the conservation status of freshwater megafauna

Among the 16 species predicted as threatened, the Amazon river dolphin (*Inia geoffrensis*) and the northern New Guinea softshell turtle (*Pelochelys signifera*) have been considered as threatened species in the newly updated assessment of the IUCN Red List (IUCN 2018b), while the big-head schizothoracin has been assessed as Critically Endangered on the Red List of China’s Vertebrates (Jiang *et al.*, 2016).

Interestingly, black carp (*Mylopharyngodon piceus*) and bighead carp (*Hypophthalmichthys nobilis*) have been predicted as threatened. These two species have been regarded as invasive species, especially in North America (Kočovský *et al.*, 2018). However, their reproduction has been severely impacted by dams, overexploitation and habitat loss, leading to sharp decline in larval abundances (Ban *et al.*, 2019). Given the large size of remaining populations and their wide distribution, black carp and bighead carp are not yet in a critical situation; however, this may change in the near future, especially considering the dire and continuously degrading situation of freshwater ecosystems in China (Song *et al.*, 2018).

The Amazon and Yangtze river basins are emerging hotspots for threatened freshwater megafauna. These two basins share some common characteristics. They harbor 50 freshwater megafauna species, and a high freshwater biodiversity in general; concurrently, they are highly underrepresented in the IUCN Red List assessment (Carrizo *et al.*, 2017; Collen *et al.*, 2014). Both basins have high levels of fishing activities, increasing water traffic and low enforcement of environmental regulations, which have already led to a major population decline or even local extinction of megafish species and river dolphins (Castello *et al.*, 2013; Xie 2017). In addition, dams have caused major effects on freshwater megafauna species in the Yangtze river basin (Dudgeon 2011). Similar effects are predicted for the Amazon river basin (Winemiller *et al.*, 2016).

Even under the mild scenario, the Amazon River basin has been highlighted as a hotspot of threatened freshwater megafauna. Hence, an assessment of the conservation status of freshwater megafauna in this area is urgently needed. Due to the high biodiversity in the Amazon River basin, 42.5% of its basis is protected (Abell *et al.*, 2018). However, a large proportion of these protected areas are IUCN Category VI protected areas, where conservation regulations are usually poorly enforced and provide questionable protection of biodiversity (Dudley *et al.*, 2010). Moreover, protection often focuses on terrestrial ecosystems, providing limited protection for freshwater biodiversity (Azevedo-Santos *et al.*, 2019; Fagundes *et al.*, 2016). Hence, an assessment of freshwater megafauna in the Amazon River basin should be backed up with additional protected areas which specifically include freshwater ecosystems (Azevedo-Santos *et al.*, 2019).

It requires comprehensive data on life-history traits, threats (e.g. spatially explicit data on the type, and the intensity and change of threats), and conservation efforts to accurately predict the conservation status of species (Murray *et al.*, 2014). However, the taxonomy of freshwater megafauna species such as river dolphins and the Arapaima in South America or the Chinese giant salamander remains inconclusive (Siciliano *et al.*, 2016; Stewart 2013; Yan *et al.*, 2018). Information on traits including spawning periodicity, fecundity, and age at maturity of many freshwater megafauna species, especially megafishes and giant turtles, is still missing. These traits are important to estimate the maximum per capita population growth rate (r_{max}), which is associated with extinction risk and important for conservation management (Hutchings *et al.*, 2012). In addition, the conservation applications of extinction-risk assessment are largely based on generation times. For example, population change over the last three generations is an important criterion to assess conservation status on the IUCN Red List (IUCN 2018a). However, information on generation time remains unknown for 65% of all megafauna species. To fill the large data gaps, field surveys and long-term monitoring are needed for freshwater megafauna.

5.5.3 Recommendations for freshwater megafauna conservation

Species cannot be considered as not-threatened, just because they are not classified by the IUCN Red List. Jaric *et al.*, (2016) suggested that species listed as Data Deficient could underlay a similar or even higher risk of extinction than assessed species. We support this notion and specifically call for an assessment of the IUCN Red List status of the 14 freshwater megafauna species that were predicted as threatened in our study (excluding the two recently assessed species, Amazon river dolphin and the northern New Guinea softshell turtle). We do realize that such an assessment requires financial support, commitment of species' experts, and time. Hence, until a full assessment of these species is conducted, monitoring schemes of their population size and distribution range should be implemented.

The "Field of Dreams" hypothesis, i.e. "if you build it they will come", is common guideline in conservation and restoration practices (Fraser *et al.*, 2015). However, given the complex habitat requirements of megafauna species, it may take years to decades to restore their required habitats. Therefore, time is critical in protecting freshwater megafauna. Indeed, we might miss the window-of-opportunity to protect these species from extinction if conservation actions are delayed as it happened for the Baiji and the Chinese paddlefish. On the basis of our results, it is important to sustain their recovery potential, even before their habitats are restored. One possible approach to do so is to support populations by artificially enhancing their reproductive success. Owing to specific knowledge on the biology of some freshwater megafauna species as well as to new technologies, artificial reproduction has been successfully conducted to enhance wild populations or to reintroduce them into previously inhabited areas for various megafauna species (Lundgren *et al.*, 2018), including beavers (Halley 2011), sturgeons (Pikitch *et al.*, 2005), or finless porpoises (Wang 2009). Hence, there is still chance that these large freshwater animals can be protected if more research and timely conservation programs are implemented. Meanwhile, conservation actions must be prioritized for highly threatened freshwater megafauna, i.e. species with very small population sizes and highly restricted distribution ranges.

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6 General discussion

The sections 6.2 and 6.5.1 have been modified from the following manuscript:

He, F. & Jähnig, S.C. Put freshwater megafauna on the table before they are eaten to extinction (to be submitted).

Advances in our knowledge and technology have allowed for the development of efficient conservation frameworks towards balancing the need for human development and maintaining biodiversity. At the same time, great accelerations in human activities have put tremendous pressures on the environment (Steffen *et al.*, 2015), resulting in species extinction at a rate which is 100 – 1000 times higher than natural background rates (Ceballos *et al.*, 2015; De Vos *et al.*, 2015). Freshwaters are losing species faster than terrestrial and marine ecosystems (Costello, 2015; McRae *et al.*, 2017), with megafauna species at high risk of extinction (Ripple *et al.*, 2019). To halt their trajectory towards extinction, timely and efficient conservation actions should be taken. This thesis provides a scientific basis for such conservation actions and has important implications for overall freshwater biodiversity conservation.

6.1 Key research findings

In this thesis I have shown the diversity and risk patterns of freshwater megafauna on different spatial scales and over time. With the body-mass threshold of 30 kg, I compiled a list of 207 extant freshwater megafauna species, including 130 fishes, 44 reptiles, 31 mammals and 2 amphibians. I mapped the global distribution of all freshwater megafauna and threatened species in **Chapter 2**. I hypothesized that diversity hotspots of freshwater megafauna would largely overlap with diversity hotspots of all freshwater species. I also showed the intensity of overall anthropogenic threats and its change from 1990 to 2010 within the distribution ranges of freshwater megafauna. Based on the published literature, I identified the main threats to freshwater megafauna in **Chapter 3**, including overexploitation, habitat degradation, dam construction, pollution and biological invasions. These threats have led to a reduction in population abundances and distribution ranges of freshwater megafauna, which has been analyzed in **Chapter 4**. I also hypothesized that freshwater megafauna populations have declined more than those of their smaller counterparts (i.e. -81% from 1970 to 2012; McRae et al., 2017). The population decline and range contraction are preludes to species extinction, which does not happen randomly among taxonomic groups or geographic regions. It is related with intrinsic traits of species and external threats posed on them (Gonzalez-Suarez *et al.*, 2012; Murray *et al.*, 2014; Wang *et al.*, 2018). In **Chapter 5**, I examined the relationships between extinction risk of freshwater megafauna and their life-history traits with generalized linear mixed models (GLMMs), as well as the effect of anthropogenic threats on such relationships. Based on these relationships, I used the selected GLMMs to predict the conservation status of the 49 unclassified freshwater megafauna species.

6.1.1 Global patterns of freshwater megafauna diversity

Freshwater megafauna species inhabit 76% of the world's main basins (level 3 HydroBASINS). The Amazon, Congo, Orinoco, Mekong and Ganges-Brahmaputra river basins are amongst the diversity hotspots of freshwater megafauna (**Chapter 2**). These basins are also diversity hotspots of overall freshwater species (Collen *et al.*, 2014). Such results confirmed my hypothesis that freshwater megafauna are associated with a high level of overall freshwater biodiversity. Indeed, freshwater megafauna diversity shows clear spatial congruence with overall freshwater biodiversity in Africa, India and Southeast Asia (Fig. 6.1), where freshwater species have been well assessed by IUCN (Collen *et al.*, 2014). Due to their large habitat requirements and/or high trophic position, freshwater megafauna usually occur in ecosystems with sufficient water resources, high geomorphic complexity and/or high levels of ecosystem productivity, where high levels of biodiversity are likely to be supported (Sergio *et al.*, 2006). In addition, these large animals often function as keystone species or ecosystem engineers and can create and maintain habitats for smaller species, thereby promoting high level of biodiversity in ecosystems they inhabit (Moore, 2006; Bakker *et al.*, 2016b).

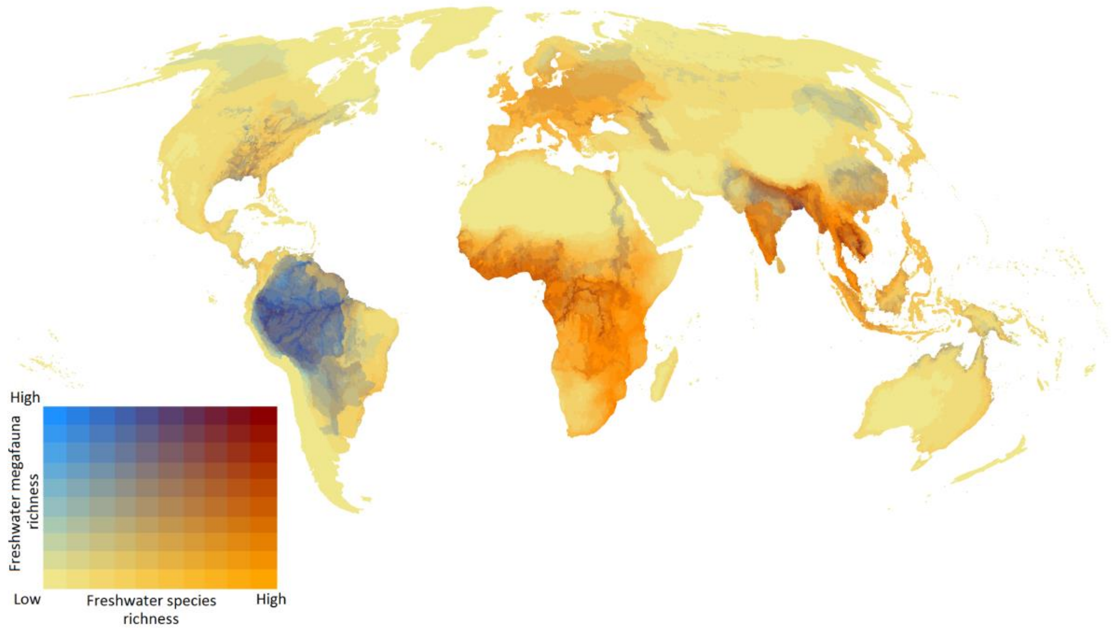

Fig. 6.1 Concordance map of freshwater megafauna species richness with overall freshwater species richness. The freshwater megafauna data were derived from Chapter 2 while the overall freshwater species data were derived from the IUCN database (detailed methods see Chapter 2 and Appendix G). Note that freshwater species in China, Russia, Middle East, Oceania, and North and South America are incompletely assessed by IUCN Red List (IUCN, 2018).

6.1.2 Anthropogenic impacts on freshwater megafauna

Anthropogenic activities are intense and have increased considerably within many diversity hotspots of freshwater megafauna (**Chapter 2**). According to IUCN Red List assessments, the Mekong and Ganges-Brahmaputra river basins have the highest number of threatened species (15 and 13 species, respectively). These two basins are also amongst the diversity hotspots of threatened freshwater species (Collen *et al.*, 2014) and are subject to high level of anthropogenic threats, in particular overexploitation (**Chapter 2**; Vörösmarty *et al.*, 2010; McIntyre *et al.*, 2016), which is the biggest threat to freshwater megafauna (**Chapter 3**, **Appendix G**). In addition to overexploitation, dam construction, habitat degradation, pollution, and biological invasions have posed further pressure on these large animals, leading to reduced fitness, disrupted reproduction and increased mortality (**Chapter 3**). The main threats to freshwater megafauna are also main threats to overall freshwater biodiversity (Dudgeon *et al.*, 2006; Reid *et al.*, 2018). Freshwater megafauna are often favored in harvest, poaching, and trophy hunting due to their high market value and the human fascination with big animals (Ripple *et al.*, 2019). Because of the large and complex habitat requirements of freshwater megafauna, there is a high risk of habitat fragmentation caused by dams, which leads to lost access to spawning and/or feeding ground.

6.1.3 Megafauna loss in freshwaters

Anthropogenic threats have caused a major population decline and range contraction of freshwater megafauna (**Chapter 4**). From 1970 to 2012, global populations of freshwater megafauna declined by 88%, which is higher than the decline rate of overall vertebrate populations in freshwater (-81%), terrestrial (-38%) or marine (-36%) ecosystems (McRae *et al.*, 2017). Decline rates of populations in Indomalaya (-99%) and Palearctic (-97%) realms, and in mega-fish (-94%) are even higher, mainly due to overexploitation and dam construction. In addition, 42% of all freshwater megafauna species have lost more than 40% of their historical distributions in Europe. Such declines mirror intense anthropogenic threats on freshwater megafauna and their susceptibility to these threats.

The extirpation of freshwater megafauna such as crocodilians and big piscivore fishes leads to simplification of food web and influences the ecological process and functioning through trophic cascading (Hanson *et al.*, 2015; Winemiller *et al.*, 2015; Hammerschlag *et al.*, 2019). It could further result in reduced resistance of communities and ecosystems to disturbances (Brose et al 2017). Many small animals and plants will lose their habitats or refuges during drought periods, if e.g. beaver dams or small pools maintained by crocodilians or hippos are gone (Moore, 2006; Bakker *et al.*, 2016b). In addition, the loss of freshwater megafauna also causes the abruption of material and nutrient cycling among freshwater, marine and terrestrial ecosystems (Doughty *et al.*, 2016). For example, salmonids migrate from oceans to freshwaters where they get caught by terrestrial predators such as bears, or die and degrade in streams after spawning, boosting local microbe and macroinvertebrate communities (Janetski *et al.*, 2009). Hippos feed on riparian vegetations while their dung is usually flushed into rivers, fertilizing water and supporting local fish populations (Pennisi, 2014). Within freshwaters, many mega-fishes migrate to upstream areas for feeding during flood season, which could also contribute to the dispersal of seeds and small organisms (Anderson *et al.*, 2011; O'Farrill *et al.*, 2013; Costa-Pereira *et al.*, 2018). Hence, the disappearance of freshwater megafauna will pose, and most likely has already had, profound impacts on other species and ecological processes in freshwaters and surrounding ecosystems.

6.1.4 Correlating extinction risk of freshwater megafauna with life-history traits and threats

Fifty-four percent of all assessed freshwater megafauna species are considered as threatened on the IUCN Red List (**Chapter 1**), which is higher than the threatened proportion of all freshwater species (Collen *et al.*, 2014). **Chapter 5** provided quantitative evidence that freshwater megafauna are characterized by extinction-prone traits (McKinney, 1997; Hutchings *et al.*, 2012) such as large body size (183 ± 388 kg; mean ± standard deviation), long lifespan (40 ± 25 years), and late maturity (6 ± 4 years). The combination of traits (i.e. lifespan, age at maturity, and fecundity) related to species' recovery potential and intensity of anthropogenic threats best explained the extinction risk (measured with conservation status on the IUCN Red List) of freshwater megafauna in GLMMs. Sixteen out of 49 unclassified freshwater megafauna species were predicted as threatened. Based on the model predictions together with IUCN Red List assessments, the Amazon and Yangtze river basins have also become diversity hotspots of threatened freshwater megafauna, in addition to the Mekong and Ganges-Brahmaputra river basins and the Caspian sea region. The IUCN Red List assessments for freshwater megafauna in these two basins are largely incomplete (**Appendix G**, **Chapter 2**) while the future of these species is at increasing risk due to rapidly growing anthropogenic threats (Castello *et al.*, 2013; Castello *et al.*, 2015; Xie, 2017).

6.2 Future challenges for freshwater megafauna

Owing to the growing human population and subsequent demand of freshwater, food and energy, the degradation in freshwater ecosystems is likely to continue in the near future (Bunn, 2016; Hermoso, 2017). The global inland capture fisheries have been growing rapidly due to developments in equipment and technique (Bartley *et al.*, 2015). Additional stress is put on freshwater megafauna by newly developed fishing forms, e.g. using river dolphins and caimans as bait to catch piracatinga (*Calophysus macropterus*) in the Amazon River basin (Brum *et al.*, 2015; da Silva *et al.*, 2018; Pimenta *et al.*, 2018).

Reid *et al.* (2018) have identified twelve emerging threats to freshwater biodiversity. Among these threats, the ongoing hydropower-dam boom is the most pressing one to freshwater megafauna as these species, including river dolphins, manatees and mega-fishes, have seasonal migration as an adaptation to natural flow regimes. This may unfold particularly strong in megafauna-rich basins such as the Amazon, Congo and Mekong river basins (**Chapter 3**, Fig. 6.2) which are currently less fragmented compared to the Danube, Mississippi, and Yangtze river basins (Grill *et al.*, 2015). The future dams will pose catastrophic impacts on freshwater megafauna by fragmenting their habitats, altering flow regimes and blocking their migratory routes. Climate change can also cause habitat loss of species such as the Caspian seal (*Pusa caspica*) and freshwater whipray (*Urogymnus dalyensis*) (Härkönen, 2008; Chin *et al.*, 2010). The combined impact of dams and climate change will add further uncertainty to the future of freshwater megafauna, particularly of those inhabiting areas below dams.

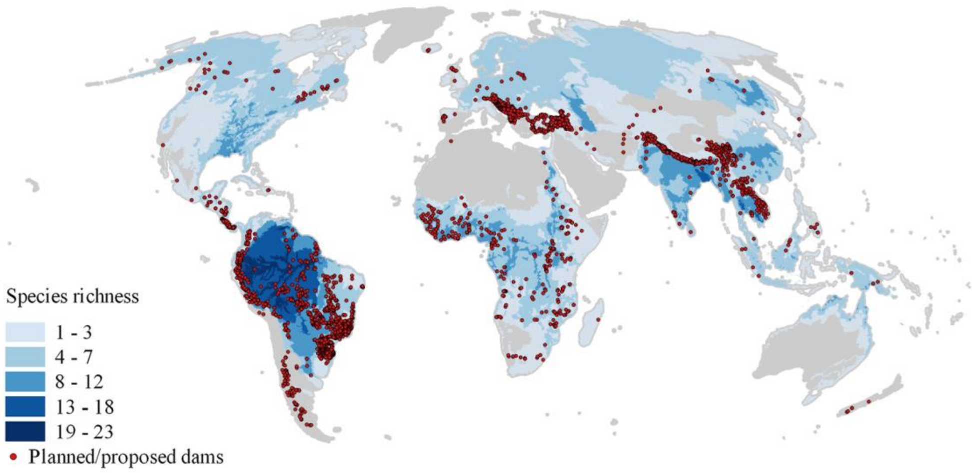

Fig. 6.2 Spatial congruence between species richness of freshwater megafauna and future hydropower dams (adapted from Zarfl et al., unpublished data).

Emerging pollutants, such as endocrine-disrupting chemicals, newer pesticides, and plastics, could also affect the fitness and reproduction of freshwater megafauna, particularly in light of their impacts on other aquatic animals (Sumpter & Jobling, 2013; Reid *et al.*, 2018). Most studies on plastic pollution (i.e. micro- and macro-plastics) have focused on its impact on marine animals including megafauna species such as sea turtles, rays, sharks and whales (Broderick *et al.*, 2015; Law, 2017; Germanov *et al.*, 2018). Given that plastic debris reported affecting marine megafauna also widely occur in freshwaters (Blettler *et al.*, 2018), negative impacts of plastic pollution (e.g. suffocation and obstruction of the digestive tract) on freshwater megafauna such as mega-fishes, giant turtles and crocodilians could be expected, due to their similar life-history traits with their marine counterparts.

Compared to terrestrial or marine megafauna, freshwater megafauna are also less recognized in conservation and biodiversity research. (**Chapter 3**). Recently, Ripple and colleagues reported that megafauna species face high level of harvesting pressure in marine, terrestrial and freshwater ecosystems (Ripple *et al.*, 2019). They define megafauna as all mammals and fishes ≥100 kg and amphibians, birds and reptiles ≥40 kg. There are 104 extant freshwater megafauna species falling under their definition (Table S6.1). However, 43 (41%) of them have not been recognized and included in their study. The rate of such neglected megafauna in freshwaters is much higher than those in terrestrial (6%, 5 out of 81 species; Table S6.2) and marine (11%; 25 out of 219 species; Table S6.3) ecosystems. Two factors contributed to the neglect of freshwater megafuana: First, many megafauna species in freshwaters are poorly studied. Information on their maximum body mass remains unknown, particularly for mega-fishes and mega-reptiles inhabiting in developing countries (**Chapter 5**). Second, even if data on their body mass have been reported, they are often not integrated in well-known database such as Amniote (Myhrvold *et al.*, 2015) and FishBase (Froese & Pauly, 2018) which have been used for Ripple et al. (2019). Similarly, 47 species (i.e. 23% of all freshwater megafuna species) remain unclassified on the IUCN Red List (IUCN, 2018) while all terrestrial megafauna have been assessed and reassessed (Ripple *et al.*, 2016).

6.3 Potential implications and limits of the thesis

The established database and findings of this thesis can have important implications for freshwater megafauna conservation: 1) The distribution of each freshwater megafauna species has been mapped to sub-catchment level based on the HydroBASINS template (level 8). This is consistent with the spatial unit used by the IUCN Red List assessments for freshwater species (IUCN, 2018) and could be directly used for future conservation assessments and planning such as identifications of key biodiversity areas. 2) The identified diversity hotspots of threatened freshwater megafauna such as the Amazon, Congo, Mekong, Ganges-Brahmaputra river basins harbor many migratory mega-fishes. The spawning areas and migration corridors for these mega-fishes largely remain unknown (Hogan, 2011). Considering hundreds of proposed dams in these basins, it is urgent to identify such key areas and take them into considerations of the dam constructions (e.g. selection of dam locations, establishment of fish passages). 3) The current fish passages are largely designed for salmonids and do not work well for non-salmonid species (Noonan *et al.*, 2012). Given that most migratory mega-fishes threatened by future dams are non-salmonid species, new fish passages considering these species should be included in the operation plans of future dams. 4) Considering the drastic population decline of freshwater megafauna and their susceptibility to extinction, monitoring the population abundance of these large animals isneeded. This is especially the case for mega-fish and giant turtles in the Global South, which have very limited population data available. For the 14 predicted-threatened species, monitoring on their populations and distributions should also be implemented before the IUCN Red List assessments are conducted. 5) The thesis underscores the importance of maintaining the recovery potential of freshwater megafauna. For species with severely impeded or disrupted reproduction and/or extremely small populations, artificial population enhancement can be a practical approach to maintain the population abundance until their habitats get restored in the future.

