Contributed Paper

Combined effects of life-history traits and human impact on extinction risk of freshwater megafauna

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Abstract: Megafauna species are intrinsically vulnerable to human impact. Freshwater megafauna (i.e., freshwater animals ≥30 kg, including fishes, mammals, reptiles, and amphibians) are subject to intensive and increasing threats. Thirty-four species are listed as critically endangered on the International Union for Conservation of Nature (IUCN). Red List of Threatened Species, the assessments for which are an important basis for conservation actions but remain incomplete for 49 (24%) freshwater megafauna species. Consequently, the window of opportunity for protecting these species could be missed. Identifying the factors that predispose freshwater megafauna to extinction can help predict their extinction risk and facilitate more effective and proactive conservation actions. Thus, we collated 8 life-history traits for 206 freshwater megafauna species. We used generalized linear mixed models to examine the relationships between extinction risk based on the IUCN Red List categories and the combined effect of multiple traits, as well as the effect of human impact on these relationships for 157 classified species. The most parsimonious model included human impact and traits related to species' recovery potential including life span, age at maturity, and fecundity. Applying the most parsimonious model to 49 unclassified species predicted that 17 of them are threatened. Accounting for model predictions together with IUCN Red List assessments, 50% of all freshwater megafauna species are considered threatened. The Amazon and Yangtze basins emerged as global diversity hotspots of threatened freshwater megafauna, in addition to existing hotspots, including the Ganges-Brahmaputra and Mekong basins and the Caspian Sea region. Assessment and monitoring of those species predicted to be threatened are needed, especially in the Amazon and Yangtze basins. Investigation of life-history traits and trends in population and distribution, regulation of overexploitation, maintaining river connectivity, implementing protected areas focusing on freshwater ecosystems, and integrated basin management are required to protect threatened freshwater megafauna in diversity hotspots.

Keywords: assessment, biodiversity, body size, IUCN Red List, prediction, recovery potential, threats, vertebrate

Efectos Combinados de los Rasgos de la Historia de Vida y el Impacto Humano sobre el Riesgo de Extinción de la Megafauna de Agua Dulce

Resumen: Las especies de megafauna son intrínsecamente vulnerables al impacto humano. La megafauna de agua dulce (es decir, los animales ≥30 kg, incluyendo peces, mamíferos, reptiles y anfibios) está sujeta a amenazas

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***Article impact statement**: Life-history traits and human impact jointly determine extinction risk of freshwater megafauna.*
Paper submitted August 16, 2019; revised manuscript accepted July 5, 2020.

Conservation Biology, Volume 35, No. 2, 643–653

DOI: 10.1111/cobi.13590

intensivas y en aumento. La Lista Roja de la UICN (Unión Internacional para la Conservación de la Naturaleza) lista a 34 especies en peligro crítico de extinción. Las evaluaciones para esta lista son un cimiento importante para las acciones de conservación, pero permanecen incompletas para 49 (24%) de las especies de megafauna de agua dulce. Como consecuencia, la ventana de oportunidad para la protección de estas especies podría perderse. La identificación de los factores que predisponen a la megafauna de agua dulce a la extinción puede ayudar a predecir el riesgo de extinción para cada especie y facilitar acciones de conservación más efectivas y proactivas. Por lo anterior, recopilamos ocho rasgos de historia de vida para 206 especies de megafauna de agua dulce. Usamos modelos lineales generalizados mixtos para examinar las relaciones entre el riesgo de extinción medido con base en las categorías de la Lista Roja de la UICN y el efecto combinado de diferentes rasgos, así como el efecto del impacto humano sobre estas relaciones para 157 especies clasificadas. El modelo más parsimonioso incluyó al impacto humano y a los rasgos relacionados con el potencial de recuperación de las especies como el ciclo de vida, edad de madurez y fecundidad. La aplicación de este modelo a las 49 especies sin clasificación pronosticó que 17 de ellas están amenazadas. Si consideramos las predicciones del modelo junto con las evaluaciones de la Lista Roja de la UICN, el 50% de todas las especies de megafauna de agua dulce están consideradas como amenazadas. Las cuencas del Amazonas y del Yangtze surgieron como puntos calientes de diversidad mundial, junto con las cuencas del Ganges-Brahmaputra y el Mekong y la región del mar Caspio. Es urgente evaluar y monitorear a aquellas especies que se pronostica estén amenazadas, especialmente en las cuencas del Amazonas y del Yangtze. Se requieren investigaciones sobre los rasgos de la historia de vida y las tendencias poblacionales y de distribución, la regulación de la sobreexplotación, el mantenimiento de la conectividad entre ríos, la implementación de áreas protegidas enfocadas en los ecosistemas de agua dulce y un manejo integrado de cuencas para proteger a la megafauna de agua dulce en los puntos calientes de diversidad.

