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Global Patterns and Drivers of Freshwater Fish Extinctions: Can We Learn From Our Losses?

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ABSTRACT

Nearly one-third of extant freshwater fish species, which account for over 50% of global fish diversity, are at risk of extinction. Despite their crucial ecological and socioeconomic importance, the extinction of freshwater fishes remains under-researched on a global scale. This is a comprehensive assessment of taxonomic, spatial, and temporal patterns of freshwater fish extinctions while identifying key extinction drivers and driver synergies. Using data from the International Union for Conservation of Nature Red List, 89 extinct freshwater fish and 11 extinct in the wild were analyzed. Taxonomic statistical analysis revealed the disproportionate impact on Cyprinidae, Leuciscidae, and Salmonidae. Estimated globally for the period 1851–2016, the modern extinction rate for freshwater fishes stands at 33.47 extinctions per million species-years (E/MSY), more than 100 times greater than the natural background extinction rate of 0.33 E/MSY. Extinction rates, when calculated per continent using the number of extinct species and the total number of species per continent, indicated that North America has the highest extinction rate (225.60 E/MSY), followed by Europe (220.26 E/MSY) and Asia (34.62 E/MSY). Although Africa is less affected, it still shows a 42-fold increase over the background rate. Bayesian modeling, reflecting cumulative species extinctions, indicated a strong association of North America and Asia with species loss (37 and 34 extinctions, respectively), a moderate one for Europe (20 extinctions) and a weak association of Africa (eight extinctions). Natural system modification, pollution, and invasive species emerged as the primary extinction drivers, often acting synergistically. Temporal trends indicate an acceleration in extinctions since the mid-20th century. This study highlights that, despite recent increases in conservation efforts, freshwater fish extinctions continue to rise, indicating the urgent need for integrated conservation strategies. Without immediate action, many species currently at risk may soon follow the same trajectory of extinction as the 100 extinct freshwater fishes of this study.

1 | Introduction

The ongoing decline in global biodiversity is expected to accelerate in the coming years, with Earth continuing to experience what many scientists refer to as the sixth mass extinction—an event driven entirely by human activities (Barnosky et al. 2011; Ceballos et al. 2015; Cowie et al. 2022; though see Bocchi et al. 2022 for a debate on this classification). This biodiversity crisis, marked by a significant rise in extinction rates over the past 100–150 years (Pimm et al. 2014; Ceballos et al. 2015), emphasizes the urgent need for an improved understanding of extinction dynamics to inform conservation strategies. Research

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indicates that current extinction rates, particularly among vertebrates, far exceed historical background levels, emphasizing the unprecedented magnitude of this crisis. In some cases, extinction rates of freshwater populations have been found to surpass those of terrestrial or marine systems (Pimm et al. 2014; del Monte-Luna et al. 2023; WWF 2024). Acknowledging the urgency of this issue, the Kunming-Montreal Global Biodiversity Framework was adopted in 2022, calling for an end to human-induced extinction of threatened species, the mitigation of biodiversity loss drivers, and a tenfold reduction in extinction rates and risks for all species, including those in freshwater ecosystems, by 2050.

Despite covering a small part of the Earth's surface, freshwater ecosystems are among the most biodiverse and ecologically significant systems on the planet (Su et al. 2021). They support approximately 51% of all known fish species, amounting to 18,898 species out of the 37,106 globally recognized (Fricke et al. 2025). Beyond their intrinsic ecological value, freshwater fishes play a crucial role in human well-being by providing essential ecosystem services, such as enhancing ecosystem resilience, regulating food webs, and supporting the nutritional needs of billions worldwide (Holmlund and Hammer 1999; Lynch et al. 2016; McIntyre et al. 2016; Funge-Smith and Bennett 2019). Yet, their populations are under severe threat due to persistent and emergent anthropogenic pressures (Reid et al. 2019). Habitat loss and degradation, pollution, overexploitation, and invasive species, exacerbated by climate change, are among the primary drivers of biodiversity loss in freshwater habitats (Reid et al. 2019; Su et al. 2021; Danet et al. 2024; Dudgeon and Strayer 2025; Sayer et al. 2025). As a result, nearly one-third (26%) of freshwater fish species now face an increasing risk of extinction, with many being narrow endemics (Sayer et al. 2025). For instance, the modern extinction rate for North American freshwater fishes was estimated to be over 800 times higher than the natural background extinction rate (Burkhead 2012), while riverine fish populations in Western Europe and the USA have experienced a mean extinction rate over the past 110 years that is approximately 112 times higher than natural extinction rates (Dias et al. 2017). Despite these alarming trends, research and conservation investment for freshwater biodiversity remains substantially outpaced by those in terrestrial and marine ecosystems (Maasri et al. 2022) with most efforts focusing on flagship or commercially valuable species (e.g., salmonids, sturgeons). As vital components to the functioning of aquatic ecosystems, freshwater fish loss could signal broader ecological disruption, with cascading effects on associated fauna and flora (Closs et al. 2016; Lee et al. 2023), and ultimately posing risks to human well-being (Ceballos et al. 2015; Taylor et al. 2016).