Uncertainties exist in the results of the thesis due to data unavailability: 1) Information on distributions of many freshwater megafauna species in South America remain limited. It did not allow mapping their current distributions precisely in high-resolution units (i.e. HydroBASINS level 8 sub-catchments). For example, exact distribution ranges of each Arapaima species (i.e. *Arapaima agassizii*, *Arapaima gigas*, *Arapaima leptosome*, and *Arapaima mapae*) remain unclear. Hence, their distributions were all covered by the *Arapaima* spp. complex map (**Chapter 2**, **Appendix G**). This could hamper the effectiveness of spatial conservation prioritizations (e.g. identification of key biodiversity area) as such analyses often require high-resolution spatial data. 2) Data on historical distributions of freshwater megafauna species outside of Europe and the USA are largely unavailable (**Chapter 4**). Hence, changes in distribution ranges of freshwater megafauna in other regions have not been shown. 3) The lack of monitoring data caused some uncertainties in tracking trends of freshwater megafauna populations, spatially in the Global South and taxonomically for mega-reptiles (**Chapter 4**). In addition, inadequate data in 1970s can lead to the underestimation of declines in freshwater megafauna populations. The reference year of 1970 was chosen to be consistent with the Living Planet Report. However, in regions such as Europe, major declines of sturgeons and beavers already happened before 1970. 4) The large gap in life-story traits including generation time, fecundity, spawning/postnatal periodicity makes it challenging to gain a comprehensive understanding the extinction risk of freshwater megafauna. The missing information in such traits can reduce the performance of model predictions as the extinction risk of freshwater megafauna is associated with their recovery potential (**Chapter 5**). 5) All the analyses were conducted at large spatial scales. It is difficult to include detailed information on local conditions (e.g. whether freshwater megafauna species are targeted in local conservation management) in such analyses. This could add uncertainties in identifying areas in need of conservation actions. 6) Threat data layers used in the thesis such as the Temporal Human Pressure Index was developed to track changes in human pressure on land. Even freshwater specific layers such as the Incident Biodiversity Threat Index, were not originally mapped with catchments or sub-catchments as units, but with latitude/longitude grids. Although these threat layers were converted into HydroBASINS to match biodiversity layers, hydrological relationships among sub-catchments were not considered in these threat layers. In addition, the mismatch of original layers and potential information loss during data conversion might weaken the accuracy of spatial congruence analysis (**Chapter 2**). Hence, more updated freshwater specific layers including harvesting pressure and fragmentation index with catchment as units are called for future studies. Such spatial and type-intensity explicitly threat layers, together with comprehensive life-history data, can considerably improve the performance of model predictions for extinction risk of freshwater megafauna.

6.4 Opportunities for freshwater megafauna conservation

Despite the dire situation of freshwater megafauna, there are still opportunities to keep these large animals on Earth if timely research and conservation are implemented. North America has set a good example for protecting them (**Chapter 2**). In addition, there is increasing attention on freshwater biodiversity conservation. The latest version of Living Planet Report by World Wide Fund For Nature (WWF) has highlighted the freshwater biodiversity crisis and received attention from other leading conservation organizations including the IUCN and Conservation International (Harrison *et al.*, 2018; WWF, 2018). National Geographic also featured the overlooked freshwater life in early 2019[1] and continues the *Monster Fish* show to highlight mega-fishes in freshwaters.

Recently, freshwater megafauna species such as Salmons, manatees, hippos and crocodilians have also been featured in Netflix documentary *Our Planet*. Features by large conservation organizations and visual media such as movies and television shows is a promising approach to raise public awareness of the freshwater biodiversity crisis, in light of their ability to reach a broader audience and to stimulate discussions (Silk *et al.*, 2018), in turn, boosting conservation.

Artificial breeding has been successful for many freshwater megafauna species such as sturgeons, crocodilians, beavers and giant salamanders (Ludwig, 2006; Halley *et al.*, 2012; Tosun, 2013; Cunningham *et al.*, 2016). In addition, reintroductions of freshwater megafauna species such as sturgeons and beavers have been implemented in European countries including Germany, France and the Netherlands (see detailed discussion in **Chapter 5**). Most of the surveyed respondents in Europe support the reestablishment of freshwater megafauna species such as the Atlantic salmon (*Salmo salar*) and sturgeon (*Acipenser* spp.) in extirpated rivers (Kochalski *et al.*, 2019). In Asia, the mugger (*Crocodylus palustris*) has been spotted recently in Bangladesh where it thought to have disappeared[2]. The population of Irrawaddy dolphin in the Mekong River basin is rebounding for the first time in 20 years[3] while spawning activity of the Chinese sturgeon (*Acipenser sinensis*) has been observed again after two years of suspended reproduction (Zhuang *et al.*, 2016). Considering the rapid developments in science and increasing conservation efforts, as well as increasing dam removals (Ding *et al.*, 2019), it allows us to remain cautiously optimistic for the future of freshwater megafauna.

6.5 Beyond megafauna: implications for freshwater biodiversity conservation

Given the human fascination on megafauna and their complex habitat requirements, freshwater megafauna have the potential to act as flagship and umbrella species to promote conservation for overall freshwater biodiversity (**Chapter 1** and **3**, **Appendix G**, Kalinkat et al., 2017). Indeed, species such as river dolphins, sturgeons and giant catfishes have already been considered as flagship species

1 http://bit.ly/mega-discussion1 (Date of access: 2019-04-05)

2 http://bit.ly/mega-discussion2 (Date of access: 2019-04-05)

3 http://bit.ly/mega-discussion3 (Date of access: 2019-04-05)

by WWF[4,5,6]. Besides this, freshwater megafauna have more potential for advancing freshwater biodiversity conservation.

6.5.1 Megafauna as surrogates to highlight gaps in freshwater conservation

Compared to their smaller counterparts, megafauna species usually receive more attention from both scientists and the general public. Therefore, they are often well studied and favored in conservation actions, particularly in terrestrial ecosystems (Ford *et al.*, 2017). However, this thesis highlights that even the largest animals in freshwaters are not well studied and remain underrepresented in conservation (**Chapter 2**, **3** and **5**, **Appendix G**), which mirrors vast gaps in knowledge and conservation of freshwater biodiversity: 1) We still know little about freshwater biodiversity. Many freshwater species are yet to be described. For example, over 240 freshwater fish species have been described per year from 2006 to 2014 (Pelayo-Villamil *et al.*, 2015). The debate on taxonomic classification of river dolphins (*Inia* spp.) and Arapaima (*arapaima* spp.) in South America is still going on (Hrbek *et al.*, 2014; Siciliano *et al.*, 2016; Watson *et al.*, 2016). In 2018, the Chinese giant salamander (*Andrias davidianus*), the largest amphibian species and once classified as a single species, has been suggested to be at least five different species which are all threatened with extinction (Yan *et al.*, 2018). In the same year, a giant salamander species (*Siren reticulata*) over 60 cm wasdescribed in U.S.A. (Graham *et al.*, 2018). 2) The IUCN Red List assessments are insufficient for freshwater species. For example, IUCN Red List assessments for 43% of all freshwater megafauna are insufficient (i.e. listed as Data Deficient or Not Evaluated) or outdated (i.e. assessments conducted more than 10 years ago, **Chapter 2**) while approximate 7000 freshwater fishes (45% of all freshwater fishes) have not been assessed[7]. The gap in assessments is particular obvious in South America for both freshwater megafauna and all freshwater species (**Chapter 2**; Collen et al., 2014), where emerging threats (e.g. hydropower dams) are expected to grow rapidly in the near future (Grill *et al.*, 2015; Zarfl *et al.*, 2015; Winemiller *et al.*, 2016; Couto & Olden, 2018). 3) Information on life-history traits for freshwater species are largely unavailable. Compared to terrestrial species, such as mammals and birds, well covered by life-history databases such as Amniote (Myhrvold *et al.*, 2015),

4 http://bit.ly/mega-discussion4 (Date of access: 2019-04-06)
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7 http://bit.ly/mega-discussion7 (Date of access: 2019-04-06)

PanTHERIA (Jones *et al.*, 2009) and EltonTraits (Wilman *et al.*, 2014), freshwater species fall far behind regarding availability of trait data. For example, life-history traits of European fishes, one of the most well-studied freshwater groups, remain largely unavailable on FishBase (Jaric *et al.*, 2019) which is widely regarded as the most comprehensive database for freshwater fishes (Froese & Pauly, 2018). 4) Although it is suggested that 15% of inland surface waters are within boundaries of protected areas (Bastin *et al.*, 2019), rivers and lakes are often used to delineate boundaries rather than being targeted in conservation goals (Darwall *et al.*, 2011). The integrated protection for most freshwater biodiversity hotspots do not reach the Aichi Target 11 of Convention on Biological Diversity (Abel *et al.*, 2017; Fig. 6.3). In addition, current protected areas and conservation management are largely based on terrestrial ecosystems and provide limited protection for freshwater species (**Appendix G**; Fagundes *et al.*, 2016; Hermoso *et al.*, 2016).

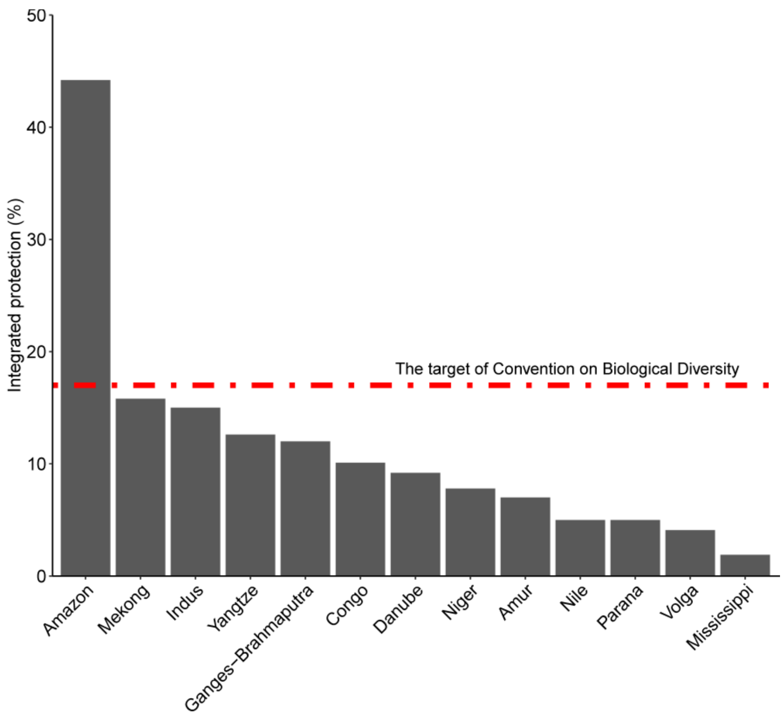

Fig. 6.3 Integrated protection levels (%) of world's large rivers (adapted from Abell et al., 2017). Red dashed line indicates the target (17%) of Convention on Biological Diversity regarding protected areas.

6.5.2 Megafauna as indicators for the integrity of freshwater ecosystems

Given their large and complex habitat requirements and high trophic positions, freshwater megafauna species are often sensitive to ecosystem dysfunction caused by overexploitation, disrupted river connectivity, altered flow regime, pollution and habitat degradation (**Chapter 3**). In addition, they are often associated with high level of overall freshwater biodiversity (Fig 6.1). Hence, the status of freshwater megafuana (e.g. changes in population and distribution) can indicate the ecological integrity of the whole basin. Indeed, river dolphins, beavers and crocodilians have been suggested as indicators for the ecological status of ecosystems they inhabit (Mazzotti *et al.*, 2009; Gomez-Salazar *et al.*, 2012; Hunter *et al.*, 2016). Although freshwater megafauna are particularly sensitive to overexploitation and dam construction, they can still reflect the pressure from pollution and invasive species within the ecosystem (**Chapter 3**).

Shifting baseline syndrome of freshwater ecosystems has been widely reported (Humphries & Winemiller, 2009; Finlayson *et al.*, 2015; Leeney & Downing, 2016). For example, Atlantic salmon (*Salmo salar*) and sturgeon (*Acipenser* spp.) have been perceived as native species in Europe by only 40% of surveyed respondents (Kochalski *et al.*, 2019). In China, the older fishermen are more likely to recognize the Baiji (*Lipotes vexillifer*) and Chinese paddlefish (*Psephurus gladius*) than younger ones. Younger generations get used to the degraded freshwater ecosystems, thereby continously lowering their expectations of natural environment and reduce their willingness to support biodiversity conservation (McClenachan *et al.*, 2018). Hence, it is important to make people aware of the previously existing megafauna species in unaffected local freshwater ecosystems to mitigate the impact of shifting baselines and establish appropriate restoration aims.

6.5.3 The potential of freshwater megafauna to strengthen links between people and freshwater life

In many countries, traditional cultures have strong links with freshwater ecosystems. Freshwater megafauna have been often integrated in traditional cultures and connected to local people by providing food, being used in cultural events and occuring in literature and local stories. For example, the lake sturgeon (*Acipenser fulvescens*) was an important food source for Menominee Indians during winter and has been associated with the story of the tribe’s orgins and their traditional religion, the Metawin (David, 1995). Sturgeons (*Acipenser* spp.) were also important components of tribal trades for Native Americans (Holzkamm & Waisberg, 2005). Crocodilians are regarded as symbols of fertility and strength and are associated with agricultural harvesting in the traditional Philippine culture (van der Ploeg et al., 2011) while mega-fishes in the Mekong basin are tightly connected with local fisheries and associate with the culture and identity of local communities (Gray et al., 2017). The Murray cod (*Maccullochella peelii*) is regarded as a cultural totem of Aboriginal communities in Australia (Noble et al., 2016). Communication and collaboration with local people are important to improve freshwater conservation (Geist, 2015). Strengthening cultural relevance of freshwater species, or re-enacting it where it has been lost, could be a promising approach to increase the public's willing to support biodiversity conservation and engage local people, especially in developing countries.

Due to reduced interactions with nature and lack of information on local biodiversity in their books, children are particularly susceptible to the extinction of biodiversity-related experience (Celis-Diez et al., 2016). Consequently, they have more knowledge on Pokemon than natural wildlife (Balmford et al., 2002). Such developments in technology and human lifestyle could also be harnessed to promote scientific outreach and biodiversity conservation in freshwaters (Sandbrook et al., 2015; Smith, 2016; Dorward et al., 2017). For example, games such as Phylo[8] could be developed to increase public knowledge of freshwater species (e.g. distributions, biological and ecological characteristics and some fun science facts). In such outreach games, information of their historical distributions of freshwater megafauna can be shown and make people aware of these locally extirpated species. Due to their spectacular appearance, complex life history, and ecological and cultural importance, freshwater megafauna are ideal candidates for nature documentaries and outreach in social media which are powerful to enhance links between people and nature (Wunder & Sheil, 2013; Toivonen et al., 2019). Hence, they hold the potential to inform the notion of freshwater biodiversity and help create momentum for freshwaters to be experienced as attractive and essential ecosystems in society.

6.6 Outlook

This thesis highlights that even the largest freshwater animals are at high risk of extinction and remain underrepresented in biodiversity research and conservation actions, which reflects a current poorly recognized global need, i.e. the conservation for freshwater biodiversity. Besides more activities in science communication and outreach to inform the public and policy makers of the crisis in freshwater

8 http://bit.ly/mega-discussion8 (Date of access: 2019-04-06)

biodiversity and engage them in freshwater conservation, further research should strive for a comprehensive understanding of these large animals. 1) Gaps in distributions, population dynamics and life-history traits of freshwater megafauna are the first issue to be tackled. This requires more field works and monitoring to uncover these data. In addition, the database of freshwater megafauna should be regularly updated and integrated in a large database such as Freshwater Information Platform[9] or the IUCN to provide easy access to these data. 2) Many freshwater megafauna species are ideal candidates for the ICARUS (International Cooperation for Animal Research Using Space) project[10], a global initiative to monitor migratory routes and living conditions of species. It can help identify key habitats (e.g. feeding, spawning and nursery grounds) of freshwater megafauna and facilitate proactive and efficient conservation actions if they can be included in such initiatives. 3) IUCN Red List assessments are necessary for species that have not been classified or have outdated assessments (i.e. assessments were conducted over 10 years ago). It is difficult to convince decision makers and initiate conservation actions for species without the sense of urgency indicated by the IUCN Red List. 4) More protected areas integrating freshwater megafauna into management goals should be established. A megafauna-based approach can be a promising strategy to promote freshwater biodiversity conservation and benefit a broad range of co-occurring species. However, prior to this, the surrogate efficiency of freshwater megafauna should be tested in different basins. 5) A synthesis of ecosystem functions and services provided by freshwater megafauna is recommended. This can inform the decision makers and general public about the importance of these large animals. Exploring potential conflicts between human and freshwater megafauna and public perceptions on them, as well as people's willingness to support conservation for these large species, can also provide insights for establishing efficient conservation strategies. 6) Conservation projects focusing on artificial population enhancement and reintroduction of freshwater megafauna are needed, together with the restoration of freshwater habitats, to keep all "*the hugest, and fiercest, and strangest*" (Wallace, 1876) freshwater life on our planet.

9 http://bit.ly/mega-discussion9 (Date of access: 2019-04-06)

10 http://bit.ly/mega-discussion10 (Date of access: 2019-04-06)

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Appendix A: Supporting information for Chapter 1

Methods

According to Web of Science, 56 journals are listed under the category of “biodiversity conservation”. Among these journals, we selected 18 journals which regularly changed their covers from 1997 to 2016 and had information available online or in the libraries (Table S1.1). Information on the species or ecosystems on cover images was collected, i.e. 1043 images with a clear focus on species and their ecosystems. Information on locations where photos were taken was also collected, if it was indicated. We followed the International Union for Conservation of Nature Red List of Threatened Species (here after IUCN Red List; IUCN, 2017) on the species name and their associated ecosystems. For some species which were not assessed by the IUCN Red List, they were assigned to a single (i.e. freshwater, marine or terrestrial) or combined ecosystem (e.g. marine and terrestrial) according to their life history. In addition, we assigned the featured landscape or habitat to a single or combined ecosystem. When a cover featured more than one ecosystem, we split the number proportionally (e.g. when both freshwater and terrestrial ecosystems were on one cover, we assigned 0.5 cover count to each of them).

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Table S1.1 Summary of cover images collected from biodiversity and conservation journals.

Journal	Period of data collection	Publication frequency
Animal Conservation*	2003-2016**	Quarterly (2003-2007) Bi-monthly (2008-2016)
Biodiversity and Conservation	1997-2012**	Monthly
Conservation Biology*	1997-2016	Bi-monthly
Conservation Letters*	1998-2016**	Bi-monthly
Diversity and Distributions*	2016**	Monthly
Ecography*	2014-2016**	Monthly
Global Change Biology*	1998-2016	8 issues per year (1997-2001) Monthly (2002-2016)
Journal for Nature Conservation	2002-2016**	Quarterly (2002-2010) Bi-monthly (2011-2016)
Journal of Applied Ecology*	1997-2016	Bi-monthly
Journal of Fish and Wildlife Management	2010-2016**	Biannual
Northeastern Naturalist	1997-2016	Quarterly
Oryx*	2007-2016	Quarterly
Pachyderm	1997-2016	Biannual (1997-2013) Annual (2014-2016)
Southeastern Naturalist	2002-2016**	Quarterly
Systematics and Biodiversity*	2003-2016**	Quarterly (2003-2014) Bi-monthly (2015-2016)
The Southwestern Naturalist	1997-2016	Quarterly
Tropical Conservation Science	2008-2016**	Quarterly (Bi-monthly in 2013)
Wildlife Society Bulletin	1997-2006; 2011-2016**	Quarterly

*These journals show the ALTmetric Attention Score for each article on their websites.

**These journals started changing cover images regularly after 1997. All cover images have been included. The Wildlife Society Bulletin has been paused between 2007 and 2010. Since 2013, Biodiversity and Conservation has stopped changing its covers.

Appendix B: Supporting information for Chapter 2

Table S2.1 List of freshwater megafauna and their conservation status. Abbreviations for IUCN Red List categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Critically Endangered (Possibly Extinct) (CR(PE)), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD) and Not Evaluated (NE). Species assessed more than ten years ago are classified as "needs updating" (IUCN, 2016). NA means Not Applicable.

