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## Global Environmental Change Advances

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## Accelerated human-induced extinction crisis in the world's freshwater mammals

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## ARTICLE INFO

## Keywords:

Aridity  
 Freshwater ecosystems  
 Pesticide pollution  
 Threatened species  
 Indigenous Peoples' lands  
 Wildlife trade  
 Protected areas  
 Sixth mass extinction

## ABSTRACT

Human activities have significantly impacted natural habitats and wildlife worldwide, particularly emphasizing repercussions for freshwater habitats and associated species. These negative impacts on freshwater fish are well known, but for mammal species that regularly use and depend on freshwater systems, there is an incomplete understanding. Here, we assessed the status of freshwater and semi-aquatic mammal species inhabiting and dependent on freshwater ecosystems (hereafter referred to as freshwater mammals) and evaluated the impact of human activities on species richness both globally and by biogeographical regions. We used structural equation modeling and simultaneous autoregressive models to assess the direct and indirect effects of seven anthropogenic-related variables on overall freshwater mammal richness. Specifically, we examined the effects of anthropogenic disturbance on the richness of threatened and non-threatened species, as well as species with decreasing and stable/increasing populations. Forty-three percent of all freshwater mammal species are classified as globally threatened by the IUCN Red List, with 50% experiencing population declines. Furthermore, 48% are affected by domestic or international trade, while 75% face threats from geographically expanding human activities. Aridity, pesticide pollution, human footprint, and croplands had the strongest negative effects on freshwater mammal richness. In contrast, the coverage of freshwater habitats (FWs), Indigenous Peoples' lands (IPLs), and protected areas (PAs) helped to sustain freshwater mammal species globally, with an even stronger positive effect at individual biogeographical regions. We conclude that FWs, IPLs, and PAs play a critical role in the conservation of freshwater mammal species, helping safeguard these species from extinction, however, freshwater ecosystems are seldom the focal point of conservation management strategies. The ongoing adverse anthropogenic impacts on these natural habitats present a potentially catastrophic and irreversible threat to global freshwater environments and the species, including humans, reliant upon them. We strongly advocate for the implementation of more robust national and international policy frameworks that endorse alternative and sustainable livelihoods. Such frameworks can play a crucial role in alleviating anthropogenic pressures, thereby aiding in the mitigation of the extinction risk faced by these vital ecosystems and the world's freshwater mammal species.

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<https://doi.org/10.1016/j.gecadv.2024.100006>

Received 13 July 2023; Received in revised form 13 February 2024; Accepted 18 February 2024

Available online 22 February 2024

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## 1. Introduction

Human activities have caused widespread environmental degradation (Pimm et al., 2014; Ceballos et al., 2015), leading to population declines and range contractions in many species, ultimately putting many of them at risk of extinction (Ceballos et al., 2017, 2020). Over the past century, nearly 200 terrestrial vertebrate species have gone extinct, with a third of the remaining extant species experiencing population declines (Ceballos et al., 2017). Current extinction rates are estimated to be 100–1000 times higher than Holocene background rates and may continue to rise in the future (Ceballos et al., 2015; De Vos et al., 2015). This loss of biodiversity is leading to a rapid degradation of critical ecosystem functions and services, posing a significant threat to fauna, flora, and human societies worldwide (Diaz et al., 2006; Oliver et al., 2015). While these pressures are visible in terrestrial ecosystems, the negative effects reverberate to the aquatic system due to the ecological links between the two.

Freshwater habitats, comprising rivers, lakes, and wetlands, occupy less than 3% of the Earth's surface, yet support approximately 10% of all known animal species and one-third of all known vertebrate species (Dudgeon et al., 2006; Balian et al., 2008). Despite their critical importance, freshwater habitats rank among the most threatened ecosystems globally, primarily due to anthropogenic activities such as wetland conversion, dam construction, pollution, and more generally, climate change (Strayer and Dudgeon, 2010; Reid et al., 2019; He et al., 2019; Tickner et al., 2020). From 1970 to 2018, the global populations of freshwater vertebrates declined by an average of 83%, with a even sharper decline in large freshwater vertebrates (He et al., 2019; Almond et al., 2020). Among these, mammal species dependent on freshwater ecosystems (hereafter referred to as 'freshwater mammals') were particularly vulnerable to human activities as most of them use both

terrestrial and freshwater habitats and are thus exposed to stressors in both environments (Veron et al., 2008) (Fig. 1).

Freshwater mammals are faced with escalating anthropogenic threats worldwide (Hood, 2020; Sanders et al., 2023). In fact, with approximately 46% of the global terrestrial surface area currently experiencing medium to high human impact, ecosystems are under threat from habitat loss and fragmentation (Jacobson et al., 2019). Human activities have had a dramatic impact on the planet, for example, the draining and conversion of wetlands for agricultural lands (Fluet-Chouinard et al., 2023) have strongly affected the survival of freshwater mammals. Indeed, relatively large-bodied freshwater mammal species such as Madagascan dwarf hippopotamus (*Hippopotamus madagascariensis*; Guldberg, 1883), Schomburgk's deer (*Rucervus schomburgki*; Blyth, 1863), and Yangtze River dolphin (*Lipotes vexillifer*; Miller, 1918) have presumably become extinct due to increasing human pressures (IUCN, 2023). The long-term viability of many freshwater mammals, and theoretically all terrestrial vertebrates, depends on their ability to persist in human-modified landscapes across the globe (Dudgeon et al., 2006; Torres-Romero et al., 2020). This is especially important given the current anthropogenic impact on the environment and the increasing rate of habitat loss worldwide, including habitats formally protected for their natural, ecological, or cultural values (i.e., protected areas), as well as lands informally managed and/or controlled by Indigenous Peoples (Maxwell et al., 2016; Jones et al., 2018; Torres-Romero et al., 2020; Torres-Romero and Giordano, 2022). Although globally protected areas support terrestrial mammal diversity (Chen et al., 2022), there are relatively few protected areas established with freshwater ecosystems in mind (Hermoso et al., 2016; Saunders et al., 2002; Suski and Cooke, 2007). The bias of protected areas towards marginal habitats and away from rich aquatic systems can be attributed to the concentration of agriculture and human settlements in highly



**Fig. 1.** Freshwater mammals with their IUCN Red List status in square brackets, from top left, clockwise: platypus *Ornithorhynchus anatinus* [Near Threatened] (Peter Scheunis CC-BY-1.0); Amazonian manatee *Trichechus inunguis* [Vulnerable] (Dan Lundberg CC-BY-2.0); Southern lechwe *Kobus leche* [Near Threatened] (Charles J Sharp CC-BY-4.0); coypu *Myocastor coypus* [Least Concern] (Petar Milosevic CC-BY-SA-3.0); Asian small-clawed otter *Aonyx cinereus* [Vulnerable] (Mathias Appel CC-BY-1.0); fishing cat *Prionailurus viverrinus* [Vulnerable] (kellinahandbasket CC-BY-2.0); Ganges River dolphin *Platanista gangetica* [Endangered] (Kukul Gogoi CC-BY-SA-4.0); Eurasian watershrew *Neomys fodiens* [Least Concern] (NathDCFC CC-BY-2.0).

productive lands (Ellis, 2011).