Human population growth and rising per capita consumption have been the leading drivers of species extinction (Pimm et al. 2014). Many studies assessing extinction drivers have relied on proxies such as human population density and economic activity (Luck et al. 2004; Davies et al. 2006; Irwin et al. 2022). Others have attempted to identify the most vulnerable species by examining life-history traits (Olden et al. 2007; Hutchings et al. 2012; Chichorro et al. 2019). A study investigating the impact of specific extinction factors on freshwater fishes found only weak effects from certain anthropogenic stressors, including river fragmentation by dams and the percentage of non-native fish species (Dias et al. 2017). Similarly, climate change models predicting future extinction rates of freshwater fishes, particularly in relation to habitat loss, suggest that only a limited number of river basins (20 out of more than 1,010) are expected to experience actual extinctions due to climate-induced habitat loss by 2090 (Tedesco et al. 2013). While these studies offer valuable insights, they often examine threats in isolation or focus on specific regions, creating a critical gap in understanding the global patterns and drivers of freshwater fish extinctions (Darwall and Freyhof 2016). This gap may hinder the development of effective conservation strategies, leaving many freshwater species and ecosystems at continued risk. A notable exception is the recent study by Sayer et al. (2025), which provides the first comprehensive global assessment of extinction risk in freshwater species, including decapod crustaceans, fishes, and odonates. A staggering one-quarter (24%) of these species are now threatened with extinction, with freshwater fish being largely affected by pollution and water management issues such as dams and water extraction, while overfishing, invasive species, and diseases also pose significant risks. Furthermore, most freshwater species are impacted by multiple threats that may have cumulative effects, emphasizing the urgent need for a holistic evaluation of how these stressors interact and impact freshwater biodiversity (Dudgeon 2019).

The present study conducts a global-scale assessment focused exclusively on extinct freshwater fishes, analyzing both the spatial and temporal patterns of species loss and the key drivers contributing to their extinction, independently and in synergy. By using an extensive and diverse dataset that integrates ecological data and anthropogenic pressures, we aim to identify the primary drivers of extinction across different regions. Specifically, our objectives are to: (a) investigate the taxonomic patterns of freshwater fish extinctions, (b) analyze the spatial and temporal trends by examining variations across continents, ecosystem types (lotic and lentic), climatic zones, and extinction drivers, (c) compare current extinction rates with historical baselines to assess the severity and acceleration of freshwater fish biodiversity loss, (d) identify the primary drivers of freshwater fish extinctions, explore their interactions, and determine whether their relative significance has changed over time, and (e) evaluate the influence of species-specific traits (such as body size or position in the water column) on extinction counts, to identify biological characteristics that increase vulnerability. Through this comprehensive assessment, we seek to deepen our understanding of the complex factors driving freshwater fish extinctions, ultimately providing a more refined and actionable foundation for conservation aimed at mitigating species loss.

2 | Materials and Methods

2.1 | Data Collection

Species data for this study were primarily obtained from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species using its advanced search criteria portal (accessed in November 2024; available at www.iucnredlist.org). We specifically focused on freshwater fishes classified as extinct (EX) and extinct in the wild (EW)—hereafter referred to as extincts—all of which inhabit inland waters. To maximize data completeness, we supplemented the IUCN Red List data with species-specific information from FishBase (www.fishbase.org) and additional peer-reviewed literature, incorporating relevant ecological, biological, and environmental attributes.

For each species, we compiled an individual dataset including taxonomic details (order, family, genus); ecological characteristics (habitat type, position in the water column, trophic level, and body size); and documented anthropogenic extinction drivers/threats. To classify the habitats previously occupied by extinct species, we utilized IUCN's Habitats Classification Scheme (Version 3.1) of the IUCN Red List. This system provides a standardized categorization of habitats, with those for inland aquatic ecosystems primarily based on the Ramsar Wetland Type Classification System (www.iucnredlist.org/resources/habitat-classification-scheme). We reviewed habitat types listed under the categories "Wetlands (inland)" and "Artificial—Aquatic" in the classification system including only those marked as "Suitable" for the species in our dataset. We then adopted the division of the overarching category "5. Wetlands (inland)" into riverine, lake and wetland habitats (the latter encompassing all other wetland habitats, except lentic and lotic ones). Species-specific traits (flow preference, position in the water column, trophic level and body size) were primarily obtained from FishBase supplemented through a targeted review of scientific literature. Information on species distributions across climate zones was also obtained from FishBase and where such data were unavailable, supplemented through review of scientific literature.