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Andrias davidianus	Chinese Giant Salamander	Amphibian	CR	Decreasing	2004	Yes	No
Andrias japonicus	Japanese Giant Salamander	Amphibian	NT	Decreasing	2004	Yes	No
Aaptosyax grypus	Mekong Giant Salmon Carp	Fish	CR	Decreasing	2011	No	Yes
Acipenser baerii	Siberian Sturgeon	Fish	EN	Decreasing	2009	No	No
Acipenser dabryanus	Yangtze Sturgeon	Fish	CR(PE)	Decreasing	2009	No	Yes
Acipenser fulvescens	Lake Sturgeon	Fish	LC	Increasing	2004	Yes	No
Acipenser gueldenstaedtii	Russian Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser medirostris	Green Sturgeon	Fish	NT	Stable	2006	No	No
Acipenser mikadoi	Sakhalin Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser naccarii	Adriatic Sturgeon	Fish	CR(PE)	Decreasing	2009	No	No
Acipenser nudiventris	Ship Sturgeon	Fish	CR	Decreasing	2009	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Acipenser oxyrinchus	Gulf Sturgeon	Fish	NT	Increasing	2006	No	No
Acipenser persicus	Persian Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser schrenckii	Amur Sturgeon	Fish	CR	Decreasing	2009	No	Yes
Acipenser sinensis	Chinese Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser stellatus	Stellate Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser sturio	Atlantic Sturgeon	Fish	CR	Decreasing	2009	No	No
Acipenser transmontanus	White Sturgeon	Fish	LC	Stable	2004	Yes	No
Anguilla reinhardtii	Speckled Longfin Eel	Fish	NE	Unknown	NA	NA	No
Arapaima agassizii		Fish	NE	Unknown	NA	NA	No
Arapaima gigas	Arapaima	Fish	DD	Unknown	1996	Yes	No
Arapaima leptosoma		Fish	NE	Unknown	NA	NA	No
Arapaima mapae		Fish	NE	Unknown	NA	NA	No
Arius gigas	Giant Sea Catfish	Fish	NT	Decreasing	2006	No	No
Aspiorhynchus laticeps	Big Head Schizothracin	Fish	NE	Unknown	NA	NA	Yes
Atractosteus spatula	Alligator gar	Fish	NE	Unknown	NA	NA	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Bagarius yarrelli	Giant Devil Catfish	Fish	NT	Decreasing	2009	No	No
Bagrus docmak	Sudan Catfish	Fish	LC	Unknown	2016	No	No
Barbus grypus	Shabout	Fish	VU	Decreasing	2013	No	No
Bathyclarias worthingtoni		Fish	LC	Unknown	2006	No	Yes
Brachyplatystoma capapretum		Fish	NE	Unknown	NA	NA	Yes
Brachyplatystoma filamentosum	Piraiba	Fish	NE	Unknown	NA	NA	No
Brachyplatystoma rousseauxii	Gilded Catfish	Fish	LC	Unknown	2007	No	No
Carcharhinus leucas	Bull Shark	Fish	NT	Unknown	2005	Yes	No
Catla catla	Catla	Fish	LC	Unknown	2009	No	No
Catlocarpio siamensis	Giant Carp	Fish	CR	Decreasing	2011	No	No
Channa marulius	Great Snakehead	Fish	LC	Unknown	2009	No	No
Chrysichthys cranchii	Kokuni	Fish	LC	Unknown	2009	No	Yes
Chrysichthys grandis	Kukumai	Fish	LC	Unknown	2006	No	Yes
Clarias gariepinus	African Catfish	Fish	LC	Unknown	2016	No	No
Clarias macrocephalus	Broadhead Catfish	Fish	NT	Decreasing	2011	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Colossoma macropomum	Cachama	Fish	NE	Unknown	NA	NA	No
Ctenopharyngodon idella	Grass Carp	Fish	NE	Unknown	NA	NA	No
Cyprinus carpio	Wild Common Carp	Fish	VU	Unknown	2008	No	No
Electrophorus electricus	Electric Eel	Fish	LC	Stable	2007	No	No
Eleutheronema tetradactylum	Fourfinger threadfin	Fish	NE	Unknown	NA	NA	No
Elopichthys bambusa	Yellowcheek	Fish	DD	Increasing	2010	No	No
Esox lucius	Northern Pike	Fish	LC	Stable	2011	No	No
Esox masquinongy	Muskellunge	Fish	LC	Stable	2011	No	No
Fontitrygon ukpam	Pincushion Ray	Fish	EN	Unknown	2005	Yes	No
Glyphis gangeticus	Ganges Shark	Fish	CR	Decreasing	2007	No	No
Glyphis garricki	New Guinea River Shark	Fish	CR	Decreasing	2003	Yes	No
Glyphis glyphis	Speartooth Shark	Fish	EN	Decreasing	2005	Yes	No
Hemibagrus maydelli	Krishna Mystus	Fish	LC	Unknown	2010	No	Yes
Hemibagrus microphthalmus	Irrawaddy Mystus	Fish	LC	Decreasing	2009	No	No
Hemibagrus wyckioides	Asian Red Tailed Catfish	Fish	LC	Stable	2011	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Heterobranchus bidorsalis	Eel-like Fattyfin Catfish	Fish	LC	Unknown	2009	No	No
Heterobranchus longifilis	Vundu	Fish	LC	Unknown	2009	No	No
Himantura dalyensis	Freshwater Whipray	Fish	LC	Unknown	2015	No	No
Himantura polylepis	Giant Freshwater Whipray	Fish	EN	Decreasing	2011	No	No
Hoplias aimara	Wolf Fish	Fish	NE	Unknown	NA	NA	No
Hucho hucho	Huchen	Fish	EN	Unknown	2008	No	Yes
Hucho perryi	Sakhalin Taimen	Fish	CR	Decreasing	2006	No	No
Hucho taimen	Siberian Taimen	Fish	VU	Decreasing	2012	No	No
Huso dauricus	Kaluga	Fish	CR	Decreasing	2009	No	Yes
Huso huso	Beluga	Fish	CR	Decreasing	2009	No	No
Hydrocynus goliath	Giant Tigerfish	Fish	LC	Unknown	2009	No	Yes
Hypophthalmichthys molitrix	Silver Carp	Fish	NT	Decreasing	2011	No	No
Hypophthalmichthys nobilis	Bighead Carp	Fish	DD	Decreasing	2010	No	No
Hypselobarbus mussullah	Hump Backed Mahseer	Fish	EN	Decreasing	2010	No	No
Ictalurus furcatus	Blue Catfish	Fish	LC	Stable	2012	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Ictiobus bubalus	Smallmouth Buffalo	Fish	LC	Stable	2012	No	No
Ictiobus cyprinellus	Bigmouth Buffalo	Fish	LC	Stable	2012	No	No
Labeo rohita	Rohu	Fish	LC	Unknown	2010	No	No
Lates angustifrons	Tanganyika Lates	Fish	EN	Decreasing	2006	No	Yes
Lates calcarifer	Barramundi	Fish	NE	Unknown	NA	NA	No
Lates japonicus	Japanese Lates	Fish	NE	Unknown	NA	NA	Yes
Lates niloticus	Nile Perch	Fish	LC	Unknown	2009	No	No
Lepisosteus osseus	Longnose Gar	Fish	LC	Stable	2012	No	No
Lota lota	Burbot	Fish	LC	Stable	2012	No	No
Luciobarbus esocinus	Pike Barbel	Fish	VU	Decreasing	2014	No	Yes
Luciocyprinus striolatus	Striped Pikecarp	Fish	EN	Decreasing	2011	No	Yes
Maccullochella ikei	Eastern Freshwater Cod	Fish	EN	Unknown	1996	No	No
Maccullochella mariensis	Mary River Cod	Fish	NE	Unknown	NA	NA	Yes
Maccullochella peelii	Murray River Cod	Fish	CR	Unknown	1996	Yes	Yes
Megalops atlanticus	Tarpon	Fish	VU	Unknown	2011	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Morone saxatilis	Striped Bass	Fish	LC	Unknown	2012	No	No
Mylopharyngodon piceus	Black Carp	Fish	DD	Unknown	2010	No	No
Myxocyprinus asiaticus	Chinese Sucker	Fish	NE	Unknown	NA	NA	No
Neoceratodus forsteri	Australian Lungfish	Fish	NE	Unknown	NA	NA	No
Oncorhynchus tshawytscha	Chinook Salmon	Fish	NE	Unknown	NA	NA	No
Pangasianodon gigas	Mekong Giant Catfish	Fish	CR	Decreasing	2011	No	Yes
Pangasianodon hypophthalmus	Striped Catfish	Fish	EN	Decreasing	2011	No	No
Pangasius pangasius	Pangas Catfish	Fish	LC	Decreasing	2009	No	No
Pangasius sanitwongsei	Giant Pangasius	Fish	CR	Decreasing	2007	No	No
Paratrygon ajereba	Manzana Ray	Fish	DD	Unknown	2004	Yes	No
Phractocephalus hemioliopterus	Redtail Catfish	Fish	NE	Unknown	NA	NA	No
Polydactylus macrochir	Grand Threadfin	Fish	NE	Unknown	NA	NA	No
Polyodon spathula	Paddlefish	Fish	VU	Unknown	2004	Yes	No
Potamotrygon brachyura	Giant Freshwater Stingray	Fish	DD	Unknown	2003	Yes	No
Potamotrygon motoro	Ocellate River Stingray	Fish	DD	Unknown	2005	Yes	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Pristis pristis	Largetooth Sawfish	Fish	CR	Decreasing	2013	No	No
Probarbus jullieni	Jullien's Golden Carp	Fish	EN	Decreasing	2011	No	No
Probarbus labeamajor	Thicklipped Barb	Fish	EN	Decreasing	2011	No	Yes
Protopterus aethiopicus	Marbled Lungfish	Fish	NE	Unknown	NA	NA	No
Psephurus gladius	Chinese Paddlefish	Fish	CR(PE)	Unknown	2009	No	Yes
Pseudoplatystoma corruscans	Spotted Sorubim	Fish	NE	Unknown	NA	NA	No
Pseudoplatystoma fasciatum	Barred Sorubim	Fish	NE	Unknown	NA	NA	No
Ptychocheilus lucius	Colorado Pikeminnow	Fish	VU	Stable	2012	No	Yes
Pylodictis olivaris	Flathead Catfish	Fish	LC	Stable	2012	No	No
Rita sacerdotum	Salween Rita	Fish	LC	Unknown	2009	No	No
Salminus brasiliensis	Dorado	Fish	NE	Unknown	NA	NA	No
Salmo marmoratus	Marble Trout	Fish	LC	Decreasing	2006	No	No
Salmo salar	Atlantic Salmon	Fish	LC	Unknown	1996	Yes	No
Salmo trutta	Brown Trout	Fish	LC	Unknown	2010	No	No
Salvelinus namaycush	Lake Trout	Fish	NE	Unknown	NA	NA	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Scaphirhynchus albus	Pallid Sturgeon	Fish	EN	Decreasing	2004	Yes	Yes
Sciades couma	Couma Sea Catfish	Fish	LC	Unknown	2009	No	No
Scomberomorus sinensis	Chinese Seerfish	Fish	DD	Unknown	2009	No	No
Silurus asotus	Amur Catfish	Fish	LC	Unknown	2010	No	No
Silurus glanis	Wels Catfish	Fish	LC	Unknown	2008	No	No
Silurus soldatovi	Soldatov's Catfish	Fish	NE	Unknown	NA	NA	No
Silurus meridionalis	Chinese Large-mouth Catfish	Fish	LC	Decreasing	2011	No	No
Sorubimichthys planiceps	Firewood Catfish	Fish	NE	Unknown	NA	NA	No
Stenodus nelma	Nelma	Fish	LC	Unknown	2008	No	No
Tor putitora	Putitor Mahseer	Fish	EN	Decreasing	2009	No	No
Tor tor	Tor Barb	Fish	NT	Decreasing	2009	No	No
Wallago attu	Wallago	Fish	NT	Decreasing	2010	No	No
Wallago leerii	Helicopter Catfish	Fish	NE	Unknown	NA	NA	No
Wallago micropogon		Fish	DD	Unknown	2011	No	No
Zungaro jahu	Manguruyu	Fish	NE	Unknown	NA	NA	Yes

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Zungaro zungaro	Guilded Catfish	Fish	NE	Unknown	NA	NA	No
Aonyx capensis	African Clawless Otter	Mammal	NT	Decreasing	2014	No	No
Aonyx congicus	Congo Clawless Otter	Mammal	NT	Decreasing	2014	No	No
Blastocerus dichotomus	Marsh Deer	Mammal	VU	Decreasing	2016	No	No
Bubalus arnee	Wild Water Buffalo	Mammal	EN	Decreasing	2008	No	No
Castor canadensis	American Beaver	Mammal	LC	Stable	2016	No	No
Castor fiber	Eurasian Beaver	Mammal	LC	Increasing	2016	No	No
Choeropsis liberiensis	Pygmy Hippopotamus	Mammal	EN	Decreasing	2015	No	No
Hippopotamus amphibius	Hippopotamus	Mammal	VU	Decreasing	2008	No	No
Hydrochoerus hydrochaeris	Capybara	Mammal	LC	Stable	2016	No	No
Inia araguaiaensis	Araguaian Boto	Mammal	NE	Unknown	NA	NA	Yes
Inia boliviensis	Bolivian River Dolphin	Mammal	NE	Unknown	NA	NA	Yes
Inia geoffrensis	Amazon River Dolphin	Mammal	DD	Unknown	2008	No	No
Kobus leche	Southern Lechwe	Mammal	LC	Stable	2008	No	No
Kobus megaceros	Nile Lechwe	Mammal	EN	Decreasing	2008	No	Yes

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Lipotes vexillifer	Baiji	Mammal	CR(PE)	Unknown	2008	No	Yes
Neophocaena asiaeorientalis ssp. *asiaeorientalis*	Yangtze Finless Porpoise	Mammal	CR	Decreasing	2012	No	Yes
Orcaella brevirostris	Irrawaddy Dolphin	Mammal	VU	Decreasing	2008	No	No
Phoca vitulina ssp. *mellonae*	Ungava Seal	Mammal	EN	Unknown	2015	No	No
Platanista gangetica ssp. *gangetica*	Ganges River Dolphin	Mammal	EN	Decreasing	2004	Yes	No
Platanista gangetica ssp. *minor*	Indus River Dolphin	Mammal	EN	Unknown	2004	Yes	Yes
Pteronura brasiliensis	Giant Otter	Mammal	EN	Decreasing	2014	No	No
Pusa caspica	Caspian Seal	Mammal	EN	Unknown	2015	No	Yes
Pusa hispida ssp. *ladogensis*	Ladoga Seal	Mammal	VU	Increasing	2015	No	Yes
Pusa hispida ssp. *saimensis*	Saimaa Seal	Mammal	EN	Increasing	2015	No	Yes
Pusa sibirica	Baikal Seal	Mammal	LC	Stable	2015	No	Yes
Sotalia fluviatilis	Tucuxi	Mammal	DD	Unknown	2010	No	Yes
Tapirus bairdii	Baird's Tapir	Mammal	EN	Decreasing	2014	No	No
Tragelaphus spekii	Sitatunga	Mammal	LC	Decreasing	2016	No	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Trichechus inunguis	Amazonian Manatee	Mammal	VU	Decreasing	2016	No	Yes
Trichechus manatus	American Manatee	Mammal	VU	Decreasing	2008	No	No
Trichechus senegalensis	African Manatee	Mammal	VU	Unknown	2015	No	No
Alligator mississippiensis	American Alligator	Reptile	LC	Unknown	1996	Yes	No
Alligator sinensis	Chinese Alligator	Reptile	CR	Unknown	1996	Yes	No
Amyda cartilaginea	Asiatic Softshell Turtle	Reptile	VU	Unknown	2000	Yes	No
Apalone ferox	Florida Softshell Turtle	Reptile	LC	Unknown	2010	No	Yes
Caiman crocodilus	Common Caiman	Reptile	LC	Unknown	1996	Yes	No
Caiman latirostris	Broad-snouted Caiman	Reptile	LC	Unknown	1996	Yes	No
Caiman yacare	Yacaré	Reptile	LC	Unknown	1996	Yes	No
Chitra chitra	Southeast Asian Narrow-headed Softshell Turtle	Reptile	CR	Unknown	2000	Yes	No
Chitra indica	Indian Narrow-headed Softshell Turtle	Reptile	EN	Unknown	2000	Yes	No
Chitra vandijki	Burmese Narrow-Headed	Reptile	NE	Unknown	NA	NA	Yes

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
	Softshell Turtle						
Crocodylus acutus	American Crocodile	Reptile	VU	Increasing	2009	No	No
Crocodylus intermedius	Orinoco Crocodile	Reptile	CR	Unknown	1996	Yes	Yes
Crocodylus johnsoni	Australian Freshwater Crocodile	Reptile	LC	Unknown	1996	Yes	No
Crocodylus mindorensis	Philippines Crocodile	Reptile	CR	Decreasing	2012	No	Yes
Crocodylus moreletii	Morelet's Crocodile	Reptile	LC	Stable	2009	No	Yes
Crocodylus niloticus	Nile Crocodile	Reptile	LC	Unknown	1996	Yes	No
Crocodylus novaeguineae	New Guinea Crocodile	Reptile	LC	Unknown	1996	Yes	Yes
Crocodylus palustris	Mugger	Reptile	VU	Stable	2009	No	No
Crocodylus porosus	Salt-Water Crocodile	Reptile	LC	Unknown	1996	Yes	No
Crocodylus rhombifer	Cuban Crocodile	Reptile	CR	Unknown	2008	No	Yes
Crocodylus siamensis	Siamese Crocodile	Reptile	CR	Decreasing	2012	No	No
Eunectes beniensis	Bolivian Anaconda	Reptile	LC	Unknown	2014	No	Yes
Eunectes deschauenseei	Dark Spotted Anaconda	Reptile	DD	Unknown	2009	No	No
Eunectes murinus	Anaconda	Reptile	NE	Unknown	NA	NA	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Eunectes notaeus	Yellow Anaconda	Reptile	NE	Unknown	NA	NA	Yes
Gavialis gangeticus	Gharial	Reptile	CR	Decreasing	2007	No	No
Macrochelys temminckii	Alligator Snapping Turtle	Reptile	VU	Unknown	1996	Yes	No
Mecistops cataphractus	Slender-snouted Crocodile	Reptile	CR	Decreasing	2013	No	No
Melanosuchus niger	Black Caiman	Reptile	LC	Unknown	2000	Yes	No
Nilssonia gangetica	Indian Softshell Turtle	Reptile	VU	Unknown	2000	Yes	No
Nilssonia leithii	Leith's Softshell Turtle	Reptile	VU	Unknown	2000	Yes	No
Nilssonia nigricans	Black Softshell Turtle	Reptile	EW	NA	2002	Yes	No
Orlitia borneensis	Bornean River Turtle	Reptile	EN	Unknown	2000	Yes	No
Osteolaemus osborni	Osborn's Dwarf Crocodile	Reptile	NE	Unknown	NA	NA	Yes
Osteolaemus tetraspis	African Dwarf Crocodile	Reptile	VU	Unknown	1996	Yes	No
Paleosuchus palpebrosus	Dwarf Caiman	Reptile	LC	Unknown	1996	Yes	No
Paleosuchus trigonatus	Smooth-fronted Caiman	Reptile	LC	Unknown	1996	Yes	No
Pelochelys bibroni	Asian Giant Softshell Turtle	Reptile	VU	Unknown	2000	Yes	Yes
Pelochelys cantorii	Cantor's Giant Softshell	Reptile	EN	Unknown	2000	Yes	No

Binomial name	Common name	Group	IUCN status	Population trend	Assessed year	Update required	Endemic species
Pelochelys signifera	Northern New Guinea Giant Softshell Turtle	Reptile	NE	Unknown	NA	NA	Yes
Podocnemis expansa	South American River Turtle	Reptile	LC	Unknown	1996	Yes	No
Rafetus swinhoei	Yangtze Giant Softshell Turtle	Reptile	CR	Unknown	2000	Yes	No
Tomistoma schlegelii	False Gharial	Reptile	VU	Decreasing	2011	No	No
Trionyx triunguis	African Softshell Turtle	Reptile	NE	Unknown	NA	NA	No

Table S2.2 Species without maps in the IUCN database* and references for their distribution information.

Binomial name	Common name	Distribution references
Acipenser baerii	Siberian Sturgeon	Ruban, 1997
Acipenser dabryanus	Yangtze Sturgeon	Wei, 2010a
Acipenser fulvescens	Lake Sturgeon	Fergus & Duckworth, 1997; NatureServe, 2010
Acipenser mikadoi	Sakhalin Sturgeon	Mugue, 2010; Shmigirilov et al., 2007
Acipenser schrenckii	Amur Sturgeon	Krykhtin & Svirskii, 1997; Ruban & Wei, 2010
Acipenser sinensis	Chinese Sturgeon	Zhuang et al., 2016
Anguilla reinhardtii	Speckled Longfin Eel	Atlas of Living Australia
*Arapaima agassizii***		Castello & Stewart, 2010
*Arapaima gigas***	Arapaima	Castello & Stewart, 2010
*Arapaima leptosoma***		Castello & Stewart, 2010
*Arapaima mapae***		Castello & Stewart, 2010
Aspiorhynchus laticeps	Big Head Schizothracin	Bain & Zhang, 2001; Froese and Pauly, 2017
Atractosteus spatula	Alligator gar	NatureServe, 2010
Brachyplatystoma capapretum		Froese & Pauly, 2017
Brachyplatystoma filamentosum	Piraiba	Froese & Pauly, 2017
Colossoma macropomum	Cachama	Froese & Pauly, 2017
Ctenopharyngodon idella	Grass Carp	Li & Fang, 1990
Eleutheronema tetradactylum	Fourfinger Threadfin	Froese & Pauly, 2017
Esox masquinongy	Muskellunge	NatureServe, 2010
Hoplias aimara	Wolf Fish	Froese & Pauly, 2017
Huso dauricus	Kaluga	Krykhtin & Svirskii, 1997

Binomial name	Common name	Distribution references
Hypophthalmichthys molitrix	Silver Carp	Wu et al., 1982
Labeo rohita	Rohu	Dahanukar, 2010
Lates calcarifer	Barramundi	Froese & Pauly, 2017
Lates japonicus	Japanese Lates	Froese & Pauly, 2017
Lota lota	Burbot	NatureServe, 2010; Froese and Pauly, 2017
Luciobarbus esocinus	Pike Barbel	Freyhof, 2014
Maccullochella ikei	Eastern Freshwater Cod	Fish of Australia
Maccullochella mariensis	Mary River Cod	Atlas of Living Australia
Maccullochella peelii	Murray River Cod	Atlas of Living Australia
Myxocyprinus asiaticus	Chinese Sucker	Zhang et al., 1999
Neoceratodus forsteri	Australian Lungfish	Encyclopedia of Life
Oncorhynchus tshawytscha	Chinook Salmon	Froese & Pauly, 2017
Phractocephalus hemioliopterus	Redtail Catfish	Froese & Pauly, 2017
Polydactylus macrochir	Grand Threadfin	Motomura et al., 2000; Froese & Pauly, 2017
Protopterus aethiopicus	Marbled Lungfish	Froese & Pauly, 2017
Psephurus gladius	Chinese Paddlefish	Wei, Q. 2010b
Pseudoplatystoma corruscans	Spotted Sorubim	Froese & Pauly, 2017
Pseudoplatystoma fasciatum	Barred Sorubim	Froese & Pauly, 2017
Rita sacerdotum	Salween Rita	Ng, 2010
Salminus brasiliensis	Dorado	Froese & Pauly, 2017
Salmo salar	Atlantic Salmon	Kottelat & Freyhof, 2007;NatureServe, 2010
Salvelinus namaycush	Lake Trout	Froese & Pauly, 2017; NatureServe,

Binomial name	Common name	Distribution references
		2010
Silurus soldatovi	Soldatov's Catfish	Froese & Pauly, 2017
Sorubimichthys planiceps	Firewood Catfish	Froese & Pauly, 2017
Tor putitora	Putitor Mahseer	Singh et al., 2009; Jha & Rayamajhi, 2010
Tor tor	Tor Barb	Desai, 2003
Wallago leerii	Helicopter Catfish	Froese & Pauly, 2017
Zungaro jahu	Manguruyu	Froese & Pauly, 2017
Zungaro zungaro	Guilded Catfish	Froese & Pauly, 2017
Eunectes notaeus	Yellow Anaconda	Santos et al., 2013
Osteolaemus osborni	Osborn's Dwarf Crocodile	Eaton, 2010

*****Including maps compiled by Freshwater Unit, IUCN, and from other IUCN related sources (e.g. Indo-Burma freshwater assessment, IUCN/Species Survival Commission Specialist Groups)

**Covered by *Arapaima* spp. complex map.

Table S2.3 Number of species and threatened species of freshwater megafauna, and mean value of IBTI and THPI in a selection of large river basins (HydroBASINS level 3).

Basin	Number of species	Number of threatened species	Mean value of IBTI	Mean value of THPI
Amazon	35	6	0.37	0.36
Congo	23	7	0.49	0.88
Orinoco	23	5	0.49	0.61
Mekong	22	15	0.76	0.71
Ganges	22	13	0.82	1.65
Mississippi	19	4	0.90	2.32
Niger	16	5	0.73	4.19
Yangtze	15	6	0.85	1.89
Paraná	15	2	0.66	2.44
Nile	13	2	0.65	2.06
Volga	12	7	0.80	-2.55
Indus	11	4	0.81	4.45
Amur	10	3	0.59	3.22
Danube	10	5	0.92	0.47

Table S2.4 Summary of the IBTI and THPI values of main basins (level 3 HydroBASINS). Sub-catchments with an IBTI value >0.75 were considered to have high levels of human pressure while those with a mean THPI value >0 were considered as having increased human pressure.

	Min.	Max.	Mean	$Q_{0.25}$	$Q_{0.5}$	$Q_{0.75}$
IBTI	0.06	1.00	0.56	0.37	0.61	0.79
THPI	-21.30	12.95	0.98	-0.30	0.61	2.63

Table S2.5 Richness of endemic freshwater megafauna species by basin

Basin	Number of basin-endemic species	Basin-endemic species
Amazon	5	*Eunectes beniensis* *Inia boliviensis* *Sotalia fluviatilis* *Trichechus inunguis** *Brachyplatystoma capapretum*
Congo	5	*Osteolaemus osborni* *Chrysichthys cranchii* *Hydrocynus goliath* *Chrysichthys grandis* *Lates angustifrons**
Mekong	4	*Aaptosyax grypus** *Luciocyprinus striolatus** *Pangasianodon gigas** *Probarbus labeamajor**
Yangtze	4	*Lipotes vexillifer** *Neophocaena asiaeorientalis* ssp. *asiaeorientalis** *Acipenser dabryanus** *Psephurus gladius**

* species considered as threatened by IUCN Red List

Table S2.6 Comparison of IUCN Red List assessments on freshwater and terrestrial megafauna (Ripple et al., 2016). Species are considered as with insufficient assessment if they are listed as Data Deficient or Not Evaluated on IUCN Red List, or their assessments were conducted ten years ago.

System	Number of species	Species assessed by IUCN (%)	Insufficient assessment (%)	Unknown population trends (%)
Freshwater	207	76	43	55
Terrestrial	101	100	0	4

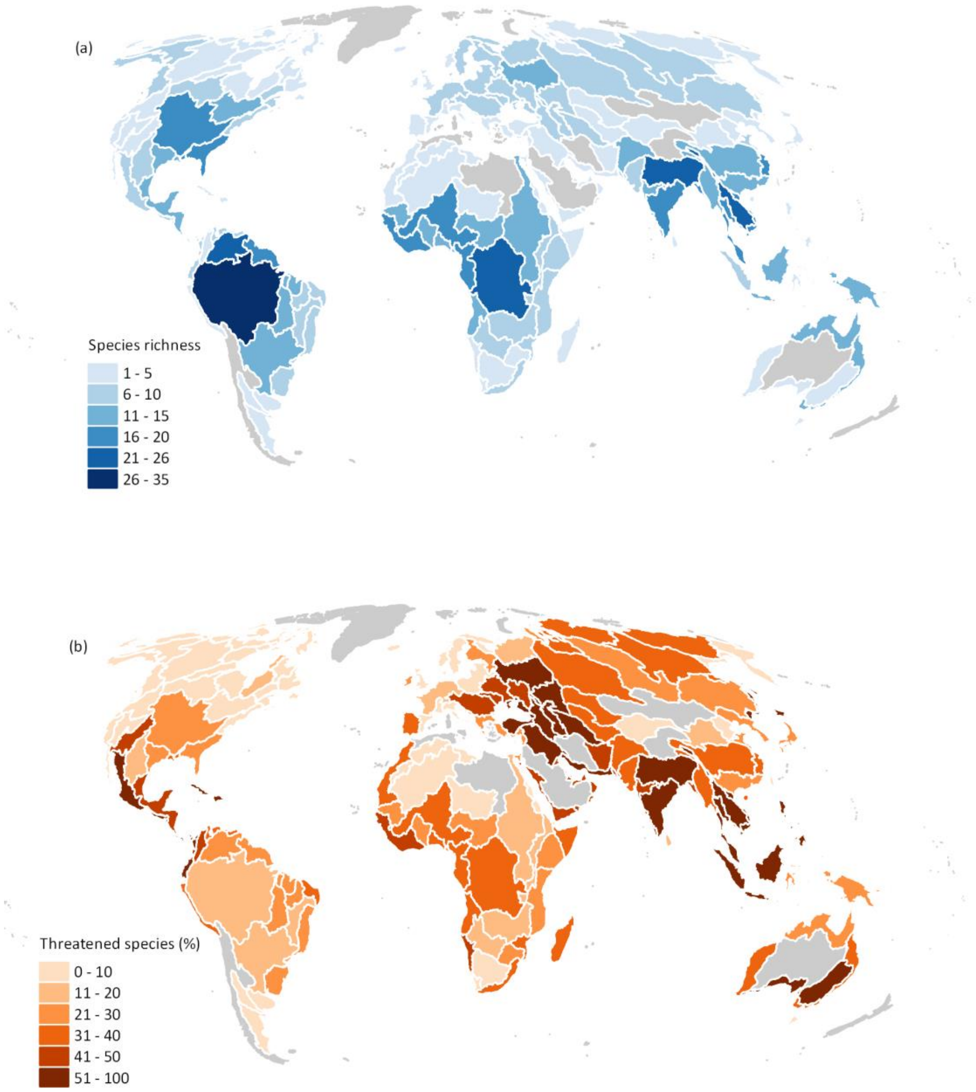

Fig. S2.1 (a) Overall species richness and (b) proportion of threatened freshwater megafauna within each main basin (HydroBASINS level 3).