Understanding the impact of human activities on species richness patterns is crucial for identifying effective conservation strategies and mitigating potential extinction risks. Accordingly, we examined the effects of various anthropogenic pressures on freshwater mammal species richness across large-scale spatial gradients. Utilizing assessment data from the IUCN Red List (IUCN, 2023), we investigated the relative significance of current human impacts and landscape attributes in shaping regional and global patterns of freshwater mammal diversity. Given that different biomes pose unique challenges to aquatic biota (Collen et al., 2014; Brum et al., 2021), we assessed whether the importance of anthropogenic factors varies among major biogeographical regions (i.e., Afrotropical, Australasian, Nearctic, Neotropical, Indo-Malayan, West Palearctic, and East Palearctic regions). Specifically, we analyzed the influence of anthropogenic and landscape factors on (i) the species richness of freshwater mammals, (ii) the number of freshwater mammal species classified as threatened (i.e., Critically Endangered, Endangered, or Vulnerable) vs. non-threatened (i.e., Least Concern or Near Threatened), and (iii) freshwater mammal species with decreasing vs. stable/increasing population trends based on the most recent Red List assessments (IUCN, 2023). Our hypothesis posited that freshwater mammal richness is particularly susceptible to escalating human

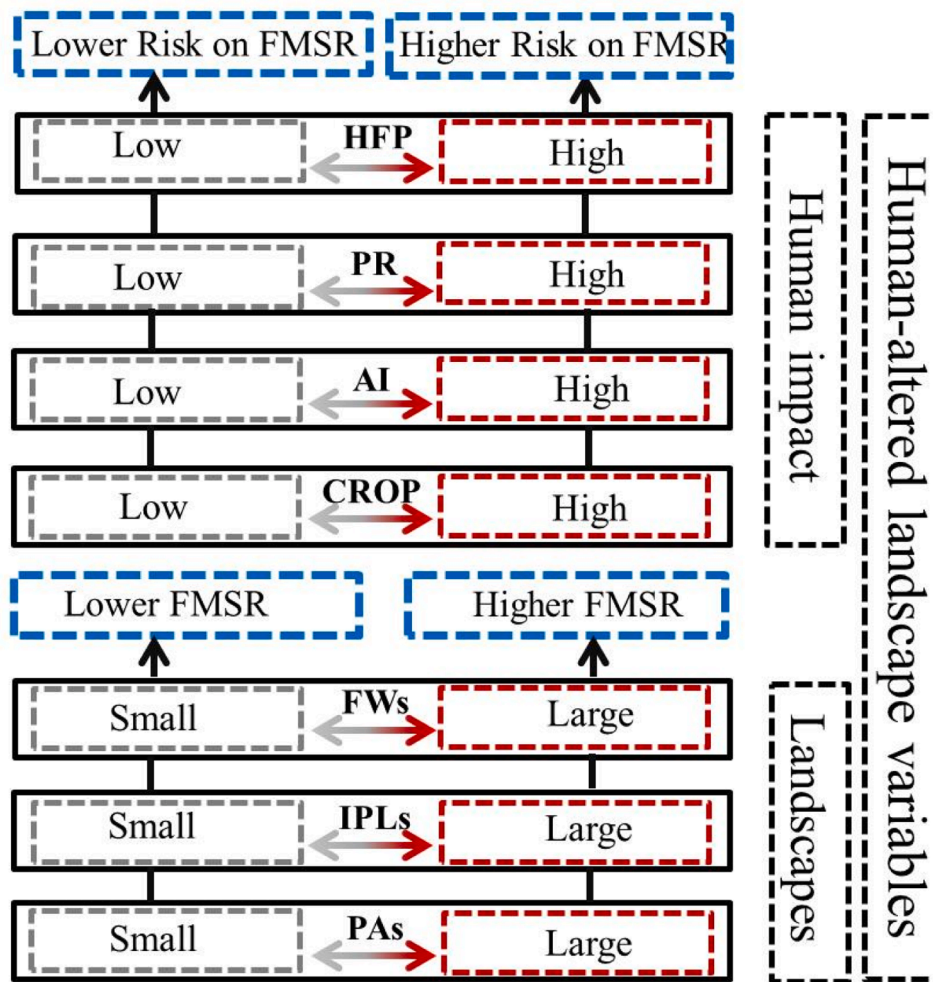
activities, including aridity, pesticide pollution, and croplands (see Fig. 2). It is generally accepted that large patch areas display higher species diversity and are more effective in preserving large-scale ecological processes compared to small patches (Torres-Romero et al., 2020; Torres-Romero and Giordano, 2022); however, it is crucial to recognize that sets of small patches typically accommodate a greater number of species compared to a single or a few larger patches (Fahrig, 2020; Torres-Romero and Giordano, 2022). As such, we anticipate that small core areas can serve as potential refuges for numerous species, playing a pivotal role in maintaining the diversity of freshwater mammals (see Fig. 2).

## 2. Methods

### 2.1. Species data

According to the IUCN Red List database (<http://www.iucnredlist.org>, accessed in June 2023), there are currently 142 extant mammal species worldwide that are associated with freshwater systems, spanning nine orders: Afrosoricida (n = 4), Carnivora (n = 24), Cetartiodactyla (n = 29), Didelphimorphia (n = 1), Eulipotyphla (n = 13), Monotremata (n = 1), Perissodactyla (n = 5), Rodentia (n = 62), and Sirenia (n = 3).

## Freshwater mammal species richness (FMSR)



**Fig. 2.** Graphical summary of predictions related to human-altered landscape variables influencing (low/high risk, and small/ high patches) on freshwater mammal species richness (FMSR) across the planet. Abbreviations: HFP (human footprint), PR (pesticide pollution risk), AI (aridity index), CROP (croplands), FWs (freshwater habitats), IPLs (Indigenous Peoples' lands), and PAs (protected areas). Note: The direction and color of the arrows indicate the level of human impact on one hand, and the size of core areas on the other, which can influence on FMSR.

While there are several mammal species that maintain close associations with freshwater systems in addition to coastal habitats (e.g., riverine and mangrove forests for proboscis monkeys *Nasalis larvatus*; Wurmb 1787), or where typically coastal species have long-term populations isolated in rivers and lakes (e.g., Irrawaddy dolphins *Orcaella brevirostris*; Owen in Gray 1866), we did not consider these species in our study. We are noting the exclusion of such species as it highlights the importance of maintaining freshwater habitats for all species that may occasionally depend on them (Minton et al., 2017; Boonratana et al., 2021). Using the IUCN database, we obtained data on the current geographic ranges (rather than historic ranges) of all extant freshwater mammal species available. We recorded each species' conservation status based on Red List assessment categories: Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), or Extinct (EX) (IUCN, 2023). Additionally, we compiled data on each species' "population trend" (i.e., declining, stable, increasing, or unknown), the primary "threats" faced by each species (e.g., agriculture and aquaculture, residential and commercial development, natural systems modification, pollution, biological resource use, energy production, and mining), as well as data on the reported "use and trade" of each species, encompassing categories such as food-human, pets/display animals, medicine-human and veterinary, research, sport hunting/specimen collecting.

We used a Behrmann equal-area global grid with a spatial resolution of 100 km × 100 km (approximately 1° at the equator) in combination with geographic range maps for each freshwater mammal species to generate a presence/absence matrix in ArcGIS 10.1 (ESRI, 2011). We excluded grid cells that contained less than 50% of the land surface and where species richness was effectively zero. This resulted in a total of 12,899 cells, each of which was assigned to one of seven biogeographical regions: Afrotropical, Australasian, Nearctic, Neotropical, Indo-Malayan, West Palearctic, and East Palearctic regions. These regions were defined in previous macroecological studies (e.g., Torres-Romero et al., 2020; Torres-Romero and Giordano, 2022).

