Received: 5 December 2022 | Accepted: 3 August 2023

DOI: 10.1111/cobi.14168

Conservation Biology

REVIEW

Extinction risk of the world's freshwater mammals

Emmalie Sanders[1] | **Skye Wassens**[1,2] | **Damian R. Michael**[2] | **Dale G. Nimmo**[1,2] | **James M. Turner**[3]

[1]School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Albury, New South Wales, Australia

[2]Gulbali Institute for Agriculture, Water and Environment, Charles Sturt University, Albury, New South Wales, Australia

[3]Institute of Biomedical and Environmental Health Research, School of Health and Life Sciences, University of the West of Scotland, South Lanarkshire, UK

Correspondence
Emmalie Sanders, 4/51 Kincaid Street, Wagga Wagga NSW 2650, Australia. Email: esanders@csu.edu.au

Article impact statement: Aquatic and semiaquatic mammals are at a greater risk of extinction than other terrestrial and freshwater taxa.

Funding information
Gulbali Institute, Grant/Award Number: Gulbali Accelerated Publication Scheme; Commonwealth Environmental Water Office, Grant/Award Number: Murrumbidgee Flow MER program; Australian Government, Grant/Award Number: AGRTP Scholarship

Abstract

The continued loss of freshwater habitats poses a significant threat to global biodiversity. We reviewed the extinction risk of 166 freshwater aquatic and semiaquatic mammals—a group rarely documented as a collective. We used the International Union for the Conservation of Nature Red List of Threatened Species categories as of December 2021 to determine extinction risk. Extinction risk was then compared among taxonomic groups, geographic areas, and biological traits. Thirty percent of all freshwater mammals were listed as threatened. Decreasing population trends were common (44.0%), including a greater rate of decline (3.6% in 20 years) than for mammals or freshwater species as a whole. Aquatic freshwater mammals were at a greater risk of extinction than semiaquatic freshwater mammals (95% CI –7.20 to –1.11). Twenty-nine species were data deficient or not evaluated. Large species (95% CI 0.01 to 0.03) with large dispersal distances (95% CI 0.03 to 0.15) had a higher risk of extinction than small species with small dispersal distances. The number of threatening processes associated with a species compounded their risk of extinction (95% CI 0.28 to 0.77). Hunting, land clearing for logging and agriculture, pollution, residential development, and habitat modification or destruction from dams and water management posed the greatest threats to these species. The basic life-history traits of many species were poorly known, highlighting the need for more research. Conservation of freshwater mammals requires a host of management actions centered around increased protection of riparian areas and more conscientious water management to aid the recovery of threatened species.

KEYWORDS
conservation, IUCN Red List, semiaquatic, threatening processes, threats, wetlands

Riesgo de extinción de los mamíferos de agua dulce

Resumen: La pérdida continua de hábitats de agua dulce representa una amenaza importante para la biodiversidad mundial. Analizamos el riesgo de extinción de 166 especies de mamíferos acuáticos y semiacuáticos de agua dulce—un grupo que se documenta pocas veces como colectivo. Usamos las categorías de la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza de diciembre 2021 para determinar el riesgo de extinción. Después comparamos este riesgo entre grupos taxonómicos, áreas geográficas y caracteres biológicos. El 30% de los mamíferos de agua dulce están categorizados como amenazados. La declinación de las tendencias poblacionales fue común (44.0%), incluyendo una mayor tasa de declinación (3.6% en 20 años) que para los mamíferos o las especies de agua dulce como conjunto. Los mamíferos acuáticos de agua dulce se encuentran en mayor riesgo de extinción que los mamíferos semiacuáticos (95%

IC -7.20 a -1.11). Veintinueve especies no contaban con suficientes datos o no estaban evaluadas. Las especies grandes (95% IC 0.01 a 0.03) con distancias de dispersión amplias (95% IC 0.03 a 0.15) tuvieron un mayor riesgo de extinción que las especies pequeñas con menores distancias de dispersión. El número de procesos amenazantes asociados a alguna especie agravó su riesgo de extinción (95% CI 0.28 a 0.77). Las principales amenazas para estas especies fueron la cacería, el desmonte de tierras para tala y agricultura, la contaminación, los desarrollos residenciales y la destrucción o modificación del hábitat causados por presas o manejo hidrológico. Se sabe poco sobre los caracteres básicos de la historia de vida de muchas especies, lo que destaca la necesidad de más investigación al respecto. La conservación de mamíferos de agua dulce requiere una serie de acciones gestoras centradas en el incremento de la protección de las áreas ribereñas y una gestión hidrológica más consciente para ayudar a la recuperación de las especies amenazadas.

PALABRAS CLAVE

amenazas, conservación, humedales, Lista Roja de la UICN, procesos amenazantes, semiacuático

INTRODUCTION

Freshwater ecosystems occupy only 0.8% of Earth's surface but are home to approximately 10% of all known animal species (Balian et al., 2008) and one third of all vertebrates (Dudgeon et al., 2006). Freshwater ecosystems are one of the most threatened. Freshwater vertebrate populations have declined by 81% since 1970, and since 1900 an estimated 71% of the world's wetlands have been lost (Davidson, 2014; McRae et al., 2017). Key threats include flow modification, water extraction, habitat destruction and degradation, invasive species, and climate change (Collen et al., 2014; Dudgeon et al., 2006; Reid et al., 2019; Strayer, 2010). Pollution of waterways from domestic, industrial, and agricultural waste products is a leading cause of freshwater system degradation in regions densely populated by humans (Collen et al., 2014; Stoett et al., 2019). Climate change represents an even greater emerging threat to freshwater systems due to more severe drought from lack of rainfall, increased aridity, and greater frequency of flooding events (Dudgeon et al., 2006; Larkin et al., 2020).

One group that is often overlooked when discussing impacts on freshwater systems is freshwater mammals. This is a highly diverse group that can be further divided into aquatic and semiaquatic mammals. Aquatic mammals are highly adapted and confined to water for all aspects of their life and cannot travel on land, such as the Amazon River dolphin (*Inia geoffrensis*) (Pacini & Harper, 2008; Veron et al., 2007). Semiaquatic mammals are less adapted to aquatic life (Dunestone & Gorman, 1998; Howell, 1930). They require land for nesting, rest, or reproduction but display an obligate connection with water in their daily activity, especially as a main food source (Hood, 2020). This includes terrestrial mammals that require water sources for food and protection but excludes species reliant only on freshwater-associated habitats, such as surrounding grasslands and not freshwater systems per se. For example, the webbed-footed tenrec (*Limnogale mergulus*), which derives its food from the water, and swamp rabbit (*Sylvilagus aquaticus*), which utilizes waterbodies to avoid predation, are semiaquatic. However, jaguars (*Panthera onca*), which hunt predominantly around waterways, and puku (*Kobus vardonii*), which graze in grassland surrounding waterways, are excluded.

Due to the global scale of the threats to freshwater ecosystems, there is an urgent need to quantify life-history traits associated with higher extinction rates in freshwater species. The International Union for the Conservation of Nature (IUCN) Red List is used to document the world's changing biodiversity and identify species most at risk of extinction and in need of conservation (IUCN, 2021). Combining IUCN assessments with data on life-history traits within taxonomic groups provides insight into why some species are more susceptible to extinction and can identify potentially threatened species that have yet to be evaluated or lack sufficient data for IUCN Red List classification (Hernández-Yáñez et al., 2022; Kopf et al., 2017; Marneweck et al., 2021). In this review, we aimed to document the key threats to freshwater mammals based on information in the IUCN Red List. We examined species' taxonomy, biogeographic location, habitat characteristics, and life-history traits to determine species' associations with extinction risk and identify groups of the greatest conservation concern.

METHODS

Species list

We compiled a comprehensive list of freshwater mammals from multiple sources. All mammalian species listed in version 2021–3 of the IUCN Red List (IUCN, 2021) as occupying freshwater systems were included ($n = 146$) as were additional species on the Freshwater Animal Diversity Assessment (FADA) (Balian et al., 2008; Véron et al., 2010), which includes aquatic and water-dependent species ($n = 152$). Because the definition of semiaquatic mammals varies greatly and new species have been described since 2010, we also consulted Hood (2020) on semiaquatic mammals ($n = 140$). These 3 sources were combined to produce a list of 203 species.

To ensure all species conformed to the scope of our review, we excluded volant species, species that do not occupy freshwater habitats, and riparian species that only use the surrounding vegetation for food or hunting grounds. We used a precautionary approach to include species deemed reliant on freshwater environments when basic ecological information was unknown. Due to the differences in levels of aquatic specialism of semiaquatic mammals, we ranked these species on 3 levels: high, moderate, and low (Appendix S1). Species with a high aquatic affinity can dive, remain submerged for extended periods, and display numerous physiological or morphological aquatic adaptations (e.g., webbing, natatory fringes, or ability to close all orifices) (Howell, 1930). Moderate species are less biologically specialized but still display some level of aquatic adaptation or behavior and instinctively seek water for protection and main dietary items (Dunstone & Gorman, 1998). Low-level species are highly associated with water, and likely seek water to avoid predation, but exact interactions are either unknown (such as rare or data deficient species) or limited to the shallows of the water's edge. Fully aquatic mammals were classified as such for comparison with semiaquatic mammals.