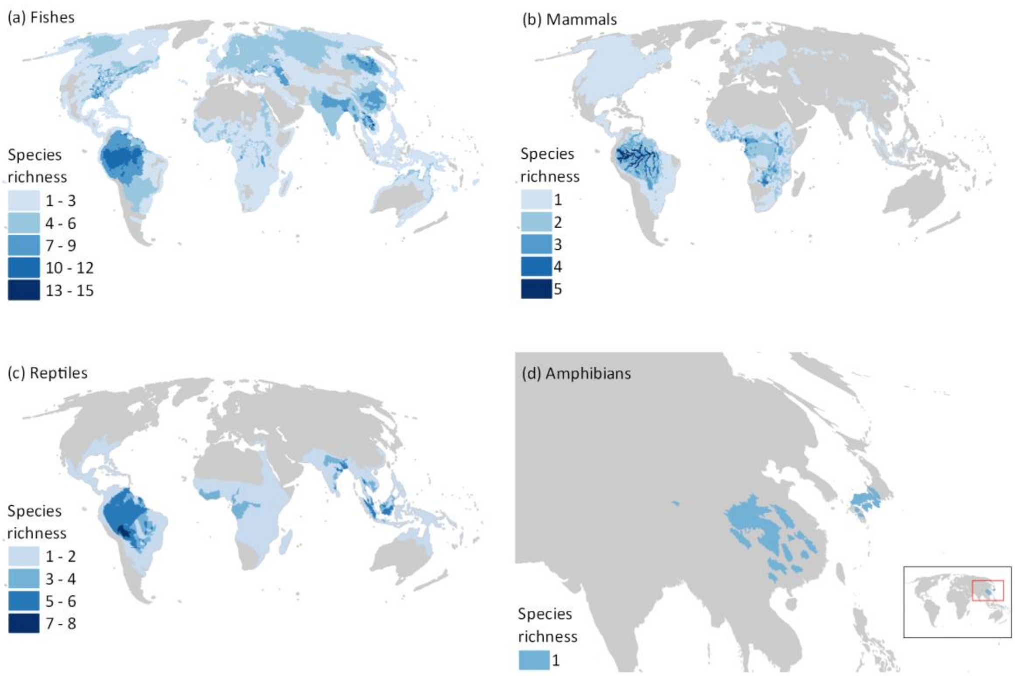

Fig S2.2 Distributions of freshwater megafauna in different taxonomic groups.

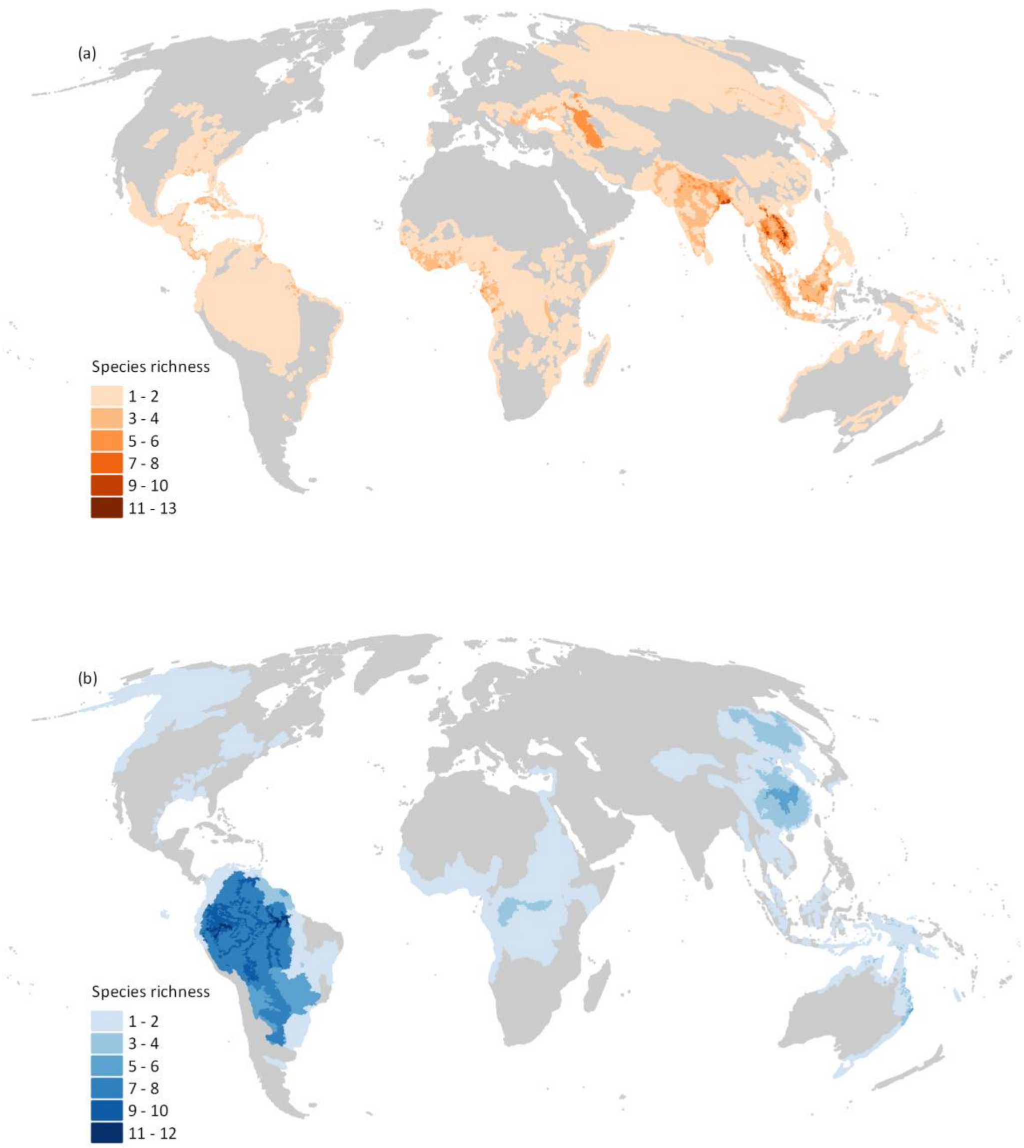

Fig. S2.3 Species richness of freshwater megafauna listed as (a) threatened, and (b) Data Deficient or Not Evaluated according to the IUCN Red List.

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Appendix C: Supporting information for Chapter 3

Methods

Collection of publications focused on megafauna

The ISI Web of Knowledge database was searched using the terms ‘TOPIC: (megafauna) OR TOPIC: (megafaunal)’ in order to identify publications focused on megafauna. The search returned 1511 records in total. These records were first checked for suitability by reading their abstracts. Articles focusing on pre-historical megafauna and megabenthos on the sea floor were excluded, leaving a total of 231 records for further review. The year of publication for each article was recorded and each article was assigned to one of four “ecosystem type” categories: marine, terrestrial, freshwater and, where an ecosystem type was not obvious from an article’s content, in general.

Conservation status of freshwater megafauna

Up to date, there is no official definition of freshwater megafauna. We define freshwater megafauna as all animals which could gain a body mass of at least 30 kg and spend an essential part of their life history in freshwater or brackish ecosystems. Based on the 30-kg threshold, we compiled a list of freshwater megafauna species, including 131 fishes, 44 reptiles, 31 mammals and 2 amphibians. We assessed each species based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species^{TM} list. The species have been evaluated and assigned to one of the following categories (IUCN, 2015): Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), Extinct (EX) and Data Deficient (DD). We calculated the proportion of threatened (Critically Endangered, Endangered or Vulnerable) species as follows: % threatened = (CR + EN + VU) / (total assessed - EX - EW - DD). We assumed that Data Deficient species have the same proportional threat status as the species for which sufficient data are available.

Threats on freshwater megafauna

We collected and reviewed threat information on the freshwater megafauna species based on published papers, scientific reports and data from the IUCN Species Information Service. Threat was grouped into five major categories: overexploitation, dam construction, habitat degradation, pollution and species invasion.

Dam construction data

The data of all hydropower dams in the Amazon, Congo and Mekong River basins were extracted from Winemiller et al (2016). We determined the number and the location of dams in each basin using QGIS (QGIS Development Team, 2015). For the Amazon River basin, the dam data in the Tocantins River basin were not included as it is not a part of the Amazon River basin according to HydroBASINS (Lehner & Grill, 2013), which we used for catchment delineation. The data of operational/under construction dams in the Ganges River basin were collected from the GranD database V1.1(Lehner *et al*., 2013). For the proposed/planned dams, data were provided by co-authors (Zarfl et al., 2015 and unpublished data). All figures were plotted with R (R Core Team, 2016).

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Appendix D: Supporting information for Chapter 4

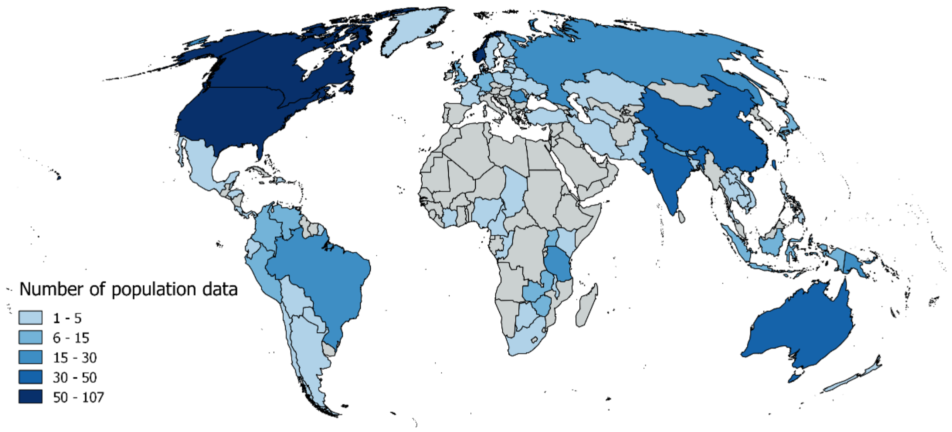

Fig. S4.1 Distributions of the population data (i.e. number of time series) of freshwater megafauna

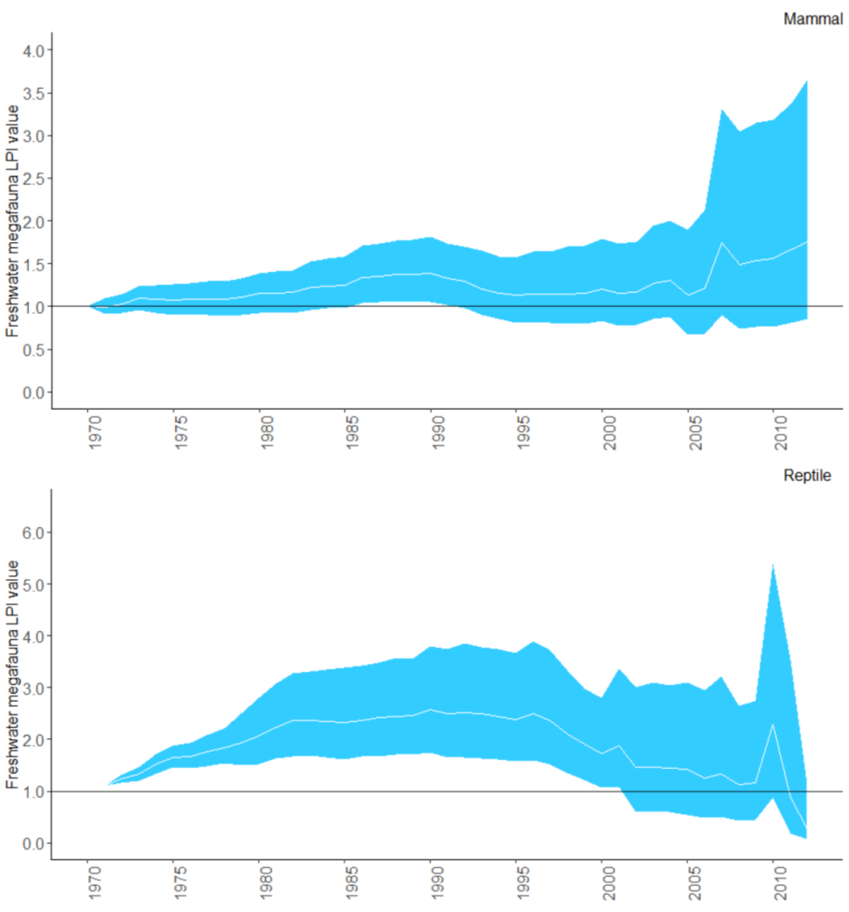

Fig. S4.2 Population change of mega-mammal (22 species; 118 time series) and mega-reptile (21 sepcies; 114 time series) species from 1970 to 2012. The value of Living Planet index (LPI) was set to 1 in the reference year 1970.

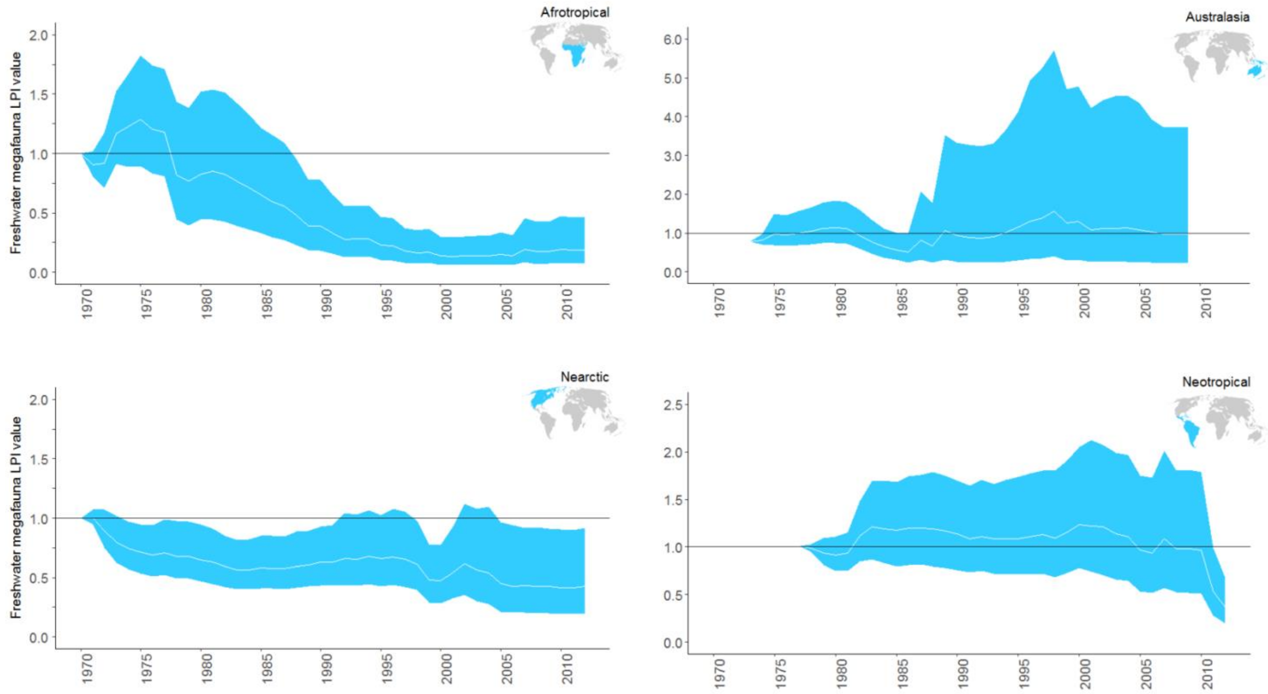

Fig. S4.3 Population change of freshwater megafauna in Afrotropical (13 species; 51 time series), Australasia (10 species; 69 time series), Nearctic (29 species; 152 time series) and Neotropical (27 species; 65 time series) realms. The value of Living Planet index (LPI) was set to 1 in the reference year 1970.

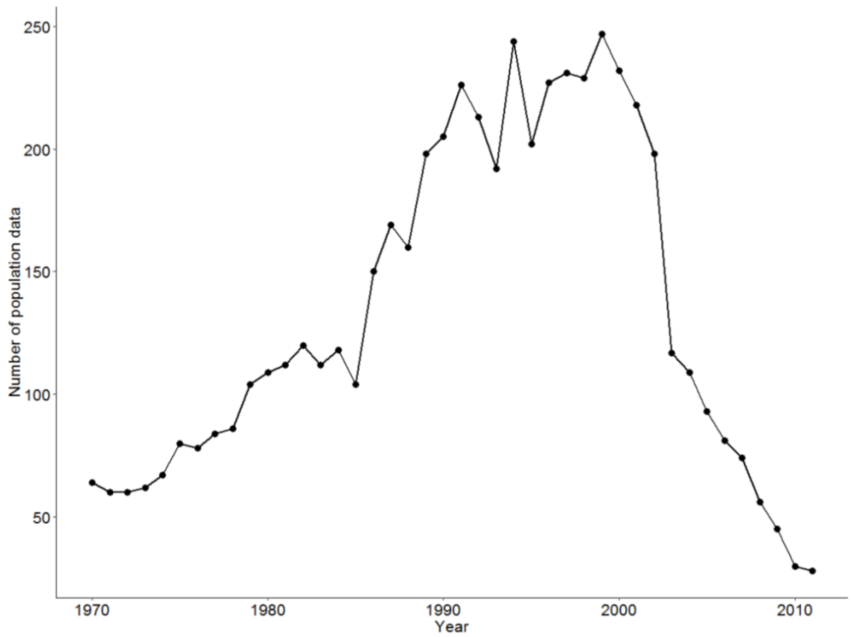

Fig. S4.4 Change in number of time series on population abundance.

Appendix E: Supporting information for Chapter 5

Table S5.1 Collected traits for FW megafauna species. Traits marked with an asterisk (*) are not included in the analysis due to data unavailability.

Trait	Unit of measurement/category
Maximum body length	cm
Maximum body mass	kg
Lifespan	year
Generation length*	year
Migration	migratory; non- migratory
Age at maturity (female)	year
Spawning/postnatal periodicity*	year
Fecundity (average number of offspring)	very low: 1-5; low: 6-20; medium: 21-200; high:201-1000; very high: >1000
Offspring type	eggs; viviparous
Hatching time* (time of hatching /gestation)	day
Habitat	aquatic; semi-aquatic
Feeding habit	herbivorous; omnivorous; carnivorous

Table S5.2 Species which were predicted as threatened by GLMM models under mild or strict scenarios. The thresholds of 0.3 and 0.7 were used for the mild and strict scenarios, respectively. T stands for threatened while NT stands for threatened.

Species name	Taxon	Scenarios with trait-based model		Scenarios with trait- and threat-based model	
		mild	strict	mild	strict
Anguilla reinhardtii	Fish	NT	T	NT	NT
Aspiorhynchus laticeps	Fish	T	T	T	T
Atractosteus spatula	Fish	NT	NT	NT	T
Elopichthys bambusa	Fish	T	T	T	T
Hypophthalmichthys nobilis	Fish	NT	T	NT	T
Lates calcarifer	Fish	NT	T	NT	NT
Maccullochella mariensis	Fish	NT	NT	NT	T
Mylopharyngodon piceus	Fish	NT	T	NT	T
Myxocyprinus asiaticus	Fish	NT	T	NT	T
Neoceratodus forsteri	Fish	NT	T	NT	T
Paratrygon ajereba	Fish	T	T	NT	T
Phractocephalus hemioliopterus	Fish	NT	T	NT	NT
Potamotrygon brachyura	Fish	T	T	T	T
Potamotrygon motoro	Fish	NT	T	NT	T
Salvelinus namaycush	Fish	NT	T	NT	T
Zungaro zungaro	Fish	NT	T	NT	NT
Inia araguaiaensis	Mammal	T	T	T	T
Inia boliviensis	Mammal	T	T	T	T
Inia geoffrensis	Mammal	T	T	T	T
Sotalia fluviatilis	Mammal	T	T	T	T
Chitra vandijki	Reptile	T	T	T	T
Eunectes deschauenseei	Reptile	NT	T	NT	NT
Eunectes murinus	Reptile	NT	T	NT	T
Eunectes notaeus	Reptile	NT	NT	NT	T
Osteolaemus osborni	Reptile	T	T	NT	T
Pelochelys signifera	Reptile	T	T	NT	T

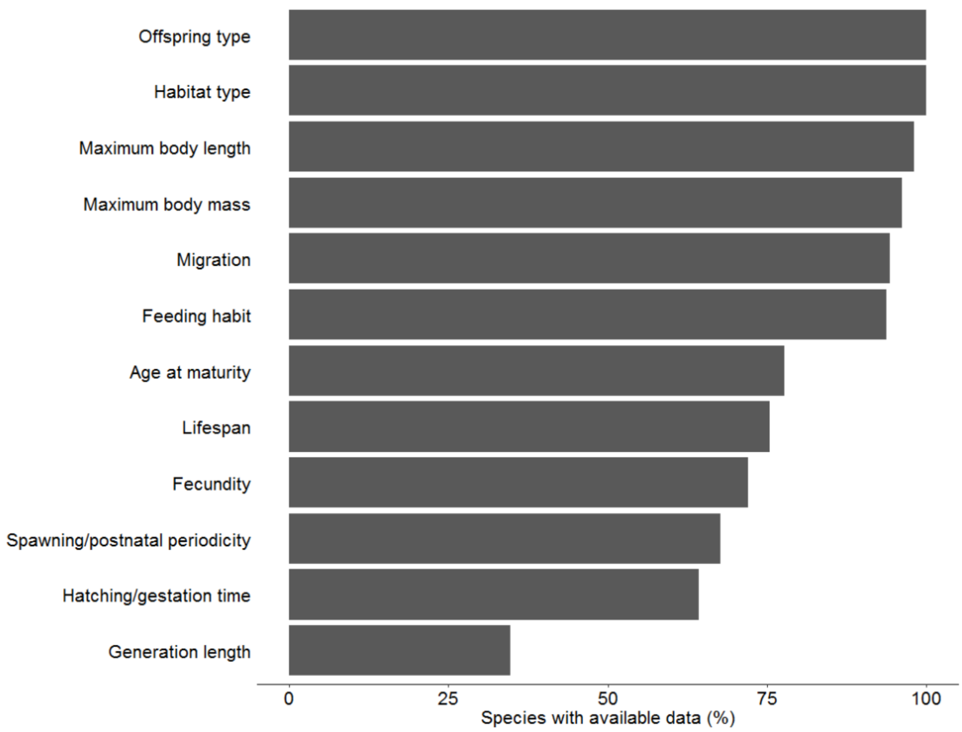

Fig. S5.1 Data availability of 12 life-history traits for freshwater megafauna species

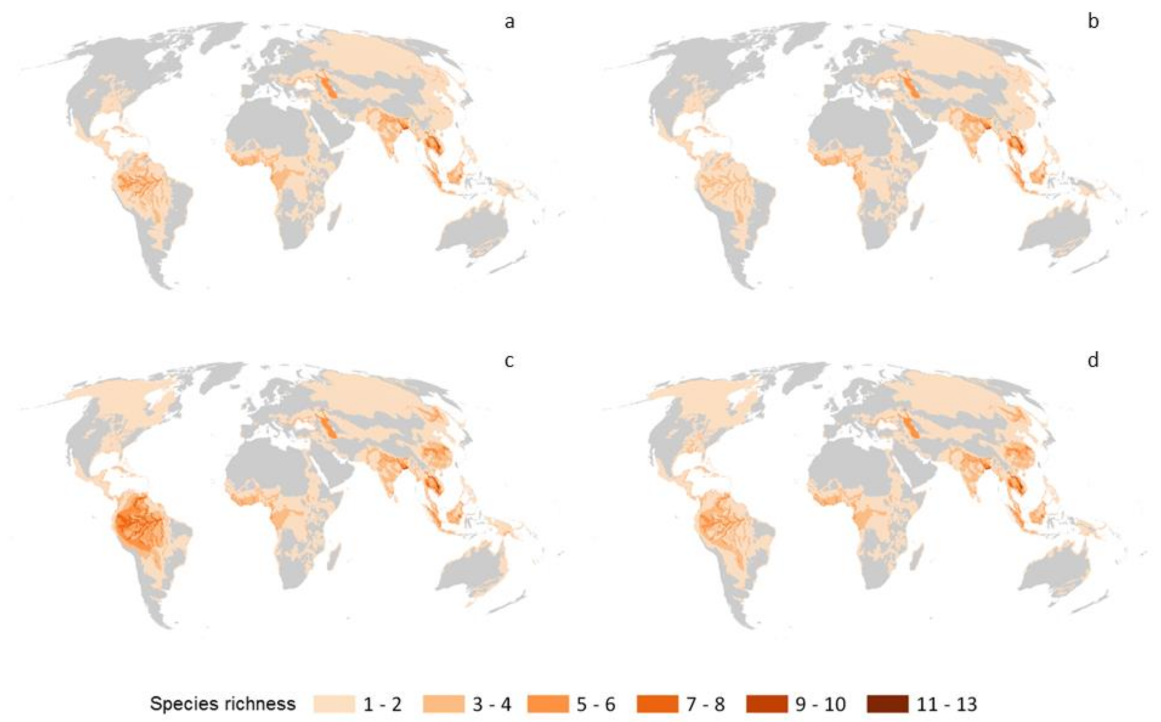

Fig. S5.2 Species richness of freshwater megafauna considered as threatened according to the IUCN Red List and model predictions: (a) only considering traits and (b) considering both traits and threats under the mild scenario; (c) only considering traits and (d) considering both traits and threats under the strict scenario.