2.2 | Spatial Analysis

Spatial distribution data on freshwater fish extinctions were collected at the continent level using HydroBASINS species range maps from the IUCN Red List. To estimate the former extent of occurrence of extinct species, we utilized species range tables from the IUCN Red List, which include HydroBASINS data to uniquely identify specific river and lake catchments.

2.3 | Temporal Analysis

We collected data on the date of last recorded occurrence in the wild for each species, sourced from the IUCN Red List. This date serves as a proxy for extinction events, allowing us to analyze extinction trends over time. When an exact date was unavailable—such as when only a decade (e.g., 1980s, 1990s) was reported—we used the beginning of the respective decade as a reference. The dataset was then used to construct temporal extinction pattern graphs—globally, across continents, and globally per driver—with 95% confidence intervals using Python (version 3.13).

2.4 | Extinction Drivers

In addition to spatial and temporal data, we systematically compiled information on the drivers of extinction for the target species. These were classified according to the IUCN Red List Threat categories, namely Biological Resource Use (BRU), Pollution (POL), Invasive Non-Native/Alien Species and Diseases (INV), Natural System Modifications (NSM), Agriculture and Aquaculture (AA), and Climate Change and Severe Weather (CLIM). For species whose precise threat(s) could not be identified, we assigned them to the "Unknown" (UKN) driver category. Additional threat categories identified in the IUCN Red List such as "Residential and Commercial Development" and "Energy Production and Mining," were consolidated into the "Other" (OTH) category.

2.5 | Data Visualization and Analysis

To visualize spatial patterns of freshwater fish extinctions across continents, we generated maps using Python (version 3.13), employing *pandas* for data processing and *geopandas* for spatial analysis.

To estimate and compare the modern and background extinction rates on both global and continental scales, we calculated extinctions per million species-years (E/MSY). This metric quantifies the contemporary extinction rates relative to the natural background rate, offering insights into the impact of anthropogenic factors on freshwater biodiversity. Following the methodologies of Ricciardi and Rasmussen (1999), Burkhead (2012), and Pimm et al. (2014), we estimated the background extinction rate based on the mean duration from origination to extinction, inferred from fossil records. For freshwater fishes, this interval is assumed to be three million years, yielding a background extinction rate of 1/3 E/MSY. The modern extinction rate was calculated using the formula:

$$\text{Modern extinction rate} = \text{Extinctions} \times 10^6 / (\text{Total number of extant species} \times \text{time period in years}).$$

In addition to point estimates derived from a Poisson model, we applied a Bayesian framework to estimate modern extinction rates, using a non-informative Gamma (1, 1) prior for the extinction rate parameter. This approach accounts for parameter uncertainty and provides full posterior distributions for regional extinction rates. Posteriors were obtained by updating the prior with observed extinction counts over a 165-year period (1851–2016), followed by drawing 10,000 samples to characterize uncertainty. Extinction rates were then scaled to E/MSY, and the posterior mean and 95% credible intervals were computed. All calculations were performed using Python (version 3.13).

For the calculation of extinction rates, the total number of freshwater fish species per continent, as listed on the IUCN Red List, was used as the baseline: Europe = 547, Asia = 5,916, North America = 988, Africa = 3,463, and Total = 10,914. For estimating the global modern extinction rate, we approximated the total number of known freshwater fish species at 18,000 (Fricke et al. 2025). Notably, no species from South America are classified as extinct. The analysis covered the period from 1851 (the first recorded extinction of a freshwater fish species) to 2016 (the most recent extinction), including species classified as EW.

Country-level maps of global extinction drivers for the four primary threat categories (BRU, POL, INV, NSM) were generated in Python (version 3.13).

2.6 | Statistical Analysis

A Bayesian logistic regression model was employed to evaluate the factors influencing the probability of a documented extinction driver effect, serving as a proxy for extinction risk across 100 species. The model incorporated predictors such as extinction driver type, taxonomic family, continent of origin (excluding Oceania, represented by a single extinct species), climate zone, habitat type, and fish traits (with trophic level omitted due to excessive sub categorical complexity) and was estimated using 12,000 posterior samples. The model was built in R using the package *rstanarm*.