IUCN Red List categories and criteria

The IUCN (2012a) Red List acknowledges 9 categories of extinction risk: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), data deficient (DD), and not evaluated (NE). Threatened categories (CR, EN, and VU) are assigned based on 5 criteria that describe different aspects of extinction risk (IUCN, 2012a): criterion A, population reduction; B, small, fragmented, or fluctuating geographic range; C, small and declining population size; D, very small or restricted populations; and E, high probability of extinction assessed through quantitative analyses.

We recorded the current IUCN Red List category for each species and criteria for inclusion in our review as of April 2021. Because uncertainty about the true extinction risk of species is introduced by DD and NE statuses, the percentage of threatened species was estimated at the best level and its lower and upper bounds (IUCN, 2021). The best estimate of extinction risk was based on the assumption that the proportion of DD and NE species follows that of threatened data-sufficient species, that is, (CR + EN + VU) / (N – EW – EX – DD – NE), where N is the total number of species included in our review. The numerator indicates the number of threatened species in the scenario, and the denominator is the total species being considered. The lower estimate is based on the assumption that all DD and NE species are not threatened: (CR + EN + VU) / (N – EW – EX). The upper estimate is based on the assumption that all DD and NE species are threatened: (CR + EN + VU + DD + NE) / (N – EW – EX). Population trend was recorded as either increasing, stable, decreasing, or unknown for all extant species.

Red List Index

The scale for the Red List Index (RLI) ranges from all taxa are EX (0) to all taxa are LC (1) (Butchart et al., 2007). The RLI tracks trends in the extinction risk of a group of species over time and includes only genuine reasons for species category changes. New information, changes in red-list criteria, and taxonomic revisions are not genuine reasons. We used backcasting to correct previous categories associated with changes that were not genuine and excluded species already EX or EW (Bubb et al., 2009). To calculate the RLI (Equation 1), we multiplied the number of evaluated non-DD species in each category by the assigned category weight (LC = 0; NT = 1; VU = 2; EN = 3; CR = 4; CR [Possibly Extinct], EX and EW = 5) (Butchart et al., 2004; IUCN Standards & Petitions Committee, 2022). The sum of these products was then divided by the total number of evaluated and data-sufficient species extant at the first year multiplied by 5. This number was subtracted from 1 to produce an RLI for the particular year the categories were taken.

$$\begin{aligned} \mathrm{RLI} = 1 - \{[(\mathrm{EX} + \mathrm{EW} + \mathrm{CR}\,(\mathrm{PE})) \times 5] + (\mathrm{CR} \times 4) \\ + (\mathrm{EN} \times 3) + (\mathrm{VU} \times 2) + (\mathrm{NT} \times 1) + (\mathrm{LC} \times 0)\} / \\ (N \times 5)\,. \end{aligned} \tag{1}$$

Due to different time delays between species assessments, RLI values were calculated only for 1996, 2008, and 2016.

Taxonomic and geographic patterns of extinction risk

We assessed taxonomic patterns of extinction risk based on the proportion of threatened species in each order and family. We recorded the biogeographic location of each species based on ranges reported in the IUCN Red List or in the literature for NE species. Location was categorized into 6 of the 8 biogeographical realms where freshwater mammals were found: Afrotropical, Australasian, Indo-Malayan, Nearctic, Neotropical, and Palearctic (Olson et al., 2001). We mapped the species richness for available species and threatened species on a global scale from shape files obtained from the IUCN Red List mammals data set (IUCN, 2021). We read relevant files into R Studio (R Core Team, 2022), with the package rgdal (Bivand et al., 2022), and retrieved species ranges with the unique function of the raster package (Hijmans, 2022). The unique layers were converted to a raster object and plotted onto world maps with the tmap package (Tennekes, 2018).

We obtained habitat data from the IUCN Red List, or relevant literature, and included subcategories of wetland habitats (IUCN, 2012b). Habitat breadth was recorded as the number of habitat areas the species could reside in and wetland breadth the number of wetland types the species occupied. We assigned a broad climate type (tropical, arid, temperate, cold, or polar) to each species based on their range overlap with the Köppen–Geiger climate map (Peel et al., 2007; Appendix S2).

Threatening processes

We recorded direct threatening processes listed in the IUCN Red List for all evaluated species. Threats were classified into 11 groups according to version 3.2 of the IUCN (2012c) Threats Classification Scheme and included residential and commercial development, agriculture and aquaculture, energy production and mining, transport and service corridors, biological resource use, human intrusions and disturbance, natural systems modifications, invasive and other problematic species, genes and diseases, pollution, geological events, and climate change and severe weather (IUCN, 2012c). Some species were recorded as not currently facing any species-level threatening processes and facing only minor threats on a subpopulation level or their current threats were unknown. Threats were recorded for ongoing and expected future threatening processes. Species affected by the top 6 threatening processes were mapped to identify where they are most at risk.

Life-history traits and extinction risk

We recorded life-history traits from the COMBINE (a Coalesced Mammal database of Intrinsic and Extrinsic traits) data set (Soria et al., 2021), IUCN Red List (IUCN, 2021), or relevant literature. Traits included body mass, trophic level, dietary breadth (amount of plant or animal groups or both that made >20% of the diet), activity period (nocturnal, diurnal, or mixed [i.e., cathemeral or crepuscular]), dispersal distance, and home range size. Sexual maturity, life span, and generation length were highly correlated ($r > 0.85$), so only generation length, with the largest sample size, was retained. Additional predictors of extinction risk included the level of aquatic specialization, realm, climate, habitat breadth, and number of threats a species is currently facing. Because range size is used in assessment criteria B for threatened species, it was not considered for analysis.

We used multilevel models to determine whether extrinsic factors and life-history traits contributed to extinction risk in freshwater mammals. The binomial threat status of threatened (EX, EW, CR, EN, and VU) and nonthreatened species (NT and LC) was used as the response variable for all models. Unevaluated and DD species were not included, leaving 137 species to model. We fit Bayesian Bernoulli univariate regression models with the brms package (Buerkner, 2017) in R Studio (R Core Team, 2022). Each model contained 2 variables: a fixed-effect variable and a random-effect variable, controlling for taxonomic differences (order and family). We ran models with 4 chains of 2000 iterations with the first 1000 iterations used as a warmup for a total of 4000 postwarmup draws. A control value of 0.99 was fitted to prevent divergent transitions; convergence was achieved for all models (Rhat = 1.00). We calculated the probability of direction (pd) to determine the existence of an effect by each parameter, which was deemed significant when the 95% credible interval excluded zero. Plots were made with the ggplot2 and ggeffects packages (Lüdecke, 2018; Wickham, 2016).

RESULTS

Categories and criteria

A total of 166 species remained after all inclusion criteria were met, representing 10 orders and 30 families (Appendix S1). Of these species, 157 have been evaluated by the IUCN. Threatened species comprised 30.1% of freshwater mammals, with 21 species (12.7%) listed as VU, 26 species (15.7%) listed as EN, and 3 species (1.8%) listed as CR. The Ethiopian amphibious rat (*Nilopegamys plumbeus*) and Baiji (*Lipotes vexillifer*) were flagged as CR possibly extinct. Three species (1.8%) were EX and 1 was EW (Appendix S1). Twenty species (12.0%) were listed as DD, 13 of which had previously been categorized but now lack sufficient information regarding taxonomy, population status, or range size (Appendix S3). Sixty-nine species (41.6%) were listed as LC and 14 species (8.4%) as NT.

Most threatened species (49.2%) were classified under criterion A (subcriteria A2, A3, and A4) due to large population reductions. Small, fragmented, or fluctuating geographic range size characterized 28.8% of threatened species, predominantly based on the extent of occurrence (B1) or total spread of the species' range (known for 107 species), rather than the area of occupancy (B2, known for 18 species). Small population size and decline, where the number of mature individuals is typically <10,000, accounted for 18.6% of threatened species (criterion C). Only the Venezuelan fish-eating rat (*Neusticomys venezuelae*) and Baiji were classified under criterion D due to their very small, restricted population containing <1000 mature individuals. No freshwater mammals were categorized by predictive quantitative analyses under criterion E.

The best estimated proportion of freshwater mammals that are threatened, based on the current proportion of evaluated threatened species, was 37.6%. The final range, from all unevaluated species being nonthreatened to all being threatened, was 30.9–48.8%. Of the 50 threatened species, 44 species faced decreasing population size, and the population trends of 4 species were unknown. Only the EN Indus river dolphin (*Platanista minor*) had an increasing population, and VU hippopotamus (*Hippopotamus amphibius*) had a stable population (Appendix S4). Overall, 27 species had stable populations, and the Eurasian beaver (*Castor fiber*) was the only other species with an increasing population trend. Unknown population trends were listed for 60 species, and decreasing trends were observed for 75 species.

Threatened species occurred in 7 of the 10 orders. All species of Perissodactyla ($n = 4$) and Sirenia ($n = 3$) were threatened. All 9 NE species belonged to Rodentia. Threatened species occurred in 19 of 30 families, with Cricetidae (7/45 species threatened), Mustelidae (6/13), and Muridae (4/35) containing the greatest number. All 4 species of Tapiridae, 3 species of Soricidae and Trichechidae, and 2 species of Felidae and Delphinidae were threatened.