Appendix F: Supporting information for Chapter 6

Table S6.1 Freshwater megafauna species falling under the definition (i.e. mammals and fishes ≥100 kg and amphibians, birds and reptiles ≥40 kg) by Ripple et al. (2019). Species marked with* are not included in Ripple et al. (2019).

Binomial name	**Body mass (kg)**	**Reference for body mass**
Acipenser baerii	210	Kottelat and Freyhof (2007)
Acipenser fulvescens	125	Carlander (1969)
Acipenser gueldenstaedtii	115	Birstein (1993)
Acipenser medirostris	159	Peterson *et al.* (1999)
Acipenser oxyrinchus	368	Mangin (1964)
Acipenser schrenckii	190	Krykhtin and Svirskii (1997)
Acipenser sinensis	600	Zhang (2001)
Acipenser sturio	400	Muus (1968)
Acipenser transmontanus	816	Lamb (1986)
Alligator mississippiensis	473	Lobaina (2014)
*Alligator sinensis**	42	(Thorbjarnarson *et al.*, 2001)
*Amyda cartilaginea**	140	(Auliya *et al.*, 2016)
Andrias davidianus	50	Wang *et al.* (2004)
*Andrias japonicus**	45	(Browne *et al.*, 2014)
*Apalone ferox**	43	(Meylan *et al.*, 2002)
Arabibarbus grypus	100	Borkenhagen (2014)
*Arapaima agassizii**	200	Castello and Stewart (2010)
Arapaima gigas	200	Castello and Stewart (2010)
*Arapaima leptosoma**	200	Castello and Stewart (2010)
*Arapaima mapae**	200	Castello and Stewart (2010)
Atractosteus spatula	137	Stone (2007)
*Bagarius yarrelli**	105	Winemiller *et al.* (2015)
Blastocerus dichotomus	102.5	Ripple *et al.* (2019)
Brachyplatystoma filamentosum	200	Boujard (1997)

Binomial name	**Body mass (kg)**	**Reference for body mass**
*Bathybagrus grandis**	190	Winemiller *et al.* (2015)
Bubalus arnee	827	Ripple *et al.* (2019)
*Caiman crocodilus**	58	Ojasti (1996)
*Caiman latirostris**	62	Ferraz *et al.* (2005)
*Caiman yacare**	58	Ojasti (1996)
Carcharhinus leucas	238	Wintner *et al.* (2002)
Catlocarpio siamensis	300	Roberts and Warren (1994)
*Chitra chitra**	202	Kitimasak *et al.* (2005)
Chitra indica	57	Das and Singh (2014)
*Chitra vandijki**	100	Platt *et al.* (2009)
Choeropsis liberiensis	275	Boisserie (2007)
Chrysichthys cranchii	135	Risch and Bagridae (1986)
Crocodylus acutus	173	Lobaina (2014)
Crocodylus intermedius	380	Lobaina (2014)
*Crocodylus johnsoni**	108	O'Gorman and Hone (2012)
*Crocodylus mindorensis**	75	(O'Gorman & Hone, 2012)
*Crocodylus moreletii**	58	Lobaina (2014)
Crocodylus niloticus	200	Hutton (1987)
*Crocodylus novaeguineae**	294	(O'Gorman & Hone, 2012)
Crocodylus palustris	200	Lobaina (2014)
Crocodylus porosus	2000	Ogamba and Abowei (2012)
Crocodylus rhombifer	215	Lobaina (2014)
Crocodylus siamensis	50	Daltry *et al.* (2003)
Eleutheronema tetradactylum	145	Grant (1978)
Eunectes murinus	156	O'Gorman and Hone (2012)
*Eunectes notaeus**	50	O'Gorman and Hone (2012)
Gavialis gangeticus	160	Stevenson and Whitaker (2010)

Binomial name	**Body mass (kg)**	**Reference for body mass**
Hippopotamus amphibius	4500	Coughlin and Fish (2009)
Hucho taimen	105	Kottelat and Freyhof (2007)F
Huso dauricus	1000	Krykhtin and Svirskii (1997)
Huso huso	3200	Kottelat and Freyhof (2007)
*Inia araguaiaensis**	207	Da Silva (2009)
*Inia boliviensis**	207	Da Silva (2009)
*Inia geoffrensis**	207	Da Silva (2009)
*Kobus leche**	128	Estes (1991)
*Kobus megaceros**	113	Bercovitch *et al.* (2009)
Lates angustifrons	100	Stone (2007)
Lates niloticus	200	Ribbink (1987)
*Lipotes vexillifer**	237	Zhou *et al.* (1977); Zhou (1986)
Luciobarbus esocinus	140	Robins (1991)
*Luciocyprinus striolatus**	100	(Baird *et al.*, 1999)
Maccullochella peelii	113	Rowland (1989)
Macrochelys temminckii	90	Jensen and Birkhead (2003)
Mecistops cataphractus	230	Lobaina (2014)
Melanosuchus niger	400	Da Silveira *et al.* (2010); Thorbjarnarson (2010); Cardoso *et al.* (2012)
*Nilssonia nigricans**	51	(O'Gorman & Hone, 2012)
Orcaella brevirostris	133	Arnold and Heinsohn (1996)
*Orlitia borneensis**	50	Halliday and Adler (2002)
*Osteolaemus osborni**	80	Lobaina (2014)
*Osteolaemus tetraspis**	80	Lobaina (2014)
Pangasianodon gigas	350	Kottelat (2001)
Pangasius pangasius	125	Ripple *et al.* (2019)
Pangasius sanitwongsei	300	Roberts and Vidthayanon (1991)
*Pelochelys bibroni**	120	Bonin *et al.* (2006)

Binomial name	**Body mass (kg)**	**Reference for body mass**
*Pelochelys cantorii**	43	Das (2008)
Phoca vitulina spp. *Mellonae**	150	Lowry (2016)
Platanista gangetica ssp. *gangetica**	108	Jefferson *et al.* (1994)
Platanista gangetica ssp. *minor**	110	Waqas *et al.* (2012)
Podocnemis expansa	90	Clauson *et al.* (1989)
Potamotrygon brachyura	120	Franco *et al.* (2011)
Pristis pristis	600	Stehman (1981)
Pristis pectinata	350	Stehman (1981)
Psephurus gladius	300	Mims and Georgi (1993)
Pseudoplatystoma corruscans	100	Tavares (1997)
Pusa hispida ssp. *saimensis**	124	(Niemi *et al.*, 2012)
*Pusa sibirica**	130	(Goodman, 2016)
*Rafetus swinhoei**	115	Jian *et al.* (2013)
Scaphirhynchus albus	130	Rochard *et al.* (1991)
Scomberomorus sinensis	131	Collette *et al.* (2011)
Silurus glanis	306	Frimodt (1995)
Tapirus bairdii	300	(Ripple *et al.*, 2019)
Tomistoma schlegelii	210	Lobaina (2014)
*Tragelaphus spekii**	125	Estes (1991)
Trichechus inunguis	480	Amaral *et al.* (2010)
Trichechus manatus	1500	Spellman (2014)
Trichechus senegalensis	500	Dodman *et al.* (2012)
*Trionyx triunguis**	45	Rozner and Shaines (2010)
*Urogymnus dalyensis**	100	Zeb Hogan (personal communication)
*Urogymnus polylepis**	600	Winemiller *et al.* (2015)
*Zungaro jahu**	150	(Agostinho *et al.*, 2003)

Table S6.2 Terrestrial megafauna species falling under the definition (i.e. mammals and fishes ≥100 kg and amphibians, birds and reptiles ≥40 kg) by Ripple et al. (2019). The body mass data were derived from Ripple et al., (2016). Species marked with* are not included in Ripple et al. (2019).

Binomial name	**Body mass (kg)**
Panthera tigris	161
Panthera leo	156
Ursus arctos	299
Ailuropoda melanoleuca	134
Ursus americanus	111
Tremarctos ornatus	105
Ursus thibetanus	104
Melursus ursinus	102
Helarctos malayanus	46
Bubalus arnee	950
Bos gaurus	825
Bos sauveli	791
Bison bonasus	676
Bos mutus	650
*Tragelaphus derbianus**	646
Bos javanicus	636
Bison bison	625
Syncerus caffer	593
Tragelaphus oryx	563
Ovibos moschatus	313
Budorcas taxicolor	295
Tragelaphus eurycerus	271
Hippotragus equinus	264
Bubalus depressicornis	257
Bubalus mindorensis	254
Hippotragus niger	236
Tragelaphus buxtoni	215
Tragelaphus strepsiceros	206
Kobus ellipsiprymnus	204
Oryx beisa	201
Oryx dammah	200
Connochaetes taurinus	199

Oryx gazella	188
Bubalus quarlesi	182
Boselaphus tragocamelus	182
Alcelaphus buselaphus	161
Connochaetes gnou	157
Damaliscus lunatus	136
*Capra sibirica**	130
Ovis ammon	114
*Capricornis sumatraensis**	111
*Capra walie**	100
Camelus ferus	555
*Lama guanicoe**	128
Alces americanus	541
Alces alces	462
Cervus elaphus	241
Rusa unicolor	178
Rucervus duvaucelii	171
Elaphurus davidianus	166
Przewalskium albirostris	162
Blastocerus dichotomus	113
Rangifer tarandus	109
Loxodonta africana	3825
Elephas maximus	3270
Equus grevyi	408
Equus quagga	400
Equus zebra	282
Equus kiang	281
Equus africanus	275
Equus ferus	250
Equus hemionus	235
Giraffa camelopardalis	965
Okapia johnstoni	230
Hippopotamus amphibius	1536
Choeropsis liberiensis	235
Gorilla beringei	149
Gorilla gorilla	113

Ceratotherium simum	2286
Rhinoceros unicornis	1844
Rhinoceros sondaicus	1750
Dicerorhinus sumatrensis	1046
Diceros bicornis	996
Hylochoerus meinertzhageni	198
Sus cebifrons	191
Sus oliveri	191
Sus philippensis	191
Sus barbatus	136
Sus ahoenobarbus	136
Tapirus indicus	311
Tapirus bairdii	294
Tapirus terrestris	169
Tapirus pinchaque	157

Table S6.3 Marine megafauna species falling under the definition (i.e. mammals and fishes ≥100 kg and amphibians, birds and reptiles ≥40 kg) by Ripple et al. (2019). The body mass data were derived from Estes et al., (2016). Species marked with* are not included in Ripple et al. (2019).

Species name	**Body mass (kg)**
*Achoerodus gouldii**	121
Acipenser baerii	210
Acipenser fulvescens	125
Acipenser gueldenstaedtii	115
Acipenser medirostris	159
Acipenser oxyrinchus	333
Acipenser schrenckii	190
Acipenser sinensis	600
Acipenser sturio	400
Acipenser transmontanus	816
Aetobatus narinari	230
Aetobatus ocellatus	200
Alopias superciliosus	363
Alopias vulpinus	348
*Aptenodytes forsteri**	45
*Arctocephalus australis**	200
*Arctocephalus forsteri**	250
*Arctocephalus gazella**	215
*Arctocephalus philippii**	140
Arctocephalus pusillus	360
Arctocephalus townsendi	160
*Arctocephalus tropicalis**	165
Argyrosomus regius	103
Atractosteus spatula	137
Bahaba taipingensis	100
Balaena mysticetus	100000
Balaenoptera acutorostrata	10000
Balaenoptera bonaerensis	10400
Balaenoptera borealis	28000
Balaenoptera edeni	25000
Balaenoptera musculus	180000
Balaenoptera physalus	74000
Berardius arnuxii	14000
Berardius bairdii	14000

Brachyplatystoma filamentosum	200
*Callorhinus ursinus**	275
Caperea marginata	3500
Carcharhinus albimarginatus	162
Carcharhinus altimus	167
Carcharhinus brachyurus	304
Carcharhinus falciformis	346
Carcharhinus leucas	316
Carcharhinus limbatus	122
Carcharhinus longimanus	167
Carcharhinus obscurus	346
Carcharhinus plumbeus	117
Carcharias taurus	158
Carcharodon carcharias	2114
Caretta caretta	450
Cetorhinus maximus	4000
Cheilinus undulatus	191
Chelonia mydas	395
Conger conger	110
Cystophora cristata	410
Dasyatis americana	135
Dasyatis centroura	300
Dasyatis thetidis	214
Delphinapterus leucas	1900
*Delphinus capensis**	235
*Delphinus delphis**	136
Dermochelys coriacea	650
Dugong dugong	1000
Eleutheronema tetradactylum	145
Epinephelus itajara	455
Epinephelus lanceolatus	400
Epinephelus malabaricus	150
Epinephelus tukula	110
Eretmochelys imbricata	127
Erignathus barbatus	430
Eschrichtius robustus	36000
Eubalaena australis	80000
Eubalaena glacialis	70000

Eubalaena japonica	80000
Eumetopias jubatus	1120
*Eusphyra blochii**	325
Feresa attenuata	225
Galeocerdo cuvier	807
Ginglymostoma cirratum	109
Globicephala macrorhynchus	3000
Globicephala melas	3500
Grampus griseus	500
Gymnosarda unicolor	131
Halichoerus grypus	310
Hexanchus griseus	590
*Himantura polylepis**	600
Himantura uarnak	120
Hippoglossus hippoglossus	320
Hippoglossus stenolepis	363
*Histriophoca fasciata**	100
Hucho taimen	105
Huso dauricus	1000
Huso huso	3200
Hydrodamalis gigas	11196
Hydrurga leptonyx	600
Hyperoodon ampullatus	7500
Hyperoodon planifrons	7500
Hyporthodus mystacinus	107
Hyporthodus nigritus	198
Indopacetus pacificus	7500
Istiompax indica	750
Istiophorus platypterus	100
Isurus oxyrinchus	505
Kajikia audax	440
Kogia breviceps	400
Kogia sima	250
Lagenodelphis hosei	200
Lagenorhynchus acutus	230
Lagenorhynchus albirostris	354
Lagenorhynchus australis	115
*Lagenorhynchus cruciger**	120

Lagenorhynchus obliquidens	200
*Lagenorhynchus obscurus**	100
Lamna ditropis	175
Lamna nasus	230
Lampris guttatus	270
Lepidochelys kempii	50
Lepidochelys olivacea	50
Leptonychotes weddellii	600
Lissodelphis peronii	100
*Lithognathus lithognathus**	141
Lobodon carcinophagus	300
Luvarus imperialis	150
Makaira mazara	170
Makaira nigricans	636
*Manta birostris**	3000
Masturus lanceolatus	2000
Megachasma pelagios	1327
Megalops atlanticus	161
Megaptera novaeangliae	36000
Mesoplodon bahamondi	1000
Mesoplodon bidens	1300
Mesoplodon bowdoini	3000
Mesoplodon carlhubbsi	1500
Mesoplodon densirostris	1000
Mesoplodon europaeus	1200
Mesoplodon gingkodens	1000
Mesoplodon grayi	1100
Mesoplodon hectori	900
Mesoplodon layardii	3000
Mesoplodon mirus	1400
Mesoplodon perrini	1200
Mesoplodon peruvianus	8000
Mesoplodon stejnegeri	1600
Mirounga angustirostris	4000
Mirounga leonina	4000
Mobula tarapacana	350
Mola mola	2300
Monachus monachus	400

Monachus schauinslandi	270
*Monachus tropicalis**	200
Monodon monoceros	1600
Mycteroperca bonaci	100
Natator depressus	84
Negaprion acutidens	461
Negaprion brevirostris	183
Neophoca cinerea	300
Notorynchus cepedianus	107
Odobenus rosmarus	1500
Odontaspis ferox	289
Ommatophoca rossi	250
Orcaella brevirostris	250
Orcaella heinsohni	200
Orcinus orca	10000
Otaria flavescens	350
Pagophilus groenlandica	190
Pangasius pangasius	195
Peponocephala electra	200
*Phoca larga**	100
*Phoca vitulina**	135
Phocarctos hookeri	400
*Phocoena spinipinnis**	105
Phocoenoides dalli	220
Physeter macrocephalus	41000
Polyprion americanus	100
Polyprion oxygeneios	100
Prionace glauca	205
Pristis microdon	600
Pristis pectinata	350
Pristis perotteti	591
Pseudorca crassidens	2200
Pteromylaeus bovinus	116
*Pusa hispida**	140
Regalecus glesne	272
Rhina ancylostoma	135
Rhincodon typus	34000
Rhynchobatus djiddensis	227

Silurus glanis	306
Somniosus microcephalus	775
Somniosus pacificus	701
*Sotalia guianensis**	100
Sousa chinensis	230
Sousa teuszii	284
Sphyrna lewini	152
Sphyrna mokarran	449
Sphyrna zygaena	400
Stenella attenuata	120
Stenella coeruleoalba	150
*Stenella frontalis**	140
Steno bredanensis	150
Stereolepis gigas	255
Taeniurops meyeni	150
Tasmacetus shepherdi	3150
Thunnus albacares	200
Thunnus maccoyii	260
Thunnus obesus	210
Thunnus orientalis	450
Thunnus thynnus	684
*Thyrsitoides marleyi**	302
Totoaba macdonaldi	100
Trichechus manatus	1655
Trichechus senegalensis	360
Tursiops aduncus	230
Tursiops truncatus	500
Ursus maritimus	100
Xiphias gladius	650
Zalophus californicus	390
Zalophus japonicus	560
Zalophus wollebaeki	250
Ziphius cavirostris	2500

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Appendix G: Freshwater megafauna: Flagships for freshwater biodiversity under threat

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Abstract:

Freshwater biodiversity is highly threatened and is decreasing more rapidly than its terrestrial or marine counterparts; yet freshwaters receive less attention and conservation investment than other ecosystems. The diverse group of freshwater megafauna, including iconic species such as sturgeons, river dolphins and turtles, could, if promoted, provide a valuable tool to raise awareness and funding for conservation. We found that freshwater megafauna inhabit every continent except Antarctica, with South America, Central Africa, South and Southeast Asia being particularly species-rich. Freshwater megafauna co-occur with up to 93% of mapped overall freshwater biodiversity. Fifty-eight percent of the 132 megafauna species included in the study are threatened, with 84% of their collective range falling outside of protected areas. Of all threatened freshwater species, 83% are found within the megafauna range, revealing the megafauna´s capacity as flagship and umbrella species for fostering freshwater conservation.

Freshwater ecosystems cover less than one percent of the planet, yet they are among the most diverse and dynamic systems globally (Strayer & Dudgeon, 2010). They provide important functions and services such as water purification, carbon sequestration and flood regulation, and thereby support human wellbeing (Russi et al., 2013). At the same time, freshwaters are among the most threatened ecosystems worldwide. They continue to be degraded rapidly and biodiversity is lost through human activities at unprecedented rates (Davidson, 2014; WWF, 2016). Indeed, one in three freshwater species is already threatened (Group, 2008), and populations are declining faster than in marine or terrestrial realms (Dudgeon et al., 2006; WWF, 2016).

Despite their critical state, freshwaters and their unique diversity remain largely neglected by the general public and within environmental policy (Cooke et al., 2013). Hence, rivers, lakes, and ground waters receive less conservation investments than most other ecosystems (Darwall et al., 2011). The reasons for this investment gap are manifold: for example, far less conservation research has focused on freshwater than terrestrial ecosystems (Di Marco et al., 2017), which subsequently influences the allocation of conservation funds (Donaldson et al., 2016). At the same time, the hidden nature of freshwater organisms leads to a lack of public awareness for them. A consequence of shifting baselines in public perception of freshwater biodiversity (Turvey et al., 2010) means we are often unaware of the rapid past and current decline of freshwater biodiversity (Humphries & Winemiller, 2009).

Terrestrial and marine megafauna species, such as rhinos, elephants, tigers, and whales have been successfully used as flagship species, gaining strong public attention for decades (Caro, 2010; Caro & O'Doherty, 1999; Hooker & Gerber, 2004; Verissimo, MacMillan, & Smith, 2011). Consequently, these species are widely targeted for conservation actions at regional to global scales (Sodhi, Butler, Laurance, & Gibson, 2011), and they continuously attract media attention and conservation funding (Global March for Elephants & Rhinos ATX, 2016; Price, 2016). Freshwater megafauna, such as the Beluga or European sturgeon (*Huso huso),* Yangtze finless porpoise *(Neophocaena asiaeorientalis* ssp. *asiaeorientalis),* or Caspian seal *(Pusa caspica*) are also large in size and spectacular in appearance (Fig. G1). Such impressive species may help generate public interest for the “hidden” freshwater biodiversity, too.

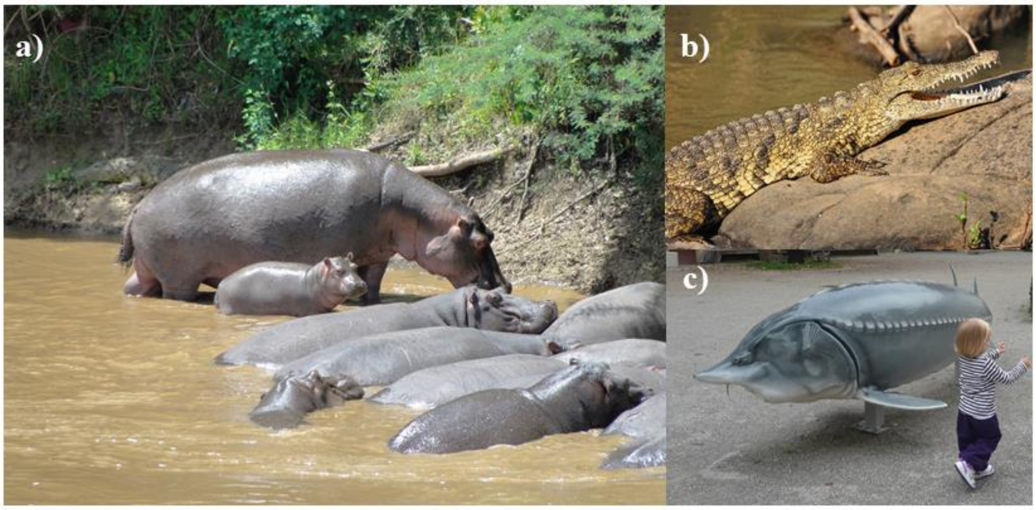

Fig. G1 Charismatic freshwater megafauna species. Left to right: (a) Large hippo (*Hippopotamus amphibious*); (b) Nile crocodile (*Crocodylus niloticus*); (c) Beluga (*Huso huso*). Photo credits: Peter Haase, F. David Carmona, and Will Darwall.

In this study, we demonstrate the potential for large-bodied freshwater species to be employed as flagship and/or umbrella species promoting the urgent need for freshwater conservation. First, we provide a synoptic and spatially-explicit assessment of the distribution and conservation status of global freshwater megafauna. As a proxy for understanding current efforts to conserve freshwater ecosystems, we quantify the spatial extent to which protected areas coincide with the distribution ranges of freshwater megafauna. Second, we investigate potential conservation umbrella effects of the freshwater megafauna through quantifying the extent to which they co-occur with other freshwater species. We also discuss possible roles for freshwater megafauna as flagship species. Third, we suggest priority scientific and policy recommendations to foster freshwater biodiversity conservation and we discuss the potential contribution of megafauna conservation to existing Multinational Environmental Agreements. The present results are expected to increase appreciation of freshwater biodiversity and support efforts to halt the largely unnoticed decline of global freshwater biodiversity.

Status and distribution of freshwater megafauna

We consider all species which require freshwater (or brackish) habitats for completing their entire life cycle as "freshwater" species (He et al. 2017). However, there is no generally accepted definition of freshwater megafauna. Indeed, there is an ongoing debate as to whether body length, mass, trophic level, functional role, or human perception and appreciation, or a combination of them, should be applied in defining megafauna (Barua, Root-Bernstein, Ladle, & Jepson, 2011; Caro & O'Doherty, 1999; Home, Keller, Nagel, Bauer, & Hunziker, 2009; Verissimo et al., 2011). Therefore, we apply a pragmatic definition considering all species with an adult mass of at least 30 kg to be classified as megafauna. A threshold of 30 kg is within the range of those applied to other taxa. For example, in terrestrial systems, a threshold of 15 kg was used for mega-carnivores and of 100 kg for mega-herbivores (Ripple et al., 2016). In marine systems, a threshold of 44 kg (100 lbs) has been applied (Estes, Heithaus, McCauley, Rasher, & Worm, 2016). A commonly used threshold for defining prehistoric megafauna of the Pleistocene is 44 kg, too (Barnosky, 2008).