## 2.2. Anthropogenic and landscape attributes

We examined four variables to assess the impact of anthropogenic activities on freshwater mammal species richness: human footprint (HFP; Venter et al., 2016), pesticide pollution risk (PR; Tang et al., 2021), aridity index (AI; Zomer et al., 2022), and croplands (CROP; Potapov et al., 2022) (see Table 1 for more detailed information for each of these variables). We used these variables as they are well-established as major causes or correlates of habitat fragmentation and loss, and are also considered primary threats to biodiversity and ecosystems, leading to accelerated extinction rates worldwide (Ceballos et al., 2017, 2020; Torres-Romero et al., 2020; Torres-Romero and Giordano, 2022; Torres-Romero et al., 2023).

We evaluated the effects of three landscape attributes: protected areas (PAs; UNEP-WCMC and IUCN, 2023), Indigenous Peoples' lands (IPLs; Garnett et al., 2018), and freshwater habitats (FWs; Lehner and Doell, 2004) (see Table 1 for more detailed information for each of these variables). These landscape variables were chosen based on their potential to maintain natural ecological processes and act as refuges for terrestrial mammals (Garnett et al., 2018; Geldmann et al., 2019; Torres-Romero et al., 2020; Torres-Romero and Giordano, 2022; Torres-Romero et al., 2023), further representing critically important core areas for safeguarding freshwater mammals (Sanders et al., 2023). We included these variables as there is support for their relative importance in previous macroecological studies, specifically studies that defined the distribution of biodiversity-related patterns and processes, including species population declines and the general extinction crisis (Garnett et al., 2018; Torres-Romero and Giordano, 2022; Torres-Romero et al., 2023). All predictor variables were resampled using 100 km x 100 km grid cells in ArcGIS 10.1 (ESRI, 2011) for

**Table 1**

Summary of predictions related to anthropogenic and landscape variables influencing global and regional freshwater mammal richness patterns. Note: 'Human pressure' represents the anthropogenic variables such as HFP, PR, AI, and CROP, while 'Conservation Lands' to landscape attributes such as FWs, IPLs and PAs, which can affect diversity depending on size (i.e., small/large core areas).

Predictor	Expected overall relationship	Rationale, Reference and Resolution
Human Footprint (HFP)	Low/High	This layer not only encompasses the most recent information of its kind but also constitutes the Human Footprint dataset, integrating various uses as proxies for human disturbance of natural systems. This data contributes to a deeper understanding of the human pressures influencing macro-ecological patterns. Furthermore, this dataset serves as a valuable tool for monitoring environmental changes and providing insights for applications in conservation science. The layer integrates global records of cumulative human pressure on the environment at a spatial resolution of approximately 1 km <sup>2</sup> . This metric is considered the most comprehensive variable, incorporating various anthropogenic pressures, including human population, built environments, light pollution, linear infrastructure (such as roadways, railways, and navigable waterways), electrical power support infrastructure, and other human land-use changes (Venter et al., 2016).
Pesticide pollution risk (PR)	Low/High	While pesticides serve the purpose of protecting crops and ensuring food safety, they also pose environmental threats, causing adverse effects on freshwater ecosystems, water quality, biodiversity, and human health. This metric incorporates the environmental pollution risk associated with 92 active ingredients most commonly used—comprising 59 herbicides, 21 insecticides, and 19 fungicides—across the globe at a 5 arc-min resolution (approximately 10 km × 10 km at the Equator) (Tang et al., 2021).
Aridity Index (AI)	Low/High	This layer is an indicator based on long-term climatic water deficits, calculated as the ratio P/PET at approximately a 1 km <sup>2</sup> resolution (30 arc seconds) (Zomer et al., 2022). Aridity is widely employed as a measure to assess the dryness of the climate at a specific location, and used as valuable predictive tool for evaluating trends, directions, magnitudes, and anticipating the impacts of climatic change, holding significant importance for agricultural production and water management. We used this layer to anticipated changes in future vertebrate biodiversity loss; we utilized this layer for a comprehensive assessment of extinction risk in freshwater mammals.
Croplands (CROP)	Low/High	Global cropland expansion has accelerated over the past two decades, replacing natural vegetation and tree cover. This trend indicates a conflict with the sustainability goal of protecting terrestrial ecosystems. This layer varies in structure from intensely managed monocultures to mosaic agricultures. Agricultural expansion and intensification pose threats to ecosystem

(continued on next page)

Table 1 (continued)

Predictor	Expected overall relationship	Rationale, Reference and Resolution
Freshwater Habitats (FWs)	Small/Large	functioning and may lead to species extinction through habitat loss and fragmentation. This variable is based on spatially explicit global estimates at a resolution of $0.025 \times 0.025$ degrees (approximately $3 \text{ km} \times 3 \text{ km}$ at the Equator) (Potapov et al., 2022). Freshwater ecosystems constitute lands with important habitats for biodiversity, and include lakes, reservoirs, rivers, and wetlands. These cover less than 3% of Earth's surface area (Lehner and Doell, 2004). Variable measured in % per grid cell.
Indigenous Peoples' Lands (IPLs)	Small/Large	This includes terrestrial land and spatial territories managed or owned by Indigenous Nations or people; they constitute most of the currently recognized terrestrial conservation land, habitat protection, and ecologically intact landscapes across the globe (Garnett et al., 2018). Variable measured in % per grid cell.
Protected Areas (PAs)	Small/Large	PAs constitute lands formally protected for their natural, ecological, or cultural values as defined by the International Union for Conservation of Nature. We included the seven distinct Protected Areas categories: Ia—Strict Nature Reserve; Ib—Wilderness Area; II—National Park; III—Natural Monument or Feature; IV—Habitat/Species Management Area; V—Protected Landscape/Seascape; and VI—Multiple Use Management & Protected Area, where the sustainable use of natural resources is permitted (UNEP-WCMC and IUCN, 2023). Variable measured in % per grid cell.

integration into our analyses. The hypothesized relationships between response and predictor variables and their detailed explanations can be found in Fig. 2 and Table 1.

### 2.3. Statistical analyses

To ensure the precision of our path analyses, we excluded species that had at least 35% of their total range outside of terrestrial habitats, resulting in a final selection of 130 freshwater mammal species (thus excluding 12 species). We examined the associations between species richness and predictor variables using Pearson product-moment correlations (PPMC). To address potential spatial autocorrelation in the PPMC, we applied a modified t-test (Dutilleul et al., 1993) to obtain unbiased estimates of significance for each correlation coefficient. We also assessed collinearity between response and predictor variables using the variance inflation factor (VIFs), with a threshold of two indicating very low collinearity (Hair et al., 2014). We then employed Structural Equation Modeling (SEM) path analysis to evaluate the direct and indirect effects of hypothesized causal relationships (Shipley, 2016). Simultaneous autoregressive, otherwise known as SAR, models were also used to assess direct and indirect associations of anthropogenic and landscape attributes. This combined approach is widely used in studies of ecological systems that involve interconnected processes in a single network (e.g., Kissling et al., 2008; Torres-Romero et al., 2023). We estimated direct effects using standardized regression coefficients, while indirect effects were identified as paths originating at the human footprint variable and passing through other variables before reaching freshwater mammal species richness (Shipley, 2016).