Red List Index

The RLI showed temporal change in the extinction risk of species assemblages. The RLI was calculated for 132 species that had been evaluated based on IUCN Red List criteria and not reported as DD or EX during the first assessment following backcasting. Not all species were reported on in the same year; new publications and category changes occurred periodically. Because the RLI requires the same number of species present each year, and many species had gaps of up to 15 years between assessment publications, we used only 3 reporting years: 1996, 2008, and 2016. Six of the 7 genuine changes that occurred after 2016 were backcast to that year because all assessments took place either in 2016 or early 2017, and the driver of the genuine change was already present. The last genuine change occurred in 2021 where the Pyrenean desman (*Galemys pyrenaicus*) was upgraded to EN and was not included in the calculation. The RLI for freshwater mammals (Appendix S5) in the 12 years between 1996 and 2008 showed a decline of 2.0% (compared with 0.8% decline in the global mammal assemblage [Hoffmann et al., 2011]) and over 20 years a decline of 3.6% (compared with a 1.6% decline in all freshwater species [IUCN, 2021]).

Geographic patterns of extinction risk

Globally, freshwater mammals were widely distributed (Figure 1a), with most species occurring in the Neotropical (56) and Afrotropical (48) realms, followed by the Palearctic (22), Indo-Malayan (17), Nearctic (13), and Australasian (10) realms. Ninety-seven species occurred in tropical climates compared with 45 species in temperate areas, 17 in cold climates, and 7 in arid regions. No freshwater mammals occurred prominently in polar climates, despite some species' extent of occurrence overlapping with small polar zones.

The Neotropical realm supported 15 threatened species (26.8%) and the Indo-Malayan realm 13 threatened species (76.5%). Eleven threatened species occurred in the Afrotropical realm, 10 occurred in the Palearctic realm, and only the water mouse (*Xeromys myoides*) was threatened in the Australasian realm (Figure 1b). Conversely, all species in the Nearctic realm are considered LC, with the exception of the DD Glacier Bay water shrew (*Sorex alaskanus*). Of the 29 unclassified DD and NE species, 13 were from the Neotropical realm, 9 from the Afrotropical, 4 Australasian, 2 Indo-Malayan, and 1 Nearctic.

Freshwater mammals occupied 11 habitat types (Appendix S6). As expected, wetlands offered the most habitat for 154 species, with 28 species exclusively occurring in wetland habitats. Forests provided habitat for 97 freshwater mammals, 55 species occurred in grasslands, and <25 species each occupied shrubland, artificial terrestrial habitats (e.g., cultivated gardens, plantations, agricultural or urban land), artificial aquatic habitats (e.g., human-made ponds, aquaculture, irrigation channels), and moist savanna (Appendix S5). Although predominantly occupying freshwater habitats, 27 species also occurred in saline environments, including marine coastal, marine intertidal (e.g., around submerged mangrove roots), marine neritic (including estuaries), and oceanic areas (Appendix S6). Seventy-two freshwater mammals had a narrow habitat breadth of 2 major habitat types, with a maximum breadth of 8 recorded for the Asian small-clawed otter (*Aonyx cinereus*) and Eurasian otter (*Lutra lutra*) (Appendix S7). Of the 154 wetland-dwelling species, most occupied permanent rivers, streams, and creeks (109 species); followed by bogs, marshes, and swamps (77 species); permanent freshwater lakes (35 species); shrub-dominated wetlands (35 species); permanent freshwater marshes (33 species); and seasonal or intermittent rivers, streams, and creeks (22 species) (Appendix S8).

Threatening processes

All threatening processes listed by the IUCN affected at least 1 freshwater mammal at 1 point in time. However, currently no geological events were considered a species-level threat. The most prevalent ongoing threats included biological resource use, agriculture and aquaculture, pollution, residential and commercial development, and modification of natural systems (Figures 2 & 3). Cropping practices, hunting, logging, agricultural runoff, housing development, and water management practices were the leading threats within the main threat categories. Transport corridors, particularly roads, railway, and shipping lanes, threatened 25 species, and current threats of 16 evaluated species were unknown. Invasive, problematic species, genes, and diseases, transport corridors, mining and energy production, and human intrusion of natural habitat each affected <12% of species (Figure 2). Minor threats that did not affect the entire population of a species, such as hunting for food or pelts, habitat loss and degradation, or poisoning of species considered pests, were reported for 15 species. Climate change effects were reported for 19 species, represented by drought (13 species), habitat shifting and alteration (7 species), storms and flooding (6 species), and temperature extremes (2 species). Of those species facing known threats, the majority were threatened by 3 (20 species) or 4 (18 species) separate processes, with a maximum of 9 effecting any 1 animal (Appendix S9).

More than half of all ongoing threatening processes were reported in the Neotropical (27.6% of threats) and Afrotropical (24.0%) realms. The Palearctic followed (19.8%), then Indo-Malayan (16.4%), Nearctic (7.6%), and Australasian (4.5%) realms. The Afrotropical realm contained the highest number of species threatened by biological resource use (20 species), agriculture and aquaculture (19 species), human disturbance (5 species), and unknown factors (14 species) (Figure 3). Pollution (19 species), agriculture and aquaculture (19 species), residential development (12 species), energy production (7 species), and minor threats (5 species) were the most prevalent in the Neotropical realm. However, this realm also contained the greatest number of species not experiencing current threats (10 species). The Palearctic realm contained the greatest number of species threatened by ecosystem modification (12 species), invasive species and diseases (7 species), transport corridors (7 species), and climate change (7 species) and showed a high concentration of species affected by water pollution (13 species).

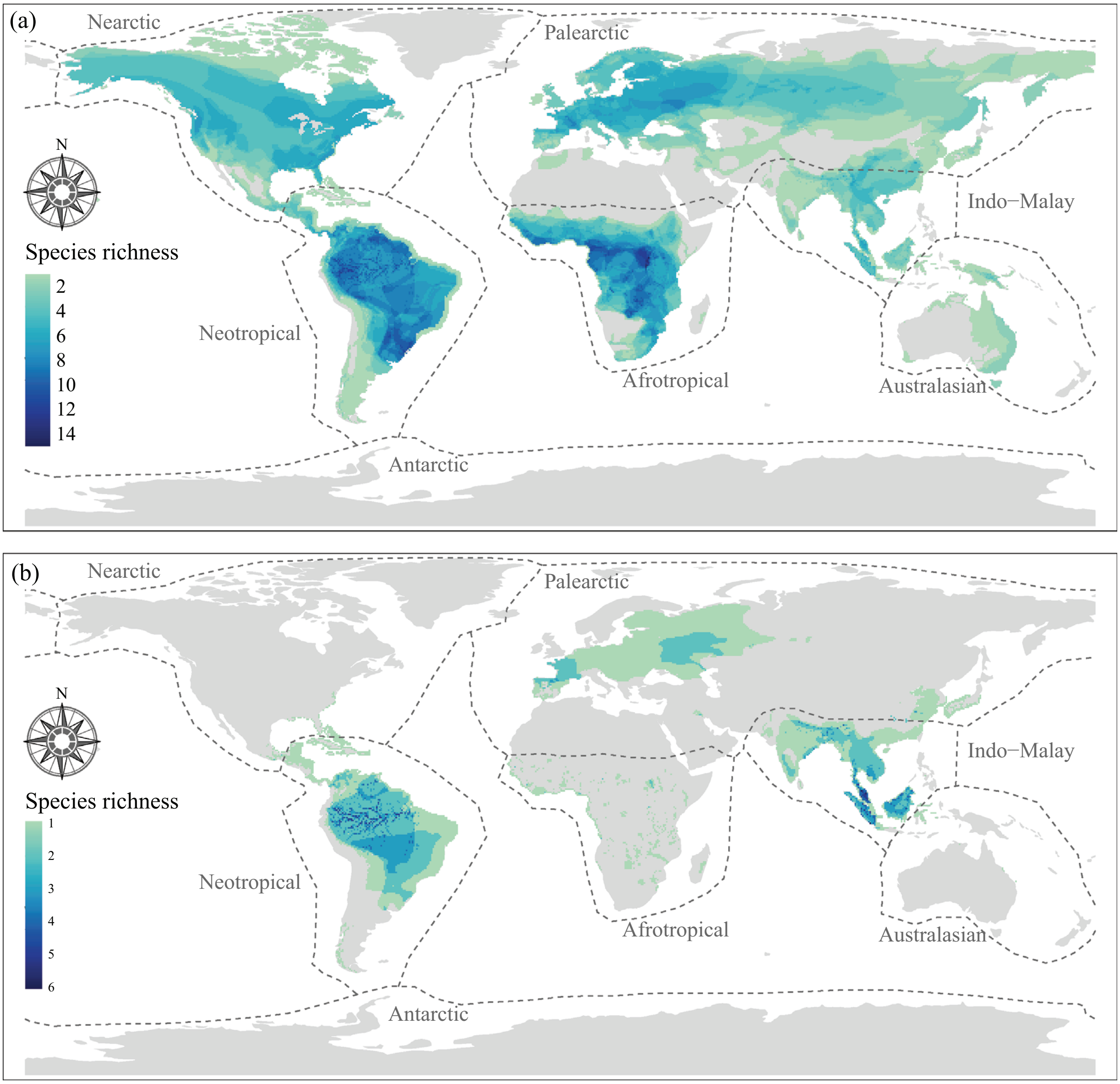

FIGURE 1 Species richness of (a) all freshwater mammals with available range maps ($n = 153$) and (b) threatened freshwater mammals ($n = 50$, including extinct in the wild).