Based on this 30 kg mass threshold we compiled a list of freshwater species that meet the threshold and, as well-known or otherwise iconic species, can serve as 'ambassadors' representative of both the freshwater megafauna and of conservation priorities for freshwater ecosystems. On this basis, we selected 132 megafauna species, including 73 fishes, 36 reptiles and 23 mammals (Table SG1). We reviewed the global conservation status of these species according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species^{TM} (hereafter Red List) (IUCN 2016b). Sixty two (58%) of the 107 species so far assessed for the Red List are classified as threatened, being Vulnerable, Endangered or Critically Endangered (Table SG1). The baiji (*Lipotes vexillifer)* and the Chinese paddlefish *(Psephurus gladius*) are Critically Endangered (Possibly Extinct). In addition, six species are Near Threatened, six species lack sufficient information to assess their conservation status (Data Deficient), and 25 species are not yet evaluated for the Red List (Table G1). Consequently, the overall level of threat to freshwater megafauna is most likely greater than presented.

Table G1 Total number and percentage of the 132 megafauna species classified in each Red List Category: EX, Extinct; EW, Extinct in the Wild; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated. Threatened categories are color coded. *baiji and Chinese paddlefish are CR (Possibly Extinct). NA = not applicable.

IUCN Red List Category	EX	EW	CR	EN	VU	NT	LC	DD	NE
Number of species	0*	1	27	18	17	6	32	6	25
Percent of assessed species	0.0	0.9	25.2	16.8	15.9	5.6	29.9	5.6	NA

Freshwater megafauna inhabit every continent except Antarctica (Fig. G2a). As expected, they mostly occur in large rivers (e.g. Amazon, Congo, Ganges, Mekong, Mississippi) and lakes (e.g. Lake Tanganyika, Tonlé Sap Lake, also the Caspian Sea), which also harbour a major share of the total freshwater fauna (Fig. G2c). Geographically, South America, Central Africa, and South and Southeast Asia are notably rich in freshwater megafauna. At the same time, South and Southeast Asia contain a relatively high proportion of threatened freshwater megafauna species (Fig. G2b).

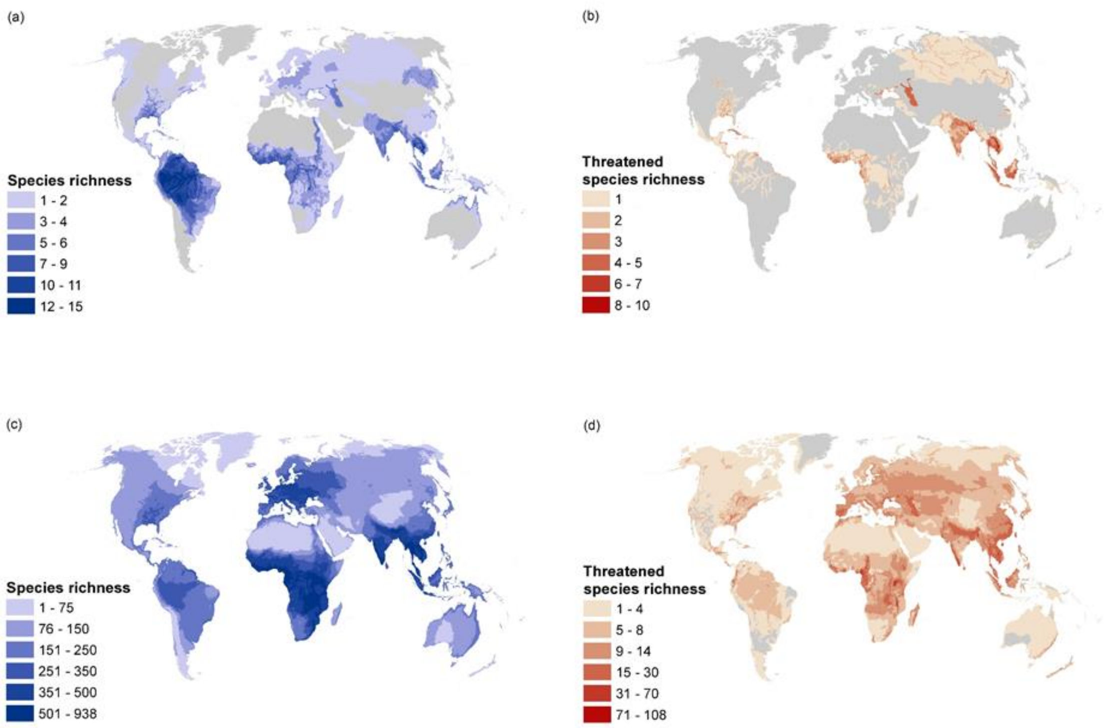

Fig. G2 Richness maps: Species richness (a) and threatened species richness (b) of freshwater megafauna. Species richness (c) and threatened species richness (d) of freshwater species exclusive of megafauna (fishes, molluscs, odonates, plants, crabs, crayfish, shrimps, turtles, mammals, birds, amphibians). Note that the Americas, Australasia, China, Russia and parts of the Middle East are incompletely assessed regions, thus richness is at least at the level depicted.

Eighty-four percent of the collective freshwater megafauna distribution ranges fall outside of protected areas (Fig. G3). Only two species, the Baikal seal (*Pusa sibirica*) and Ungava seal (*Phoca vitulina* ssp. *mellonae*), have more than half of their range within protected areas (Table SG2). Large rivers show particularly low levels of protected area coverage. For example, the Mekong and Ganges rivers are poorly protected in terms of the proportion of catchment area protected or maintenance of their natural flow regimes (Abell, Lehner, Thieme, & Linke, 2017; Harrison et al., 2016), this despite supporting a highly diverse freshwater megafauna. We conclude, therefore, that freshwater species are currently not gaining sufficient conservation attention.

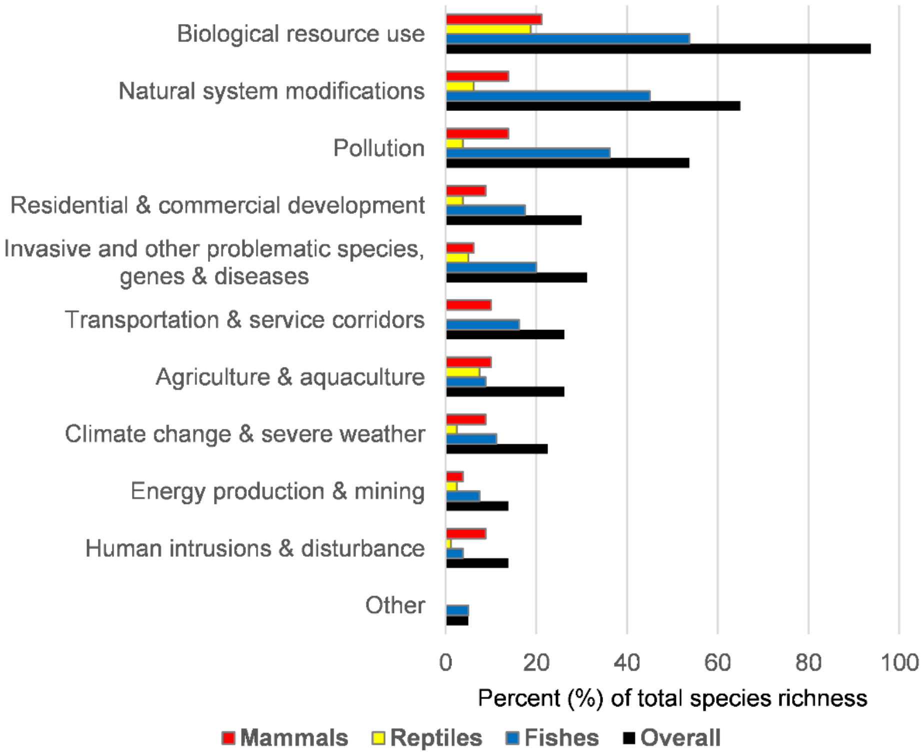

Fig. G3 Gap analysis between the World Database on Protected Areas (WDPA) and freshwater megafauna 'Extant' and 'Probably Extant' records (PRESENCE = 1 and 2) shows that 84% of the collective freshwater megafauna range is outside protected areas.

Protected areas are widely considered by the Convention on Biological Diversity (CBD) (Leadley et al., 2014) as a primary tool for conservation of biodiversity. The CBD recommends that 17 % of terrestrial and freshwater systems should be protected. However, such area-based targets have been shown ineffective in protecting freshwater biodiversity, attributed in part to a current lack of information on the distribution and global extent of wetlands (Abell et al., 2017; Juffe-Bignoli et al., 2016; Watson, Dudley, Segan, & Hockings, 2014). Moreover, many protected areas do not incorporate freshwaters as specified conservation targets per se; hence, effective protection is often only incidental and more often absent (Pittock et al., 2015; Reis et al., 2017; Saunders, Meeuwig, & Vincent, 2002). Rivers, for example, are commonly used to delineate protected area boundaries rather than being considered as a key component of conservation plans (Abell, Allan, & Lehner, 2007). Where freshwater species ranges do fall within protected areas, they often remain exposed to threats propagated from outside this area due to pronounced hydrological connectivity gradients up- and downstream (Pittock et al., 2015). However, when thoughtfully selected, megafauna species requirements can guide area targets and boundaries for protected areas, resulting in major financial support and strong political commitment as shown for marine and terrestrial species (Hooker & Gerber, 2004; Ripple et al., 2017).

The key threats to freshwater megafauna species are overexploitation (94% of the analyzed species), habitat alteration (65%), and pollution (54%) (Fig. G4 & G5 and Box G1). The current data suggest that freshwater species are affected by unsustainable population declines caused by humans acting as “super-predators” as in marine and terrestrial ecosystems (Darimont et al. 2015). In addition to general harvesting for food, ‘megafishes’ are also subject to increasing pressure from anglers as trophy catches (Maxwell, Fuller, Brooks, & Watson, 2016; Stone, 2007). Water abstraction and dam construction (Table SG3 & SG4) alter flow, sediment and temperature regimes, fragment river networks, and drain and isolate wetlands, thereby affecting home ranges, migratory routes and access to spawning sites of megafauna species (Davidson, 2014). Agricultural, industrial, and urban pollutants propagate through catchments and affect freshwater megafauna (Pittock et al., 2015). Overall, these threats, single or in combination, lead to a decline of populations, a reduction of genetic variability, and ultimately to species extinction (He et al., 2017).

Fig. G4 Threats to freshwater megafauna. Left: (a) The Beluga (*Huso huso*) is Critically Endangered due to overfishing, poaching, and habitat modification. Belugas migrate upstream to spawn; however, impoundments have destroyed most of the species' spawning grounds. Right top to bottom: (b) The Three Gorges Dam on the Yangtze River increases water temperatures which causes delays and reduces the spawning activity of the Chinese sturgeon (*Acipenser sinensis*); (c) Boat traffic, and pollution such as from intense sand mining in Poyang Lake (photo from 2010) and associated vessel strikes are common threats to freshwater megafauna. Photo credits: Jörg Freyhof, Pedro Vásquez Colmenares, Sonja C. Jähnig; Photo (b) Three Gorges Dam by P.V. Colmenares published under CC BY-NC 2.0 license, https://www.flickr.com/photos/pvcg/3412711352/sizes/o/

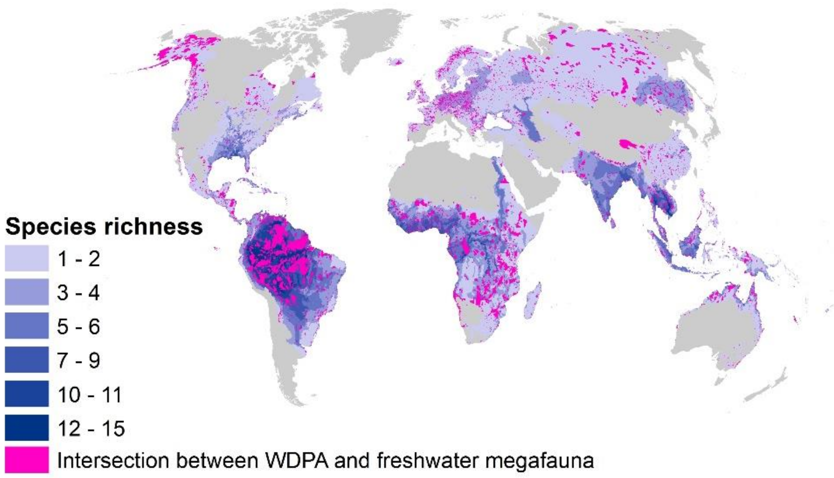

Fig. G5 The main threats affecting freshwater megafauna (as a percentage of total species richness).

Box G1. Charismatic freshwater megafauna species

Freshwater megafauna species require freshwater (or brackish) habitat for completing any critical stage in the species life cycle. In addition to their potential to act as flagship species, megafauna species fulfill important ecological roles, such as ecosystem engineers; e.g., the Large Hippo (*Hippopotamus amphibious*; Fig. G1) alters floodplain habitats, the river morphology and fertilizes floodwaters, which has an effect on the productivity of fish populations. The large hippo is primarily threatened by illegal hunting and loss of habitats due to conflicting human population growth, development and agriculture. The Nile crocodile (*Crocodylus niloticus*, Fig. G1) was hunted for its skin almost to extinction in many locations, but was rather successfully protected due to the development of crocodile farming which now satisfies human demands. After years of being classified as "Endangered", in 1996 the status of the Nile crocodile improved to "least concern" (but the Red List notes this status requires updating). The Beluga, or European sturgeon (*Huso huso*) (Fig. G1 & G4) is the largest freshwater fish in the world as demonstrated by the life sized model of it at the National Park Donau-Auen offices, Austria.

As most megafauna species are threatened by multiple pressures, an integrated management approach is required to protect and increase their populations over the long term (Abell et al., 2007; Pittock et al., 2015). An immediate priority is to address overexploitation. However, protected areas alone will not be sufficient to protect and improve freshwater megafauna, certainly while harvesting remains unsustainable. Impacts of the global boom in hydropower dams such as in the Amazon, Congo and Mekong river basins (Winemiller et al., 2016; Zarfl, Lumsdon, & Tockner, 2015) also represent priority areas for attention if freshwater species declines are to be reversed. Unsustainable abstraction of water is likewise a major concern in the dry regions of the world such as the Ganges-Brahmaputra and Indus river basins.

Co-occurrence of freshwater megafauna with other freshwater biodiversity

Based on the most comprehensive, spatially-explicit biodiversity data set available up to now, 93% of all assessed freshwater biodiversity co-occurs with the freshwater megafauna species (Fig. G2, Table SG5). Overall, 60% of the world's threatened freshwater species are found within the collective freshwater megafauna range, varying from 24% (odonates) to 87% (turtles) (Table SG6). Indeed, the level of co-occurrence is expected to be even higher because the spatial distribution and the conservation status of freshwater biodiversity are not yet fully assessed for many regions of the world. Therefore, an effective conservation of megafauna species will most likely benefit many additional freshwater species. A similar "umbrella" effect has recently been demonstrated for terrestrial megafauna (Branton & Richardson, 2011; Ripple et al., 2016). For example, conservation efforts targeting the giant panda (*Ailuropoda melanoleuca*) in China (Li & Pimm, 2016) protect co-occurring species such as the threatened golden snub-nosed monkey (*Rhinopithecus roxellana),* blackthroat (*Calliope obscura*), and Liangbei toothed toad (*Oreolalax liangbeiensis*). Similarly, the jaguar conservation network in South America, established to maintain habitat quality and connectivity, benefits co-occurring mammal species such as the highly threatened lowland tapir (*Tapirus terrestris*) (Thornton et al., 2016).

Whether such an umbrella effect can be realized strongly depends on the role megafauna species have on ecosystem functioning (Ford, Cooke, Goheen, & Young, 2017). Although freshwater megafauna might take a central role in food webs (Brose et al., 2017), for most species their ecological role is yet to be determined. The presence of top-down or bottom-up processes are likely to determine the potential wider benefits of their conservation such that, in some cases, smaller species might be more effective as conservation priorities (Ford et al. 2017). However, it has been argued that top-down control is greater in water than on land (Shurin et al. (2002) and references therein). At the same time, we need to be aware that it may be challenging to develop effective conservation strategies for freshwater megafauna species on account of their large home ranges, complex life cycles, and distinct movement dynamics.

Additionally, conservation efforts for freshwater biodiversity must consider headwater rivers and streams too. Although headwaters themselves contain few megafauna species, they are essential in supporting the biodiversity of entire river systems, including megafauna species present in downstream sections (Meyer et al., 2007).

Knowledge gaps and next steps

Information gaps on the global distribution and status of freshwater megafauna need to be filled to ensure evidence-based and effective conservation strategies, regionally and globally. One priority is to identify sites of importance to conservation of freshwater species. Key Biodiversity Areas (KBAs), defined as "sites contributing significantly to the global persistence of biodiversity" (IUCN, 2016), need to be identified and validated for freshwaters for most of the world (but see Holland, Darwall, and Smith (2012)).

Evidence-based conservation planning depends further on baseline information on species; this includes regularly updated and comprehensive Red List assessments, with a priority focus on additional research for Data Deficient species and new assessments of the many species yet to be evaluated. Conservation planning might also focus on the identification of Evolutionarily Distinct and Globally Endangered (EDGE) species (The Zoological Society of London, 2016) based on an updated phylogeny. Such baseline information would include refined and validated distribution maps including spawning areas and migration routes. Eventually, a freshwater megafauna Red List Index could be developed to track change over time within global monitoring programs.

Based on the information for critical sites and species, systematic conservation planning approaches – as opposed to ad-hoc conservation planning; (Hermoso, Kennard, & Linke, 2015) – may further help improve the representation of freshwater biodiversity within protected area networks. However, climate change impacts on megafauna distributions have to be considered too, in particular in relation to potential boundary modifications for protected areas (Pittock et al., 2015).

Finally, long-term data are available for only few, mainly commercially important megafauna populations, such as Chinook salmon (*Oncorhynchus tshawytscha*), Atlantic salmon (*Salmo salar*), sturgeons, or crocodiles. Such data are fundamental to track the status and the trends of megafauna species (WWF 2016).

The potential conservation benefits of flagship and umbrella freshwater species, sometimes referred to as "freshwater pandas" (Kalinkat et al., 2017) have only been considered for a few regions. Ebner et al. (2016), for example, presented Australian freshwater flagship species, including several megafauna species, arguing for an audience-targeted nomination of species which would receive conservation action. Promotion of flagship species needs to be targeted to specific regions and/or stakeholders, such as recreational or commercial fishers, scientists, environmental managers, water resource users, or indigenous people to consider their differing perceptions of nature and biodiversity (Cooke et al., 2013). Successful examples for such targeted flagship promotion are the largetooth sawfish (*Pristis pristis*) or the smaller bodied axolotl (*Ambystoma mexicanum*) (Barua et al., 2011; Bride, Griffiths, Meléndez-Herrada, & McKay, 2008; Ebner et al., 2016). Likewise, identification of threats common to all species (Donaldson et al. 2016) is an essential precursor to development of effective management strategies benefiting both megafauna and other co-occurring species.

The contribution of freshwater megafauna to the provision of ecosystem services requires further investigation. Many species are of importance to livelihoods, such as through contributions to national and local fisheries (Petrere, Barthem, Córdoba, & Gómez, 2004), recreational fisheries (Jensen et al., 2009), or tourism (Solomon, Corey-Luse, & Halvorsen, 2004). Freshwater megafauna, such as the taimen and other large fishes are already known to be important for recreational fisheries (Granek et al., 2008), and other species, such as river dolphins bring important tourism benefits (de Sá Alves, Andriolo, Orams, & de Freitas Azevedo, 2012).

Closing the knowledge gaps for freshwater megafauna will help achieve two major goals: (1) Raising political will as needed to conserve freshwater megafauna and freshwater biodiversity in general, and (2) identifying flagship species targeted to specific regions or stakeholders (Verissimo et al., 2011).

Policy relevance

To counteract the ongoing decline in freshwater biodiversity, conservation actions are required at multiple spatial scales (Sodhi et al., 2011). At the local scale, priority activities include habitat restoration, creation of protected freshwater areas, control of illegal hunting, and recovery plans for threatened species. At the regional scale, measures include cooperation among neighboring countries, such as regulation of international wildlife trade and transboundary river basin management. At the global scale, the impact of climate change on freshwater ecosystems has to be addressed.

Multinational Environmental Agreements aim to improve the status of freshwater biodiversity, such as through regulating trade and advocating international cooperation. For example, 29 freshwater megafauna species are represented in the Convention on Migratory Species (CMS) and 69 species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Table SG7). The Secretariat of the CMS has already recognized the need to strengthen measures to protect transboundary migratory freshwater fishes, which include many of the 'megafishes' (Hogan, 2011; Stone, 2007). Improved knowledge of freshwater megafauna and leveraging megafauna species to generate attention and action for freshwater biodiversity could help achieve the targets of international conventions.

For example, actions implemented for conservation of freshwater megafauna could simultaneously help reach multiple Aichi Targets: reducing fragmentation and degradation of freshwater habitats (Target 5), improving long-term sustainability of freshwater fisheries (Target 6), decreasing pollution effects in freshwater ecosystems (Target 8), improving the effectiveness of freshwater protected areas (Target 11), and, closing data gaps regarding the conservation status of freshwater species, which will allow better monitoring of trends in species extinctions, and implementation of actions to reverse those trends (Target 12). Moreover, knowledge of and attention to freshwater megafauna can support the Ramsar Convention to maintain or restore the ecological character of Ramsar sites, through effective planning and integrated management (Target 5 of Ramsar's 2016-2024 Strategic Plan; Resolution XII.2; (Ramsar Conference of the Contracting Parties, 2015)). Freshwater megafauna can also highlight and help shape the application of two targets of the Sustainable Development Goals (SDGs): "The protection and restoration of water-related ecosystems, including wetlands, rivers, aquifers and lakes" (Target 6.6) and "the conservation, restoration, and sustainable use of terrestrial and inland freshwater ecosystems and their services" (Target 15.1) (United Nations, 2016). Associated with target 15 is the process of safeguarding terrestrial and freshwater key biodiversity areas around the world. Finally, megafauna data can be used to identify transboundary basins where large migratory fishes provide important natural resources that benefit multiple nations, and guide management decisions for programs such as the Intergovernmental

Platform on Biodiversity and Ecosystem Services (Díaz et al., 2015), the Transboundary Waters Assessment Programme (TWAP), and the UN Watercourses Convention 2015 (UN Watercourses Convention, 2016; Verissimo et al., 2011).

Summary and outlook

Freshwater is both a resource for human use as well as part of a diverse mix of ecosystems containing a unique biodiversity. The unusually large and fast decline in freshwaters is a product of their relatively small extent and distinct internal connectivity, also with close links to surrounding terrestrial areas. Freshwater ecosystems are quickly and significantly affected by overharvesting of regional fishes, shellfishes, and plants, over-abstraction of water, pollution, and fragmentation of rivers. The effective management of these threats is further complicated when river catchments cross political or administrative borders (WWF 2016).

Despite these major challenges, and the high value of freshwater ecosystems in terms of biodiversity, livelihoods and economics, the fact that freshwater ecosystems are declining at greater rates than other systems suggests that there is less investment in their conservation and management. Therefore, there is a major conflict between human use of freshwater and conservation of freshwater ecosystems. As the availability of freshwater, both spatially and temporally, is predicted to decrease in many regions in the future, this conflict is likely to increase. Solutions to the water supply crisis have focused on engineering approaches such as construction of dams for water storage and power generation, inter-basin water transfers, or construction of dikes and channels for flood protection. Frequently, these measures will accelerate the decline in freshwater biodiversity as fundamental habitats and connectivity are degraded or lost (Green et al., 2015; Harrison et al., 2016; Vörösmarty et al., 2010). Resolving this conflict may be possible if the ecosystem services provided by diverse and intact freshwaters become more widely acknowledged and the species in freshwaters become better known and valued.

Freshwater megafauna have a great potential, yet to unfold, to communicate to the public, policy makers, and donors the immense value of freshwater ecosystems, including a unique biodiversity. Here, we provide spatially explicit and quantitative data, supporting a better use of freshwater megafauna as a conservation tool. The results and recommendations presented here demonstrate the potential for freshwater megafauna to generate greater public awareness and political will to better support conservation of freshwater ecosystems and to stop, or even reverse, their current widespread and tragic decline.

