Received: 19 September 2022 | Revised: 1 March 2023 | Accepted: 2 March 2023

DOI: 10.1111/fwb.14073

ORIGINAL ARTICLE

Freshwater Biology WILEY

Do alien species affect native freshwater megafauna?

Xing Chen[1,2] | Sonja C. Jähnig[1,3] | Jonathan M. Jeschke[1,2] | Thomas G. Evans[1,2,4] | Fengzhi He[1,3,5]

[1]Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[2]Institute of Biology, Freie Universität Berlin, Berlin, Germany

[3]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany

[4]Ecologie Systématique et Evolution, Université Paris-Saclay, Gif-sur-Yvette, France

[5]Department of Biology, Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) and Section for Ecoinformatics and Biodiversity, Aarhus University, Aarhus C, Denmark

Correspondence
Fengzhi He, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.
Email: fengzhi.he@igb-berlin.de

Funding information
China Scholarship Council (CSC); German Academic Exchange Service (DAAD; PRIME programme); Bundesministerium für Bildung und Forschung (BMBF; 033W034A); Leibniz Association (Freshwater Megafauna Futures)

Abstract

1. Freshwater megafauna species (i.e., animals that can reach a body mass ≥30 kg, including fish, reptiles, mammals, and amphibians) play important roles in freshwater systems (e.g., by influencing habitat structure, trophic dynamics, or the dispersal of smaller species). As they tend to be large and charismatic, they may also function as flagship umbrella species in future freshwater conservation initiatives. Despite this, as a group they are highly threatened, and our knowledge of the nature of these threats is limited. In this study, we aim to improve our understanding of the impacts of alien species on native freshwater megafauna.

2. We undertook the first global assessment of the impacts of alien species on native freshwater megafauna using the Environmental Impact Classification for Alien Taxa (EICAT) framework. We conducted a literature review to identify published and grey literature on impacts, which we quantified and categorised by their severity and type, following the EICAT guidelines.

3. Negative impacts on native freshwater megafauna were caused by 61 alien species from a diverse range of taxonomic groups, including both freshwater and terrestrial alien species, and both vertebrates and invertebrates. They adversely affected 44 of 216 native freshwater megafauna species, including amphibians, fish, mammals, and reptiles. The Great Lakes Basin had the highest number of affected megafauna species (six of the 14 freshwater megafauna species it supports, mainly fish). Impacts occurred through a broad range of mechanisms (10 of the 12 identified mechanisms under EICAT); predation and competition were the most frequently reported mechanisms. Some impacts were relatively minor, adversely affecting the performance of individuals of native freshwater megafauna species. However, some reported impacts did cause declining populations of native freshwater megafauna species, and one impact contributed to the local extinction of the ship sturgeon (*Acipenser nudiventris*) in the Aral Sea. The vulnerability of native freshwater megafauna species to different types of impact varies during different life-cycle stages (egg, juvenile, and adult).

4. Our understanding of impacts posed by alien species on native freshwater megafauna is limited because data are unavailable for many regions, particularly the Global

Thomas G. Evans and Fengzhi He contributed equally to this work.

South, including hotspots for freshwater megafauna diversity such as the Amazon, Congo, Mekong, and Ganges-Brahmaputra basins. Freshwater megafauna species are often subject to multiple threats, which makes it difficult to determine the significance of alien species impacts relative to other threats such as habitat degradation and overexploitation. In addition, short-term studies are likely to be masking the severity of the impacts identified. We call for more long-term studies that attempt to identify population-level impacts, and for studies that identify impacts in data-deficient regions.

5. The EICAT assessments undertaken for this study will be reviewed by the EICAT Authority and subsequently incorporated into the IUCN EICAT database. They may be used to guide future research and conservation actions.

KEYWORDS

biological invasions, competition, EICAT, freshwater biodiversity, invasive alien species

1 | INTRODUCTION

Freshwater ecosystems, including lakes, rivers, and wetlands, are among the most diverse ecosystems on Earth (Strayer & Dudgeon, 2010; Wetzel, 2001). Although only covering about 3% of the Earth's surface (Lehner & Döll, 2004), they support approximately one-third of all known vertebrate species and half of all described fish species (Balian et al., 2008; Carrete Vega & Wiens, 2012). They also provide vital contributions to people, for example enabling the transportation of goods, providing opportunities for recreation, supplying fertile soils for agriculture, and regulating flood events (Postel & Carpenter, 1997; Vári et al., 2022). Despite this, freshwater ecosystems are among the world's most vulnerable ecosystems; the proportion of species that are threatened or extinct is much higher in freshwaters when compared to terrestrial or marine realms (Costello, 2015). Indeed, over 25% of assessed freshwater species are considered threatened (evaluated as being Vulnerable, Endangered, or Critically Endangered on the International Union for Conservation of Nature's [IUCN] Red List of Threatened Species), and more than 260 freshwater species are extinct (IUCN, 2022). This may be because freshwater ecosystems are subject to multiple stressors that act together to negatively affect freshwater species (Reid et al., 2019).

Freshwater megafauna species (i.e., animals that can reach a body mass ≥ 30 kg) include, for example, river dolphins, hippos, crocodilians, large turtles, sturgeons, and giant salamanders. They often have important ecological roles as ecosystem engineers or keystone species (Hammerschlag et al., 2019; Moore, 2006). For example, the hippopotamus (*Hippopotamus amphibius*) alters floodplain habitats and river morphology, and transfers large amounts of nutrients from grasslands to freshwater ecosystems, influencing the diversity of invertebrate and fish species in the ecosystems it occupies (Stears et al., 2018; Subalusky et al., 2015). Freshwater megafauna including river dolphins and piscivore megafish are top predators and have a profound influence on local trophic dynamics (Hammerschlag et al., 2019), while megafish species are often highly mobile and facilitate dispersal of smaller species (Correa et al., 2015; Lopes-Lima et al., 2017). Furthermore, many freshwater megafauna species are considered to be charismatic, and as such may play important roles in future conservation initiatives (e.g., as flagship umbrella species; He, Jähnig, et al., 2021a; Kalinkat et al., 2017). Despite this, they tend to be long-lived with slow life-history traits (e.g., long lifespan and late maturity), which makes them vulnerable to human impacts (He, Langhans, et al., 2021b; WWF, 2020) because individuals lost from a population are not replaced at a rate fast enough to prevent declines in that population (sensu Webb, 2002). For example, the incubation period for eggs of Australian freshwater crocodiles (*Crocodylus johnsoni*) is typically 75–85 days (which gives predators, including alien wild boar [*Sus scrofa*], an adequate opportunity to consume their eggs) (Webb et al., 1983). Freshwater megafauna also often require a variety of habitats to complete their life cycle (He, Langhans, et al., 2021), and impacts on any one of these habitats may adversely affect their ability to reproduce (Schlosser, 1991). Hence, freshwater megafauna are threatened by a diverse range of activities. For example, harvesting of their meat, skin, and eggs has led to a collapse of local populations of sturgeons, beavers, turtles, and giant salamanders (He & Jähnig, 2019; Ripple et al., 2019). Recreational fishing has contributed to the decline of the Siberian taimen (*Hucho taimen*; Jensen et al., 2009). Dams and levees have reduced the connectivity of rivers that freshwater megafauna inhabit, which has restricted their access to spawning and nesting sites (He, Thieme, et al., 2021c). As a consequence, between 1970 and 2012, global monitored populations of freshwater megafauna declined by 88% (He et al., 2019).

Alien species (i.e., species that have been introduced deliberately or unintentionally by human activities to areas outside of their natural distribution) are a critical threat to biodiversity (Pyšek et al., 2020). They are one of the causes of 33% of all animal species extinctions and 25% of all plant species extinctions since 1500 CE (Blackburn et al., 2019). The number of alien species has grown continuously across the world over the last 2 centuries, and rates of their introduction continue to rise (Seebens et al., 2017). The connectivity of freshwater ecosystems fosters the spread of alien species, which is furthered by human activities such as aquaculture and shipping (Francis & Chadwick, 2011; Moorhouse & Macdonald, 2015). In addition, many freshwater alien species are adapted to disturbances (e.g., drought and flood) and can survive in a range of conditions, which increases their chance of survival and establishment in regions into which they are introduced (Francis & Chadwick, 2011; Strayer, 2010). The introduction of alien species can have catastrophic impacts on local freshwater ecosystems, including the freshwater megafauna species they support. For example, the introduction of the Nile perch (*Lates niloticus*) to Lake Victoria caused the extinction of approximately 200 species of fish through predation and competition (Goldschmidt et al., 1993) and led to population declines of several native freshwater megafauna species, including the marbled lungfish (*Protopterus aethiopicus*), African sharptooth catfish (*Clarias gariepin*), and Sudan catfish (*Bagrus docmak*) (Goudswaard & Whitte, 1997). Despite these observed impacts, the influence of alien species on freshwater megafauna has received limited attention in comparison to impacts associated with other types of threat, such as overexploitation and dam construction (He et al., 2017).