Palabras Clave: amenazas, biodiversidad, evaluación, Lista Roja UICN, potencial de recuperación, predicción, tamaño corporal, vertebrado

摘要: 大型淡水动物包含体重超过30千克的鱼类, 哺乳动物, 爬行动物和两栖动物。这些动物易受人类活动影响且面临着日益增长的威胁。其中34种动物已经被国际自然保护联盟(IUCN)濒危物种红色名录评估为极危; 与此同时, 49种大型淡水动物未受到充分的灭绝风险评估。保护这些动物的时机可能会因此错过。鉴别影响大型淡水动物灭绝风险的因素能够帮助开展积极主动且有效的保护行动。我们收集了206个物种的8类生活史特征并运用广义混合线性模型分析了其中157种受到充分评估的物种的红色名录等级与它们的生活史特征以及分布范围内人类活动强度的关系。筛选出的最优模型包含了人类活动强度以及与物种恢复潜能相关的生活史特征, 如寿命, 性成熟时间和繁殖能力。49种未受到充分评估的大型淡水动物中的17种被最优模型预测为受威胁物种。如果综合考虑红色名录评估和模型预测结果, 全球半数大型淡水动物应该被列为受威胁物种。长江和亚马逊流域也应同恒河, 湄公河以及里海区域一起被视为受威胁的大型淡水动物多样性热点区域。为了保护受威胁的大型淡水动物, 在这些多样性热点地区应进行物种生活史调查和物种种群数量和分布范围监测并限制过度捕捞, 维持河流的连通性, 以及建立保护区。

关键词: 生物多样性, 评估, IUCN红色名录, 脊椎动物, 物种大小, 恢复潜能, 预测, 威胁

Introduction

Accelerated biodiversity loss is one of the biggest challenges humankind is currently facing (Pimm et al. 2014; Ceballos et al. 2015; IPBES 2019); species extinction rates are 100–1000 times higher than background rates (Ceballos et al. 2015; De Vos et al. 2015). The extinction risk of species depends on their intrinsic traits, human impact, and the interaction among them (Owens & Bennett 2000; González-Suárez et al. 2013; Murray et al. 2014).

Life-history traits play a crucial role in determining the vulnerability of species to extinction (e.g., Reynolds et al. 2005; Pearson et al. 2014; Wang et al. 2018). Hence, quantifying the relationship between species traits and extinction risk has been of increasing interest in ecological and conservation research (Cardillo & Meijaard 2012; Gonzalez-Suarez et al. 2012; Murray et al. 2014). Previous studies show that large 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 life span, late maturity, and low population density. Consequently, it is argued that large-bodied animals (i.e., megafauna) are particularly susceptible to extinction (Ripple et al. 2016; Ripple et al. 2019). However, this hypothesis has been challenged. Small-bodied fish and amphibian species, for example, are at similar or even higher extinction risk than their larger counterparts (Olden et al. 2007; Kopf et al. 2017; Ripple et al. 2017). Hence, extinction risk of species is most likely determined by a combination of several traits rather than a single trait (McKinney 1997; Lee & Jetz 2011; Pearson et al. 2014).

Human impact on the environment is increasing in the Anthropocene, accelerating biodiversity loss (Pimm et al. 2014; Ceballos et al. 2015). Freshwaters are among the most threatened ecosystem globally (Reid et al. 2019; Tickner et al. 2020). Freshwater species face not only intense threats in the aquatic environment, such as overexploitation, flow modification, fragmentation, and species invasion, but are also influenced by land-based processes including land-use change and pollution (Vörösmarty et al. 2010). Understanding how intrinsic traits and human impact shape species' extinction risk can help predict extinction risk of unclassified species as well as facilitate proactive conservation actions (e.g., predicting their susceptibility to future threats) (Cardillo & Meijaard 2012; Murray et al. 2014).

The conservation status assigned by the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (IUCN 2018) is widely used as a proxy of species' extinction risk (Gonzalez-Suarez et al. 2012; Murray et al. 2014). According to IUCN Red List assessments, 54% of all classified freshwater megafauna species are threatened (He et al. 2018). From 1970 to 2012, global freshwater megafauna populations declined 88% (He et al. 2019). At the same time, they are underrepresented in monitoring and conservation actions, compared with terrestrial or marine megafauna (Carrizo et al. 2017; He & Jähnig 2019). For example, 49 of 207 freshwater megafauna species remain unclassified (i.e. listed as data deficient or not evaluated) (IUCN 2018) due to insufficient data on population size, distribution pattern, underlying threats, and lack of expertise and financial resources.

In light of the current, unprecedented freshwater megafauna crisis, there is an urgent need to identify species that are at major risk of extinction and to prioritize conservation actions accordingly. Therefore, a challenge is to fill the information gap in IUCN Red List assessments of freshwater megafauna. Given that most unclassified freshwater megafauna species occur in the Global South and there are few data on their current population size and distributions (He et al. 2018, 2019), completing IUCN Red List assessments requires considerable expert engagement and is time consuming and likely expensive. A promising approach to close the information gap is to predict their probabilities of being threatened based on relationships between life-history traits, human impact, and extinction risk (Cardillo & Meijaard 2012; Murray et al. 2014).