Acknowledgments

The data will be archived through the Freshwater Information Platform (http://www.freshwaterplatform.eu) and metadata published through the Freshwater Metadata Journal.

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Appendix H: Supporting information for Appendix G

Data

The IUCN Red List of Threatened Species™

The Red List assessment process assigns a species to one of the following Categories as a measure of the risk of global extinction: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), Extinct (EX) and Data Deficient (DD) (Group, 2008). The data exported from the Red List still included some Categories that have been decommissioned (i.e., no longer used). These Categories were combined with the appropriate current Red List Categories as follows; species assessed as Lower Risk/conservation dependent (LR/cd) and Lower Risk/near threatened (LR/nt) were incorporated within the current Category NT, and species assessed as Lower Risk/least concern (LR/lc) were incorporated within the Category LC. The decommissioned Categories will gradually be removed from the Red List as the species within them are reassessed according to the current Categories. Along with assigning a Red List Category, the Red List assessments collate information including threats, habitats, country occurrence, and use and trade. Our Red List export was current as of 5th May 2016.

Geographic distributions

Where possible, species geographic distributions are mapped as part of the Red List assessment process. The distributions are mapped to sub-catchments allowing delineation and analysis, and hence conservation planning and practical management interventions, to take place at the appropriate ecological scale. Mapping to sub-catchments also enables consideration of biological and ecological processes, such as species migrations and threat propagation, mediated by catchment connectivity (Nel et al., 2009). To define sub-catchments, we used HydroBASINS, a global standardized hydrological framework that delineates catchments at multiple resolutions and includes network connectivity information (B. Lehner, 2012; Bernhard Lehner & Grill, 2013). We analyzed distribution data at the HydroBASINS level 8 sub-catchment scale (catchment area: 538.3 ± 649.45 km^2; mean ± SD). ‘Presence’ within each sub-catchment is indicated according to the nature and certainty of occurrence, based on observation and inference, and is coded as Extant, Probably Extant, Possibly

Extant, Possibly Extinct, Extinct (post 1500), and Presence Uncertain. 'Origin' is coded as Native, Reintroduced, Introduced, Vagrant, and Origin Uncertain (www.iucnredlist.org/technical-documents/spatial-data). We spatially transferred existing reptile, mammal, and fish distribution maps that were not originally mapped to HydroBASINS sub-catchments via a semi-automated process. Finally, we individually validated these maps to ensure correct data transfer to the catchment framework. Where a map was not available, we created a map based on descriptions from the IUCN Red List and other sources.

For the overall freshwater biodiversity assessment, we used species distribution data for eleven freshwater groups: 1776 plants, 1505 odonates, 1277 crabs, 4221 amphibians, 2182 birds, 141 mammals, 734 shrimps, 504 crayfish, 270 turtles, 2021 molluscs, and 6647 fishes. Not all of these groups are comprehensively assessed on the Red List, but we included all available data to also inform conservation of those partially assessed groups.

World Database on Protected Areas (WDPA)

For the gap analysis, we performed spatial coverage analyses using the World Database on Protected Areas (WDPA) dataset (IUCN and UNEP-WCMC, 2016). We used a pre-processed layer provided by the United Nations Environment Programme World Conservation Monitoring Centre (UNEP WCMC). In this layer, all points and polygons with STATUS = "not reported" and STATUS = "proposed" and all UNESCO MAB (The United Nations Educational, Scientific and Cultural Organization Man and the Biosphere Programme) reserves had been removed. These data were removed because the features may include large areas that do not meet the definition of protected areas (Juffe-Bignoli et al., 2014). Our WDPA layer was current as of April 2016.

CMS and CITES

We sourced information on species representation in the Convention on Migratory Species (CMS) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) from the Species+ database (www.speciesplus.net/). The CMS Appendix I lists threatened migratory species and CMS Appendix II lists migratory species requiring international cooperation (www.cms.int/en). CITES Appendix I lists "species that are the most endangered among CITES-listed animals and plants. They are threatened with extinction and CITES prohibits international trade in specimens of these species except when the purpose of the import is not commercial...". CITES Appendix II lists "species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled." CITES Appendix III lists "species included at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation" (www.cites.org).

Analysis

Species list

We selected 132 freshwater megafauna species (Table SG1) with reference to published weight data (Table SG8).

Conservation status

We collated IUCN Red List assessment data for all 132 species, where available, as of May 5th, 2016. We summarized conservation status of the freshwater megafauna as the mid-point estimate (MID) of the percentage of threatened species (i.e., assuming the Data Deficient (DD) species are threatened in the same proportion as the species for which there are sufficient data) as follows: % threat = (CR + EN + VU) / (total assessed – EX – EW – DD).

Geographic distributions

We derived global species richness maps from the individual species Red List maps. We summarized the spatial data into species richness and threatened species richness maps for megafauna and overall freshwater biodiversity, using 'Extant' (PRESENCE = 1) and 'Probably Extant' (PRESENCE = 2) records within each HydroBASINS sub-catchment (Fig. G2). Furthermore, we used the distribution data on the remaining freshwater species to run a co-occurrence analysis with the megafauna (Tables SG5 and SG6).

Threats

We extracted threat data, collated during Red List assessments from the IUCN Species Information Service (SIS) for each species where available. We summarized the percentage of species affected by each threat category for mammals, fishes, reptiles, and megafauna overall. We reviewed the threats at each of the three levels (levels 0, 1, and 2) of detail within the threat classification hierarchy (Fig. G5 and Tables SG3 & SG4).

Gap analysis

We filtered the species ranges to only include 'Extant' (PRESENCE = 1) and 'Probably Extant' (PRESENCE = 2) records. We projected all spatial data to WGS_1984 Cylindrical Equal Area to ensure correct calculation of areas. We then intersected the set of corresponding HydroBASINS with the WDPA layer. We aggregated the total area (km^2) of each HydroBASINS that is overlapped by a protected area from the individual intersecting segments. Thus, we calculated the area of each species range that is covered by protected areas from the component HydroBASINS overlaps (Table SG2). We visualized the WDPA overlaps with the 'Extant' and 'Probably Extant' records of megafauna to evaluate the spatial distribution of gaps (Fig. G3).

CMS and CITES

We summarized the presence of species within the CMS and CITES conventions (Table SG7).

All analyses were conducted using custom R scripts with R version 2.15.2 (R Core Team, 2012) and ArcGIS (ESRI, 2015).

Table SG1 Species list and status from the International Union for Conservation of Nature (IUCN) Red List of Threatened speciesTM. Sorted by Red List Category EX, Extinct; EW, Extinct in the Wild; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated.

Binomial	**Common Name**	**Class**	**Red List Category**
Nilssonia nigricans	Black Soft-shell Turtle, Black Softshell Turtle	Reptilia	EW
Acipenser gueldenstaedtii	Russian sturgeon	Actinopterygii	CR
Acipenser mikadoi	Sakhalin Sturgeon	Actinopterygii	CR
Acipenser nudiventris	Ship Sturgeon, Spiny Sturgeon	Actinopterygii	CR
Acipenser persicus	Persian Sturgeon	Actinopterygii	CR
Acipenser schrenckii	Amur Sturgeon	Actinopterygii	CR
Acipenser sinensis	Chinese Sturgeon	Actinopterygii	CR
Acipenser stellatus	Stellate Sturgeon, Sevruga, Star Sturgeon	Actinopterygii	CR
Acipenser sturio	Common Sturgeon, Atlantic Sturgeon,	Actinopterygii	CR
Catlocarpio siamensis	Giant Carp, Giant Barb	Actinopterygii	CR

Binomial	**Common Name**	**Class**	**Red List Category**
Huso dauricus	Kaluga	Actinopterygii	CR
Huso huso	Beluga, Giant Sturgeon, European Sturgeon, Great Sturgeon	Actinopterygii	CR
Maccullochella peelii	Murray Cod, Murray River Cod	Actinopterygii	CR
Pangasianodon gigas	Mekong Giant Catfish, Giant Catfish	Actinopterygii	CR
Pangasius sanitwongsei	Giant Pangasius, Paroon Shark, Pangasid-catfish, Pla Thepa	Actinopterygii	CR
Pristis pristis	Largetooth Sawfish	Chondrichthyes	CR
Pristis pectinata	Smalltooth Sawfish, Wide Sawfish	Chondrichthyes	CR
Psephurus gladius	Chinese Paddlefish	Actinopterygii	CR*
Lipotes vexillifer	Yangtze River Dolphin, Whitefin Dolphin	Mammalia	CR*
Neophocaena asiaeorientalis ssp. *asiaeorientalis*	Yangtze Finless Porpoise	Mammalia	CR
Alligator sinensis	Chinese Alligator, China Alligator	Reptilia	CR
Chitra chitra	Southeast Asian Narrow-headed Softshell Turtle	Reptilia	CR
Crocodylus intermedius	Orinoco Crocodile	Reptilia	CR

Binomial	**Common Name**	**Class**	**Red List Category**
Crocodylus rhombifer	Cuban Crocodile	Reptilia	CR
Crocodylus siamensis	Siamese Crocodile	Reptilia	CR
Gavialis gangeticus	Gharial, Indian Gharial	Reptilia	CR
Mecistops cataphractus	Slender-snouted Crocodile, African Slender-snouted Crocodile	Reptilia	CR
Rafetus swinhoei	Yangtze Giant Softshell Turtle	Reptilia	CR
Acipenser baerii	Siberian sturgeon	Actinopterygii	EN
Argyrosomus hololepidotus	Madagascar Kob, Madagascar Meagre	Actinopterygii	EN
Himantura polylepis	Giant freshwater stingray	Chondrichthyes	EN
Hucho hucho	Danube Salmon, Huchen	Actinopterygii	EN
Hypselobarbus mussullah	Hump Backed Mahseer	Actinopterygii	EN
Lates angustifrons	Tanganyika Lates	Actinopterygii	EN
Probarbus jullieni	Jullien's Golden Carp, Seven-striped Barb	Actinopterygii	EN

Binomial	**Common Name**	**Class**	**Red List Category**
Probarbus labeamajor	Thicklipped Barb	Actinopterygii	EN
Scaphirhynchus albus	Pallid Sturgeon	Actinopterygii	EN
Tor putitora	Putitor Mahseer, Golden Mahaseer	Actinopterygii	EN
Choeropsis liberiensis	Pygmy Hippopotamus	Mammalia	EN
Kobus megaceros	Nile Lechwe	Mammalia	EN
Platanista gangetica ssp. *gangetica*	Ganges River Dolphin, Ganges Susu, Ganges Dolphin	Mammalia	EN
Platanista gangetica ssp. *minor*	Indus River Dolphin, Susu, Indus Dolphin	Mammalia	EN
Pusa caspica	Caspian Seal	Mammalia	EN
Chitra indica	Indian Narrow-headed Softshell Turtle, Narrow-headed Softshell Turtle	Reptilia	EN
Orlitia borneensis	Bornean River Turtle, Malaysian Giant Turtle	Reptilia	EN
Pelochelys cantorii	Cantor's Giant Softshell Turtle, Frog-faced Softshell Turtle	Reptilia	EN
Hucho taimen	Siberian Taimen, Mongolian Taimen, Siberian Salmon, Taimen	Actinopterygii	VU

Binomial	Common Name	Class	Red List Category
Luciobarbus esocinus	Pike Barbel	Actinopterygii	VU
Megalops atlanticus	Tarpon	Actinopterygii	VU
Polyodon spathula	Paddlefish, Spadefish, Duckbill Cat, Spoonbill Cat	Actinopterygii	VU
Hippopotamus amphibius	Hippopotamus, Large Hippo, Common Hippopotamus	Mammalia	VU
Orcaella brevirostris	Irrawaddy Dolphin, Snubfin Dolphin	Mammalia	VU
Trichechus inunguis	Amazonian Manatee, South American Manatee	Mammalia	VU
Trichechus manatus	American Manatee, West Indian Manatee	Mammalia	VU
Trichechus senegalensis	African Manatee, Seacow, West African Manatee	Mammalia	VU
Amyda cartilaginea	Asiatic Softshell Turtle, Southeast Asian Softshell Turtle	Reptilia	VU
Crocodylus acutus	American Crocodile	Reptilia	VU
Crocodylus palustris	Mugger, Muggar, Broad-snouted Crocodile, Marsh Crocodile	Reptilia	VU
Macrochelys temminckii	Alligator Snapping Turtle	Reptilia	VU
Nilssonia leithii	Leith's Softshell Turtle	Reptilia	VU

Binomial	**Common Name**	**Class**	**Red List Category**
Osteolaemus tetraspis	African Dwarf Crocodile, West African Dwarf Crocodile	Reptilia	VU
Pelochelys bibroni	Asian Giant Softshell Turtle, Striped New Guinea Softshell Turtle	Reptilia	VU
Tomistoma schlegelii	False Gharial, Tomistoma, Sunda Gharial, Malayan Gharial	Reptilia	VU
Acipenser medirostris	Green Sturgeon	Actinopterygii	NT
Acipenser oxyrinchus	Gulf Sturgeon	Actinopterygii	NT
Arius gigas	Giant Sea Catfish	Actinopterygii	NT
Carcharhinus leucas	Bull Shark	Chondrichthyes	NT
Hypophthalmichthys molitrix	Silver Carp	Actinopterygii	NT
Wallago attu	Wallago (Giant sheatfish)	Actinopterygii	NT
Acipenser fulvescens	Lake Sturgeon	Actinopterygii	LC
Acipenser transmontanus	White Sturgeon	Actinopterygii	LC

Binomial	**Common Name**	**Class**	**Red List Category**
Chrysichthys cranchii	Kokuni, Kokuni, Manora	Actinopterygii	LC
Clarias gariepinus	African Catfish, Sharptooth Catfish	Actinopterygii	LC
Hemibagrus maydelli	Krishna Mystus	Actinopterygii	LC
Hemibagrus wyckioides	Asian Red Tailed Catfish, Red fin bagrus	Actinopterygii	LC
Heterobranchus longifilis	Catfish, Sampa, Vundu, Vundu	Actinopterygii	LC
Hydrocynus goliath	Giant tigerfish, Giant tigerfish	Actinopterygii	LC
Ictalurus furcatus	Blue Catfish	Actinopterygii	LC
Labeo rohita	Rohu	Actinopterygii	LC
Lates niloticus	Nile Perch, Victoria Perch, African Snook	Actinopterygii	LC
Morone saxatilis	Striped Bass	Actinopterygii	LC
Pylodictis olivaris	Flathead Catfish	Actinopterygii	LC
Salmo salar	Atlantic Salmon, Black Salmon	Actinopterygii	LC
Salmo trutta	Brown Trout, Sea Trout	Actinopterygii	LC

Binomial	**Common Name**	**Class**	**Red List Category**
Silurus glanis	Wels Catfish	Actinopterygii	LC
Hydrochoerus hydrochaeris	Capybara	Mammalia	LC
Kobus leche	Southern Lechwe	Mammalia	LC
Pusa sibirica	Baikal Seal	Mammalia	LC
Tragelaphus spekii	Sitatunga, Marshbuck	Mammalia	LC
Alligator mississippiensis	American Alligator, Mississippi Alligator	Reptilia	LC
Apalone ferox	Florida Softshell Turtle	Reptilia	LC
Caiman crocodilus	Common Caiman, Spectacled Caiman	Reptilia	LC
Caiman latirostris	Broad-snouted Caiman	Reptilia	LC
Caiman yacare	Yacaré	Reptilia	LC
Crocodylus johnsoni	Australian Freshwater Crocodile, Johnson's Crocodile	Reptilia	LC
Crocodylus moreletii	Morelet's Crocodile, Belize Crocodile	Reptilia	LC
Crocodylus niloticus	Nile Crocodile	Reptilia	LC

Binomial	**Common Name**	**Class**	**Red List Category**
Crocodylus porosus	Salt-Water Crocodile, Estuarine Crocodile	Reptilia	LC
Melanosuchus niger	Black Caiman	Reptilia	LC
Paleosuchus palpebrosus	Dwarf Caiman, Cuvier's Smooth-fronted Caiman	Reptilia	LC
Podocnemis expansa	South American River Turtle, Arrau, Giant South American Turtle	Reptilia	LC
Arapaima gigas	Arapaima, Pirarucu	Actinopterygii	DD[a]
Potamotrygon brachyura	Giant Freshwater Stingray	Chondrichthyes	DD
Scomberomorus sinensis	Chinese Seerfish	Actinopterygii	DD
Wallago micropogon	Walaga	Actinopterygii	DD
Inia geoffrensis	Amazon River Dolphin, Boutu	Mammalia	DD
Sotalia fluviatilis	Tucuxi, Bouto Dolphin	Mammalia	DD
Arapaima agassizii	n/a	Actinopterygii	NE[a]

Binomial	Common Name	Class	Red List Category
Arapaima leptosoma	n/a	Actinopterygii	NE[a]
Arapaima mapae	n/a	Actinopterygii	NE[a]
Atractosteus spatula	Alligator gar	Actinopterygii	NE
Brachyplatystoma filamentosum	Kumakuma	Actinopterygii	NE
Colossoma macropomum	Cachama	Actinopterygii	NE
Ctenopharyngodon idella	Grass Carp	Actinopterygii	NE
Eleutheronema tetradactylum	Fourfinger threadfin	Actinopterygii	NE
Lates calcarifer	Barramundi	Actinopterygii	NE
Oncorhynchus tshawytscha	Chinook Salmon	Actinopterygii	NE
Polydactylus macrochir	Grand Threadfin	Actinopterygii	NE
Pseudoplatystoma corruscans	Spotted sorubim	Actinopterygii	NE
Pseudoplatystoma fasciatum	Barred sorubim	Actinopterygii	NE
Silurus soldatovi	Soldatov's catfish	Actinopterygii	NE

Binomial	**Common Name**	**Class**	**Red List Category**
Wallago leerii	Tapah	Actinopterygii	NE
Zungaro zungaro	Guilded Catfish	Actinopterygii	NE
Inia araguaiaensis	Araguainan River dolphin	Mammalia	NE
Inia boliviensis	Bolivian River dolphin	Mammalia	NE
Phoca vitulina ssp. *mellonae*	Seal Lake Seal or Ungava Seal	Mammalia	NE
Pusa hispida ssp. *ladogensis*	Ladoga Seal	Mammalia	NE
Pusa hispida ssp. *saimensis*	Saimaa Ringed Seal	Mammalia	NE
Chitra vandijki	Burmese Narrow-Headed Softshell Turtle	Reptilia	NE
Eunectes murinus	Anaconda	Reptilia	NE
Osteolaemus osborni	Osborn's dwarf crocodile	Reptilia	NE
Trionyx triunguis	African Softshell Turtle	Reptilia	NE

Note: [a]Covered by *Arapaima* spp. complex map. *Possibly Extinct.

Table SG2 Protected area (PA) coverage (km2) per species for catchments where the species is tagged as 'Extant' or 'Probably Extant' (PRESENCE = 1 and 2).

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Pusa sibirica	32835	32718	99.6
Phoca vitulina ssp. *mellonae*	8257	7120	86.2
Kobus leche	334770	163472	48.8
Colossoma macropomum	6821773	2945334	43.2
Zungaro zungaro	6825621	2945587	43.2
Brachyplatystoma filamentosum	7387788	3130930	42.4
Melanosuchus niger	6121171	2572893	42.0
Podocnemis expansa	6012060	2520214	41.9
Inia geoffrensis	2451980	1025499	41.8
Trichechus inunguis	1548182	645008	41.7
Arapaima spp.	3020991	1257287	41.6
Inia boliviensis	162469	66876	41.2

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Sotalia fluviatilis	1318983	538836	40.9
Crocodylus intermedius	619088	237930	38.4
Caiman crocodilus	9510272	3386756	35.6
Pseudoplatystoma fasciatum	10027741	3370646	33.6
Paleosuchus palpebrosus	10600204	3476516	32.8
Pusa hispida ssp. *saimensis*	5512	1773	32.2
Oncorhynchus tshawytscha	2615911	838485	32.1
Hippopotamus amphibius	3105015	958757	30.9
Megalops atlanticus	1053043	313900	29.8
Hydrochoerus hydrochaeris	12609846	3730146	29.6
Lates calcarifer	196605	57373	29.2
Eunectes murinus	5571884	1524645	27.4
Hucho hucho	141200	35611	25.2

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Tor putitora	48328	11927	24.7
Kobus megaceros	177684	40584	22.8
Trichechus manatus	225075	51217	22.8
Pristis pectinata	174098	39109	22.5
Choeropsis liberiensis	166731	37398	22.4
Hydrocynus goliath	476718	100609	21.1
Tragelaphus spekii	4710209	976576	20.7
Polydactylus macrochir	989974	204336	20.6
Crocodylus johnsoni	1107835	226023	20.4
Crocodylus acutus	2311771	468589	20.3
Carcharhinus leucas	3194925	636424	19.9
Acipenser medirostris	184686	35708	19.3
Arius gigas	927163	178599	19.3

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Eleutheronema tetradactylum	83164	15788	19.0
Pristis pristis	1193375	222445	18.6
Osteolaemus osborni	2134344	388391	18.2
Crocodylus moreletii	516320	92166	17.9
Trichechus senegalensis	679978	121481	17.9
Probarbus labeamajor	59447	10560	17.8
Caiman yacare	2730413	483597	17.7
Crocodylus niloticus	17808043	3075338	17.3
Heterobranchus longifilis	3155678	546576	17.3
Clarias gariepinus	9627325	1617590	16.8
Inia araguaiaensis	426343	71089	16.7
Osteolaemus tetraspis	3181842	524297	16.5
Huso huso	225613	36981	16.4

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Salmo trutta	6311935	1006499	15.9
Lates niloticus	5253473	822092	15.6
Probarbus jullieni	200364	30461	15.2
Trionyx triunguis	5320848	792269	14.9
Salmo salar	5924169	874356	14.8
Mecistops cataphractus	3617566	532753	14.7
Caiman latirostris	4691656	668644	14.3
Acipenser sturio	23896	3326	13.9
Crocodylus siamensis	1771248	244117	13.8
Wallago micropogon	515629	71057	13.8
Catlocarpio siamensis	534100	71680	13.4
Chrysichthys cranchii	930505	120905	13.0
Wallago leerii	528021	68870	13.0

Binomial	**Range Area (km²)**	**PA Coverage (km²)**	**% Coverage**
Pelochelys bibroni	305452	39372	12.9
Crocodylus porosus	6335641	812918	12.8
Crocodylus rhombifer	114852	14755	12.8
Pangasius sanitwongsei	299487	38358	12.8
Hemibagrus wyckioides	475447	60144	12.7
Hypophthalmichthys molitrix	5305300	656600	12.4
Orcaella brevirostris	787343	94364	12.0
Acipenser sinensis	102118	12121	11.9
Amyda cartilaginea	2707564	323284	11.9
Neophocaena asiaeorientalis ssp. *asiaeorientalis*	102118	12121	11.9
Tomistoma schlegelii	258900	29916	11.6
Acipenser mikadoi	29665	3343	11.3
Silurus glanis	7696293	859734	11.2

Binomial	Range Area (km^2)	PA Coverage (km^2)	% Coverage
Chitra chitra	388360	42933	11.1
Acipenser schrenckii	206968	22246	10.7
Silurus soldatovi	2246081	238641	10.6
Acipenser baerii	1073267	112610	10.5
Orlitia borneensis	799675	82164	10.3
Acipenser transmontanus	536007	54862	10.2
Pelochelys cantorii	1476768	150430	10.2
Acipenser fulvescens	2057561	195430	9.5
Apalone ferox	255285	24042	9.4
Pseudoplatystoma corruscans	3274795	307768	9.4
Ctenopharyngodon idella	284831	25933	9.1
Hucho taimen	12147557	1105351	9.1
Wallago attu	5476456	499767	9.1

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Potamotrygon brachyura	1409231	125147	8.9
Huso dauricus	158408	13926	8.8
Maccullochella peelii	226452	19930	8.8
Alligator sinensis	113716	9858	8.7
Acipenser gueldenstaedtii	945921	79998	8.5
Acipenser stellatus	1001700	79226	7.9
Pangasianodon gigas	83694	6370	7.6
Crocodylus palustris	3964340	295871	7.5
Labeo rohita	4118178	303473	7.4
Hypselobarbus mussullah	179276	12719	7.1
Argyrosomus hololepidotus	73870	5068	6.9
Nilssonia leithii	500974	34249	6.8
Lates angustifrons	32707	2186	6.7

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Acipenser oxyrinchus	805433	48045	6.0
Morone saxatilis	708013	41601	5.9
Himantura polylepis	373212	20768	5.6
Acipenser persicus	633075	34542	5.5
Nilssonia nigricans	93833	4941	5.3
Chitra indica	2596136	132731	5.1
Platanista gangetica ssp. *gangetica*	368677	18714	5.1
Alligator mississippiensis	1431075	68979	4.8
Platanista gangetica ssp. *minor*	68142	3173	4.7
Rafetus swinhoei	104326	4742	4.5
Atractosteus spatula	382507	16950	4.4
Gavialis gangeticus	695665	29926	4.3
Acipenser nudiventris	521938	22120	4.2

Binomial	**Range Area (km^2)**	**PA Coverage (km^2)**	**% Coverage**
Chitra vandijki	226869	9161	4.0
Hemibagrus maydelli	218848	8186	3.7
Ictalurus furcatus	1147486	41791	3.6
Macrochelys temminckii	1036973	36433	3.5
Scomberomorus sinensis	48431	1623	3.4
Pylodictis olivaris	3056769	98801	3.2
Polyodon spathula	1016185	31721	3.1
Pusa hispida ssp. *ladogensis*	17988	514	2.9
Scaphirhynchus albus	287261	8189	2.9
Pusa caspica	374357	9660	2.6
Luciobarbus esocinus	542507	7999	1.5

Table SG3 Number and percentage of species affected within each IUCN Red List threat category (level 1).