Understanding the impacts of alien species on biodiversity is crucial for the development of efficient and effective management strategies to protect them from extinction (Jeschke et al., 2014; Kumschick et al., 2015). The Environmental Impact Classification for Alien Taxa (EICAT) protocol provides a systematic approach for categorising the impacts of alien species (Blackburn et al., 2014) and has been adopted by the IUCN to assess the environmental impacts of alien species (IUCN, 2020a, 2020b). It has been used to assess the impacts of several groups of alien species in terrestrial ecosystems, including birds (Evans et al., 2016, 2021), mammals (Allmert et al., 2021; Hagen & Kumschick, 2018; Volery et al., 2021), gastropods (Kesner & Kumschick, 2018), and plants (Canavan et al., 2019; Jansen & Kumschick, 2022). However, with the exception of amphibians (Kumschick et al., 2017), EICAT has not been used to carry out a global-scale assessment of the effects of alien species in freshwater ecosystems. As alien species are widely distributed across freshwater ecosystems and can have significant adverse impacts (Francis & Chadwick, 2011; Moorhouse & Macdonald, 2015; Strayer, 2010), such an assessment may provide important information that informs future research to identify and mitigate impacts, to the benefit of imperilled native freshwater megafauna species.

In this study, we use EICAT for the first time to undertake a global assessment of the environmental impacts of alien species on native freshwater megafauna. We aim to answer the following three questions: (1) Which freshwater megafauna species have been affected by alien species, and where do these impacts occur? (2) In what way, and how severely, are freshwater megafauna species affected by alien species? (3) Do the types of impacts sustained by freshwater megafauna vary across different stages of their life cycle? Freshwater megafauna species reach a very large final body size, and we therefore expect them to be more vulnerable to the impacts of many alien species in their egg and juvenile stage than they are as adults.

2 | METHODS

2.1 | Literature review

An updated version of the published list of freshwater megafauna taxa was collected from He et al. (2018), comprising 134 fishes, 47 reptiles, 33 mammals, and two amphibians. Their conservation status was collected from the IUCN Red List of Threatened Species (hereafter IUCN Red List; IUCN, 2022). We conducted a literature review to search for evidence documenting the impacts of alien species on each of these native freshwater megafauna species. Following Evans et al. (2016), we used terms describing alien species in combination with the scientific and common names of each freshwater megafauna species to search for literature on the Web of Science and Google Scholar. For example, the search string for the Nile crocodile was: ("invasive" OR "alien" OR "non-indigenous" OR "non-native" OR "introduced" OR "exotic") AND ("Nile crocodile" OR "*Crocodylus niloticus*"). We screened the titles and abstracts of articles to identify those that were relevant and reviewed the reference list published in each selected relevant article to identify additional references. We included articles describing impacts in the wild, or impacts identified through experiments. Articles written in either English or Chinese were considered. We also reviewed information on each freshwater megafauna species published on the IUCN Red List, CABI's Invasive Species Compendium (http://www.cabi.org/isc/), the Global Invasive Species Database of the Invasive Species Specialist Group (http://www.iucngisd.org/gisd/), and USGS's Nonindigenous Aquatic Species (https://nas.er.usgs.gov/).

Impact records were divided into three groups. The first included direct observations of impacts in the wild or established through laboratory experiments, which may be used for EICAT assessments (group 1). The second contained references that could not be included in the EICAT assessment for various reasons (group 2). For example, these references provided no direct observation of impacts (e.g., they are review articles) or no evidence of a negative impact (e.g., potential impacts were inferred). Some articles documented positive impacts whilst others focused on stocked native species rather than individuals in the wild. These references were also not included in our analysis. The third group contained references that were excluded because we could not assess the complete article due to access restrictions (group 3). The following data were extracted from studies in group 1: names of alien species and affected native freshwater megafauna species; description of observed impact; location of impact; and life-cycle stage of affected freshwater megafauna species (egg, juvenile, or adult).

2.2 | Distribution mapping

We obtained the native ranges of each freshwater megafauna species (He et al., 2018) and used level-3 HydroBASINS as spatial units to map their distributions (Lehner & Grill, 2013). HydroBASINS delineates catchments at a global scale based on their topographic position and hydrological connections and provides hierarchical sub-basins with 12 levels. Level-3 HydroBASINS mainly corresponds to large river basins such as the Amazon, Congo, Ganges-Brahmaputra, Mekong, Mississippi, Nile, and Yangtze basins. We assigned each recorded impact on a native freshwater megafauna species to one or more level-3 HydroBASINS at this scale. We also categorised each alien species by the continent of its origin and by the continent where it caused impacts (i.e., Africa, Asia, Europe, North America, Oceania, and South America). If an alien species was native to more than one continent and/or caused impacts on more than one continent, we assigned it to the category *multiple* continents.

2.3 | EICAT assessment

We assessed the impacts of alien species on native freshwater megafauna following the EICAT guidelines (IUCN, 2020a, 2020b; Volery et al., 2020). We assigned each impact record by its type to one of 12 impact mechanisms: competition; predation; hybridisation; transmission of disease; parasitism; poisoning/toxicity; bio-fouling or other direct physical disturbance; grazing/herbivory/browsing; chemical impact on ecosystem; physical impact on ecosystem; structural impact on ecosystem; and indirect impact through interaction with other species. We also assigned each impact record by its severity to one of five impact severity categories: minimal concern (MC) if no discernible impact was identified; minor (MN) if the alien species reduced the performance of individuals of a native freshwater megafauna species; moderate (MO) if the alien species caused a decline in the population of a native freshwater megafauna species; major (MR) if the alien species caused the local extinction of a native freshwater megafauna species (but this could be reversed if alien species were removed); and massive (MV) if the alien species caused the global extinction of a native freshwater megafauna species or the local extirpation of a native freshwater megafauna species that is not naturally reversible (i.e., the locally extirpated freshwater megafauna could not recolonise the area even if the alien species were removed). When interactions between alien species and native freshwater megafauna were observed but the available data were insufficient to assess the magnitude of any impacts, these records were classified as being data deficient (DD) under EICAT. We categorised impacts on each freshwater megafauna species by their affected life-cycle stage (i.e., egg, juvenile, and adult). We assigned impacts on viviparous megafauna (e.g., hippos, beavers) by either juvenile or adult stage as they give birth to living young. Freshwater megafauna species affected by hybridisation were classified as adults. In some cases, life-cycle stages were inferred based on the body length and body mass of the affected freshwater megafauna taxa. We assigned a confidence level of low, medium, or high to each impact record to indicate the probability of our EICAT assessment being accurate (IUCN, 2020a, 2020b). For example, confidence levels may be affected by data quality, the spatial and temporal scale of the observed data, and the presence of confounding factors that make it difficult to determine the cause of an impact. All EICAT assessments were reviewed by at least two co-authors to minimise subjectivity.

When calculating the number and percentage of each impact mechanism and severity category, we only included unique records. For example, if two or more records documented the same species interaction (i.e., between one alien species and one native freshwater species) with the same impact mechanism in the same level-3 HydroBASINS, only one record was counted. We examined the distribution of impacts across impact severity and life-cycle stage using contingency table tests (unconditional exact tests) with the *FunChisq* package (Zhong & Song, 2019) in R (R Core Team, 2021). For impact severity, due to small sample sizes in some categories of interest, we grouped EICAT categories as follows: MC and MN impacts = less severe impacts; MO, MR, or MV impacts = harmful impacts. The *FunChisq* package generated an *estimate* for each contingency table, which is a number between 0 and 1, where 1 represents a complete mathematical dependency of the two variables and 0 represents complete independence.