Researchers emphasized previously the importance of body size and species' recovery potential in determining extinction risk of vertebrates (e.g., Hutchings et al. 2012; Kopf et al. 2017; Wang et al. 2018). Hence, we hypothesize that body size and traits related to species' recovery potential (e.g., fecundity and age at maturity) determine the vulnerability of freshwater megafauna to extinction. In addition, freshwater megafauna species are subject to intense human impact, including overexploitation, habitat degradation, and fragmentation (Carrizo et al. 2017; He et al. 2017; Ripple et al. 2019). We expect that including interactions between life-history traits and human impact will further improve the model performance in explaining extinction risk of freshwater megafauna—compared with solely trait-based models. Thus, we first explored the relationship between extinction risk of freshwater megafauna and individual traits. In the second step, we examined the relationships between extinction risk of freshwater megafauna and the combined effect of multiple traits and the influence of human impact (i.e., quantified as incident biodiversity threat index [IBTI], an aggregate index that integrates information on multiple threats; Vörösmarty et al. 2010) on these relationships by applying generalized linear mixed models. Finally, based on these relationships, we aimed to predict the extinction risk of 49 unclassified freshwater megafauna species based on the most parsimonious models. Accounting for IUCN Red List assessments and model predictions, we mapped the global distribution of threatened freshwater megafauna and featured the basins in urgent need of assessment and conservation.

Methods

Extinction Risk

We used conservation status of freshwater megafauna assigned by the IUCN Red List as a proxy for extinction risk. Following the IUCN Red List (IUCN 2018), we considered threatened species those listed as critically endangered, endangered, or vulnerable and species listed as least concern or near threatened as not threatened. Among the 158 species with sufficient assessments, 85 species were categorized as threatened and 72 species as not threatened. One species (i.e., the black softshell turtle [*Nilssonia nigricans*]) was excluded from further analyses because it was assessed as extinct in the wild and could not be considered either threatened or not threatened. The remaining 49 species were listed as not evaluated (i.e., no assessment had been conducted to evaluate the conservation status of the taxon) or data deficient (i.e., taxon assessed but existing information is insufficient to evaluate conservation status [IUCN 2018]).

Life-History Traits

For each freshwater megafauna species, we initially compiled information on 12 traits but only 8 traits were included in the analysis based on data availability and variation (details on all traits and trait selection are in Supporting Information): maximum body mass, life span, migration, age at maturity (female), fecundity (i.e., average number of offspring), offspring type, habitat type, and feeding habits. To avoid autocorrelation and circularity, size of geographic range was excluded intentionally because it is used by the IUCN Red List as one of the key criteria to evaluate extinction risk of species (IUCN 2018).

Relationships Among Extinction Risk, Traits, and Human Impact

To explore the relationships among extinction risk of freshwater megafauna and their traits and human impact, a 2-step approach was used. In the first step, relationships between extinction risk of freshwater megafauna and individual traits were examined separately. When traits were measured quantitatively (i.e., maximum body mass, life span, and age at maturity), the interrelationships were examined by applying generalized linear mixed models (GLMMs) with binomial distribution. This allowed us to estimate relationships between continuous data on traits and binomial data on extinction risk (threatened or not threatened). For species assessed as critically endangered, endangered, or vulnerable, the probability of being threatened was 1, whereas the probability of being threatened for species assessed as least concern or near threatened was 0. In this step, combined effects of different traits were not considered. Only 1 trait was used as the fixed factor in each GLMM, and taxonomic information (class, order, and family) was included in the models as a nested random factor to control for the potential influence of phylogenetic relatedness (i.e., phylogenetically related species could have more similar traits). All the quantitative trait data were $\log_{10}$ transformed. When the traits (i.e., feeding habits, habitat type, migration, and offspring type) were described with categorized data, the proportion of threatened species in each category was compared. Although fecundity was quantified as the average number of offspring, we categorized the values into 5 levels according to the average number of offspring because information on the exact number of offspring remains unknown for 27% of all species, especially for fish (Supporting Information).

We also applied a GLMM with a nested random factor to examine the relationship between extinction risk of freshwater megafauna and the intensity of human impact. The intensity of overall human impact was measured with an average value of the incident biodiversity threat index (IBTI) within each species' distribution range. The IBTI is an aggregate index that combines information on multiple threats, including pollution, catchment disturbance, river fragmentation, harvesting pressure, and species invasion (Vörösmarty et al. 2010). It provides a comprehensive measurement of overall human impact on freshwater ecosystems. We converted information on freshwater megafauna distribution and IBTI into the HydroBASINS level 8 subcatchments (Lehner & Grill 2013). Details on the methods are in Supporting Information.

In the second step, we fitted GLMMs with binomial distribution to identify which combinations of traits and IBTI explained extinction risk of freshwater megafauna best. Two sets of models were fitted in this step. For the first set of models, only the traits of freshwater megafauna were used as fixed factors, and nested taxonomy was included as a random factor. In the second set of models, we added IBTI as a potential fixed factor to examine the influence of human impact on the linkage between extinction risk and traits. We included the 157 classified species in the models. With the 2 most parsimonious models selected in each set of models (i.e., 1 model included only traits and 1 model considered both traits and IBTI) based on the Akaike information criterion (AIC) (details in Supporting Information), we predicted extinction risks (i.e., threatened or not threatened) for the 49 unclassified species listed as not evaluated or data deficient. The GLMM models predicted the probabilities (range from 0 to 1) of the unclassified species being threatened. Species with the respective probabilities >0.5 were considered threatened (hereinafter referred to as medium scenario). To demonstrate potential variability in the extinction risk of these unclassified species, 2 additional scenarios were explored, with thresholds for the probability of 0.3 and 0.7, that reflected a strict or an optimistic categorization. For example, species with predicted threatened probabilities >0.3 were considered threatened under the strict scenario, whereas only species with predicted probabilities of being threatened >0.7 were considered threatened under the optimistic scenario.