To test for driver synergies, extinction driver co-occurrence (globally and at the continental level), we employed a Bayesian modeling framework that quantifies pairwise associations between drivers globally and within each continent (i.e., Africa, Asia, Europe, and North America). Data on the presence (1) or absence (0) of a specific driver for each species were compiled into binary matrices, with each column representing a driver and each row corresponding to a species. We analyzed pairwise relationships between all possible combinations of driver variables using Bayesian Poisson regression models. Specifically, for each pair of drivers (A, B), we modeled the presence of driver B as a function of driver A using the following specification:

$$B_i \sim \text{Poisson}(\lambda_i), \log(\lambda_i) = \beta_0 + \beta_1 A i$$

where λ_i is the expected rate of driver B given driver A for species $_i$. We ran each model with 4 chains and 3,000 posterior draws, resulting in robust posterior distributions of the intercept term (β_0) representing the baseline log co-occurrence rate. From each model, we extracted the posterior mean, 95% credible intervals (2.5th and 97.5th percentiles) of the intercept, and the raw count of species exhibiting both drivers.

For the statistical analyses, the following extinction drivers were used as predictors: BRU, INV, NSM, CLIM, AA, OTH, and UKN (following the categorization in our database). The single species from the boreal climate zone was excluded from the analysis due to insufficient data. For size analysis, extinct species were grouped into two categories: small species (< 15 cm in length) and large species (> 15 cm in length). Size data were unavailable for 13 species.

3 | Results

3.1 | Taxonomic Patterns of Extinctions

So far, a total of 100 freshwater fish species have been recorded as EX, of which 11 species are classified as EW (Table S1). These species represent 0.52% of all known freshwater fish species, 0.64% of the assessed freshwater fish species, and 0.91% of the freshwater fish fauna of the continents examined in this study. The family Cyprinidae exhibited the highest number of extinctions, with 22 species lost, with most (17 species) recorded in Asia (Figure 1a). Leuciscidae ranked closely second, with 20 extinctions, primarily in North America (12 species, Figure 1a), while Salmonidae accounted for 19 extinctions, with most (14 species) recorded in Europe. Other (less) affected families included Cyprinodontidae, Poeciliidae, and Cichlidae, with eight, five, and four extinctions, respectively. Collectively, all other families contributed to 22 extinctions, with fewer than three species per family (Figure 1a). Building on these patterns, our statistical analysis revealed that several families exhibit elevated extinction risk, with varying levels of statistical support (Table S2). Specifically, Cyprinidae showed the highest estimated effect among all families (mean = 1.2, SD = 4.9, CI: −5.2 to 7.4), suggesting higher extinction vulnerability, with Leuciscidae and Salmonidae also displaying a high mean (mean = 1.1, SD = 4.4, CI: −4.7 to 6.7 and mean = 1.1, SD = 4.5, CI: −4.8 to 6.8), which supports increased extinctions, albeit with high variability. Cyprinodontidae, in contrast, displayed a moderate mean (mean = 0.8, SD = 3.2, CI: −3.4 to 4.8), which points to a potential increase in extinction probability, followed by Poeciliidae (mean = 0.6, SD = 2.5, CI: −2.6 to 3.7); Cichlidae (mean = 0.5, SD = 2.1, CI: −2.3 to 3.2); and Goodeidae (mean = 0.4, SD = 1.7, CI: −1.8 to 2.5). Catostomidae (mean = 0.2, SD = 1.1, CI: −1.2 to 1.6); Clupeidae (mean = 0.2, SD = 1.1, CI: −1.2 to 1.6); and Xenocyprididae (mean = 0.2, SD = 1.1, CI: −1.2 to 1.6) displayed a slight positive effect. In contrast, the rest of the families, such as, for example, Acipenseridae (mean = −0.1, SD = 0.4, CI: −0.6 to 0.4); Aphaniidae (mean = −0.1, SD = 0.4, CI: −0.5 to 0.4); and Atherinopsidae (mean = −0.1, SD = 0.4, CI: −0.6 to 0.4), all showed negligible effects on extinction risk, with narrow credible intervals tightly centered around zero.

At the genus level, *Barbodes* (Cyprinidae) was the most affected, with 15 extinct species, all from a single lake in Asia (Figure 1b). This was followed by *Coregonus* (Salmonidae), with 13 extinctions. The genus *Cyprinodon* (Cyprinodontidae) accounted for six extinctions, all involving North American pupfishes, while *Notropis* (Leuciscidae), which includes four species of shiners, experienced extinctions primarily in North America. The remaining extinctions were distributed across 48 genera, with no more than three species per genus (Figure 1b).