3 | RESULTS

3.1 | Spatial distribution

Negative impacts on native freshwater megafauna were reported in 45 level-3 HydroBASINS (Figure 1) and affected 44 species (28 fishes, 11 reptiles, four mammals, and one amphibian; Table S1). A quarter of these species were threatened (listed as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List). The Great Lakes Basin had the highest number of affected freshwater megafauna (six species), followed by the Mississippi Basin (five), and the western European coastal region (four). Some freshwater megafauna-rich basins, such as the Mekong and Ganges-Brahmaputra basins, had few affected freshwater megafauna species, and no reported impacts were identified in others, including the Amazon, Orinoco, and Congo basins.

Twenty-three alien species (i.e., 38% of the 61 alien species that negatively affected native freshwater megafauna) were native to North America. Of these, 12 were introduced to other areas in North America that were outside of their native ranges (e.g., smallmouth bass, *Micropterus dolomieu*; alewife, *Alosa pseudoharengus*). The other 11 species were introduced to other continents (Figure S1). Over a quarter of all identified alien species (16 species) were native to more than one continent; eight species were introduced to more than one continent. None of the identified alien species that affected freshwater megafauna were native to Oceania.

3.2 | Taxonomic distribution

Among the 61 alien species that posed a negative impact on native freshwater megafauna, 36 (59%) were fish. Negative impact reports were found for other taxonomic groups, including mammals (five reports), crustaceans and plants (four each), reptiles (three), and amphibians, molluscs, and worms (two each). Eight alien species caused negative impacts on three or more native freshwater megafauna

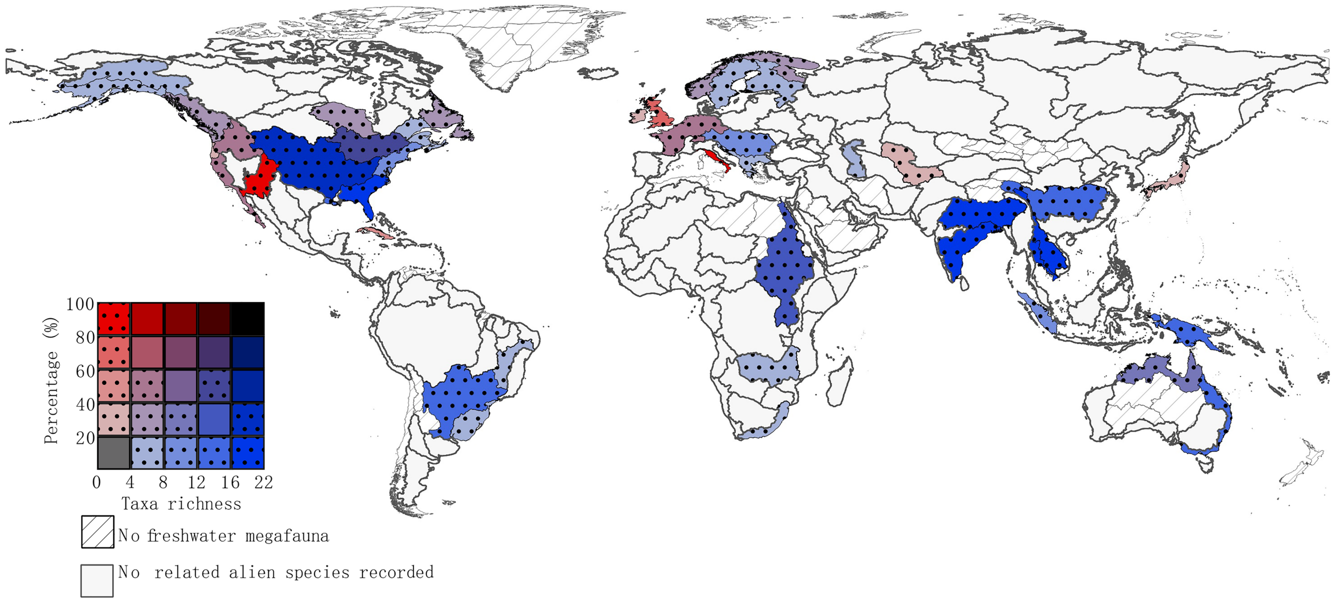

FIGURE 1 Taxa richness of native freshwater megafauna and percentage of impacted native freshwater megafauna in each HydroBASINS level-3 catchment. Alien species that posed impacts on native freshwater megafauna were recorded from catchments shown with black dots.

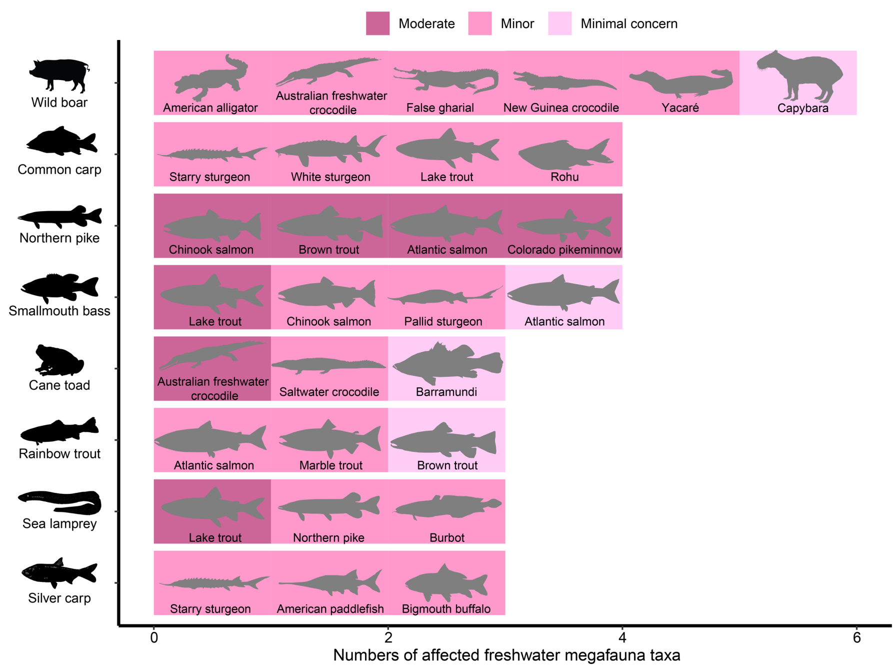

FIGURE 2 Alien species that affected at least three native freshwater megafauna taxa categorised by the severity of impacts caused.

species (Figure 2). Three of these alien species were also freshwater megafauna species (common carp, *Cyprinus carpio*; northern pike, *Esox lucius*; and silver carp, *Hypophthalmichthys molitrix*). The alien species affecting the highest number of native megafauna species (six) was a terrestrial mammal, the wild boar.

3.3 | Impact mechanisms and severity

In total, 257 impact records with sufficient information to identify the severity and mechanism of impact were extracted from 209 reports. Competition and predation were the most widely reported impact mechanisms (Figure S2), being associated with 44% and 31% of all impact records, respectively. Groups of alien species tended to affect native freshwater megafauna through different types of impact mechanisms (Figure 3a). Predation was the most common impact caused by alien mammals (75%), crustaceans (72%), and fish (44%), whilst poisoning/toxicity dominated for alien amphibians (75%) due to the extensive impacts of the cane toad (*Rhinella marina*) in Australia where poisoning/toxicity was the most frequently reported impact mechanism. Parasitism was the most common impact caused by alien worms.