Table 1. Summary of generalized linear mixed models (GLMMs) used to evaluate relationships between extinction risk of freshwater megafauna and individual traits and incident biodiversity threat index (IBTI).*.

Model	*Fixed factor*	*Estimate*	*SE*	z	p (>|z|)
1	Maximum body mass	1.40	0.56	2.51	0.012
2	Life span	3.23	0.98	3.30	<0.001
3	Age at maturity	3.03	0.91	3.32	<0.001
4	IBTI	3.18	1.59	2.00	0.046

**Only 1 trait or IBTI was used as the fixed factor in each GLMM, and taxonomic information (i.e., class, order, and family) was included as the nested random effect.*

Results

On average freshwater megafauna (all 207 species) had a maximum body mass of 169 kg (SD 276). Mean life span of these large animals was 40 years (SD 25), and mean age of maturity (female) was 6 years (SD 4). Without considering the combined impacts of traits, GLMMs showed that the probability of species being threatened was positively associated with maximum body mass (slope coefficient 1.40 [SE 0.56], $p = 0.012$), life span (3.23 [SE 0.98], $p < 0.001$), and age at maturity (3.03 [SE 0.91], $p < 0.001$) for the 157 classified freshwater megafauna species (Table 1). Freshwater megafauna with high fecundity (i.e., large number of offspring) included a lower

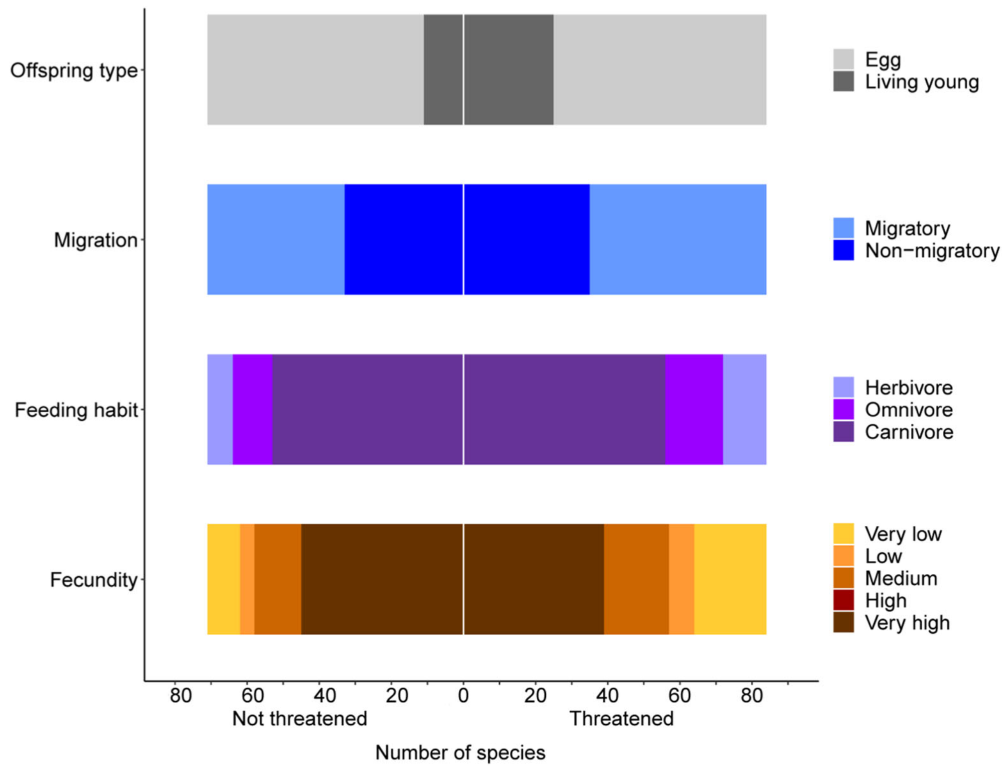

Figure 1. Numbers of threatened and nonthreatened species of freshwater megafauna with different traits. The category of fecundity was determined based on the average number of offspring (very low, 1–5; low, 6–20; medium, 21–200; high, 201–1000; very high, >1000).

Table 2. The 2 most parsimonious generalized linear mixed models selected in each set of models related to extinction risk of freshwater megafauna[a].