We constructed SEM models at both the global and the seven biogeographical regional levels. We developed SEM models for globally threatened species and those species with declining population trends, following a general or global path. To minimize spatial autocorrelation on inference from SEMs (Legendre and Legendre, 1998), we used standardized regression coefficients ( $\beta$ ) in SAR models with species richness as the response variable (see Kissling et al., 2008). For each SEMs, we used standardized regression coefficients to rank the importance of each predictor in SEM models. The use of SAR models reduces spatial autocorrelation under a variety of spatial pattern scenarios (Kissling and Carl, 2008), and thus allows us to control for these effects. We conducted all statistical analyses in R 3.4.0 (R Core Team, 2020), using the 'spdep' (Bivand, 2015) and 'semPlot' (Epskamp, 2019) packages.

## 3. Results

### 3.1. Global freshwater mammal species patterns

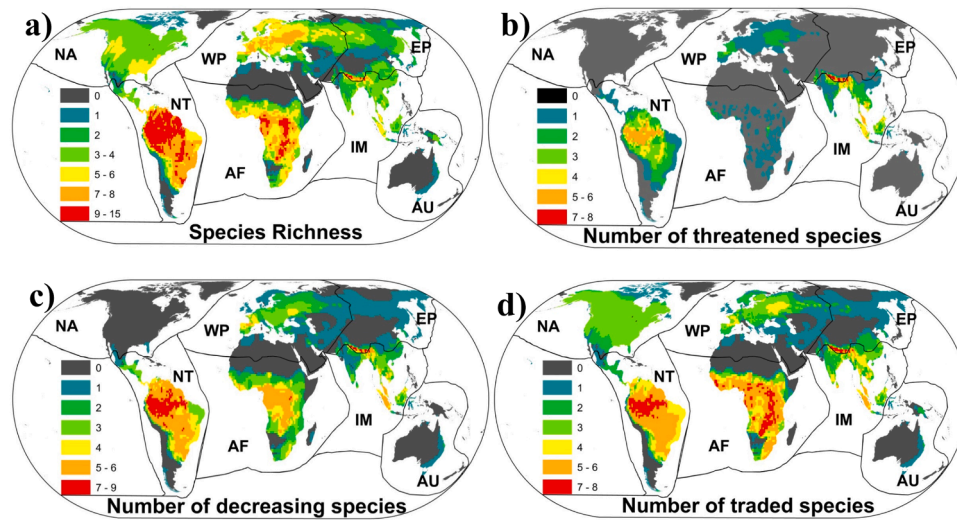
Globally, the Neotropical region has the highest freshwater mammal species richness, followed by the Afrotropical, West Palearctic, Indo-Malayan, East Palearctic, Nearctic, and Australasian regions (Fig. 3a). For species categorized as globally threatened by the IUCN (2023), most occur in Neotropical and Indo-Malayan regions (Fig. 3b). Furthermore, the Neotropical, Indo-Malayan, and Afrotropical regions have the most species listed with declining populations and largest trade use (Fig. 3c, d).

Of the 126 extant freshwater mammal species with sufficient assessments (i.e., listed as CR, EN, VU, NT and LC), 43% ( $n = 54$ ) were assessed as threatened (i.e., listed as CR, EN, or VU) in the IUCN Red List (Fig. 4a), while Père David's deer (*Elaphurus davidianus* Milne-Edwards 1866) was listed as Extinct in the Wild; however, this species has been reintroduced into various areas of China and as of 2021, nearly 9000 Père David's deer roam freely in over 80 populations (Dayuan et al., 2022). Approximately 11% ( $n=15$ ) of freshwater mammal species had insufficient assessments (i.e., listed as Data Deficient), with most of those belonging to the order Rodentia ( $n=12$ ; Fig. 4a). The proportions of threatened species varied between orders, for example, Rodentia (16%), Eulipotyphla (31%), Carnivora (41%), Afrosoricida (50%), Cetartiodactyla (69%), Perissodactyla (100%) and Sirenia (100%) (Fig. 4c).

Considering the species assessments with known population trends ( $n=100$ ), 71% had declining populations, while 26% had a stable population (Fig. 4b). Only three species (i.e., Eurasian beaver *Castor fiber*; Linnaeus 1758, Indus River dolphin *Platanista minor* Owen 1853, Indian rhinoceros *Rhinoceros unicornis*; Linnaeus 1758) had increasing populations reported in their assessments. Population trends of 41 species remained unknown. The proportion of freshwater mammal species with declining populations varied between orders: Rodentia (26%), Eulipotyphla (46%), Sirenia (67%), Carnivora (71%), Afrosoricida (75%), Cetartiodactyla (75%), Perissodactyla (80%), Didelphimorphia (100%), and Monotremata (100%) (Fig. 4d). Furthermore, expanding human activities and their consequences (e.g., commercial development, agriculture, habitat modification, pollution, climate change, and other anthropogenic disturbances) were listed as threats to ~75% of freshwater mammal species, while ~48% were listed as exposed to wildlife trade use (Fig. 4e, f).

### 3.2. Path analysis models

According to our SEM analyses, protected areas ( $\beta=0.314$ ) are the most important predictor of mammalian diversity with a direct positive effect on freshwater mammal species richness. In addition, aridity index ( $\beta=0.305$ ), pesticide pollution risk ( $\beta=0.188$ ), and human footprint ( $\beta=0.101$ ) were the most important factors found to decrease freshwater mammal species richness across the globe (Fig. 5). For threatened species richness, aridity ( $\beta=0.441$ ) emerged as the principal predictor with



**Fig. 3.** Spatial diversity patterns of freshwater mammal species at the global scale were generated by overlaying species ranges obtained from the International Union for the Conservation of Nature (IUCN, 2023) on a 100 km<sup>2</sup> resolution grid. The maps represent the following: global freshwater mammal species richness (a); number of threatened species (b), number of species with decreasing populations (c), and number of traded species (d). Biogeographical regions abbreviations are as follows: Afrotropical (AT), Australasian (AU), Nearctic (NA), Neotropical (NT), Indo-Malayan (IM), West Palearctic (WP), and East Palearctic (EP).

a high-risk direct effect, while human footprint ( $\beta = -0.172$ ) was an important predictor with a low-risk effect; Indigenous Peoples' lands ( $\beta = 0.298$ ), freshwater habitats ( $\beta = 0.137$ ) and protected areas ( $\beta = 0.128$ ) were secondarily important in explaining freshwater species richness patterns, with these landscape variables all showing positive effects (Fig. 5). In contrast, the most important variable in explaining richness patterns for non-threatened species was protected areas ( $\beta = 0.269$ ) with a strong positive effect, followed by aridity ( $\beta = 0.264$ ) and pesticide pollution ( $\beta = 0.146$ ), which all showed high-risk effects and thus high levels of importance (Fig. 5). Freshwater habitats ( $\beta = 0.111$ ) and indigenous peoples' lands ( $\beta = -0.101$ ) also emerged as important variables with positive and negative associations on non-threatened species richness, respectively. Specifically, smaller Indigenous Peoples' lands tended to protect more threatened species than larger ones. Moreover, aridity ( $\beta = 0.401$ ) showed positive effects for freshwater mammal species with decreasing population trends and thus emerged as the principal predictor with a high level of risk in explaining these patterns; protected areas ( $\beta = 0.303$ ) and Indigenous Peoples' lands ( $\beta = 0.067$ ) were also important predictors with positive effects (Fig. 5). Conversely, for species with non-decreasing population trends, FWs ( $\beta = 0.289$ ) and Indigenous Peoples' lands ( $\beta = -0.234$ ) emerged as important positive and negative predictors, respectively (Fig. 5).