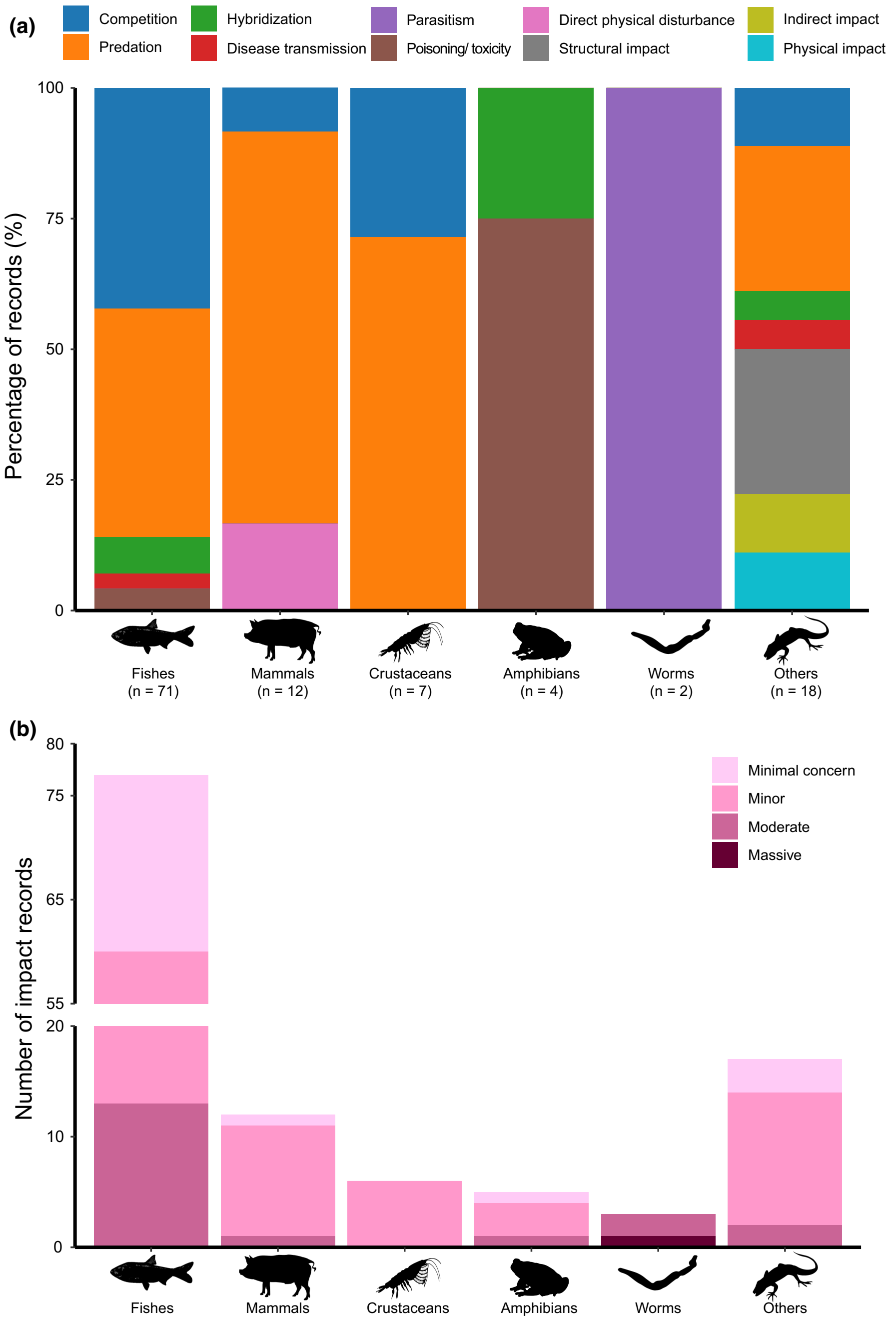

FIGURE 3 (a) Percentage of alien species as categorised by the mechanism of their impacts on native freshwater megafauna, and (b) number of impact records of alien species group, categorised by impact severity.

We identified 58 records of interactions between alien species and native freshwater megafauna where the impact mechanism or magnitude could not be identified due to inadequate information. This resulted in 15 alien species being categorised as DD under EICAT (e.g., water hyacinth, *Pontederia crassipes*). These impact records involved 21 native freshwater megafauna species. Five of these species, including hippopotamus and beluga (*Huso huso*), were completely DD under EICAT (i.e., the severity and mechanism of impact on these freshwater megafauna species could not be established).

Among those records with sufficient information to evaluate the impact magnitude, 83% were MC or MN (Figure 3b). A further 16% were MO, causing declining populations of 14 native freshwater megafauna species. No MR impacts were identified (i.e., reversible local population extinctions), but one MV impact was identified (i.e., gill fluke contributing to the irreversible local extinction of ship sturgeon [*Acipenser nudiventris*] in the Aral Sea). Northern pike had harmful impacts on the highest number of native freshwater megafauna species (four). We found no significant differences in the severity of impacts that were sustained by different taxonomic groups of native freshwater megafauna species (Table S2) or associated with different impact mechanisms (Table S3).

3.4 | Life-cycle stage

Impacts were caused through four mechanisms during the egg stage, and through eight during the juvenile and adult stages (Figure 4). Impacts were caused through two mechanisms (i.e., predation and

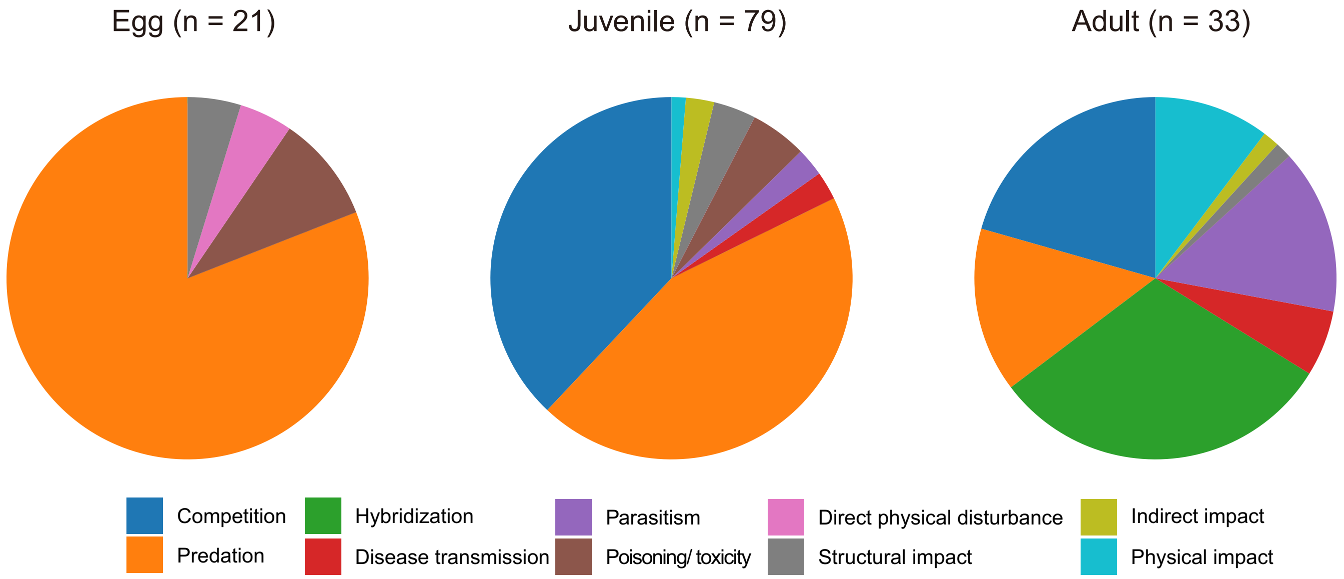

FIGURE 4 Percentage of native species impact records as categorised by impact mechanisms and life-cycle stages.

structural impact on ecosystem) during all three life-cycle stages. Impacts caused by direct physical disturbance only occurred during the egg stage. Predation impacts accounted for 81% of all records for the egg stage; 30% for the juvenile stage and 15% for the adult stage. A decline in the proportion of all records that were associated with competition was observed from the juvenile stage (38%) to adult stage (24%). Impact mechanisms and severity were nonrandomly distributed across life-cycle stage (Tables 1 and 2). In particular, there were more records describing competition between alien species and juvenile freshwater megafauna than would be expected by chance, and fewer records of predation on adult freshwater megafauna than would be expected by chance. In addition, there were fewer records of damaging impacts during the egg stage and more during the adult stage than would be expected by chance.

4 | DISCUSSION

Alien species are found in most major river basins worldwide, and their impacts on native freshwater megafauna species have been recorded across many regions of the world. However, we observed major data gaps in many regions. As economic development influences the availability of impact data on alien species, fewer data tend to be available in developing countries (Bellard & Jeschke, 2016; Evans et al., 2018; Evans & Blackburn, 2020; Pyšek et al., 2008). It is therefore possible that the impacts of alien species on freshwater megafauna are going unnoticed in the Global South. We also acknowledge that as we carried out our literature review using search terms in English, we might not have found all available information published in other languages (Nuñez & Amano, 2021).