The Indo-Malayan realm contained a high proportion of species threatened by resource use (16 species), agriculture (15 species), and urban and residential development (11 species).

The IUCN assessments of 18 species predicted they will be affected by further threatening processes in the next century, including climate change, housing development, mining and wood plantations, dams and surface water abstraction, industrial and military effluents, and noise pollution. This included 8 species of otters—3 of which are currently threatened—that will be affected by habitat alteration, drought, and flooding. The 2 extinct Madagascan hippopotamuses were likely threatened by overhunting (Hansford et al., 2021), and Nelson's rice rat (*Oryzomys nelsoni*) was likely driven to extinction by competition with the invasive black rat (*Rattus rattus*) (Timm et al., 2017). The extinction of Père David's deer (*Elaphurus davidianus*) in the wild was attributed to habitat loss associated with housing development, agricultural crops, and hunting (Jiang & Harris, 2016).

Life-history traits and predictors of extinction risk

Despite the majority of freshwater mammals being listed as LC, many species remain poorly known and basic data on life-history traits are lacking. For instance, home range data were only available for 34 species. Body mass was a strong indicator of extinction risk; the greater the mass, the more likely to be threatened (Table 1; Figure 4). We also found the probability of a species being threatened increased as dispersal distance and number of threats to a species increased (Table 1; Figure 4). Habitat breadth, wetland breadth, activity cycles (diurnal,

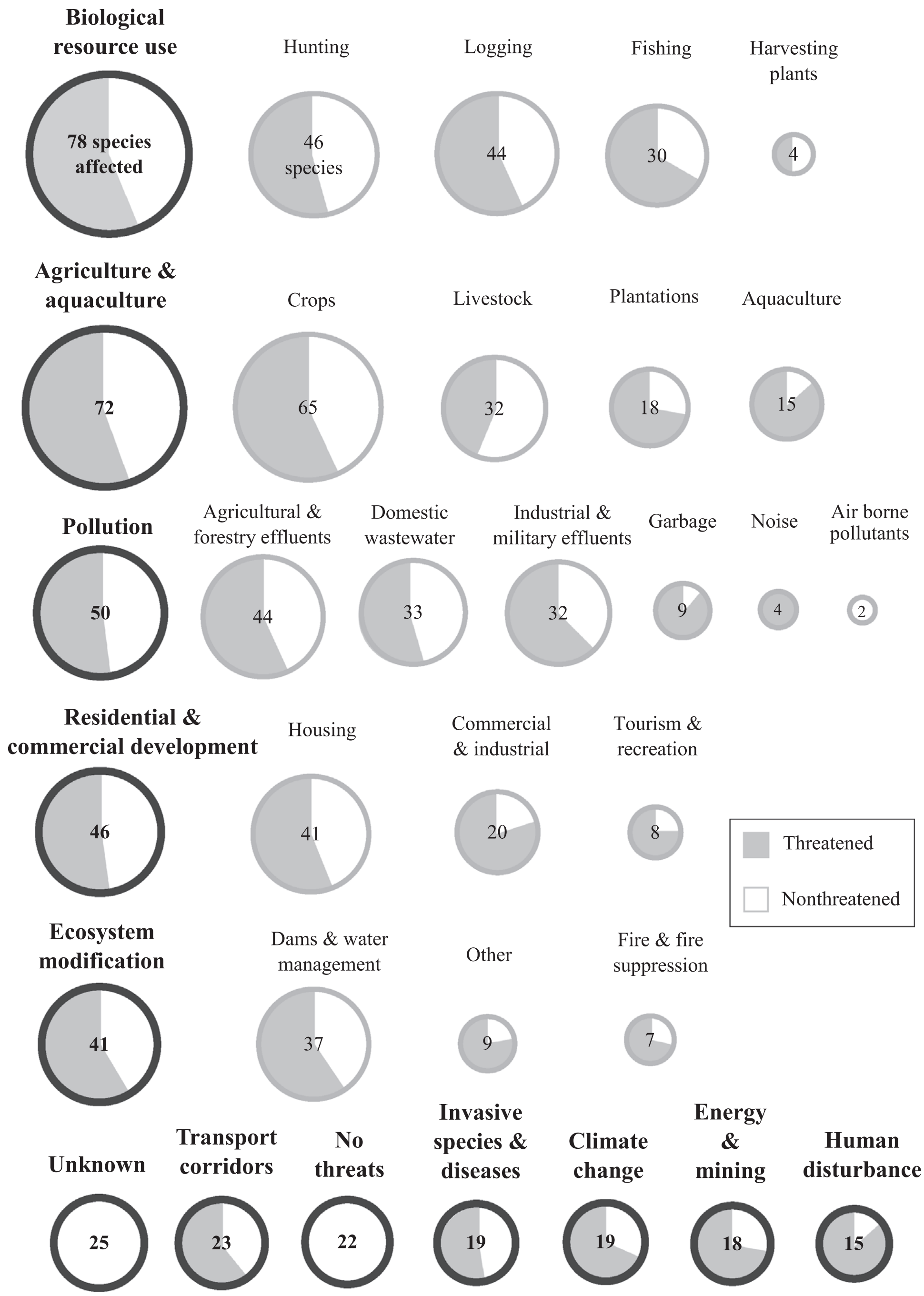

FIGURE 2 Number of freshwater mammals affected by each threatening process and the proportion (pie charts) of threatened species affected based on the International Union for the Conservation of Nature Threats Classification Scheme 3.2 (IUCN, 2012c) (first 5 circles on the left, 5 greatest threats; threats aligned to the right of top 5 threats, respective subcategory threats; bottom row, other threats that affect freshwater mammals).

nocturnal, or mixed), and trophic level had no effect on extinction risk (95% CI contained zero). Although the degree of aquatic specialization in semiaquatic mammals had no effect on their risk of extinction, fully aquatic mammals were at a significantly greater risk of extinction than semiaquatic mammals (Table 1; Figure 5a).

The Indo-Malayan realm contained the greatest proportion of threatened species (b = 3.05, pd = 99.95%, 95% CI 1.07 to 5.32), whereas the Nearctic had the lowest proportion of threatened species (b = −5.28, pd = 99.85%, 95% CI −11.56 to −1.07). No difference was observed between the proportion of species in the remaining realms (Figure 5b). Only cold climates were associated with a comparatively low extinction risk (b = −3.49, pd = 99.25%, 95% CI −6.53 to −0.63) (Appendix S10).