Threat Category (Level 1)	**SpRich**	**pcnt**	**FSpRich**	**Fishes%**	**RSpRich**	**Reptiles%**	**MSpRich**	**Mammals%**
Fishing & harvesting aquatic resources	66	82.5	42	52.5	13	16.2	11	13.8
Dams & water management/use	52	65.0	36	45.0	5	6.2	11	13.8
Agricultural & forestry effluents	35	43.8	23	28.7	3	3.8	9	11.2
Industrial & military effluents	34	42.5	22	27.5	2	2.5	10	12.5
Domestic & urban waste water	25	31.2	18	22.5	2	2.5	5	6.2
Commercial & industrial areas	19	23.8	12	15.0	2	2.5	5	6.2
Shipping lanes	19	23.8	12	15.0	NA	NA	7	8.8
Housing & urban areas	18	22.5	10	12.5	3	3.8	5	6.2
Invasive non-native/alien species/diseases	16	20.0	14	17.5	1	1.2	1	1.2
Problematic native species/diseases	16	20.0	9	11.2	2	2.5	5	6.2
Hunting & trapping terrestrial animals	15	18.8	1	1.2	7	8.8	7	8.8

Threat Category (Level 1)	SpRich	pcnt	FSpRich	Fishes%	RSpRich	Reptiles%	MSpRich	Mammals%
Droughts	12	15.0	5	6.2	1	1.2	6	7.5
Mining & quarrying	10	12.5	6	7.5	2	2.5	2	2.5
Annual & perennial non-timber crops	10	12.5	2	2.5	4	5.0	4	5.0
Marine & freshwater aquaculture	10	12.5	6	7.5	2	2.5	2	2.5
Excess energy	9	11.2	5	6.2	NA	NA	4	5.0
Temperature extremes	8	10.0	5	6.2	1	1.2	2	2.5
Logging & wood harvesting	8	10.0	5	6.2	1	1.2	2	2.5
Habitat shifting & alteration	6	7.5	2	2.5	2	2.5	2	2.5
Garbage & solid waste	6	7.5	6	7.5	NA	NA	NA	NA
Recreational activities	6	7.5	3	3.8	NA	NA	3	3.8
Livestock farming & ranching	5	6.2	1	1.2	1	1.2	3	3.8
Tourism & recreation areas	5	6.2	2	2.5	1	1.2	2	2.5

Threat Category (Level 1)	**SpRich**	**pcnt**	**FSpRich**	**Fishes%**	**RSpRich**	**Reptiles%**	**MSpRich**	**Mammals%**
War, civil unrest & military exercises	5	6.2	NA	NA	NA	NA	5	6.2
Other ecosystem modifications	4	5.0	NA	NA	2	2.5	2	2.5
Other threat	4	5.0	4	5.0	NA	NA	NA	NA
Storms & flooding	3	3.8	1	1.2	NA	NA	2	2.5
Oil & gas drilling	2	2.5	NA	NA	1	1.2	1	1.2
Roads & railroads	2	2.5	1	1.2	NA	NA	1	1.2
Wood & pulp plantations	2	2.5	NA	NA	1	1.2	1	1.2
Work & other activities	2	2.5	NA	NA	1	1.2	1	1.2
Air-borne pollutants	1	1.2	1	1.2	NA	NA	NA	NA
Fire & fire suppression	1	1.2	NA	NA	NA	NA	1	1.2
Introduced genetic material	1	1.2	NA	NA	1	1.2	NA	NA

Abbreviations: SpRich, Species richness; FSpRich, Fish species richness; RSpRich, Reptile species richness, MSpRich, Mammal species richness; pcnt, percent; NA, not applicable.

Table SG4 Number and percentage of species affected within each IUCN Red List threat category (level 2).

Threat Category (Level 2)	**SpRich**	**pcnt**	**FSpRich**	**Fishes%**	**RSpRich**	**Reptiles%**	**MSpRich**	**Mammals%**
Intentional use: (subsistence/small scale) [harvest]	46	57.5	34	42.5	7	8.8	5	6.2
Dams (size unknown)	44	55.0	33	41.2	2	2.5	9	11.2
Type Unknown/ Unrecorded	33	41.2	22	27.5	3	3.8	8	10.0
Unintentional effects: (subsistence/small scale) [harvest]	31	38.8	23	28.7	5	6.2	3	3.8
Intentional use: (large scale) [harvest]	28	35.0	23	28.7	2	2.5	3	3.8
Unintentional effects: (large scale) [harvest]	28	35.0	18	22.5	1	1.2	9	11.2
Soil erosion, sedimentation	21	26.2	16	20.0	2	2.5	3	3.8
Intentional use (species is the target)	13	16.2	NA	NA	7	8.8	6	7.5
Unspecified species	13	16.2	12	15.0	NA	NA	1	1.2
Sewage	12	15.0	9	11.2	NA	NA	3	3.8
Oil spills	11	13.8	8	10.0	NA	NA	3	3.8
Motivation Unknown/ Unrecorded	10	12.5	6	7.5	NA	NA	4	5.0

Threat Category (Level 2)	SpRich	pcnt	FSpRich	Fishes%	RSpRich	Reptiles%	MSpRich	Mammals%
Scale Unknown/ Unrecorded	10	12.5	6	7.5	2	2.5	2	2.5
Abstraction of ground water (unknown use)	8	10.0	6	7.5	NA	NA	2	2.5
Persecution/ control	7	8.8	1	1.2	3	3.8	3	3.8
Large dams	6	7.5	5	6.2	1	1.2	NA	NA
Agro-industry farming	6	7.5	1	1.2	2	2.5	3	3.8
Herbicides and pesticides	6	7.5	5	6.2	NA	NA	1	1.2
Thermal pollution	6	7.5	5	6.2	NA	NA	1	1.2
Abstraction of surface water (agricultural use)	4	5.0	2	2.5	1	1.2	1	1.2
Nutrient loads	4	5.0	4	5.0	NA	NA	NA	NA
Named species	4	5.0	2	2.5	2	2.5	NA	NA
Noise pollution	4	5.0	1	1.2	NA	NA	3	3.8
Run-off	4	5.0	3	3.8	NA	NA	1	1.2
Small-holder farming	4	5.0	1	1.2	1	1.2	2	2.5

Threat Category (Level 2)	**SpRich**	**pcnt**	**FSpRich**	**Fishes%**	**RSpRich**	**Reptiles%**	**MSpRich**	**Mammals%**
Nomadic grazing	3	3.8	NA	NA	NA	NA	3	3.8
Abstraction of surface water (commercial use)	2	2.5	1	1.2	NA	NA	1	1.2
Abstraction of surface water (domestic use)	2	2.5	1	1.2	NA	NA	1	1.2
Abstraction of surface water (unknown use)	2	2.5	NA	NA	2	2.5	NA	NA
Agro-industry plantations	2	2.5	NA	NA	1	1.2	1	1.2
Unintentional effects (species is not the target)	2	2.5	NA	NA	1	1.2	1	1.2
Abstraction of ground water (agricultural use)	1	1.2	NA	NA	1	1.2	NA	NA
Industrial aquaculture	1	1.2	NA	NA	1	1.2	NA	NA
Seepage from mining	1	1.2	1	1.2	NA	NA	NA	NA
Small-holder grazing, ranching or farming	1	1.2	NA	NA	NA	NA	1	1.2
Trend Unknown/ Unrecorded	1	1.2	NA	NA	NA	NA	1	1.2

Abbreviations: SpRich, Species richness; FSpRich, Fish species richness; RSpRich, Reptile species richness, MSpRich, Mammal species richness; pcnt, percent; NA, not applicable.

Table SG5 Number of all assessed freshwater species with 'Extant' and 'Probably Extant' records (PRESENCE = 1 and 2, P1&P2) and percentage spatial overlap with the megafauna species ranges.

	Amphibians	**Birds**	**Decapods**	**Fishes**	**Mammals**	**Molluscs**	**Odonata**	**Plants**	**Turtles**	**All Taxa**
A: Number of assessed species	4375	2283	2630	7620	150	3495	2784	1880	183	25400
B: Number of assessed species with P1&2 records	3972	2016	2441	5956	122	1836	1313	1201	167	19024
C: Number of assessed species with P1&2 records in the megafauna range	3739	1970	2266	5648	119	1398	1285	1094	160	17679
C as % of A	85	86	86	74	79	40	46	58	87	70
C as % of B	94	98	93	95	98	76	98	91	96	93

Note: Decapods comprise crabs, crayfish and shrimps.

Table SG6 Number of all assessed threatened (i.e. CR, EN, VU) freshwater species with 'Extant' and 'Probably Extant' records (PRESENCE = 1 and 2, P1&P2) and percentage spatial overlap with the megafauna species ranges.

	Amphibians	**Birds**	**Decapods**	**Fishes**	**Mammals**	**Molluscs**	**Odonata**	**Plants**	**Turtles**	**All Taxa**
A: Number of threatened species	1171	226	483	1824	54	1021	265	319	102	5465
B: Number of threatened species with P1&2 records	1071	204	421	1237	43	623	72	203	92	3966
C: Number of threatened species with P1&2 records in megafauna range	960	182	387	1058	41	364	64	148	89	3293
C as % of A	82	81	80	58	76	36	24	46	87	60
C as % of B	90	89	92	86	95	58	89	73	97	83

Note: Decapods comprise crabs, crayfish and shrimps.

Table SG7 Megafauna species representation with international conventions; Convention on Migratory Species (CMS) and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Acipenser gueldenstaedtii		1999		1998	
Acipenser mikadoi		1999		1998	
Acipenser nudiventris		1999		1998	
Acipenser persicus		1999		1998	
Acipenser schrenckii		1999		1998	
Acipenser sinensis		1999		1998	
Acipenser stellatus	1985	1999		1998	
Acipenser sturio	2005	1999	1983		
Catlocarpio siamensis					
Huso dauricus		1999		1998	
Huso huso		1979		1998	
Maccullochella peelii					
Pangasianodon gigas	1979		1975		
Pangasius sanitwongsei					
Pristis pectinata	2014	2014	2007		
Pristis pristis	2014	2014	2007		
Psephurus gladius		1999		1998	
Lipotes vexillifer			1979		
Alligator sinensis			1975		
Chitra chitra			2013		
Chitra vandijki			2013		
Crocodylus intermedius			1975		
Crocodylus rhombifer			1975		

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Crocodylus siamensis			1975		
Gavialis gangeticus	1979		1975		
Mecistops cataphractus			1992		
Nilssonia leithii				2013	
Nilssonia nigricans			1975		
Orlitia borneensis				2013	
Podocnemis expansa	1979	1979		1975	
Rafetus swinhoei				2013	
Acipenser baerii		1999	-	1998	
Argyrosomus hololepidotus					
Himantura polylepis					
Hucho hucho					
Hypselobarbus mussullah					
Lates angustifrons					
Probarbus jullieni			1975		
Probarbus labeamajor					
Scaphirhynchus albus				1998	
Tor putitora					
Choeropsis liberiensis				1975	
Kobus megaceros					
Platanista gangetica ssp. *gangetica*	2002	1991	1981		
Platanista gangetica ssp. *minor*	2002	1999	1981		
Pusa caspica					
Chitra indica				2013	
Pelochelys cantorii				2003	

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Hucho taimen					
Luciobarbus esocinus					
Megalops atlanticus					
Polyodon spathula				1998	
Hippopotamus amphibius				1995	
Neophocaena asiaeorientalis ssp. *asiaeorientalis*		1979*[a]			
Orcaella brevirostris	2009	1991[b]	2005		
Trichechus inunguis		2002	1975		
Trichechus manatus	1999	1999	1975		
Trichechus senegalensis	2009	2002[c]	2013		
Amyda cartilaginea				2005	
Crocodylus acutus			2005	2005	
Crocodylus palustris			1975		
Macrochelys temminckii					2006
Osteolaemus tetraspis			1992		
Pelochelys bibroni				2003	
Tomistoma schlegelii			1975		
Trionyx triunguis				2016	
Acipenser medirostris		1999		1998	
Acipenser oxyrinchus				1998	
Arius gigas					

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Carcharhinus leucas					
Hypophthalmichthys molitrix					
Wallago attu					
Acipenser fulvescens		1979		1998	
Acipenser transmontanus				1998	
Chrysichthys cranchii					
Clarias gariepinus					
Hemibagrus maydelli					
Hemibagrus wyckioides					
Heterobranchus longifilis					
Hydrocynus goliath					
Ictalurus furcatus					
Labeo rohita					
Lates niloticus					
Morone saxatilis					
Salmo salar					
Salmo trutta					
Silurus glanis					
Hydrochoerus hydrochaeris					
Kobus leche				1979	
Phoca vitulina mellonae					
Pusa sibirica					
Tragelaphus spekii					
Alligator mississippiensis				1979	
Apalone ferox					2016

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Caiman crocodilus				1977	
Caiman latirostris			1997	1997	
Caiman yacare				1977	
Crocodylus johnsoni				1977	
Crocodylus moreletii			2010	2010	
Crocodylus niloticus			2010	2010	
Crocodylus porosus		1979	1995	1995	
Melanosuchus niger			2007	2007	
Paleosuchus palpebrosus				1977	
Arapaima gigas				1975	
Potamotrygon brachyura					2017
Scomberomorus sinensis					
Wallago micropogon					
Inia geoffrensis		1991		2003	
Sotalia fluviatilis		1979	1979		
Arapaima agassizii					
Arapaima leptosoma					
Arapaima mapae					
Atractosteus spatula					
Brachyplatystoma filamentosum					
Colossoma macropomum					
Ctenopharyngodon idella					
Eleutheronema tetradactylum					
Lates calcarifer					

Binomial	**CMS Appendices**		**CITES Appendices**		
	I	II	I	II	III
Oncorhynchus tshawytscha					
Polydactylus macrochir					
Pseudoplatystoma corruscans					
Pseudoplatystoma fasciatum					
Pylodictis olivaris					
Silurus soldatovi					
Wallago leerii					
Zungaro zungaro					
Inia araguaiaensis				2014	
Inia boliviensis				2003	
Pusa hispida ssp. *ladogensis*					
Pusa hispida ssp. *saimensis*					
Eunectes murinus				1977	
Osteolaemus osborni			1992		

Note: *Parent species; [a]ASCOBANS; [b]CMS, Pacific Islands Cetaceans; [c]CMS, Western African Aquatic Mammals

Table SG8 Weight references for each megafauna species.

Binomial	**Weight (kg)**	**Reference**
Acipenser baerii	210	Kottelat and Freyhof (2007)
Acipenser fulvescens	125	Carlander (1969)
Acipenser gueldenstaedtii	115	Birstein (1993)
Acipenser medirostris	159	Peterson, Eschmeyer, and Herald (1999)
Acipenser mikadoi	80	Shilin (1995); Shmigirilov, Mednikova, and Israel (2007)
Acipenser nudiventris	80	Rochard, Williot, Castelnaud, and Lepage (1991)
Acipenser oxyrinchus	368	Mangin (1964)
Acipenser persicus	70	Vecsei and Artyukhin (2001)
Acipenser schrenckii	190	Krykhtin and Svirskii (1997)
Acipenser sinensis	600	Zhang (2001)
Acipenser stellatus	80	Frimodt (1995)
Acipenser sturio	400	Muus (1968)
Acipenser transmontanus	816	Lamb (1986)
Alligator mississippiensis	473	Lobaina (2014)
Alligator sinensis	38	J. Thorbjarnarson, Wang, and He (2001)
Andrias davidianus	50	Wang et al. (2004)
Arapaima spp.	200	Castello and Stewart (2010)
Argyrosomus hololepidotus	71	Trewavas (1977)
Arius gigas	50	Ita (1984)
Atractosteus spatula	137	Stone (2007)
Brachyplatystoma filamentosum	200	Boujard (1997)
Caiman crocodilus	58	Ojasti (1996)
Caiman latirostris	62	Ferraz, Bonach, and Verdade (2005)
Caiman yacare	58	Ojasti (1996)

Binomial	**Weight (kg)**	**Reference**
Carcharhinus leucas	238	Wintner, Dudley, Kistnasamy, and Everett (2002)
Catlocarpio siamensis	300	Roberts and Warren (1994)
Chitra chitra	202	Kitimasak, Thirakhupt, Boonyaratpalin, and MOLL (2005)
Chitra indica	57	I. Das and Singh (2014)
Chitra vandijki	100	Platt, Platt, Win, and Rainwater (2009)
Choeropsis liberiensis	275	Boisserie (2007)
Chrysichthys cranchii	135	Risch and Bagridae (1986)
Clarias gariepinus	60	Robins (1991)
Crocodylus acutus	173	Lobaina (2014)
Crocodylus intermedius	380	Lobaina (2014)
Crocodylus johnsoni	31	Walsh (1989)
Crocodylus moreletii	58	Lobaina (2014)
Crocodylus niloticus	200	Hutton (1987)
Crocodylus palustris	200	Lobaina (2014)
Crocodylus porosus	2000	Ogamba and Abowei (2012)
Crocodylus rhombifer	215	Lobaina (2014)
Crocodylus siamensis	50	Daltry et al. (2003)
Ctenopharyngodon idella	50	Cudmore and Mandrak (2004)
Eleutheronema tetradactylum	145	Grant (1978)
Eunectes murinus	200	Miller, Radi, Stiver, and Thornhill (2004)
Gavialis gangeticus	160	Stevenson and Whitaker (2010)
Hemibagrus maydelli	58	Jayaram (1995)
Hemibagrus wyckioides	80	Hee and Rainboth (1999); Roberts (1993)
Heterobranchus longifilis	55	Skelton (2001)
Himantura chaophraya	600	Last and Stevens (2009)
Hippopotamus amphibius	4500	Coughlin and Fish (2009)

Binomial	Weight (kg)	Reference
Hucho hucho	52	Nikolskii (1957)
Hucho taimen	105	Kottelat and Freyhof (2007)F
Huso dauricus	1000	Krykhtin and Svirskii (1997)
Huso huso	3200	Kottelat and Freyhof (2007)
Hydrochoerus hydrochaeris	81	Ferraz et al. (2005)
Hydrocynus goliath	50	Robins (1991)
Hypophthalmichthys molitrix	50	Krykhtin and Svirskii (1997)
Hypselobarbus mussullah	90	Talwar and Jhingran (1991)
Ictalurus furcatus	68	Frimodt (1995)
Inia araguaiaensis	207	Da Silva (2009)
Inia boliviensis	207	Da Silva (2009)
Inia geoffrensis	207	Da Silva (2009)
Kobus leche	128	Estes (1991)
Kobus megaceros	113	Bercovitch, Loomis, and Rieches (2009)
Labeo rohita	45	Frimodt (1995)
Lates angustifrons	100	Stone (2007)
Lates calcarifer	60	Larson (2001)
Lates niloticus	200	Ribbink (1987)
Lipotes vexillifer	237	Kaiya Zhou (1986); K Zhou, Qian, and Li (1977)
Luciobarbus esocinus	140	Robins (1991)
Maccullochella peelii	113	Rowland (1989)
Macrochelys temminckii	90	Jensen and Birkhead (2003)
Mecistops cataphractus	230	Lobaina (2014)
Megalops atlanticus	161	Claro (1994)

Binomial	**Weight (kg)**	**Reference**
Melanosuchus niger	400	Cardoso, de Souza, Menezes, Pereira, and Tortelly (2012); Da Silveira, Ramalho, Thorbjarnarson, and Magnusson (2010); J. B. Thorbjarnarson (2010)
Morone saxatilis	57	Peterson et al. (1999)
Neophocaena asiaeorientalis asiaeorientalis	61	Yang et al. (2008)
Oncorhynchus tshawytscha	61	Morrow (1980)
Orcaella brevirostris	133	Arnold and Heinsohn (1996)
Orlitia borneensis	50	Halliday and Adler (2002)
Osteolaemus osborni	80	Lobaina (2014)
Osteolaemus tetraspis	80	Lobaina (2014)
Paleosuchus palpebrosus	37	Campos, Sanaiotti, and Magnusson (2010)
Pangasianodon gigas	350	Kottelat (2001)
Pangasius sanitwongsei	300	Roberts and Vidthayanon (1991)
Pelochelys bibroni	120	Bonin, Devaux, and Dupré (2006)
Pelochelys cantorii	43	I Das (2008)
Phoca vitulina spp. *mellonae*	70	Smith (2000)
Platanista gangetica	108	T. Jefferson, Leatherwood, and Webber (1994)
Platanista gangetica ssp. *minor*	110	Waqas, Malik, and Khokhar (2012)
Podocnemis expansa	90	Clauson, Timm, and Albuja Viteri (1989)
Polydactylus macrochir	30	Motomura, Iwatsuki, Kimura, and Yoshino (2000)
Polyodon spathula	90	McClane (1978)
Potamotrygon brachyura	120	Oddone, Canziani, and Charvet (2012)
Pristis pristis	600	Stehman (1981)
Pristis pectinata	350	Stehman (1981)

Binomial	**Weight (kg)**	**Reference**
Probarbus jullieni	70	Roberts and Baird (1995)
Probarbus labeamajor	70	Roberts and Warren (1994)
Psephurus gladius	300	Mims and Georgi (1993)
Pseudoplatystoma corruscans	100	Tavares (1997)
Pseudoplatystoma fasciatum	70	Le Bail, Keith, and Planquette (2000)
Pusa caspica	66	Ikemoto et al. (2004)
Pusa hispida ssp. *ladogensis*	70	Popov (1979)
Pusa hispida ssp. *saimensis*	100	Sipilä and Hyvärinen (1998)
Pusa sibirica	90	Popov (1982)
Pylodictis olivaris	50	Brown, Perillo, Kwak, and Horwitz (2005)
Rafetus swinhoei	115	Jian, Hai-Tao, Cheng, and Lian-Xian (2013)
Salmo salar	46	Dymond (1963)
Salmo trutta	50	Muus and Dahlstrom (1981)
Scaphirhynchus albus	130	Rochard et al. (1991)
Scomberomorus sinensis	131	Collette et al. (2011)
Silurus glanis	306	Frimodt (1995)
Silurus soldatovi	40	Berg (1962)
Sotalia fluviatilis	40	T. A. Jefferson (1993)
Tomistoma schlegelii	210	Lobaina (2014)
Tor putitora	54	Rahman (1989)
Tragelaphus spekii	100	Estes (1991)
Trichechus inunguis	480	Amaral, da Silva, and Rosas (2010)
Trichechus manatus	1500	Spellman (2014)
Trichechus senegalensis	500	Dodman, Dagou Diop, and Beye (2012)
Trionyx triunguis	45	Rozner and Shaines (2010)
Wallago attu	45	Achakzai, Baloch, Saddozai, and Memon (2013)

Binomial	**Weight (kg)**	**Reference**
Wallago leerii	86	Roberts (1989)
Wallago micropogon	96	Roberts (1993)
Zungaro zungaro	50	Le Bail et al. (2000)

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Statement of academic integrity

I hereby certify that the submitted thesis "Diversity and risk patterns of freshwater megafauna: A global perspective" is my own work and that all published or other sources of material consulted in its preparation have been indicated. I have clearly pointed out any collaboration that has taken place with other researchers and stated my own personal share in the investigations in the Thesis outline. I confirm that this work has not been submitted to any other university or examining body for a comparable academic award.

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List of publications

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12. **He, F.**, Langhans, S.D., Zarfl, C., Wanke, R., Tockner, K. & Jähnig, S.C. Extinction risks of freshwater megafauna: The combined effects of life-history traits and anthropogenic threats. (to be submitted)

13. **He, F.**, Jähnig, S.C., Wetzig A. & Langhans, S.D. The untapped potential of cover images to promote underrepresented biodiversity (to be submitted).

14. **He, F.** & Jähnig, S.C. Put freshwater megafauna on the table before they are eaten to extinction (to be submitted).