Most impacts sustained by native freshwater megafauna are caused by alien fish. This is likely to be because most of the native freshwater megafauna species sustained impacts are also fish species. Nevertheless, native freshwater megafauna species are also affected by alien species from other taxonomic groups, including species that are predominantly terrestrial. Indeed, alien species with impacts on three or more native freshwater megafauna species include amphibians (cane toad) and mammals (wild boar). Other alien species with impacts include flatworms (gill fluke), crustaceans (rusty crayfish, *Faxonius rusticus*), crocodilians (spectacled caiman, *Caiman crocodilus*), comb jellies (sea walnut, *Mnemiopsis leidyi*), and flowering shrubs (Siam weed, *Chromolaena odorata*). This diverse range of alien species is one of the reasons for native freshwater megafauna being affected by 10 different impact mechanisms.

Alien species causing impacts on native freshwater megafauna tend to be relatively large. As the most frequently recorded impact mechanisms are predation and competition (i.e., accounting for 75% of all identified records), this may be because their size enables them to prey on, and compete with, other megafauna species (Cucherousset et al., 2012; Eby et al., 2006). In Cuba, the spectacled caiman competes with two native crocodile species (American crocodile, *Crocodylus acutus*; Cuban crocodile, *Crocodylus rhombifer*) and preys on juvenile Cuban crocodiles (Targarona et al., 2010). Hybridisation with alien species also affects native freshwater megafauna, and some of these alien species are also large, being freshwater megafauna themselves. For example, the introduction of the brown trout (*Salmo trutta*) to Slovenia led to a decline in the population of the native marble trout (*Salmo marmoratus*) due to genetic introgression (Fumagalli et al., 2002). Hybridisation between the alien Chinese giant salamander (*Andrias davidianus*) and the native Japanese giant salamander (*Andrias japonicus*) has also been widely observed in Japan (Fukumoto et al., 2015).

Nevertheless, some small alien species can affect native freshwater megafauna, but generally through different impact mechanisms. For example, native species are susceptible to the impacts

TABLE 1 Contingency table (chi-squared test) showing the actual and expected number of impacts associated with each impact mechanism for juvenile and adult stages.

	Competition	Predation	Hybridisation	Poisoning/toxicity	Others	Total
Juvenile	30	35	0	4	10	79
	27.29 (0.27)	*30.16* (0.78)	*5.75* (5.75)	*4.31* (0.02)	*11.49* (0.20)	
Adult	8	7	8	2	6	31
	10.71 (0.69)	*11.84* (1.98)	*2.25* (14.64)	*1.69* (0.06)	*4.51* (0.50)	
Total	38	42	8	6	16	110

$\chi^2 = 24.86$, $df = 4$, $p < 0.01$, estimates = 0.23.
Expected values are displayed in italics. Individual χ^2 values are displayed in parentheses. Due to small sample sizes, transmission of diseases to native species, direct physical disturbance, structural impact on ecosystem, and indirect impacts through interactions with other species were combined as Others.

TABLE 2 Contingency table (chi-squared test) showing the actual and expected number of less severe and harmful impacts for each life-cycle stage.

	Egg	Juvenile	Adult	Total
Less severe impacts (minimal concern and minor)	21	63	22	106
	17.39 (0.75)	*61.28* (0.05)	*27.33* (1.04)	
Harmful impacts (moderate, major, and massive)	0	11	11	22
	3.61 (3.61)	*12.72* (0.23)	*5.67* (5.01)	
Total	21	74	33	128

$\chi^2 = 7.31$, $df = 2$, $p = 0.02$, estimates = 0.19.
Expected values are displayed in italics. Individual χ^2 values are displayed in parentheses.

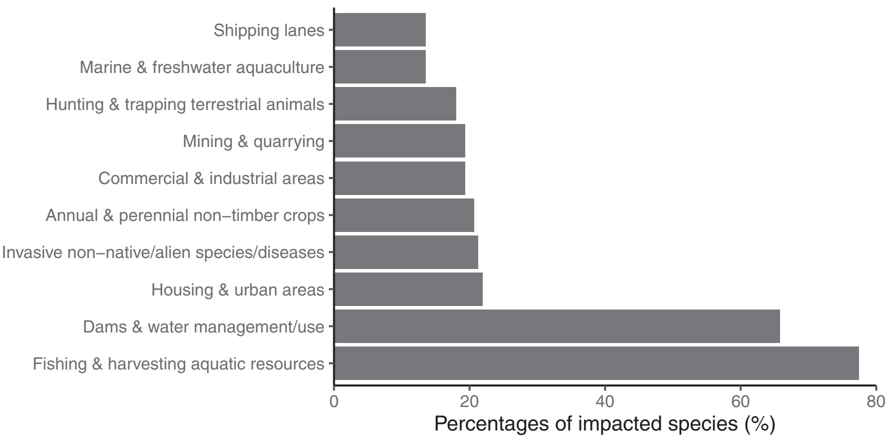

FIGURE 5 The 10 main threats to global freshwater megafauna according to IUCN Red List assessments ($n = 155$ freshwater megafauna species that have detailed information on threat categories in their assessment reports; IUCN, 2022).

of small alien parasites with which they have no coevolutionary history (sensu Saul & Jeschke, 2015). The introduction of the stellate sturgeon (*Acipenser stellatus*) to the Aral Sea also resulted in the unknown, accidental introduction of gill flukes (as a parasite of the stellate sturgeon). Gill flukes were observed in native ship sturgeons, reaching a density of 100–300 or sometimes even up to 600 individuals per ship sturgeon. About 150–200 mL of fish blood would be consumed by 300–400 gill fluke individuals per day (Bauer et al., 2002). Combined with overexploitation, dam construction, and increased salinity, this caused the local extinction of ship sturgeon in the Aral Sea (Gesner et al., 2010; Zholdasova, 1997).

Indeed, freshwater megafauna species are subject to a broad range of threats (Figure 5), and we found several examples of alien species impacts combining with some of these threats. For example, predation by the sea lamprey has caused a decline in the population of the lake trout (*Salvelinus namaycush*) in the Great Lakes, but overfishing has also contributed to this decline (Smith & Tibbles, 1980). It is difficult to determine the significance of alien species impacts in these cases, and some threats, such as overexploitation and habitat loss and degradation, may have stronger negative impacts on freshwater megafauna than alien species (He et al., 2017). Threats such as dam construction and climate change (Albert et al., 2021; Reid et al., 2019; Xi et al., 2021) may facilitate the establishment and spread of alien species (Johnson et al., 2008; Rahel & Olden, 2008). Extreme weather events associated with climate change may increase the chance that alien species in captive environments escape to the wild. For example, approximately 10,000 tonnes of five alien sturgeon species escaped from aquaculture farms into the Yangtze

River due to an extreme flooding event (Gao et al., 2017). These alien sturgeon species may be competing with the native Chinese sturgeon (*Acipenser sinensis*), which is critically endangered (Ju et al., 2019).

Impacts on native freshwater megafauna tend to be relatively weak, with only a few studies reporting impacts causing declining populations. However, the true severity of many impacts may be underestimated due to a lack of long-term monitoring (Pergl et al., 2020). Many studies on predation determined that an alien species preyed on a native freshwater megafauna species (i.e., an MN impact) but did not extend this research to determine whether this predation caused a declining population of the native species (i.e., an MO impact). This may be because documenting population-level changes in natural habitats requires considerably more time and effort than studying individual-level responses. However, where long-term monitoring data does exist, reductions in native freshwater megafauna populations have been documented. From 1987 to 1995, the impacts of the northern pike were studied after its introduction to Lake Skjeltjønna, Norway, revealing a decline in the native brown trout population across all age groups due to pike predation (Hesthagen et al., 2015). Monitoring of the population dynamics of Australian freshwater crocodiles from 1978 to 2013 revealed that the cane toad invasion reduced their population by approximately 70% on the Daly River, Australia (an MO impact; Fukuda et al., 2016). A related study that only considered the diet contents of dead Australian freshwater crocodiles identified impacts to the individual level (an MN impact; Doody et al., 2009).