Across the Nearctic region, the direct positive effect of freshwater habitats ( $\beta = 0.416$ ) was the most important predictor in explaining general species richness patterns, while pesticide pollution ( $\beta = 0.311$ ) and croplands ( $\beta = 0.143$ ) were the second most important predictor variables showing a high risk to freshwater mammals. However, Indigenous Peoples' lands ( $\beta = -0.223$ ) also emerged as an important predictor with negative effects on freshwater mammal species, meaning that small Indigenous Peoples' lands are protecting a greater number of species compared to larger Indigenous Peoples' lands (Fig. 6).

In the Neotropics, aridity ( $\beta = 0.316$ ) and pesticide pollution ( $\beta = 0.121$ ) exerted the most significant positive effects on species richness patterns, while freshwater habitats ( $\beta = 0.111$ ) exhibited positive effects. Additionally, pesticide pollution ( $\beta = 0.121$ ) exerted a high risk with positive influence on croplands, while croplands ( $\beta = 0.229$ ) had a substantial impact on protected areas (Fig. 6).

In the East Palearctic, our results revealed that aridity ( $\beta = 0.267$ ), croplands ( $\beta = 0.163$ ), and human footprint ( $\beta = 0.142$ ) exerted high-risk impacts on species richness patterns. Additionally, the presence of large protected areas ( $\beta = 0.072$ ) and small Indigenous Peoples' lands ( $\beta =$

$-0.061$ ) emerged as important predictors for these freshwater mammal species. Similar to our findings in the Neotropics, pesticide pollution ( $\beta = 0.072$ ) demonstrated a strong influence on croplands (Fig. 6).

In the West Palearctic region, aridity ( $\beta = 0.254$ ), pesticide pollution ( $\beta = 0.225$ ), and croplands ( $\beta = 0.173$ ) exhibited high-risk impacts on overall freshwater mammal richness. Furthermore, we identified that large protected areas ( $\beta = 0.117$ ) and small Indigenous Peoples' lands ( $\beta = 0.107$ ) had positive effects on these species (Fig. 5). Additionally, pesticide pollution ( $\beta = 0.118$ ) strongly influenced freshwater habitats, and this pollution ( $\beta = 0.636$ ) also had a substantial impact on croplands (Fig. 6).

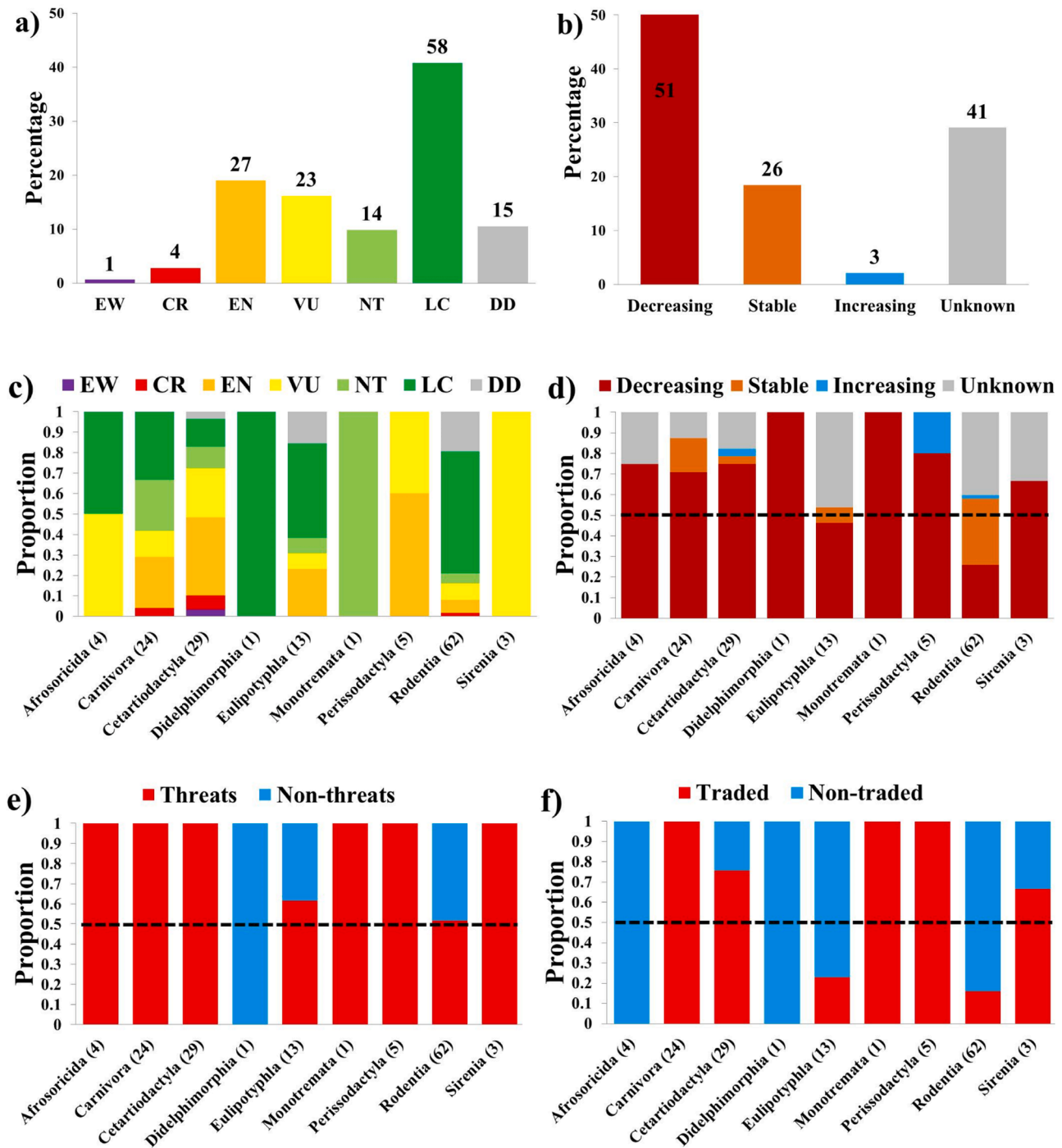
In the Afrotropical region, aridity ( $\beta = 0.521$ ) and pesticide pollution ( $\beta = 0.125$ ) had a high-risk impact on freshwater mammal species. However, protected areas ( $\beta = 0.241$ ) and Indigenous Peoples' lands ( $\beta = -0.066$ ) emerged as important factors in protecting these species with positive and negative associations, respectively. Across the region, large protected areas and small Indigenous Peoples' lands tended to protect a greater number of species. Additionally, pesticide pollution ( $\beta = 0.292$ ) had a high impact on croplands, while croplands ( $\beta = 0.134$ ) also exhibited a strong impact on Indigenous Peoples' lands (Fig. 6).