Conservation Biology

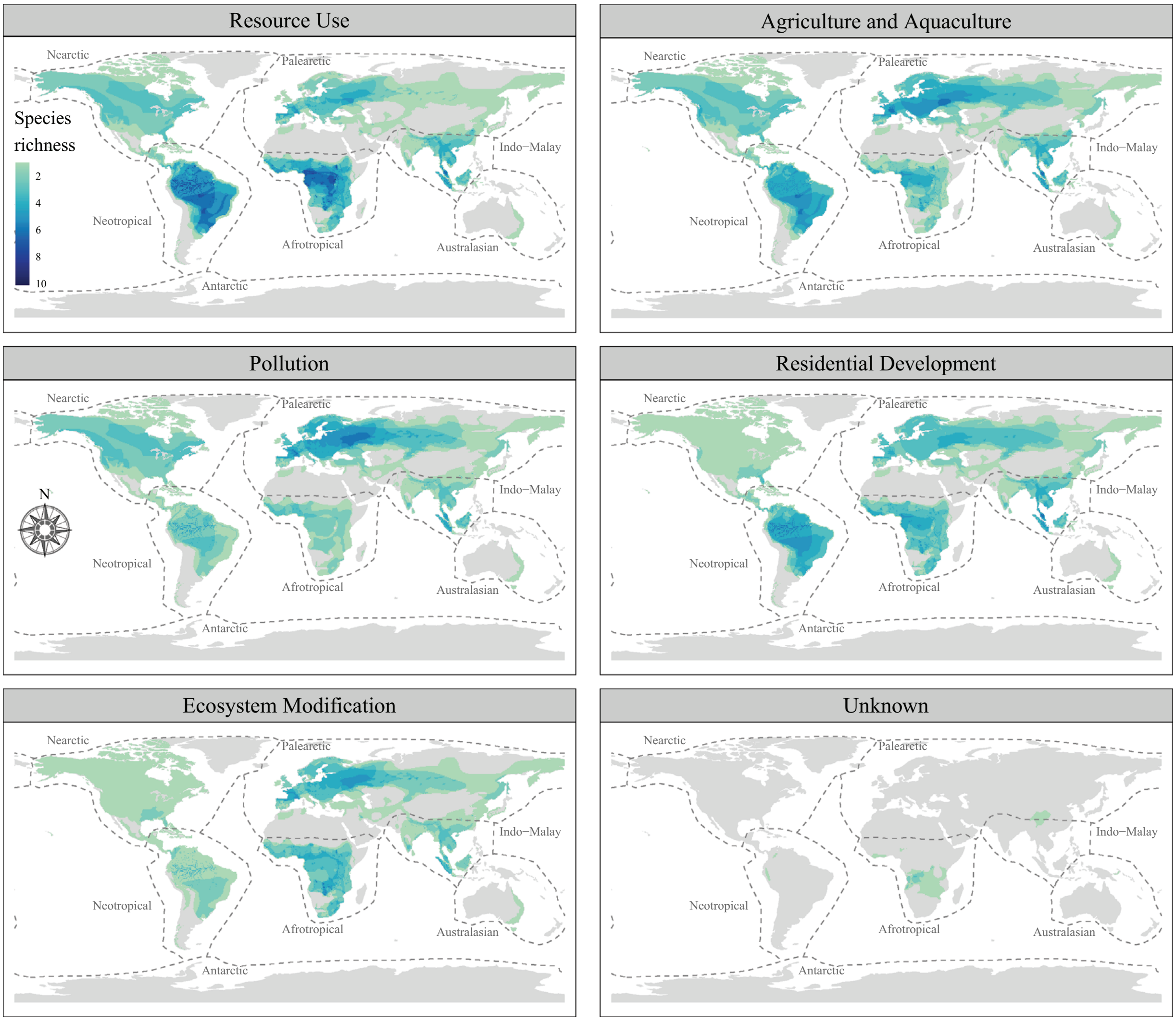

FIGURE 3 Species richness of freshwater mammals with available range maps ($n = 153$ species) relative to threats from resource use ($n = 78$), agriculture and aquaculture ($n = 72$), pollution ($n = 50$), residential development ($n = 46$), ecosystem modification ($n = 42$), and unknown process ($n = 15$).

TABLE 1 Results of univariate Bayesian regression models predicting the effect of life-history and extrinsic factors on the extinction risk of freshwater mammals.

Predictor	Estimate	pd (%)[a]	95% CI	n	Conditional R^2[b]	Marginal R^2[b]
Body mass	0.02	100	0.01 to 0.03[c]	135	0.23 (0.14–0.32)	0.21 (0.11–0.29)
Dispersal distance	0.08	99.62	0.03 to 0.15[c]	125	0.16 (0.07–0.25)	0.15 (0.01–0.23)
Number of threats	0.51	100	0.28 to 0.77[c]	128	0.31 (0.20–0.40)	0.25 (0.13–0.36)
Aquatic mammal[d]	−3.67	99.86	−7.20 to −1.11[c]	137	0.25 (0.11–0.37)	0.09 (0.02–0.16)
Habitat breadth	−0.04	61.27	−0.34 to 0.25	135	0.20 (0.09–0.30)	0.01 (0.00–0.04)
Dietary breadth	0.37	93.23	−0.11 to 0.86	126	0.22 (0.10–0.32)	0.02 (0.00–0.09)
Generation length	0.00	97.85	−0.00 to 0.00	107	0.46 (0.35–0.55)	0.20 (0.00–0.39)
Year described	0.01	99.75	0.00 to 0.02	137	0.28 (0.16–0.37)	0.08 (0.00–0.15)
Home range size	−0.00	51.05	−0.04 to 0.03	34	0.24 (0.00–0.41)	0.01 (0.00–0.09)

[a]Probability of direction, which describes certainty of the effect direction.
[b]Credible intervals in parentheses.
[c]Significant result at the 95% credible interval.
[d]Comparison of extinction risk between aquatic mammals and semiaquatic mammals.

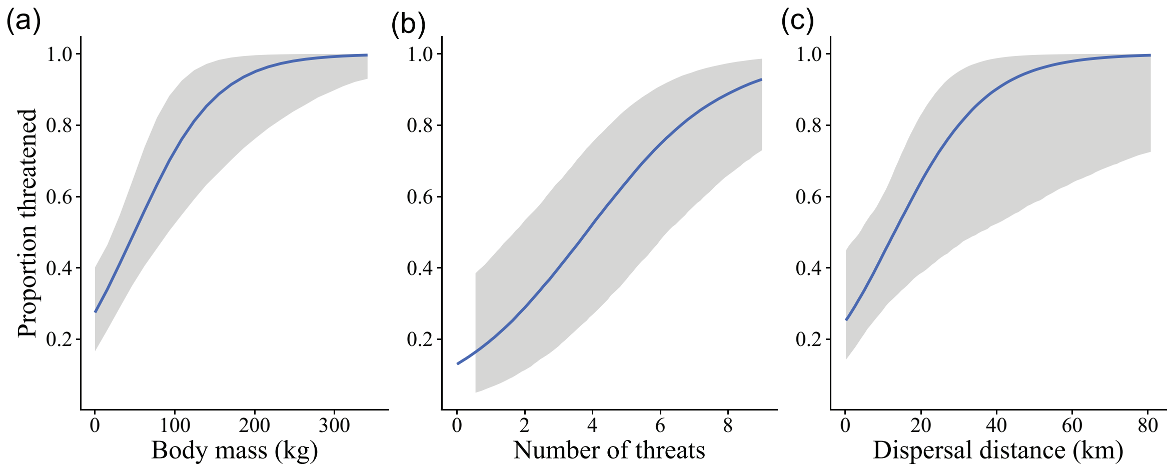

FIGURE 4 The effect of (a) body mass ($n = 124$ species) (limited to 350 kg because the proportion of threatened species plateaus when body mass is >300 kg [max body mass 1500 kg]), (b) compounding threatening processes ($n = 117$), and (c) dispersal distances ($n = 125$) on the threatened status of freshwater mammals evaluated by the International Union for the Conservation of Nature (shading, 95% credible interval).

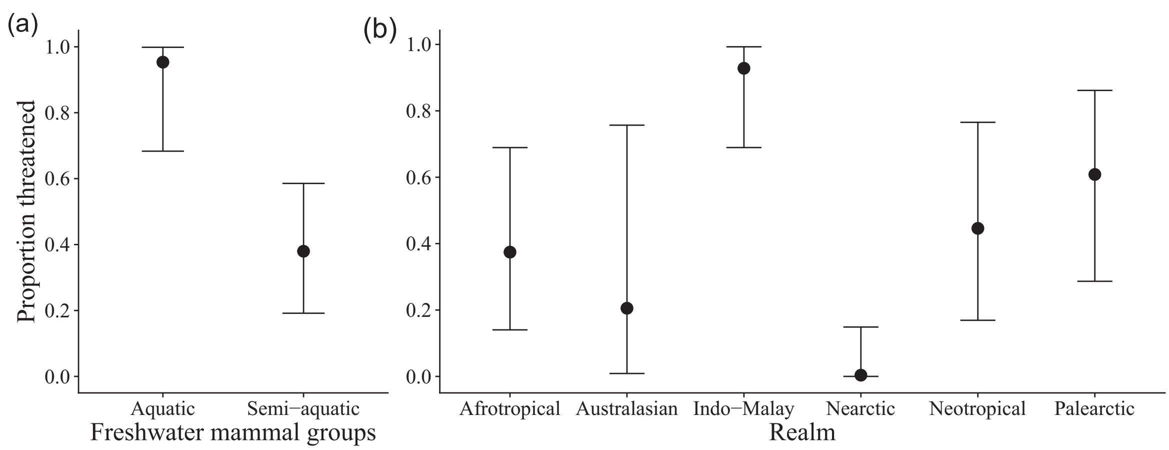

FIGURE 5 Proportion of threatened species for (a) fully aquatic ($n = 11$) and semiaquatic ($n = 155$) freshwater mammals and (b) freshwater mammals by biogeographical realm (bars, 95% credible interval).

DISCUSSION

We considered the extinction risk of 166 species of freshwater mammals in relation to their current and historical conservation status in the IUCN Red List. Despite gaps in knowledge of the basic biology of many species, particularly those listed as LC, it was clear that freshwater mammals had a higher risk of extinction and rate of decline compared with the global assemblage of mammals and freshwater animals in general. The best estimate of the true proportion of threatened species was 37.6%, which is higher than all freshwater taxa (32%; Collen et al., 2014) and terrestrial mammals (26%; IUCN, 2021). Similarly, freshwater mammals had a much greater proportion of species with declining populations (44.0%) than freshwater vertebrates (26.3%) and all mammals (32.0%) (IUCN, 2021; WWF, 2020). The rate of decline of 3.6% over 20 years equates to the IUCN Red List status of 6 species increasing by at least 1 category within the next 2 decades. With the world's vertebrate populations having already declined 68% in the past 50 years, this is a concerning trend for freshwater mammals (WWF, 2020).

Dangers of data deficiency

The elevated extinction risk of freshwater mammals highlights the need for greater study of DD and unevaluated species. Data-deficient species exhibit a higher probability of being threatened than data-sufficient species, making the status of DD particularly precarious by masking the severity of their true situation (Bland et al., 2015; Borgelt et al., 2022; Dudgeon, 2020). Predictions of the extinction risk of DD mammals are that 63.5% are already threatened (Bland et al., 2015), suggesting that the pessimistic upper estimate of the proportion of threatened freshwater mammals of 48.8% may be more accurate. A lack of current population assessments is responsible for the lapse in categorization of many DD species, which highlights the importance of developing monitoring programs. Here, as much as 65% of DD freshwater mammals had been categorized along with other highly threatened species, such as the EN Amazon River dolphin (*Inia geoffrensis*) (da Silva et al., 2018), as DD for multiple assessments before being uplisted from their previous status.