Impact severity may have also been underestimated because many studies we identified were carried out under laboratory conditions. Given their large body size, long lifespan, and large habitat requirements, it is challenging to observe impacts on freshwater megafauna throughout their entire life cycle under laboratory conditions. Indeed, many experiments were solely concerned with impacts on individual native species rather than populations. Furthermore, under EICAT, impacts identified through experiments can be classified as no more severe than MN (Volery et al., 2020). Whether the MN impacts identified in these studies actually have more severe consequences for native freshwater megafauna in the wild remains unknown.

We identified a tendency for impacts to be more damaging during the adult stage and less damaging during the egg stage (i.e., no population-level impacts were identified at the egg stage). We feel that this may be due to a lack of long-term studies undertaken on impacts during the egg stage, and we do not place much emphasis on this result. Indeed, this seems plausible, as the large size of both juvenile and adult freshwater megafauna means that they are less susceptible to predation than they are during the egg stage. For example, juvenile lake sturgeons (*Acipenser fulvescens*) show a strong anti-predator response when exposed to the alien rusty crayfish, but nonetheless, their eggs are vulnerable to predation (Crossman et al., 2018). Red fire ants (*Solenopsis invicta*) introduced from South America to Florida prey on the eggs of American alligators (*Alligator mississippiensis*), causing reduced hatching success (Allen et al., 1997; Reagan et al., 2000), but negative impacts caused by red fire ants on juvenile or adult American alligators have not been recorded. Thus, the maximum recorded EICAT impact sustained by a native freshwater megafauna species may vary over its life span. Taking into account life-cycle stage when undertaking EICAT assessments may provide important insights that inform measures to protect native freshwater megafauna species. For example, the predation risk posed by largemouth bass (*Micropterus salmoides*) on green sturgeon (*Acipenser medirostris*) decreases as the size of the sturgeon increases, and is negligible once the sturgeon is 20 cm long (Baird et al., 2020).

During our assessments, we noticed that some impacts did not fit within any of the established EICAT mechanisms. For example, alewife contain thiaminase which can cause thiamine deficiency in the eggs of native fish that feed on it. This has increased mortality in Atlantic salmon and lake trout fry (Fitzsimons et al., 1995; Ketola et al., 2000; Ladago et al., 2020). There is no suitable mechanism for this impact, which we eventually assigned to *poisoning/toxicity* even though the mechanism does not accurately reflect the impact. It is worth noting that the interactions between alien species and other threats also represent emerging stressors to freshwater megafauna, which might not be captured by the current EICAT framework. For example, consumption of alien Mozambique tilapias (*Oreochromis mossambicus*) contaminated with toxins associated with severe pollution caused the death of over 100 gharials (*Gavialis gangeticus*) in the Chambal and Yamuna rivers in India (Stevenson, 2015). Although we assigned this impact to the *poisoning/toxicity* mechanism, it does not really fit, as the tilapias do not normally contain toxins. To account for this, we suggest that the *indirect impacts through interaction with other species* mechanism could be amended to also include interactions with *other factors* (i.e., *indirect impacts through interactions with other species or other factors*).

Our study highlights the vulnerability of native freshwater megafauna to the impacts of alien species, which have caused population declines of 14 freshwater megafauna species and contributed to the local extinction of one species (the ship sturgeon in the Aral Sea). We show that native freshwater megafauna species are vulnerable to impacts from a broad range of alien species and through many different impact mechanisms. Indeed, we observed clear differences in main impact mechanisms associated with the different life-cycle stages of freshwater megafauna (egg, juvenile, and adult). On the one hand, we observed that documented impacts of alien species on native freshwater megafauna tend to be relatively weak. On the other hand, the more severe (population-level) impacts sustained by native freshwater megafauna may be going unnoticed because of the short-term nature of many impact studies, and also because of a lack of research being undertaken in the Global South, including megafauna-rich basins such as the Amazon, Congo, Mekong, and Ganges-Brahmaputra. We call for long-term monitoring studies to more accurately assess the severity of the impacts sustained by native freshwater megafauna species, and for studies in data-deficient regions where the impacts of alien species on freshwater megafauna species are likely to be going unnoticed. Finally, we found several alien freshwater megafauna species (e.g., Asian carps, northern pike, brown trout) to have negative impacts on native freshwater megafauna. To the best of our knowledge, a synthesis of the impacts of alien freshwater megafauna within freshwater ecosystems is missing, and yet they are likely to have adverse impacts because introduced large freshwater animals can profoundly influence local trophic dynamics (Cucherousset et al., 2012; Eby et al., 2006). Indeed, given that freshwater megafauna are often ecosystem engineers or top predators, and that many freshwater megafauna species have been introduced to regions outside of their native ranges, future research focusing on the impacts of alien freshwater megafauna is warranted.

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods: X.C., S.C.J., J.M.J., T.G.E., F.H. Conducting the research, data analysis, data interpretation: X.C., T.G.E., F.H. Preparation of figures and tables: X.C., F.H. Writing: X.C., S.C.J., J.M.J., T.G.E., F.H.

ACKNOWLEDGMENTS

This study has been supported by the China Scholarship Council (CSC) and is a contribution to the Leibniz Competition project Freshwater Megafauna Futures and the Alliance for Freshwater Life. F.H. acknowledges support by the PRIME programme of the German Academic Exchange Service (DAAD) with funds from the German Federal Ministry of Education and Research (BMBF). T.E. acknowledges support from the Alexander von Humboldt Foundation. We also acknowledge support by the Bundesministerium für Bildung und Forschung (BMBF; 033W034A). We would like to express our gratitude to Dr Thomas Mehner and all participants of the scientific writing workshop at the Leibniz Institute of Freshwater Ecology and Inland Fisheries for their constructive comments on an early version of the manuscript. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All the identified literature and data used for EICAT assessments are available at https://doi.org/10.18728/igb-fred-822.0.

ORCID

Sonja C. Jähnig https://orcid.org/0000-0002-6349-9561
Jonathan M. Jeschke https://orcid.org/0000-0003-3328-4217
Thomas G. Evans https://orcid.org/0000-0002-7528-2773
Fengzhi He https://orcid.org/0000-0002-7594-8205

REFERENCES

Albert, J. S., Destouni, G., Duke-Sylvester, S. M., Magurran, A. E., Oberdorff, T., Reis, R. E., Winemiller, K. O., & Ripple, W. J. (2021). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio*, *50*(1), 85–94.

Allen, C. R., Rice, K. G., Wojcik, D. P., & Percival, H. F. (1997). Effect of red imported fire ant envenomization on neonatal American alligators. *Journal of Herpetology*, *31*(2), 318–321.

Allmert, T., Jeschke, J. M., & Evans, T. (2021). An assessment of the environmental and socio-economic impacts of alien rabbits and hares. *Ambio*, *51*(5), 1314–1329.

Baird, S. E., Steel, A. E., Cocherell, D. E., Poletto, J. B., Follenfant, R., & Fangue, N. A. (2020). Experimental assessment of predation risk for juvenile green sturgeon, *Acipenser medirostris*, by two predatory fishes. *Journal of Applied Ichthyology*, *36*(1), 14–24.

Balian, E. V., Segers, H., Martens, K., & Lévéque, C. (2008). The freshwater animal diversity assessment: An overview of the results. *Freshwater Animal Diversity Assessment*, *595*, 627–637.

Bauer, O. N., Pugachev, O. N., & Voronin, V. N. (2002). Study of parasites and diseases of sturgeons in Russia: A review. *Journal of Applied Ichthyology*, *18*(4–6), 420–429.

Bellard, C., & Jeschke, J. M. (2016). A spatial mismatch between invader impacts and research publications. *Conservation Biology*, *30*(1), 230–232.

Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, *17*(4), 203–207.

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Anthony, A., Richardson, D. M., Sendek, A., Vilà, M., Wilson, J. R. U., Winter, M., … Bacher, S. (2014). A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, *12*(5), e1001850.

Canavan, S., Kumschick, S., Le Roux, J. J., Richardson, D. M., & Wilson, J. R. U. (2019). Does origin determine environmental impacts? Not for bamboos. *Plants*, *People*, *Planet*, *1*(2), 119–128.

Carrete Vega, G., & Wiens, J. J. (2012). Why are there so few fish in the sea? *Proceedings of the Royal Society B: Biological Sciences*, *279*(1737), 2323–2329.

Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., & Anderson, J. T. (2015). Neotropical fish–fruit interactions: Eco-evolutionary dynamics and conservation. *Biological Reviews*, *90*(4), 1263–1278.

Costello, M. J. (2015). Biodiversity: The known, unknown, and rates of extinction. *Current Biology*, *25*(9), R368–R371.

Crossman, J. A., Scribner, K. T., Forsythe, P. S., & Baker, E. A. (2018). Lethal and non-lethal effects of predation by native fish and an invasive crayfish on hatchery-reared age-0 lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817). *Journal of Applied Ichthyology*, *34*(2), 322–330.

Cucherousset, J., Blanchet, S., & Olden, J. D. (2012). Non-native species promote trophic dispersion of food webs. *Frontiers in Ecology and the Environment*, *10*(8), 406–408.

Doody, J. S., Green, B., Rhind, D., Castellano, C. M., Sims, R., & Robinson, T. (2009). Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*, *12*(1), 46–53.

Eby, L. A., Roach, W. J., Crowder, L. B., & Stanford, J. A. (2006). Effects of stocking-up freshwater food webs. *Trends in Ecology & Evolution*, *21*(10), 576–584.

Evans, T., & Blackburn, T. M. (2020). Global variation in the availability of data on the environmental impacts of alien birds. *Biological Invasions*, *22*(3), 1027–1036.

Evans, T., Jeschke, J. M., Liu, C., Redding, D. W., Şekercioğlu, Ç. H., & Blackburn, T. M. (2021). What factors increase the vulnerability of native birds to the impacts of alien birds? *Ecography*, *44*(5), 727–739.

Evans, T., Kumschick, S., & Blackburn, T. M. (2016). Application of the environmental impact classification for alien taxa (EICAT) to a global assessment of alien bird impacts. *Diversity and Distributions*, *22*(9), 919–931.

Evans, T., Pigot, A., Kumschick, S., Şekercioğlu, Ç. H., & Blackburn, T. M. (2018). Determinants of data deficiency in the impacts of alien bird species. *Ecography*, *41*(8), 1401–1410.

Fitzsimons, J. D., Huestis, S., & Williston, B. (1995). Occurrence of a swim-up syndrome in Lake Ontario Lake trout in relation to

contaminants and cultural practices. *Journal of Great Lakes Research*, *21*(S1), 277–285.
Francis, R. A., & Chadwick, M. A. (2011). *Invasive alien species in freshwater ecosystems: A brief overview. In A handbook of global freshwater invasive species* (pp. 3–21). (Ed: R.A. Francis). Routledge.
Fukuda, Y., Tingley, R., Crase, B., Webb, G., & Saalfeld, K. (2016). Long-term monitoring reveals declines in an endemic predator following invasion by an exotic prey species. *Animal Conservation*, *19*(1), 75–87.
Fukumoto, S., Ushimaru, A., & Minamoto, T. (2015). A basin-scale application of environmental DNA assessment for rare endemic species and closely related exotic species in rivers: A case study of giant salamanders in Japan. *Journal of Applied Ecology*, *52*(2), 358–365.
Fumagalli, L., Snoj, A., Jesenšek, D., Balloux, F., Jug, T., Duron, O., Brossier, F., Crivelli, A. J., & Berrebi, P. (2002). Extreme genetic differentiation among the remnant populations of marble trout (*Salmo marmoratus*) in Slovenia. *Molecular Ecology*, *11*(12), 2711–2716.
Gao, Y., Liu, J. Y., Zhang, T. T., Feng, G. M., Zhang, T., Yang, G., & Zhuang, P. (2017). Escaped aquacultural species promoted the alien species invasion in the Yangtze River: A case study of sturgeons. *Chinese Journal of Ecology*, *36*(6), 1739–1745.
Gesner, J., Freyhof, M., & Kottelat, J. (2010). *Acipenser nudiventris. The IUCN red list of threatened species*: E.T225A13038215. https://doi.org/10.2305/IUCN.UK.2010-1.RLTS.T225A13038215.en Accessed on May 27, 2022.
Goldschmidt, T., Witte, F., & Wanink, J. (1993). Cascading effects of the introduced Nile perch on the Detritivorous/Phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology*, *7*(3), 686–700.
Goudswaard, K. P., & Whitte, F. (1997). The catfish fauna of Lake Victoria after the Nile perch upsurge. *Environmental Biology of Fishes*, *49*(1), 21–43.
Hagen, B. L., & Kumschick, S. (2018). The relevance of using various scoring schemes revealed by an impact assessment of feral mammals. *NeoBiota*, *75*(38), 37–75.
Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R., & Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in Ecology & Evolution*, *34*(4), 369–383.
He, F., Bremerich, V., Zarfl, C., Geldmann, J., Langhans, S. D., David, J. N. W., William, D., Tockner, K., & Jähnig, S. C. (2018). Freshwater megafauna diversity: Patterns, status and threats. *Diversity and Distributions*, *24*(10), 1395–1404.
He, F., & Jähnig, S. C. (2019). Put freshwater megafauna on the table before they are eaten to extinction. *Conservation Letters*, *12*, e12662.
He, F., Jähnig, S. C., Wetzig, A., & Langhans, S. D. (2021). More exposure opportunities for promoting freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(12), 3626–3635.
He, F., Langhans, S. D., Zarfl, C., Wanke, R., Tockner, K., & Jähnig, S. C. (2021). Combined effects of life-history traits and human impact on extinction risk of freshwater megafauna. *Conservation Biology*, *35*(2), 643–653.
He, F., Thieme, M., Zarfl, C., Grill, G., Lehner, B., Hogan, Z., Tockner, K., & Jähnig, S. C. (2021). Impacts of loss of free-flowing rivers on global freshwater megafauna. *Biological Conservation*, *263*, 109335.
He, F., Zarfl, C., Bremerich, V., David, J. N. W., Hogan, Z., Kalinkat, G., Tockner, K., & Jähnig, S. C. (2019). The global decline of freshwater megafauna. *Global Change Biology*, *25*(11), 3883–3892.
He, F., Zarfl, C., Bremerich, V., Henshaw, A., Darwall, W., Tockner, K., & Jaehnig, S. C. (2017). Disappearing giants: A review of threats to freshwater megafauna. *Wiley Interdisciplinary Reviews Water*, *4*(3), e1208.
Hesthagen, T., Sandlund, O. T., Finstad, A. G., & Johnsen, B. O. (2015). The impact of introduced pike (*Esox lucius* L.) on allopatric brown trout (*Salmo trutta* L.) in a small stream. *Hydrobiologia*, *744*(1), 223–233.
IUCN. (2020a). *Guidelines for using the IUCN environmental impact classification for alien taxa (EICAT) categories and criteria – version 1.1 (Vol. 1, Issue September)*. IUCN.
IUCN (Ed.). (2020b). *IUCN EICAT categories and Criteria.The environmental impact classification for alien taxa* (1st ed.). IUCN. https://doi.org/10.2305/IUCN.CH.2020.05.en.X + Xpp
IUCN. (2022). The IUCN red list of threatened species. Version 2022-2. https://www.iucnredlist.org
Jansen, C., & Kumschick, S. (2022). A global impact assessment of acacia species introduced to South Africa. *Biological Invasions*, *24*(1), 175–187.
Jensen, O. P., Gilro, D. J., Hogan, Z., Allen, B. C., Hrabik, T. R., Weidel, B. C., Chandra, S., & Jake Vander Zanden, M. (2009). Evaluating recreational fisheries for an endangered species: A case study of taimen, Hucho taimen, in Mongolia. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(10), 1707–1718.
Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., Gaertner, M., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Winter, M., & Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, *28*(5), 1188–1194.
Johnson, P. T., Olden, J. D., & Vander Zanden, M. J. (2008). Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment*, *6*(7), 357–363.
Ju, R. T., Li, X., Jiang, J. J., Wu, J., Liu, J., Strong, D. R., & Li, B. (2019). Emerging risks of non-native species escapes from aquaculture: Call for policy improvements in China and other developing countries. *Journal of Applied Ecology*, *57*(1), 85–90.
Kalinkat, G., Cabral, J. S., Darwall, W., Ficetola, G. F., Fisher, J. L., Giling, D. P., Gosselin, M.-P., Grossart, H.-P., Jähnig, S. C., Jeschke, J. M., Knopf, K., Larsen, S., Onandia, G., Pätzig, M., Saul, W.-C., Singer, G., Sperfeld, E., & Jarić, I. (2017). Flagship umbrella species needed for the conservation of overlooked aquatic biodiversity. *Conservation Biology*, *31*(2), 481–485.
Kesner, D., & Kumschick, S. (2018). Gastropods alien to South Africa cause severe environmental harm in their global alien ranges across habitats. *Ecology and Evolution*, *8*(16), 8273–8285.
Ketola, H. G., Bowser, P. R., Wooster, G. A., Wedge, L. R., & Hurst, S. S. (2000). Effects of thiamine on reproduction of Atlantic Salmon and a new hypothesis for their extirpation in Lake Ontario. *Transactions of the American Fisheries Society*, *129*(2), 607–612.
Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pysek, P., Ricciardi, A., Bacher, S., Blackburn, T. M., Dick, J. T. A., Evans, T., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D. M., Sendek, A., & Winter, M. (2015). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *Bioscience*, *65*(1), 55–63.
Kumschick, S., Vimercati, G., de Villiers, F. A., Mokhatla, M. M., Davies, S. J., Thorp, C. J., Rebelo, A. D., & Measey, G. J. (2017). Impact assessment with different scoring tools: How well do alien amphibian assessments match? *NeoBiota*, *33*(1), 53–66.
Ladago, B. J., Futia, M. H., Ardren, W. R., Honeyfield, D. C., Kelsey, K. P., Kozel, C. L., Riley, S. C., Rinchard, J., Tillitt, D. E., Zajicek, J. L., & Marsden, J. E. (2020). Thiamine concentrations in lake trout and Atlantic salmon eggs during 14 years following the invasion of alewife in Lake Champlain. *Journal of Great Lakes Research*, *46*(5), 1340–1348.
Lehner, B., & Döll, P. (2004). Development and validation of a global database of lakes, reservoirs and wetlands. *Journal of Hydrology*, *296*(1–4), 1–22.
Lehner, B., & Grill, G. (2013). Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. *Hydrological Processes*, *27*(15), 2171–2186.
Lopes-Lima, M., Sousa, R., Geist, J., Aldridge, D. C., Araujo, R., Bergengren, J., Bespalaya, Y., Bódis, E., Burlakova, L., Van Damme, D., Douda, K., Froufe, E., Georgiev, D., Gumpinger, C.,