In the Indo-Malayan region, aridity ( $\beta = 0.231$ ) was the most important factor influencing high risk on freshwater mammal species richness patterns. Landscape attributes, i.e., Indigenous Peoples' lands ( $\beta = 0.216$ ), freshwater habitats ( $\beta = 0.171$ ), and protected areas ( $\beta = 0.152$ ), all had direct positive effects predicting greater freshwater mammal species richness. Furthermore, pesticide pollution ( $\beta = 0.104$ ) had a strong effect on croplands (Fig. 6).

Lastly, within the Australasian region, the impact of aridity ( $\beta = 0.378$ ) and pesticide pollution ( $\beta = 0.171$ ) emerged as the most significant high-risk factors influencing freshwater mammal species richness. Meanwhile, large freshwater habitats ( $\beta = 0.269$ ), small Indigenous Peoples' lands ( $\beta = -0.182$ ), and protected areas ( $\beta = -0.014$ ) exhibited strong effects on these regional species. Pesticide pollution ( $\beta = 0.503$ ;  $\beta = 0.226$ ) strongly influenced both croplands and freshwater habitats respectively, while aridity ( $\beta = 0.203$ ) also affected freshwater habitats (Fig. 6).

#### 4. Discussion

Alarmingly, a significant portion of mammal species that depend on freshwater ecosystems is under threat, with 43% classified as globally

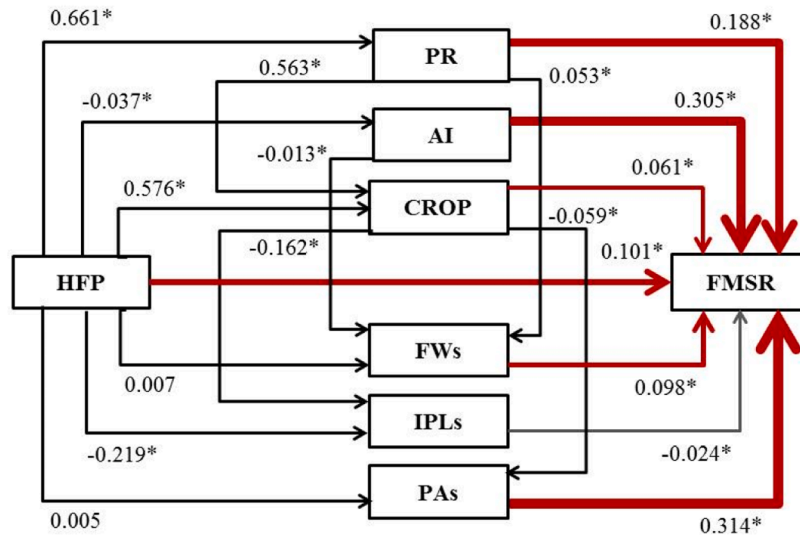


**Fig. 4.** (a) Summary of freshwater mammal species' statuses based on the most recent assessment according to the IUCN Red List (2023), with the category codes as follows: EW = Extinct in the Wild, CR=Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient.; (b) percentage of freshwater mammal species, according to reported population trends (i.e., decreasing, stable, increasing and unknown); (c) global proportion of freshwater mammal species within each IUCN Red List category, evaluated by taxonomic orders; (d) global proportion of freshwater mammal species' population trends (i.e., decreasing, stable, increasing and unknown), evaluated by taxonomic orders; (e) proportion of each order containing freshwater mammal species that is listed as under "Threats" from various human activities; (f) proportion of each order containing freshwater mammal species that are reported under the general "Use and Trade" classification according to the IUCN (2023), of which more than 50% of species listed as CR, EN, VU, NT, and LC are under threats from use and trade. Please note that the dashed line represents 50%.

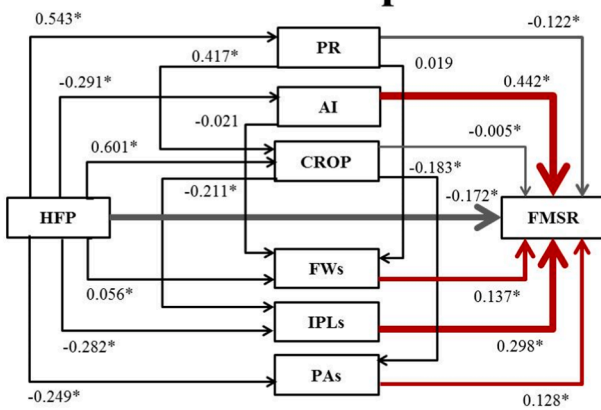
threatened (i.e., listed as CR, EN, or VU on the IUCN Red List) and 71% experiencing declining populations. Our results show that the global hotspots of freshwater mammal diversity are predominantly situated in tropical, subtropical, and temperate regions, with particularly high diversity in the Neotropical region (Daga et al., 2020), where anthropogenic activities such as pollution, deforestation, hydropower

development, and wildlife trade pose significant threats. It is worth noting that the proportion of threatened freshwater mammal species in our study is likely underestimated, as the 15 species classified as Data Deficient presumably represent globally threatened species (Bland et al., 2015). Our findings highlight the substantial impact of expanding anthropogenic pressures on freshwater habitats, directly contributing to