Set[b]	*Fixed factors*	*Estimate*	*SE*	z	p (>|z|)	*AIC*	*AUC*	R^2
1	Life span	9.66	2.98	3.25	0.001	177	0.70	0.62
	Age at maturity	19.43	5.91	3.29	0.001			
	Life span:age at maturity	−11.20	3.66	−3.06	0.002			
2	Life span	9.87	3.00	3.29	<0.001	170	0.77	0.66
	Age at maturity	21.84	6.25	3.50	<0.001			
	Fecundity	−0.70	0.28	−2.48	0.013			
	Life span:age at maturity	−12.34	3.81	−3.24	0.001			
	IBTI	5.65	1.95	2.90	0.004			

[a] *The response variable was the extinction risk of freshwater megafauna (i.e., threatened or not threatened). Taxonomy (i.e., class, order, and family) was used as a nested random factor to control for potential phylogenetic relatedness. Abbreviations: AIC, Akaike information criterion; AUC, area under the curve; IBTI, incident biodiversity threat index.*
[b] *The models in set 1 includes only traits, whereas models in set 2 include both traits and IBTI.*

proportion of threatened species compared with species with low fecundity (Fig. 1). Migratory and viviparous megafauna exhibited a greater extinction risk than non-migratory and egg-laying species, respectively. Herbivorous megafauna species had the highest proportion of threatened species, followed by omnivorous and carnivorous megafauna. A positive association was also observed between the probability of species being threatened and the average IBTI within their distribution ranges (3.18 [SE 1.59], $p = 0.046$) (Table 1).

When multiple life-history traits were considered in the GLMMs, life span (9.66 [SE 2.98], $p = 0.001$), age at maturity (19.43 [SE 5.91], $p = 0.001$), and their interaction (−11.20 [SE 3.66], $p = 0.002$) were included in the most parsimonious model (Table 2 & Supporting Information). When both life-history traits and IBTI were considered, life span (9.87 [SE 3.00], $p < 0.001$), age at maturity (21.84 [SE 6.25], $p < 0.001$), and their interaction (−12.34 [SE 3.81], $p = 0.001$) remained in the most parsimonious model, and fecundity (−0.70 [SE 0.28], $p = 0.013$) and IBTI (5.65 [SE 1.95], $p = 0.004$) were also included.

The predictions of the 2 most parsimonious models under the medium scenario were similar. Seventeen

Table 3. Freshwater megafauna species predicted to be threatened by the most parsimonious model considering both traits and human impact under the medium scenario (i.e. species with predicted threatened probability > 0.5).

Scientific name	*Common name*	*Taxonomic group*
Aspiorhynchus laticeps	big-head schizothoracin	fish
Elopichthys bambusa	yellowcheek carp	fish
Hypophthalmichthys nobilis	bighead carp	fish
Myxocyprinus asiaticus	Chinese sucker	fish
Mylopharyngodon piceus	black carp	fish
Neoceratodus forsteri	Australian lungfish	fish
Paratrygon aiereba	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

species, out of 49 species with insufficient data, were predicted to be threatened when both traits and human impact were considered, including 10 fishes, 3 reptiles, and 4 mammals (Table 3). When only traits were considered in the model, only 1 (i.e., ocellate river stingray [*Potamotrygon motoro*]) of the 17 aforementioned species was not predicted to be threatened. The speckled longfin eel (*Anguilla reinhardtii*) and barramundi (*Lates calcarifer*) were predicted to be threatened. Accounting for both evaluations (i.e. IUCN Red List assessments and our model predictions), 50% of all freshwater megafauna species were considered threatened. Under the optimistic scenario, the portion of threatened freshwater megafauna was 46% when only traits were considered in the model and 48% when both traits and IBTI were considered (Supporting Information). Under the strict scenario, the portion increased to 55% and 52%, respectively. Although the 2 most parsimonious models did not show major differences in the included traits and predictions under the medium scenario, a lower AIC value (i.e., from 177 to 170) and higher explained variance (i.e., from 62% to 66%) occurred when IBTI was considered in the GLMM. This outcome indicated that model performance improved when both intrinsic traits and human impact were taken into account.

Among the 17 species predicted as threatened when both traits and human impact were considered under the medium scenario, 7 species (41%) occur in South America, particularly in the Amazon basin, and 5 species (29%) in China. The remaining 5 species occur in Africa, Australia, North America, and Southeast Asia. Accounting for all these species predicted as threatened, the Amazon and Yangtze basins appeared as new global diversity hotspots of threatened freshwater megafauna (Fig. 2), in addition to existing hotspots (i.e., the Ganges-Brahmaputra and Mekong basins and the Caspian Sea region) according to IUCN Red List assessments (Supporting Information). The Amazon basin was highlighted as a diversity hotspot of threatened freshwater megafauna species by both models under all 3 scenarios (Fig. 2 & Supporting Information).

Discussion

Extinction Risk of Freshwater Megafauna

Freshwater megafauna species are characterized by large body size, long life span, and late maturity, which are usually considered extinction-prone traits (McKinney 1997; Hutchings et al. 2012; Ripple et al. 2017). These traits are characteristic of a slow life-history strategy (i.e., *K*-selected strategy, low maximum rate of population growth and a low recovery potential after disturbance [McKinney 1997; Purvis et al. 2000]). We also observed a significant positive relationship between intensity of human impact and extinction risk of freshwater megafauna. This was expected because previous studies suggest large animals are particularly vulnerable to anthropogenic impacts (Ripple et al. 2016; Winemiller et al. 2016*b*; He et al. 2017).