There was an extreme variation in the former area of occupancy of the extinct species, ranging from 1.67 to 1,411,016 km^2 (mean = 32,083, SD = 15,426). The most widespread species was the Chinese paddlefish (*Psephurus gladius*) which was formerly native to the Yangtze and Yellow River basins in China. This was followed by the Volga shad (*Alosa volgensis*) once native to the Volga River in the Russian Federation; the Dabry's sturgeon (*Acipenser dabryanus*) which also inhabited the Yangtze and Yellow River basins; and the Thicktail chub (*Gila crassicauda*), native to the Sacramento and San Joaquin Rivers in California. Conversely, the Lake Sidi Ali trout (*Salmo pallaryi*), once confined to a single lake in Morocco, had the smallest distribution area. This was followed by the Ören whitefish (*Coregonus trybomi*), previously found in only one Swedish lake (Lake Ören) and the Morat whitefish (*Coregonus restrictus*) which was native to Lake Morat in Switzerland.

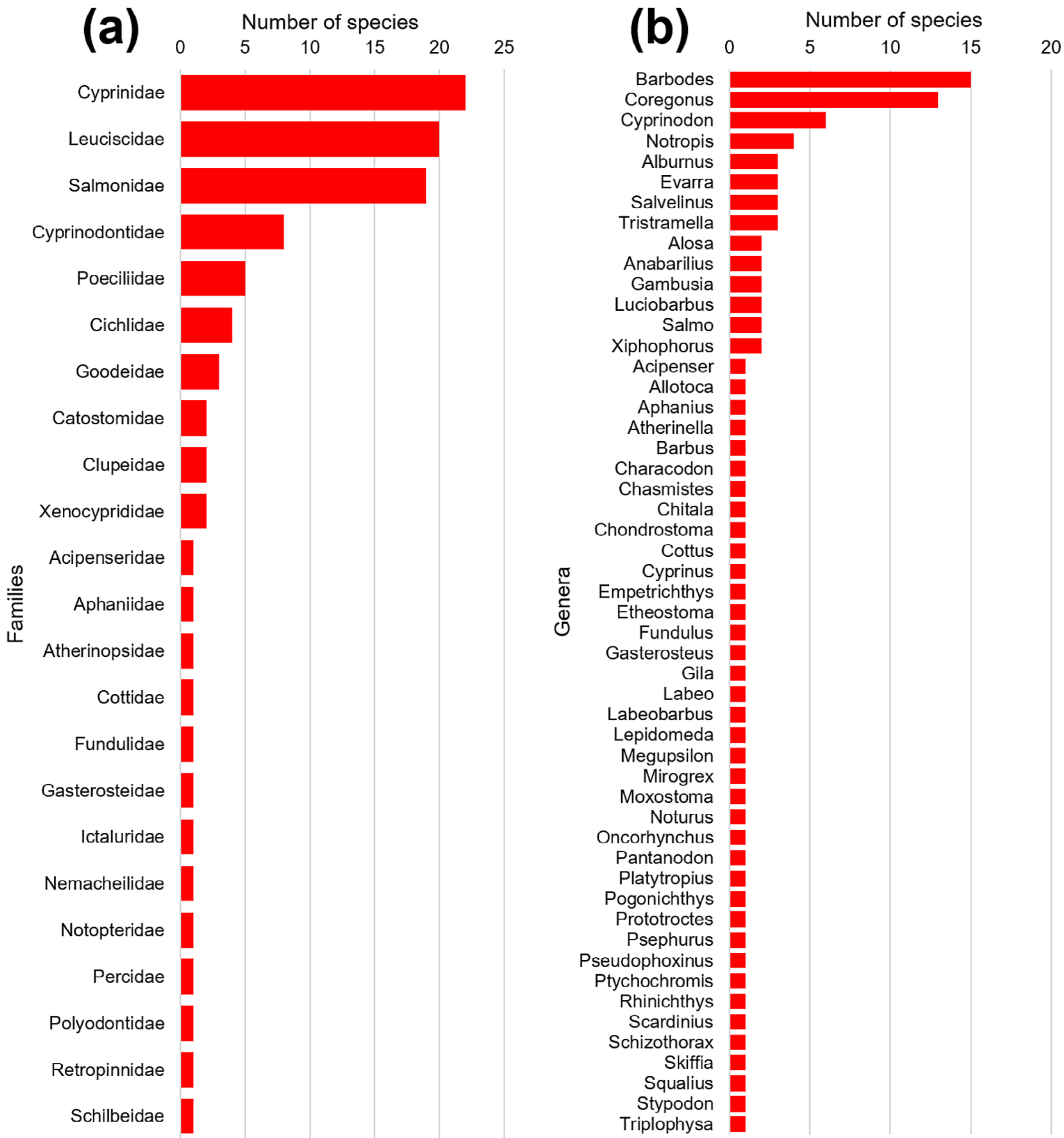

FIGURE 1 | Family (a) and genus (b) level distribution of freshwater fish extinctions.