Karatayev, A., Kebapçi, Ü., Killeen, I., Lajtner, J., Larsen, B. M., ... Zogaris, S. (2017). Conservation status of freshwater mussels in Europe: State of the art and future challenges. *Biological Reviews*, *92*(1), 572–607.

Moore, J. W. (2006). Animal ecosystem engineers in streams. *Bioscience*, *56*(3), 237–246.

Moorhouse, T. P., & Macdonald, D. W. (2015). Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews Water*, *2*(1), 1–8.

Nuñez, M. A., & Amano, T. (2021). Monolingual searches can limit and bias results in global literature reviews. *Nature Ecology & Evolution*, *5*(3), 264.

Pergl, J., Pyšek, P., Essl, F., Jeschke, J. M., Courchamp, F., Geist, J., Hejda, M., Kowarik, I., Mill, A., Musseau, C., Pipek, P., Saul, W.-C., von Schmalensee, M., & Strayer, D. (2020). Need for routine tracking of biological invasions. *Conservation Biology*, *34*(5), 1311–1314.

Postel, S., & Carpenter, S. R. (1997). Freshwater ecosystem services. In G. C. Daily (Ed.), *Natures services: Societal dependence on natural ecosystems* (pp. 195–214). Island Press.

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., ... Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534.

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, *23*(5), 237–244.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.r-project.org/

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, *22*(3), 521–533.

Reagan, S. R., Ertel, J. M., & Wright, V. L. (2000). David and Goliath retold: Fire ants and alligators. *Journal of Herpetology*, *34*(3), 475–478.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873.

Ripple, W. J., Wolf, C., Newsome, T. M., Betts, M. G., Ceballos, G., Courchamp, F., Hayward, M. W., Van Valkenburgh, B., Wallach, A. D., & Worm, B. (2019). Are we eating the world's megafauna to extinction? *Conservation Letters*, *12*(3), e12627.

Saul, W. C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters*, *18*(3), 236–245.

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *Bioscience*, *41*(10), 704–712.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*(1), 1–9.

Smith, B. R., & Tibbles, J. J. (1980). Sea lamprey (Petromyzon marinus) in lakes Huron, Michigan, and superior: History of invasion and control, 1936–78. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(11), 1780–1801.

Stears, K., McCauley, D. J., Finlay, J. C., Mpemba, J., Warrington, I. T., Mutayoba, B. M., Power, M. E., Dawson, T. E., & Brashares, J. S. (2018). Effects of the hippopotamus on the chemistry and ecology of a changing watershed. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(22), E5028–E5037.

Stevenson, C. J. (2015). Conservation of the Indian gharial *Gavialis gangeticus*: Successes and failures. *International Zoo Yearbook*, *49*(1), 150–161.

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*(Suppl. 1), 152–174.

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358.

Subalusky, A. L., Dutton, C. L., Rosi-Marshall, E. J., & Post, D. M. (2015). The hippopotamus conveyor belt: Vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology*, *60*(3), 512–525.

Targarona, R. R., Soberón, R. R., Tabet, M. A., & Thorbjarnarson, J. B. (2010). *Cuban crocodile Crocodylus rhombifer. Crocodiles: Status, survey and conservation action plan* (3rd ed., pp. 114–118). Crocodile Specialist Group.

Vári, A., Podschun, S. A., Erős, T., Hein, T., Pataki, B., Iojă, I. C., Adamescu, C. M., Gerhardt, A., Gruber, T., Dedić, A., Ćirić, M., Gavrilović, B., & Báldi, A. (2022). Freshwater systems and ecosystem services: Challenges and chances for cross-fertilization of disciplines. *Ambio*, *51*(1), 135–151.

Volery, L., Bacher, S., Blackburn, T. M., Bertolino, S., Evans, T., Genovesi, P., Kumschick, S., Roy, H. E., Smith, K. G., & Bacher, S. (2020). Improving the environmental impact classification for alien taxa (EICAT): A summary of revisions to the framework and guidelines. *NeoBiota*, *62*, 547–567.

Volery, L., Jatavallabhula, D., Scillitani, L., Bertolino, S., & Bacher, S. (2021). Ranking alien species based on their risks of causing environmental impacts: A global assessment of alien ungulates. *Global Change Biology*, *27*(5), 1003–1016.

Webb, G. J. (2002). Conservation and sustainable use of wildlife-an evolving concept. *Pacific Conservation Biology*, *8*(1), 12–26.

Webb, G. J. W., Buckworth, R., & Charlie Manolis, S. (1983). *Crocodylus johnstoni* in the McKinlay river, N.T. VI. * nesting biology. *Wildlife Research*, *10*(3), 607–637.

Wetzel, R. G. (2001). *Freshwater ecosystems. In Encyclopedia of biodiversity: Second edition* (pp. 560–569). Academic Press.

WWF. (2020). In R. E. A. Almond, M. Grooten, & T. Petersen (Eds.), *Living planet report – Bending the curve of biodiversity loss*. WWF.

Xi, Y., Peng, S., Ciais, P., & Chen, Y. (2021). Future impacts of climate change on inland Ramsar wetlands. *Nature Climate Change*, *11*(1), 45–51.

Zholdasova, I. (1997). Sturgeons and the Aral Sea catastrophe. In V. J. Birstein, J. R. Waldman, & W. E. Bemis (Eds.), *Sturgeon biodiversity and conservation* (pp. 373–380). Kluwer Academic Publishers.

Zhong, H., & Song, M. (2019). A fast exact functional test for directional association and cancer biology applications. *IEEE/ACM Transactions on Computational Biology and Bioinformatics*, *16*(3), 818–826.

SUPPORTING INFORMATION

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

How to cite this article: Chen, X., Jähnig, S. C., Jeschke, J. M., Evans, T. G., & He, F. (2023). Do alien species affect native freshwater megafauna? *Freshwater Biology*, *68*, 903–914. https://doi.org/10.1111/fwb.14073