Although a significantly positive relationship exhibited between body size and extinction risk, body size was not included in either of the 2 most parsimonious models; it appeared only in alternative models. This is consistent with the findings of Gonzalez-Suarez et al. (2012), but in contrast to studies indicating that body size is one of the most important traits correlated with extinction risk of vertebrates, such as fishes (Olden et al. 2007; Kopf et al. 2017), mammals (Purvis et al. 2000; Cardillo et al. 2005), and birds (Wang et al. 2018). Generally, both very large- and very small-bodied animals are thought to

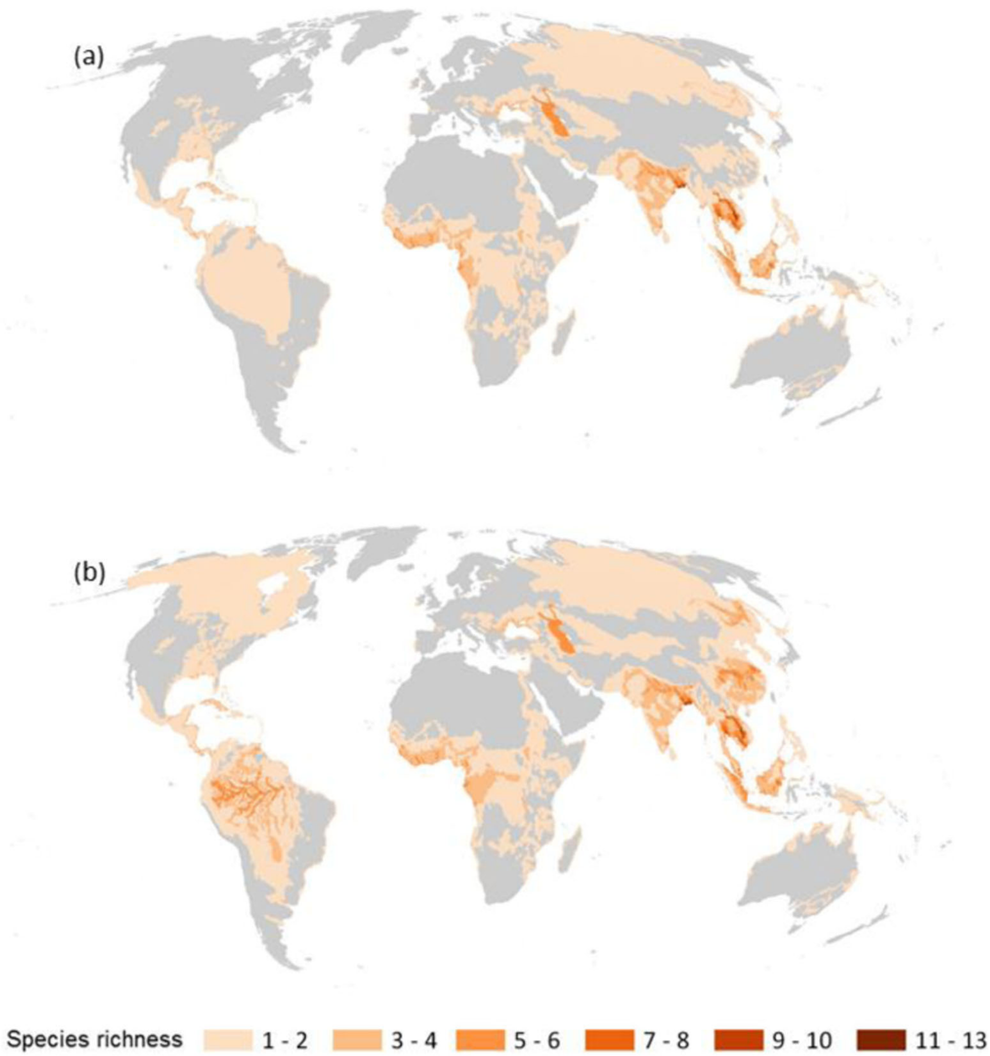

Figure 2. Species richness of freshwater megafauna (a) categorized as threatened according to the International Union for Conservation of Nature (IUCN) Red List and (b) categorized as threatened according to the IUCN Red List and prediction of the most parsimonious model considering both trait and human impact under the medium scenario (i.e., species with predicted threatened probability >0.5).

face high levels of extinction risk (e.g., Reynolds et al. 2005; Olden et al. 2007; Ripple et al. 2017). Body size is regarded as an important factor in determining extinction risk of species because of its correlation with other factors, such as distribution range and dispersal ability, that strongly influence species resistance to extinction (McKinney 1997). For freshwater megafauna, these correlations could be weakened because body size is already used as a main selection factor for megafauna species based on a body-mass threshold (He et al. 2017). For example, freshwater megafauna species with large body mass, 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 freshwater megafauna species, such as the Atlantic salmon (*Salmo salar*). Instead, body size is often negatively associated with population abundance (Cotgreave 1993), which is jointly determined by traits such as fecundity, age at maturity, and reproductive life span as well as by human impact (McKinney 1997; Hutchings et al. 2012).