3.2 | Spatial and Temporal Patterns of Freshwater Fish Extinctions

The global cumulative number of extinct freshwater fish species showed a continental variation, reflecting distinct regional drivers and vulnerabilities. North America and Asia have experienced the highest modern extinctions, followed by Europe and Africa, with lower but still notable extinctions over the past two centuries (Figures 2 and 3). Consistent with these patterns, species from Asia and North America showed the strongest statistical associations with extinction, each with very high estimated probabilities of species loss (0.95 and 0.94, respectively; 90% CIs: 0.90–0.98 and 0.89–0.97), marked by strong effect sizes and narrow, entirely positive intervals (Table S3). Europe showed a moderate association (0.82; 90% CI: 0.65–0.92), indicating a likely positive effect, while Africa displayed the weakest and most uncertain pattern (0.62; 90% CI: 0.33–0.84).

Temporal trends indicate an acceleration in freshwater fish extinctions globally during the modern period. By the early 20th century, 10 species had been lost, marking the onset of modern extinction patterns. A steep rise began in the mid-20th century, with 50 species extinctions recorded by the 1960s. This trend intensified during the 1970s and 1980s and by the 2010s, with the cumulative number of extinct freshwater fish species reaching 100 species (Figure 3). North America experienced the highest cumulative extinctions, with the trajectory accelerating sharply from the mid-20th century onward, reaching 37 extinct species by the 2010s (Figure 3). Asia exhibited a similar accelerating pattern totaling about 34 species by the end of the 20th century. Europe demonstrated a more gradual increase, culminating in 20 extinctions, with five species having imprecise last recorded dates. Africa experienced an even slower and more subdued rise, with only eight species lost.

3.3 | Modern Versus Background Extinction Rates

The modern extinction rate of freshwater fishes (E/MSY) estimated globally for the period 1851–2016 is 33.47 E/MSY (95% CI: 21.11–45.83). This figure exceeds the natural background extinction rate of 0.33 E/MSY by more than 100-fold. Regional disparities in extinction rates are pronounced. North America