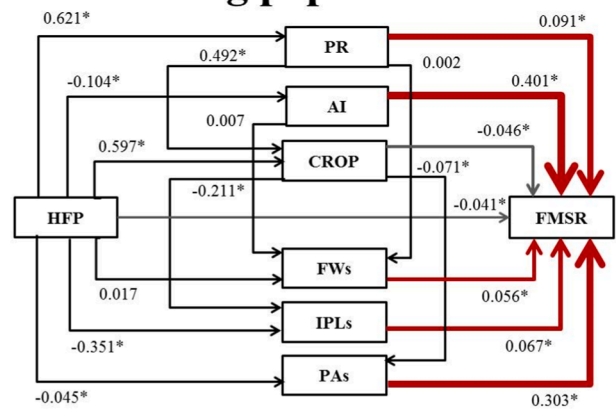
# Global



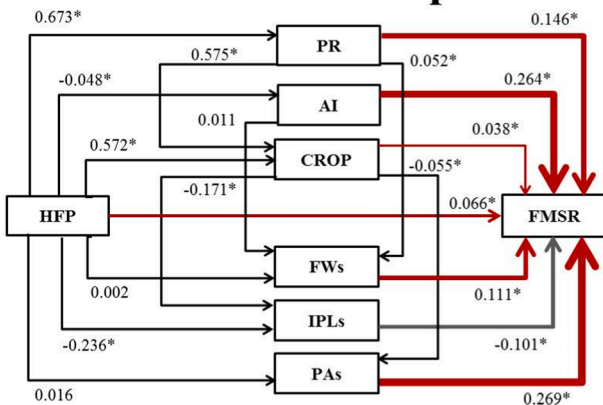
## Threatened species



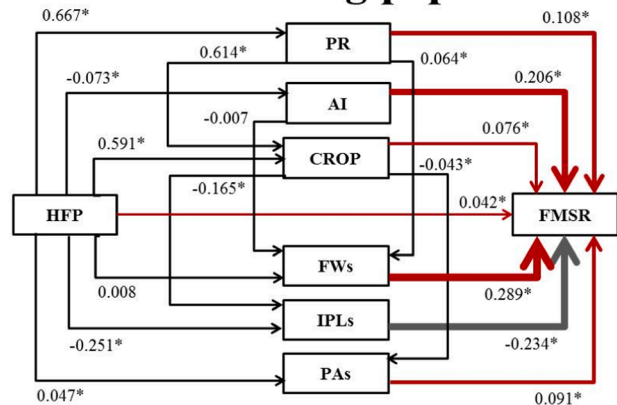
## Decreasing population trend



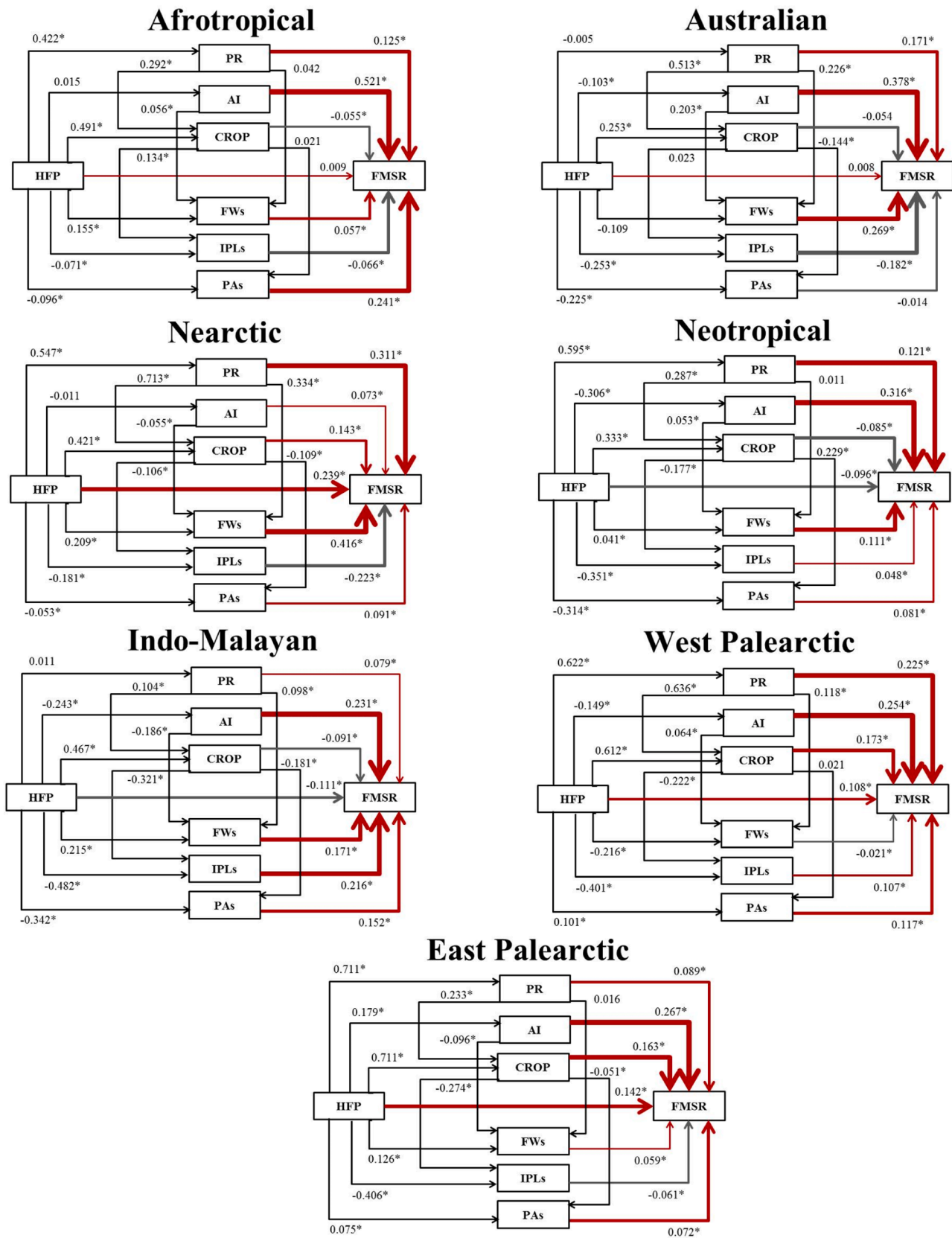
## Non- threatened species



## Non-decreasing population



**Fig. 5.** Structural equation models (SEMs) representing direct and indirect effects of human activities and landscape conditions on global freshwater mammal diversity, as well as threatened vs. non-threatened freshwater mammal species, and freshwater mammal species with decreasing vs. non-decreasing population trends. Arrows (red= high risk; grey = low risk) represent path coefficients (i.e., direct effects), with weighted lines (i.e., thickness) being proportional to the effects of standardized regression coefficients. Abbreviations are: HFP, human footprint; PR, pesticide pollution risk; AI, aridity index; CROP, cropland; FWs, freshwater habitats; IPLs, Indigenous Peoples' lands; PAs, protected areas; and FMSR, freshwater mammal species richness. Significance levels of each path are shown: \*P < 0.05. Note: See Fig. 1 for anticipated relationships between response predictors on freshwater mammals.



**Fig. 6.** Structural equation models (SEMs) represent the direct and indirect effects of human activities and landscape conditions across biogeographical regions. Arrows (red= high risk; grey = low risk) represent path coefficients (i.e., direct effects), with weighted lines (i.e., thickness) being proportional to the effects of standardized regression coefficients. Abbreviations are: HFP, human footprint; PR, pesticide pollution risk; AI, aridity index; CROP, cropland; FWs, freshwater habitats; IPLs, Indigenous Peoples' lands; PAs, protected areas; and FMSR, freshwater mammal species richness. Significance levels of each path are shown: \*P < 0.05. Note: See Fig. 1 for anticipated relationships between response predictors on freshwater mammals.

the high percentages of both threatened species and species with declining populations among freshwater mammals.

Freshwater ecosystems face numerous and severe threats, including overexploitation of water and habitat loss due to expanding agricultural activities, urbanization, dam construction, channelization, and more generally, climate change (Strayer and Dudgeon, 2010; Vörösmarty et al., 2010; He et al., 2018; Sanders et al., 2023). The increasing anthropogenic presence in these freshwater habitats has negatively impacted the persistence and survival of freshwater mammals, leading to direct human-wildlife conflicts, such as those between humans and otters or hippopotamuses (Kanga et al., 2012; Cook et al., 2022). Similar activities have also resulted in the loss of critical habitats for freshwater mammals, particularly in wetlands, which are disappearing three times faster than forests (Tickner et al., 2020). Currently, approximately 21% of inland wetlands (equivalent to 3.4 million km<sup>2</sup>) have been lost due to drainage for farmland and the conversion of wetlands into rice fields, accounting for nearly 80% of the total global wetland loss since the 1700s (Fluet-Chouinard et al., 2023). Our results align with these concerning trends as we identified various factors, including high levels of aridity, pesticide pollution, and cropland, which exhibit robust negative impacts on freshwater habitats. Our findings underscore the urgent need for comprehensive and targeted conservation efforts to protect freshwater mammal species and their delicate ecosystems.