Most DD freshwater mammals are small rodents or shrews (<100 g), which either inhabit areas that are difficult to survey (e.g., Rowe et al., 2014) or are taxonomically uncertain, such as *Dasymys* spp. and potentially *Colomys goslingi* (Giarla et al., 2021; Mullin et al., 2005). Resolutions of species complexes are important, for instance, 2 *Dasymys* species that contained 6 newly described species were previously considered LC based on their large geographic range (Mullin et al., 2005; Taylor, 2016). These ranges are now known to be disjunct, with the potential for higher threat classification, for example, the EN montane shaggy rat (*Dasymys montanus*) with its fragmented and declining range (Kennerley, 2016). Such poorly known and newly erected or described DD mammals are among the most likely to be threatened (Bland et al., 2015; Liu et al., 2022; Padial & De la Riva, 2006). Therefore, the IUCN Red List must keep up with increasing taxonomic inflation (Padial & De la Riva, 2006).

Other methods of assessment should also be considered when evaluating species that may lack sufficient population or geographical range data. Although no freshwater mammals were categorized under criterion E (quantitative analysis), using remote methods such as population viability analysis or estimating extinction risks from genetic or habitat status may help prevent species being listed as DD (Mace et al., 2008; Wilder et al., 2023). The use of historic range data in determining the degree of range reduction under criterion B may present another option for difficult-to-survey species, such as the platypus (*Ornithorhynchus anatinus*), which has had dramatic range declines, highlighting its need for reassessment (Hawke et al., 2019).

Threatened species hotspots

Tropical areas have the richest biological diversity of vertebrates (Ceballos & Brown, 1995), followed by temperate regions (Mace et al., 2005), and this pattern holds true for freshwater mammals. Our species richness maps revealed the Neotropical and Afrotropical realms supported the highest concentrations of species, with the highest proportion of threatened species residing in the Indo-Malay—particularly in Malaysia and Indonesian islands of Sumatra and Kalimantan (Figure 1). This region has the highest rate of deforestation globally, driven by logging, crop plantations (particularly palm oil), road construction, and residential development (Dudgeon, 2022; Hughes, 2018; Stibig et al., 2014). Current measures to reduce deforestation have been unsuccessful; clearing continues to increase with demand for housing and plantation products, despite this process being identified as a major threat to biodiversity in the region (Hughes, 2018). Population declines of freshwater megafauna are also greatest in the Indo-Malay region, further attributed to overexploitation and dam construction (He et al., 2019).

Other hotspots of threatened species included the Palearctic (particularly France, Spain, and Russia), Neotropics (Brazil, Venezuela, Bolivia, and Paraguay), and fragments of the Afrotropics (South Sudan). The main threats identified included biological resource use, agriculture, residential development, pollution, and ecosystem modification, where the greatest effects were evident in the Palearctic. The most prevalent impact of ecosystem modification was from water management practices and dams. Although the importance of biogeographical region was clear, the number of occupied habitats did not significantly affect species extinction risk, despite narrow habitat breadth (indicating a more specialized habitat niche) being one of the strongest traits indicative of species more prone to extinction (Chichorro et al., 2019). It is uncertain why this occurred, although it is likely associated with the high levels of total human disturbance (Riggio et al., 2020) in realms with high proportions of threatened freshwater mammals. Significant relationships between habitat type and extinction risk may be observed if species are assessed on a finer scale (e.g., subspecies or populations).

Hunting, logging, and agriculture

Overall, the greatest threats to freshwater mammals are biological resource use—through hunting and logging—and agriculture. Targeted hunting and overexploitation affected almost one third of freshwater mammals, including 21 protected species. Overharvesting of freshwater resources is largely associated with the ease of accessibility and exploitation of freshwater areas compared with hunting in expansive terrestrial refuges (Antunes et al., 2016; Dudgeon, 2020). Freshwater aquatic species are also less resilient to overexploitation; the effects of historic hunting practices still affect current populations (Antunes et al., 2016). Agricultural practices affect freshwater mammals directly via habitat loss as well as indirectly by contributing to other threatening processes (Erisman et al., 2016). Within the IUCN agricultural threat categories, cropping and livestock production were the greatest threats. Indirectly, agricultural effluents contributed to over one third of the species threated by pollution. Agriculture is also the largest consumer of freshwater, contributing to the effects of water abstraction (Shiklomanov, 1993; Stoett et al., 2019).

Interestingly, two thirds of the threats freshwater mammals face are based in the terrestrial system, largely due to crops and livestock, expanding housing developments, timber plantations, mining or road development, and the consequential land clearing often required. Similarly, the effects of habitat loss and degradation—particularly from logging and urban development—affect >80% of all freshwater animals (Collen et al., 2014). Over one quarter of threats potentially affect both terrestrial and aquatic habitats, including pollution, human recreational activities, ecosystem modification, drought, or introduced species. Subsequently, only 12% of threats affect the aquatic system directly, including aquaculture, shipping lanes, fishing, harvesting of aquatic resources, and, most predominantly, dams and water management. Water management practices currently threaten 37 freshwater mammals with many overarching effects. Large impoundments and altered downstream hydrology can cause habitat fragmentation, drive changes in food availability, and restrict movement across the landscape (Barbarossa et al., 2020; Singh et al., 2021; Soukhaphon et al., 2021; Wu et al., 2019). Particularly for fully aquatic mammals, dams are a barrier for dispersal that can drastically restrict gene flow, as has been seen with the Irrawaddy dolphin (*Orcaella brevirostris*), which persists in 3 declining populations along the Mekong River (Dudgeon, 2022). Altered flows and cold-water releases further affect foraging, nesting, or breeding behaviors of several freshwater mammals (Escoda et al., 2019; Hawke et al., 2019; Pedroso et al., 2014; Wu et al., 2019). Dams and water traffic also contribute to noise pollution, which can increase stress and affect echolocation and communication efficiency of aquatic mammals (Dey et al., 2019).

Predisposition for extinction

Life-history traits have been used to assess the likelihood of species extinction or decline and predict IUCN Red List categories of unevaluated species (Bland et al., 2015; Cardillo, 2003; Hoffmann et al., 2011; Kopf et al., 2017; Rija et al., 2020). Here, only body mass and dispersal distance had a significant influence on the extinction risk of species. In a trend following that for all mammals and freshwater megafauna, heavier freshwater mammals are at a higher risk of extinction (He et al., 2019; Hernández-Yáñez et al., 2022; Hoffmann et al., 2011; Rija et al., 2020; Ripple et al., 2017) because they typically have longer life spans and generation lengths, greater maturation ages, longer gestation periods, and lower reproductive output (Cardillo, 2003; Cardillo et al., 2005; He et al., 2019; Stearns, 1983; Whitmee & Orme, 2013). Species that disperse long distances are exposed to a greater number of potential threats when moving across large areas, which makes them susceptible to habitat alteration and increases their risk of extinction. This is a common issue for potamodromous fish, which migrate purely within freshwater systems and are highly threatened by reduced connectivity (Deinet et al., 2020; Dudgeon, 2020).

Although large freshwater mammals with greater dispersal distances are of greatest conservation concern, small species, which represent the majority (107 species <1 kg), should not be ignored. Small species receive less attention and research than large species, despite many being at the same risk of endangerment (Bland et al., 2015; Marneweck et al., 2021). Rodentia was the largest order represented in our analyses, yet even poorly known and threatened rodents were not recommended for further research in their IUCN assessments (Rivas, 2018; Weksler & Timm, 2017). Indeed, it is highly likely that there are species, such as the rakali (*Hydromys chrysogaster*), that require an elevated risk status but remain LC owing to a lack of basic ecological knowledge (Williams, 2019).

Recommendations for freshwater mammal conservation

Our results imply that the number of threats freshwater mammals face can combine to increase their risk of extinction. With the increasing prevalence of threats to freshwater environments and interactions emerging between threatening processes (Geary et al., 2019), it is important efforts are taken to manage impacts from multiple stressors (Reid et al., 2019). Given the threats we identified, freshwater mammals would benefit from improved protection of freshwater and surrounding riparian habitats; greater hunting prevention; improved management of industrial, domestic, and agricultural pollution; and greater freshwater connectivity.

Greater protection and restoration of freshwater systems and surrounding habitats may mitigate the stresses induced by agriculture, urban and industrial development, and logging. Protection can be provided through formal means, such as with protected areas (listed locally or through initiatives such as the Ramsar Convention) or through policy aimed to maintain freshwater connectivity (Maasri et al., 2021; Tickner et al., 2020). The installation of buffer and livestock exclusion zones around freshwater habitats can also be achieved on smaller scales by landholders (Kauffman et al., 2022; Luke et al., 2019; McCormack, 2023; Rhodes et al., 2002; Singh et al., 2021). Such methods not only improve general habitat quality, but also act as a filter to reduce nutrient runoff. Although previous legislative efforts have been unsuccessful in curbing freshwater pollution (Dudgeon, 2020), improved wastewater treatment, regulation of industrial pollution, and sustainable agricultural practices have led to promising improvements in water quality (McCormack, 2023; Tickner et al., 2020). Improved fishing regulations, antipoaching strategies, and poverty alleviation to limit overharvesting, bycatch, and illegal hunting can also mitigate threats associated with biological resource use (Dudgeon, 2020; Rija et al., 2020; Tickner et al., 2020). Lack of water connectivity created through intense regulation of waterways and dams is a significant threat to freshwater biodiversity. We recommend the ecological and hydrological needs of freshwater mammals be considered in all future water infrastructure plans. Environmental flows ("the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems" [Arthington et al., 2018, p. 4]) are another key to restoring freshwater ecosystem function (Dudgeon, 2022; McCormack, 2023). Further methods to restore natural watering and flooding processes include the removal of obsolete dams and levees and greater protection of remaining free-flowing systems to prevent negative effects of river regulation (Dudgeon, 2020; He et al., 2021; Tickner et al., 2020).