Abundance-related traits, including fecundity, age at maturity, and reproductive life span, determine the recovery potential of species after disturbance caused by threats (McKinney 1997; Hutchings et al. 2012). For example, age at maturity and life span jointly determine the reproductive life span. Given the multiple and intense threats that freshwater megafauna are exposed to (Carrizo et al. 2017; He et al. 2017; Ripple et al. 2019), their ability to cope with various threats is particularly crucial for maintaining stable populations. For example, species with early maturity and high fecundity would have a higher probability of surviving intense harvesting pressure (Hutchings et al. 2012). On the one hand, freshwater megafauna, such as sturgeons, freshwater sharks and rays, river dolphins, crocodilians, and giant turtles, only reach maturity after 5–10 years or even later (e.g. female green sturgeons [*Acipenser medirostris*] typically reach maturity after 17 years, and Nile crocodiles [*Crocodylus niloticus*] reach maturity after 12 years). Hence, the probability is high that they will be captured before reaching maturity. On the other hand, species such as sturgeons, crocodilians, and giant turtles have a long life span, which enables individuals to reproduce for many years despite late maturity. Hence, their populations may recover if habitats are restored before long reproductive life spans end. Compared with mammal and reptile megafauna in freshwaters, fish megafauna have many more offspring. Fish megafauna should, therefore, be more resistant to extinction. However, this is not always the case. Even if fish megafauna make it to the age of maturity, their access to spawning grounds is often blocked by dams (Winemiller et al. 2016*b*). Alteration of natural environmental conditions (e.g., flow and thermal regimes and natural substrates) due to dams and dredging also greatly affect their reproduction success (He et al. 2017). Hence, it is necessary to combine life-history traits and human impact in extinction risk analyses (Murray et al. 2014); phylogenetic influences should also be considered.

Predicting the Extinction Risk of Freshwater Megafauna

Among the 17 species predicted as threatened, the Amazon river dolphin (*Inia geoffrensis*), the Australian lungfish (*Neoceratodus forsteri*), and the Northern New Guinea softshell turtle (*Pelochelys signifera*) are categorized as threatened in the newly updated assessment of the IUCN Red List (IUCN 2019), and the big-head schizothoracin (*Aspiorhynchus laticeps*) and Chinese sucker (*Myxocyprinus asiaticus*) are categorized as critically endangered on the Red List of China's Vertebrates (Jiang et al. 2016). The Araguaian river dolphin (*Inia araguaiaensis*) and the Bolivian river dolphin (*Inia boliviensis*) were also assessed under the name *Inia geoffrensis* due to the ongoing debate on their taxonomy (Hrbek et al. 2014).

Interestingly, the black carp (*Mylopharyngodon piceus*) and the bighead carp (*Hypophthalmichthys nobilis*) were predicted to be threatened. These 2 species are regarded as invasive, especially in North America (Kočovský et al. 2018). However, wild populations in their native range have been severely negatively affected by dams, overexploitation, and habitat degradation, which have led to sharp declines in larval abundances (Ban et al. 2019). Given the large size of remaining populations and their wide distributions, the black carp and the bighead carp are not yet in a critical situation (Jiang et al. 2016; Xie 2017). 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 basins are emerging hotspots for threatened freshwater megafauna. These 2 basins share some common characteristics. They jointly harbor 50 freshwater megafauna species and high freshwater biodiversity in general, and these species are highly underrepresented in IUCN Red List assessments (Carrizo et al. 2017). Both basins have high levels of fishing activities, increasing water traffic, and low enforcement of environmental regulations, which have already led to major population declines or even local extinctions of fish megafauna and river dolphins (Wang 2009; Castello et al. 2013; Xie 2017). In addition, dams have had major effects on freshwater megafauna species in the Yangtze basin (Xie 2017). Similar effects are predicted for the Amazon basin (Winemiller et al. 2016*a*).

Even under the optimistic scenario, the Amazon basin is considered a hotspot of threatened freshwater megafauna. Hence, IUCN Red List assessments of freshwater megafauna in this area are urgently needed. Due to the high level of biodiversity in the Amazon basin, 42.5% of its basin is under protection (Abell et al. 2017). However, a large proportion of these protected areas are IUCN category VI protected areas, where conservation regulations are usually poorly enforced and, therefore, provide questionable protection for biodiversity (Dudley et al. 2010). Moreover, management often focuses on terrestrial ecosystems and thus provides limited protection for freshwater biodiversity (Fagundes et al. 2016; Azevedo-Santos et al. 2018). Hence, in the Amazon basin an expansion of protected areas and enhanced management that specifically target freshwater habitats and species are required (Azevedo-Santos et al. 2018).