In accordance with prior research (Hood, 2020; Sanders et al., 2023), our results reveal that the expansion of agricultural activities has a detrimental impact on freshwater systems, affecting the habitats of freshwater mammals and subsequently leading to population declines and range contractions. Similarly, pollution associated with agriculture further degrades the health of freshwater habitats (Collen et al., 2014; Fouchy et al., 2019; Inostroza et al., 2017) and exposes species to pesticides and other toxic chemicals (Eccles et al., 2017; Wainstein et al., 2022), thereby diminishing water quality and increasing species mortality. Our findings underscore the vital role of healthy freshwater habitats in supporting freshwater mammal species, yet if land conversion and pollution continue at an unchecked rate, the richness and abundance of these species will continue to rapidly decline. Unfortunately, most inland wetlands lack adequate protection (Reis et al., 2017), thus urgent action is required to address the threats faced by freshwater habitats, preventing further biodiversity loss and maintaining the essential ecosystem services they provide. Additionally, the creation of new protected areas should consider the entirety of aquatic environments, covering entire basins, rivers, and other freshwater habitats (Azevedo-Santos et al., 2019). Implementing such effective conservation measures includes promoting connectivity in freshwater environments, sustainably managing water resources, and reducing or eliminating pesticide use in agriculture.

Beyond habitat degradation resulting from agricultural activities and pollution, our study sheds light on the adverse impact of climate change, specifically assessed through aridity gradients. Consequently, climate change can significantly influence the available freshwater habitat for mammal species with limited ranges (Brum et al., 2021). To support these critically threatened species, conservation policy frameworks should prioritize monitoring and mitigation of climatic disturbances within biogeographical regions (Brito-Morales et al., 2018). In fact, Malhi et al. (2008) proposed the preservation of the core Amazon basin as a biological refuge due to its high biodiversity and anticipated resilience to global warming. Our analyses demonstrate that threatened species experiencing population declines, especially those in the Australasian, Afrotropical, Indo-Malayan, Neotropic, and Palearctic regions, are at substantial risk of drought under high-aridity scenarios, underscoring the urgent need for conservation actions to mitigate the impacts of climate change. Our results align with previous findings that highlight the significant influence of aridification risks on mammal distribution, exacerbating the effects of warming and potentially diminishing the effectiveness of protected areas in the future (Shi et al., 2021).

The presence and proximity of core areas and refuges (i.e., protected

areas) are positively associated with global freshwater mammal species richness, species with stable or increasing populations, and non-threatened species, a finding that is consistent with a recent global assessment of terrestrial mammals (Chen et al., 2022). Protected areas offer a variety of vital resources to freshwater mammals, including food, protective cover and escape options, and suitable resting and breeding locations, thereby reducing the potential impact of human pressures (Torres-Romero et al., 2020). Protected areas focused on freshwater biodiversity conservation, however, are few and far between (Hermoso et al., 2016; Saunders et al., 2002; Suski and Cooke, 2007), therefore, preserving freshwater systems remains critically important for ensuring the long-term survival of wildlife populations (Watson et al., 2014; Torres-Romero and Giordano, 2022).

Currently, freshwater ecosystems are not adequately covered by existing protected areas (Abell et al., 2017). Even within these protected areas, the integrity of freshwater habitats can be compromised by anthropogenic activities upstream, such as pollution and flow modification (Abell et al., 2017; Acreman et al., 2020). Additionally, the construction or proposed construction of dams within protected areas poses a significant concern, while dams upstream or downstream of protected areas may be equally harmful (Thieme et al., 2020). Moreover, small to medium-sized freshwater mammals, or species deemed less iconic or charismatic, may receive insufficient conservation attention when compared to terrestrial counterparts, such as large carnivores. These overlooked species are often neglected in conservation decision-making and the management of protected areas (Saunders et al., 2002; May-Collado and Agnarsson, 2011; Hermoso et al., 2016; He et al., 2021). Given these challenges, it is crucial to prioritize conservation actions aimed at protecting freshwater species and restoring their habitats to reverse the current decline in freshwater biodiversity (Tickner et al., 2020). Collaborative efforts with local communities, policymakers, and conservation organizations are essential for the long-term survival of freshwater mammal populations, both at the individual species level and within distinct freshwater regions (Acreman et al., 2020). Moreover, conservation policies and strategies should not only prioritize the preservation of core areas and refuges that provide vital resources for these species, but also the multi-directional connectivity of freshwater systems to enhance biodiversity protection (Linke et al., 2011). By emphasizing these conservation priorities and considering the feasibility of successful strategies, we can work towards ensuring the persistence and well-being of freshwater mammal populations in the face of mounting threats (Dudgeon et al., 2006; Strayer and Dudgeon, 2010).

Lastly, we would like to note that the IUCN Red List dataset is continually evolving and being refined as new species information is made available (Chen et al., 2022; Schmidt et al., 2023). Empirical tests have shown reasonable concordance to the accuracy of the IUCN Red List species distributions, though some minor errors (e.g. Chen et al., 2022) will always present a potential caveat that may create a marginal bias. However, to model species globally, using a standardized database such as the IUCN Red List, which plays a pivotal role in setting standards for conservation and sustainable development, is the best current option.

#### 4.1. Conclusions

We are currently facing the sixth mass extinction crisis, and insufficient funding presents a critical threat to the ability of protected habitats to safeguard biodiversity and provide valuable benefits to society and humanity (Harrison et al., 2018). Studies indicate a significant funding shortfall of US\$1 to US\$2 billion annually for effective management of existing areas, while establishing and managing an expanded protected-area system would require at least US\$4 billion per year over the next decade (Bruner et al., 2004). This funding deficit raises serious concerns about the effectiveness of protected habitats in addressing biodiversity loss, as inconsistent and inadequate funding flow hinders

proper management activities (Bruner et al., 2004). Urgent action must be taken to ensure continuous financing for protected habitats to minimize biodiversity loss, and foster a future where healthy and natural habitats are indispensable for sustainable development worldwide (Darwall et al., 2011).

Furthermore, it is imperative to confront the urgent and substantial threats faced by freshwater mammals, resulting from global wildlife trade and human activities that drive population decline. To protect these vulnerable species, it is crucial to implement new conservation and ecosystem management practices (Darwall et al., 2011), including the establishment of additional protected areas and indigenous peoples' lands, alongside the preservation of more freshwater habitats (Acreman et al., 2020). It is important to recognize that even heavily impacted freshwater ecosystems can still play a vital role in the survival of these species, so long as they are managed appropriately. Therefore, we strongly advocate for the implementation of feasible and effective policies and conservation strategies that integrate landscape mosaic management. By embracing this holistic approach, we can enhance biodiversity conservation and ensure the long-term sustainability of our ecosystems and the continued existence of freshwater mammals worldwide. We call upon policymakers, conservationists, and communities to collaborate toward these goals. Immediate political, economic, and social efforts are crucial to prevent further extinctions of freshwater species and make a significant impact in safeguarding the invaluable diversity of freshwater mammals for the benefit of future generations.

#### CRedit authorship contribution statement

**Vincent Nijman:** Writing – review & editing, Writing – original draft, Visualization, Validation, Data curation. **Fengzhi He:** Writing – review & editing. **Timothy M. Eppley:** Writing – review & editing, Writing – original draft, Visualization, Validation. **Erik Joaquin Torres-Romero:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jason Fisher:** Writing – review & editing, Writing – original draft.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

#### Acknowledgments

We are grateful to the Editor in Chief Dr. Inés Ibáñez, AE Dr. Miaogen, as well as three anonymous reviewers, for their useful and constructive comments on the manuscript. This study was supported by a postdoctoral fellowship from Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCyT -Mexico) to E.J.T-R.

#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecadv.2024.100006](https://doi.org/10.1016/j.gecadv.2024.100006).

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