ACKNOWLEDGMENTS

The IUCN is acknowledged for the use of its information, range maps, and classification of species. Funding was provided by the Australian Government Research and Training program, Gulbali Accelerated Publication Scheme, and the Murrumbidgee

Monitoring Evaluation and Research program funded by the Commonwealth Environmental Water Office.

Open access publishing facilitated by Charles Sturt University, as part of the Wiley - Charles Sturt University agreement via the Council of Australian University Librarians.

ORCID

Emmalie Sanders https://orcid.org/0000-0002-1051-1854

REFERENCES

Antunes, A. P., Fewster, R. M., Venticinque, E. M., Peres, C. A., Levi, T., Rohe, F., & Shepard, G. H. (2016). Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Science Advances*, *2*, e1600936.

Arthington, A. H., Bhaduri, A., Bunn, S. E., Jackson, S. E., Tharme, R. E., Tickner, D., Young, B., Acreman, M., Baker, N., Capon, S., Horne, A. C., Kendy, E., McClain, M. E., Poff, N. L., Richter, B. D., & Ward, S. (2018). The Brisbane declaration and global action agenda on environmental flows (2018). *Frontiers in Environmental Science*, *6*, 45.

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

Barbarossa, V., Schmitt, R. J. P., Huijbregts, M. A. J., Zarfl, C., King, H., & Schipper, A. M. (2020). Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 3648–3655.

Bivand, R., Keitt, T., & Rowlingson, B. (2022). *rgdal: Bindings for the 'Geospatial' Data Abstraction Library*. R package version 1.5-32. https://CRAN.R-project.org/package=rgdal

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

Borgelt, J., Dorber, M., Høiberg, M. A., & Verones, F. (2022). More than half of data deficient species predicted to be threatened by extinction. *Communications Biology*, *5*, 679.

Bubb, P. J., Butchart, S. H. M., Collen, B., Dublin, H., Kapos, V., Pollock, C., Stuart, S. N., & Vié, J.-C. (2009). *IUCN Red List Index—Guidance for national and regional use*. IUCN.

Butchart, S. H. M., Resit Akçakaya, H., Chanson, J., Baillie, J. E. M., Collen, B., Quader, S., Turner, W. R., Amin, R., Stuart, S. N., Lusseau, D., & Hilton-Taylor, C. (2007). Improvements to the Red List Index. *PLoS ONE*, *2*, e140.

Butchart, S. H. M., Stattersfield, A. J., Bennun, L. A., Shutes, S. M., Akçakaya, H. R., Baillie, J. E. M., Stuart, S. N., Hilton-Taylor, C., & Mace, G. M. (2004). Measuring global trends in the status of biodiversity: Red List Indices for birds. *PLoS Biology*, *2*, e383.

Bürkner, P. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*, 1–28. doi: https://doi.org/10.18637/jss.v080.i01

Cardillo, M. (2003). Biological determinants of extinction risk: Why are smaller species less vulnerable? *Animal Conservation*, *6*, 63–69.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., Orme, C. D., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*, 1239–1241.

Ceballos, G., & Brown, J. H. (1995). Global patterns of mammalian diversity, endemism, and endangerment. *Conservation Biology*, *9*, 559–568.

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229.

Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., Pollock, C., Richman, N. I., Soulsby, A., & Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, *23*, 40–51.

da Silva, V., Trujillo, F., Martin, A., Zerbini, A. N., Crespo, E., Aliaga-Rossel, E., & Reeves, R. (2018). *Inia geoffrensis*. The IUCN Red List of Threatened Species 2018: e.T10831A50358152.

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*, 934–941.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, M. L., Tickner, D., Waldman, J., … Berkhuysen, A. (2020). *The Living Planet Index (LPI) for migratory freshwater fish: Technical report*. World Fish Migration Foundation.

Dey, M., Krishnaswamy, J., Morisaka, T., & Kelkar, N. (2019). Interacting effects of vessel noise and shallow river depth elevate metabolic stress in Ganges river dolphins. *Scientific Reports*, *9*, 15426.

Dudgeon, D. (2020). *Freshwater biodiversity: Status, threats and conservation* (Ecology, biodiversity and conservation). Cambridge University Press.

Dudgeon, D. (2022). *Threatened freshwater animals of tropical East Asia: Ecology and conservation in a rapidly changing environment*. Routledge.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, *81*, 163–182.

Dunstone, N., & Gorman, M. L. (1998). *Behaviour and ecology of riparian mammals*. Cambridge University Press.

Erisman, J. W., Eekeren, N. v., Wit, J. d., Koopmans, C., Cuijpers, W., Oerlemans, N., & Koks, B. J. (2016). Agriculture and biodiversity: A better balance benefits both. *AIMS Agriculture and Food*, *1*, 157–174.

Escoda, L., Fernández-González, Á., & Castresana, J. (2019). Quantitative analysis of connectivity in populations of a semi-aquatic mammal using kinship categories and network assortativity. *Molecular Ecology Resources*, *19*, 310–326.

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., & Tulloch, A. I. T. (2019). Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *Journal of Applied Ecology*, *56*, 1992–1997.

Giarla, T. C., Demos, T. C., Monadjem, A., Hutterer, R., Dalton, D., Mamba, M. L., Roff, E. A., Mosher, F. M., Mikes, V., Kofron, C. P., & Kerbis Peterhans, J. C. (2021). Integrative taxonomy and phylogeography of *Colomys* and *Nilopegamys* (Rodentia: Murinae), semi-aquatic mice of Africa, with descriptions of two new species. *Zoological Journal of the Linnean Society*, *192*, 206–235.

Hansford, J. P., Lister, A. M., Weston, E. M., & Turvey, S. T. (2021). Simultaneous extinction of Madagascar's megaherbivores correlates with late Holocene human-caused landscape transformation. *Quaternary Science Reviews*, *263*, 106996.

Hawke, T., Bino, G., & Kingsford, R. T. (2019). A silent demise: Historical insights into population changes of the iconic platypus (*Ornithorhynchus anatinus*). *Global Ecology and Conservation*, *20*, e00720.

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*, 3883–3892.

Hernández-Yáñez, H., Kim, S. Y., & Che-Castaldo, J. P. (2022). Demographic and life history traits explain patterns in species vulnerability to extinction. *PLoS ONE*, *17*, e0263504.

Hijmans, R. (2022). *raster: Geographic data analysis and modeling*. R package version 3.5-29. https://CRAN.R-project.org/package=raster

Hoffmann, M., Belant, J. L., Chanson, J. S., Cox, N. A., Lamoreux, J., Rodrigues, A. S. L., Schipper, J., & Stuart, S. N. (2011). The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2598–2610.

Hood, G. A. (2020). *Semi-aquatic mammals: Ecology and biology*. John Hopkins University Press.

Howell, A. B. (1930). *Aquatic mammals: Their adaptation to life in the water*. Charles C Thomas.

Hughes, A. C. (2018). Have Indo-Malaysian forests reached the end of the road? *Biological Conservation*, *223*, 129–137.

International Union for Conservation of Nature (IUCN). (2012a). *IUCN Red List categories and criteria, version 3.1, second edition*. Author.

International Union for Conservation of Nature (IUCN). (2012b). *IUCN Red List Habitats Classification Scheme: Version 3.1*. https://www.iucnredlist.org/resources/habitat-classification-scheme

International Union for Conservation of Nature (IUCN). (2012c). *IUCN Red List Threats Classification Scheme: Version 3.2*. https://www.iucnredlist.org/resources/threat-classification-scheme

International Union for Conservation of Nature (IUCN). (2021). *The IUCN Red List of Threatened Species: Version 2021–3*. https://www.iucnredlist.org/

IUCN Standards and Petitions Committee. (2022). *Guidelines for using the IUCN Red List categories and criteria: Version 15*. Prepared by the Standards and Petitions Committee.

Jiang, Z., & Harris, R. B. (2016). *Elaphurus davidianus*. The IUCN Red List of Threatened Species 2016: e.T7121A22159785.

Kauffman, J. B., Coleman, G., Otting, N., Lytjen, D., Nagy, D., & Beschta, R. L. (2022). Riparian vegetation composition and diversity shows resilience following cessation of livestock grazing in northeastern Oregon, USA. *PLoS ONE*, *17*, e0250136.

Kennerley, R. (2016). *Dasymys montanus* (Errata version published in 2017). The IUCN Red List of Threatened Species 2016: e.T6270A115080657.

Kopf, R. K., Shaw, C., & Humphries, P. (2017). Trait-based prediction of extinction risk of small-bodied freshwater fishes. *Conservation Biology*, *31*, 581–591.