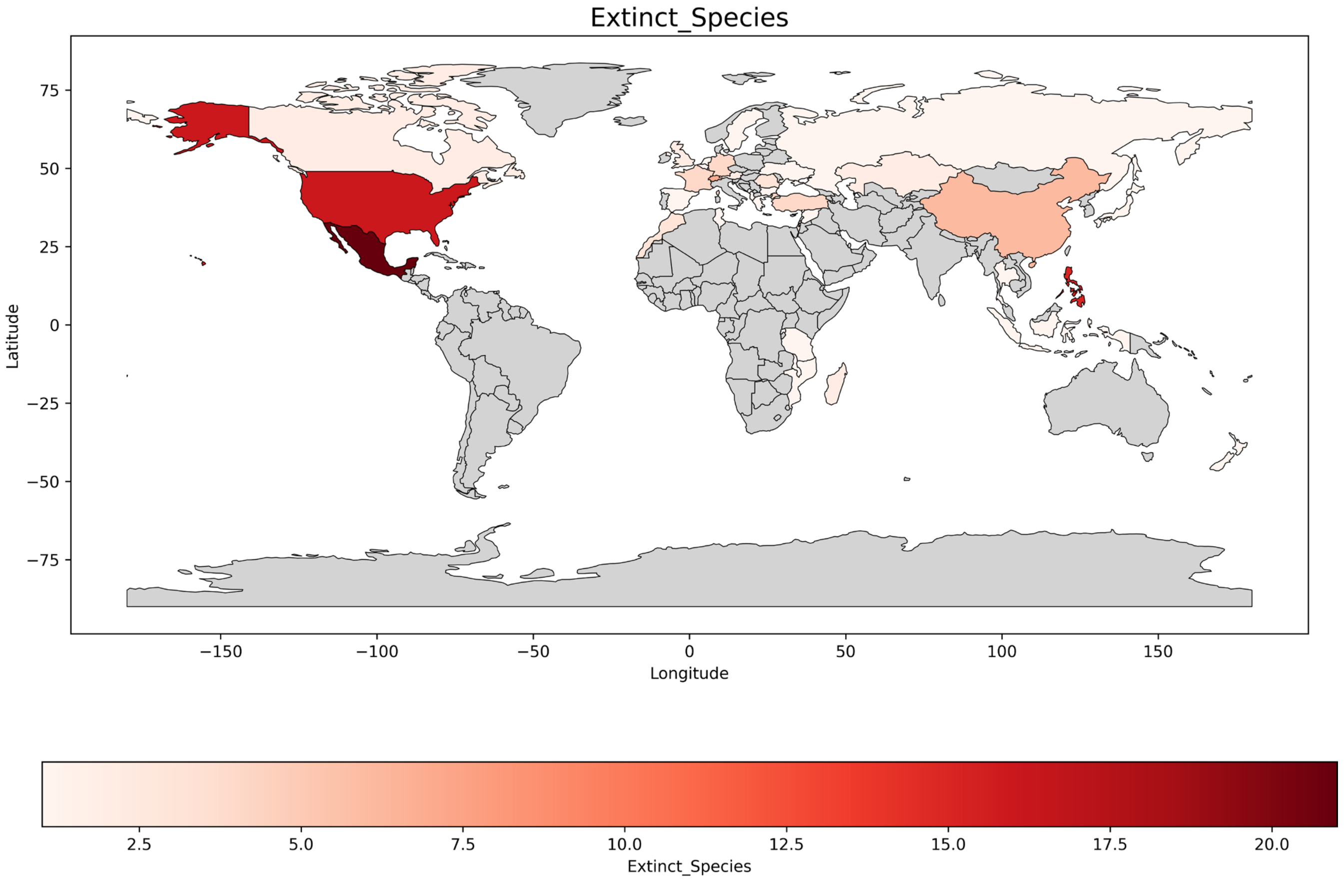

FIGURE 2 | Geographic distribution of extinct freshwater fish species by continent and country revealing regional extinction hotspots. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

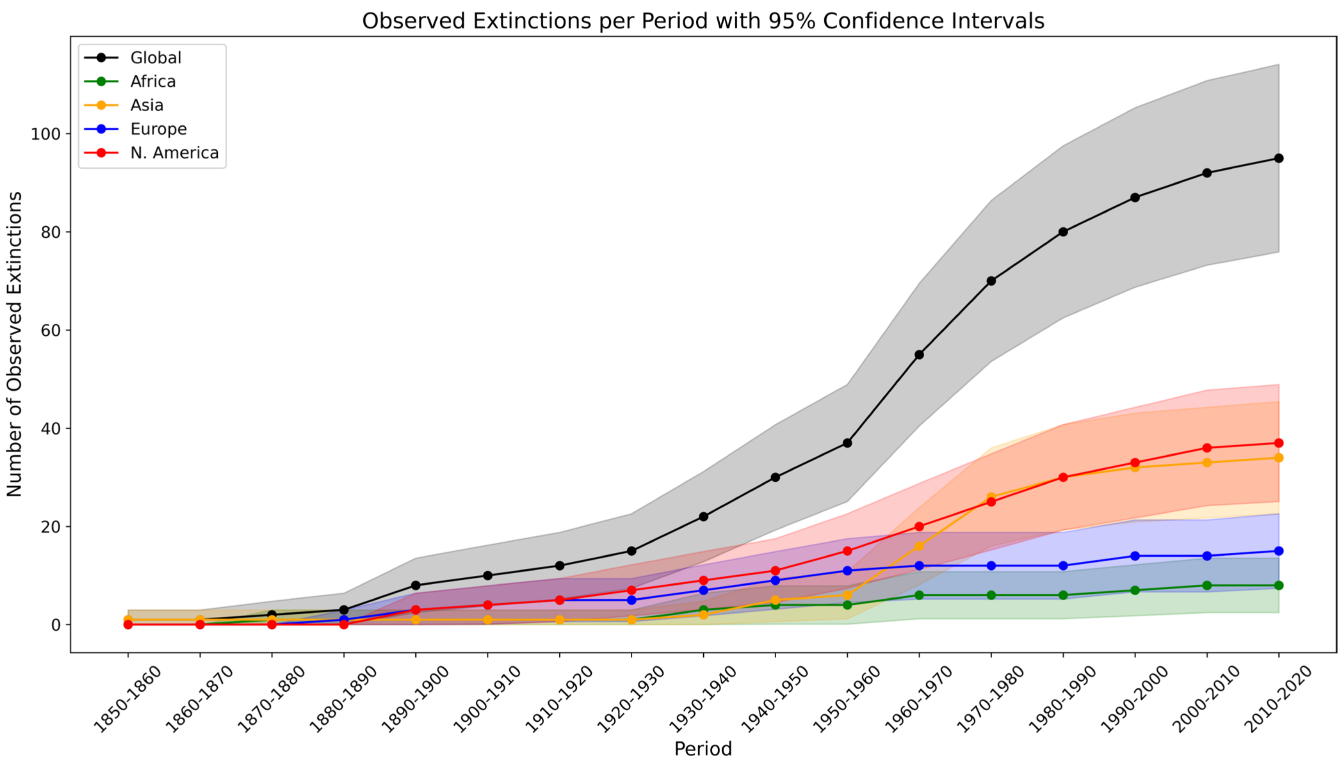

FIGURE 3 | Cumulative observed extinctions of freshwater species globally and by continent with confidence intervals. Note five species from the Global and Europe trends were excluded due to imprecise last recorded dates (e.g., May trout *Salmo schiefermuelleri*, last recorded in the 19th century).