Comprehensive information on geographic distribution, life-history traits, phylogeny, threats (e.g., spatially explicit data on the type, intensity, and rate of change of stressors), and conservation efforts are needed to accurately predict the extinction risk of species (Murray et al. 2014). However, even the taxonomy of freshwater megafauna species, such as river dolphins, arapaima (*Arapaima* spp.) in South America, and the Chinese giant salamander, remains inconclusive (Stewart 2013; Hrbek et al. 2014; Yan et al. 2018). Information on traits including spawning periodicity, generation time, fecundity, and age at maturity is still missing, especially for fish megafauna and giant turtles. These traits correlate with extinction risk (e.g., Jager et al. 2008; McKinney 1997; Liu et al. 2017) and inform estimates of maximum per capita rate of population growth ($r_{\max}$), which is associated with extinction risk of species and, hence, important for conservation (Hutchings et al. 2012). In addition, the conservation applications of extinction-risk assessments are largely based on generation times. For example, population change over the last 3 generations is an important criterion for assignment of conservation status (IUCN 2018). However, information on generation time remains unknown for 65% of all megafauna species. To fill these information and knowledge gaps, field surveys and long-term monitoring, as well as basic ecological research focusing on the life history of these species, are needed.

Recommendations for Freshwater Megafauna Conservation

Species should not be considered not threatened just because they are not classified as such by the IUCN Red List. Species listed as data deficient could have a similar or even higher risk of extinction than assessed species (Jarić et al. 2016). Hence, we call for IUCN Red List assessments for freshwater megafauna species that we predicted to be threatened, excluding the Amazon river dolphin, Australian lungfish, and northern New Guinea softshell turtle because they have been assessed recently by IUCN (2019). We realize such assessments require financial support, commitment of species' experts, and time. Monitoring their population size and distribution range should be implemented at the earliest opportunity.

Time is critical in protecting freshwater megafauna (He & Jähnig 2019). The window of opportunity to protect these species from extinction could be missed if conservation actions are delayed, as happened for the baiji (*Lipotes vexillifer*) and the Chinese paddlefish (*Psephurus gladius*) (Xie 2017; Zhang et al. 2020). On the basis of our results, it is important to sustain the reproduction and recovery potential of freshwater magafauna. Freshwater megafauna species are often targeted for their meat and eggs and as game fish and are used in traditional medicine (He et al. 2017; Ripple et al. 2019; He & Jähnig 2019). Hence, establishing harvesting regulations is crucial to protect these species from overexploitation, to maintain their reproduction potential (e.g., avoid removing individuals before maturity), and to allow recovery of populations (Winemiller et al. 2016*b*). Moreover, given that most freshwater megafauna are migratory species, maintaining river connectivity is important so they can access spawning and feeding grounds (He et al. 2017; Grill et al. 2019; Winemiller et al. 2016*a*). More studies are required to improve knowledge on their life histories and identify critical areas (e.g., spawning grounds) that need protection. Such information could also help optimize dam locations and operations (e.g., fish passage and flow management), especially in regions such as the Amazon, Congo, Mekong, and Ganges-Brahmaputra basins. These basins harbor many migratory freshwater megafauna species that are, however, potentially threatened by hundreds of proposed dams (Winemiller et al. 2016*a*). In addition, more protected areas focusing on freshwater ecosystems and integrated basin management, planned and implemented together with local communities, are required (Fagundes et al. 2016; Finlayson et al. 2018). Such initiatives can benefit both freshwater megafauna and smaller freshwater species (Campos-Silva et al. 2018). Additional actions include the reintroduction of megafauna species into previously inhabited areas, as done with the Eurasian beaver (*Castor fiber*) (Halley 2011), or artificial breeding to enhance wild populations, as done with sturgeons (Pikitch et al. 2005). Hence, opportunities to protect freshwater megafauna exist, but more research and timely conservation programs need to be implemented now.

Acknowledgments

This work was carried out within the SMART Joint Doctorate (Science for the MAnagement of Rivers and their Tidal systems), funded with the support of the Erasmus Mundus program of the European Union, and is a contribution to the Leibniz Competition project Freshwater Megafauna Futures. S.D.L was supported by the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie Actions (grant agreement 748625). C.Z. acknowledges funding through the Junior Professorship Program of the Ministry for Science, Research and Culture (MWK), Baden-Württemberg, Germany. S.C.J. was funded through the GLANCE project (Global Change Effects in River Ecosystems, 01 LN1320A; German Federal Ministry of Education and Research, BMBF). We thank K.L. Laskowski for advice on statistical analysis and 3 anonymous reviewers for constructive comments on a previous version of the article.

Supporting Information

Appendix S1 Methods. Appendix S2 Selected traits for freshwater megafauna species. Appendix S3 Summary of data availability for the eight traits which were considered in the models. Appendix S4 The most parsimonious GLMM model with the lowest AIC (Akaike Information Criterion) and five alternative models in each model set[a]. Appendix S5 Species, which were predicted as threatened by GLMMs under the optimistic or strict scenario. Appendix S6 Number of species and threatened species of freshwater megafauna in selected large river basins. Appendix S7 Data availability of 12 life-history traits for freshwater megafauna species. Appendix S8 Species richness of freshwater megafauna categorized as threatened according to the IUCN Red List and prediction of the most parsimonious model considering only traits under the medium scenario. Appendix S9 Species richness of freshwater megafauna considered as threatened according to IUCN Red List and model predictions.

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