Larkin, Z. T., Ralph, T. J., Tooth, S., Fryirs, K. A., & Carthey, A. J. R. (2020). Identifying threshold responses of Australian dryland rivers to future hydroclimatic change. *Scientific Reports*, *10*, 6653–6653.

Liu, J., Slik, F., Zheng, S., & Lindenmayer, D. B. (2022). Undescribed species have higher extinction risk than known species. *Conservation Letters*, *15*, e12876.

Luke, S. H., Slade, E. M., Gray, C. L., Annammala, K. V., Drewer, J., Williamson, J., Agama, A. L., Ationg, M., Mitchell, S. L., Vairappan, C. S., & Struebig, M. J. (2019). Riparian buffers in tropical agriculture: Scientific support, effectiveness and directions for policy. *Journal of Applied Ecology*, *56*, 85–92.

Lüdecke, D. (2018). ggeffects: tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*, 772. https://doi.org/10.21105/joss.00772

Mace, G., Masundire, H., Baillie, J., Ricketts, T., Brooks, T., Hoffmann, M., Stuart, S., Balmford, A., Purvis, A., Reyers, B., Wang, J., Revenga, C., Kennedy, E., Naeem, S., Alkemade, R., Allnutt, T., Bakarr, M., Bond, W., Chanson, J., … Williams, P. (2005). Biodiversity. In R. Hassan, R. Scholes, & N. Ash (Eds.), *Ecosystems and human well-being: Current state and trends* (Vol. 1, pp. 77–122). Island Press.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akcakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J., & Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, *22*, 1424–1442.

Marneweck, C., Butler, A. R., Gigliotti, L. C., Harris, S. N., Jensen, A. J., Muthersbaugh, M., Newman, B. A., Saldo, E. A., Shute, S. K., Titus, K. L., Yu, S. W., & Jachowski, D. S. (2021). Shining the spotlight on small mammalian carnivores: Global status and threats. *Biological Conservation*, *255*, 109005.

Maasri, A., Jähnig, S. C., Adamescu, M. C., Adrian, R., Baigun, C., Baird, D. J., Batista-Morales, A., Bonada, N., Brown, L. E., Cai, Q., Campos-Silva, J. V., Clausnitzer, V., Contreras-MacBeath, T., Cooke, S. J., Datry, T., Delacámara, G., de Meester, L., Dijkstra, K-D. B., Do, V. T., & Worischka, S. (2022). A global agenda for advancing freshwater biodiversity research. *Ecology Letters*, 25, 255–263. https://doi.org/10.1111/ele.13931

McCormack, M. (2023). *Farmer willingness to adopt mitigation measures for water quality improvements*. Agricultural Economics Society 97th Annual Conference, Coventry, UK. https://doi.org/10.22004/ag.econ.334532

McRae, L., Deinet, S., & Freeman, R. (2017). The diversity-weighted living planet index: Controlling for taxonomic bias in a global biodiversity indicator, *PLOS ONE*, *12*, e0169156.

Mullin, S. K., Pillay, N., & Taylor, P. J. (2005). The distribution of the water rat *Dasymys* (Muridae) in Africa: A review. *South African Journal of Science*, *101*, 117–124.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience*, *51*, 933–938.

Pacini, N., & Harper, D. M. (2008). Aquatic, semi-aquatic and riparian vertebrates. In D. Dudgeon (Ed.), *Tropical stream ecology* (pp. 147–197). Academic Press.

Padial, J. M., & De la Riva, I. (2006). Taxonomic inflation and the stability of species lists: The Perils of Ostrich's behavior. *Systematic Biology*, *55*, 859–867.

Pedroso, N. M., Marques, T. A., & Santos-Reis, M. (2014). Response of otters to environmental changes imposed by the construction of large dams. *Aquatic Conservation*, *24*, 66–80.

Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Science*, *11*, 1633–1644.

R Core Team. (2022). *R: A language and environment for statistical computing* (Version 4.2.1). R Foundation for Statistical Computing. https://www.R-project.org/

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*, 849–873.

Rhodes, H. M., Leland, J. L. S., & Niven, B. E. (2002). Farmers, streams, information, and money: Does informing farmers about riparian management have any effect? *Environmental Management*, *30*, 0665–0677.

Riggio, J., Baillie, J. E. M., Brumby, S., Ellis, E., Kennedy, C. M., Oakleaf, J. R., Tait, A., Tepe, T., Theobald, D. M., Venter, O., Watson, J. E. M., & Jacobson, A. P. (2020). Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. *Global Change Biology*, *26*, 4344–4356.

Rija, A. A., Critchlow, R., Thomas, C. D., & Beale, C. M. (2020). Global extent and drivers of mammal population declines in protected areas under illegal hunting pressure. *PLoS ONE*, *15*, e0227163.

Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 10678–10683.

Rivas, B. A. (2018). *Neusticomys venezuelae*. The IUCN Red List of Threatened Species: e.T14744A22336822.

Rowe, K. C., Achmadi, A. S., & Esselstyn, J. A. (2014). Convergent evolution of aquatic foraging in a new genus and species (Rodentia: Muridae) from Sulawesi Island, Indonesia. *Zootaxa*, *3815*, 541–564.

Shiklomanov, I. A. (1993). World fresh water resources. In P. Gleick (Ed.), *Water in crisis* (pp. 13–24). Oxford University Press.

Singh, R., Tiwari, A. K., & Singh, G. S. (2021). Managing riparian zones for river health improvement: An integrated approach. *Landscape and Ecological Engineering*, *17*, 195–223.

Soria, C. D., Pacifici, M., Di Marco, M., Stephen, S. M., & Rondinini, C. (2021). COMBINE: A coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, *102*, e03344.

Soukhaphon, A., Baird, I. G., & Hogan, Z. S. (2021). The impacts of hydropower dams in the mekong river basin: A review. *Water*, *13*, 265.

Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, *41*, 173–187.

Stoett, P., Davies, J., Armenteras, D., Hills, J., McRae, L., Zastavniouk, C., Bailey, R., Butler, C., Dankelman, I., Garcia, K., Godfrey, L., Kirilenko, A., Lemke, P., Liggett, D., Mudd, G., Seager, J., Wright, C. Y., & Zickgraf, C. (2019). *Global environment outlook - GEO-6: Healthy planet, healthy people*. Cambridge University Press doi: https://doi.org/10.1017/9781108627146

Stibig, H. J., Achard, F., Carboni, S., Raši, R., & Miettinen, J. (2014). Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences*, *11*, 247–258.

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

Taylor, P. J. (2016). *Dasymys incomtus* (Errata version published in 2017). The IUCN Red List of Threatened Species: e.T6269A115080446.

Tennekes, M. (2018). tmap: Thematic maps in R. *Journal of Statistical Software*, *84*, 1–39.

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A. J., Leondard, P., McClain, M. E., Olden, J.

D., … Young, L. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *Bioscience*, *70*, 330–342.

Timm, R., Álvarez-Castañeda, S. T., & Lacher, T. (2017). *Oryzomys nelsoni*. The IUCN Red List of Threatened Species 2017: e.T15583A22388135.

Véron, G., Patterson, B. D., & Reeves, R. (2010). *Vertebrates-Mammals checklist*. http://fada.biodiversity.be/group/show/58

Veron, G., Patterson, B. D., & Reeves, R. (2007). Global diversity of mammals (Mammalia) in freshwater. In: Balian, E. V., Lévêque, C., Segers, H., Martens, K. (eds) Freshwater Animal Diversity Assessment. Developments in Hydrobiology, 198. https://doi.org/10.1007/978-1-4020-8259-7_59

Weksler, M., & Timm, R. (2017). *Oryzomys gorgasi* (Errata version published in 2018). The IUCN Red List of Threatened Species: e.T115554360A123796971.

Whitmee, S., & Orme, C. D. L. (2013). Predicting dispersal distance in mammals: A trait-based approach. *Journal of Animal Ecology*, *82*, 211–221.

Wilder, A. P., Supple, M. A., Subramanian, A., Mudide, A., Swofford, R., Serres-Armero, A., Steiner, C., Koepfli, K., Genereux, D. P., Kalsson, E. K., Lindblad-Toh, K., Marques-Bonet, T., Munoz Fuentes, V., Foley, K., Meyer, W. K., Ryder, O. A., Shapiro, B., Andrews, G., Armstrong, J. C., … Zhang, X. (2023). The contribution of historical processes to contemporary extinction risk in placental mammals. *Science*, *380*, eabn5856.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York.

Williams, G. A. (2019). *Distribution and status of the Australian water-rat/rakali (Hydromys chrysogaster) in the greater ACT region*. A report by the Australian Platypus Conservancy to the Wettenhall Environmental Trust.

World Wildlife Fund (WWF). (2020). *Living Planet Report 2020: Bending the curve of biodiversity loss*. Author.

Wu, H., Chen, J., Xu, J., Zeng, G., Sang, L., Liu, Q., Yin, Z., Dai, J., Yin, D., Liang, J., & Ye, S. (2019). Effects of dam construction on biodiversity: A review. *Journal of Cleaner Production*, *221*, 480–489.

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: Sanders, E., Wassens, S., Michael, D. R., Nimmo, D. G., & Turner, J. M. (2024). Extinction risk of the world's freshwater mammals. *Conservation Biology*, *38,* e14168. https://doi.org/10.1111/cobi.14168