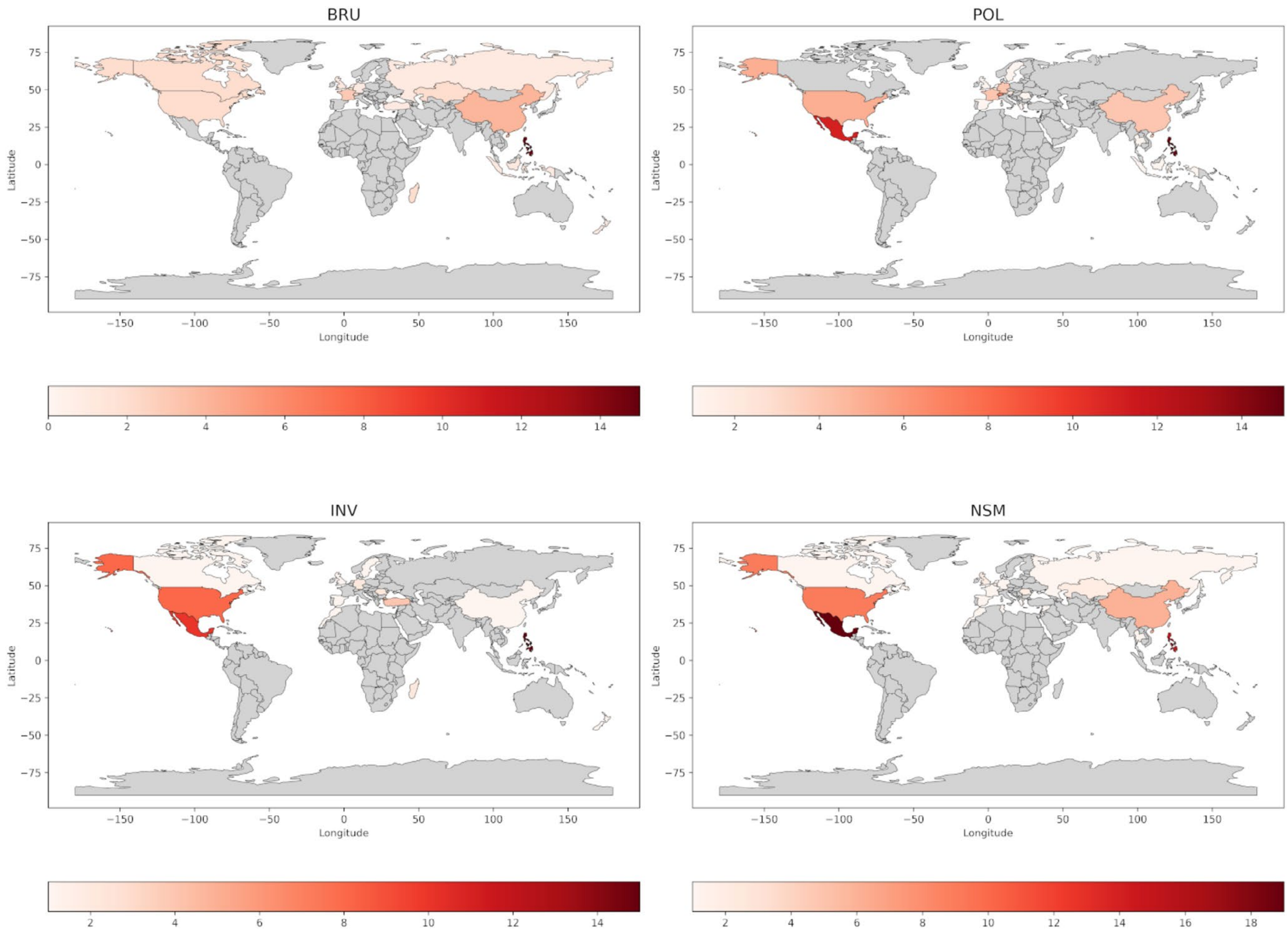

FIGURE 4 | Global extinction driver maps per country for the four major drivers of freshwater fish extinctions, indicating regional extinction hotspots, that is, Philippines and Mexico. Extinction drivers: BRU, Biological Resource Use; INV, Invasive Non-Native/Alien Species and Diseases; NSM, Natural System Modifications; POL, Pollution. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

exhibits the highest extinction rate, at 225.60 E/MSY (95% CI: 196.16–255.03), representing a 684-fold increase over the background rate. Europe follows with a rate of 220.26 E/MSY (95% CI: 191.17–249.34), which is 667 times greater than the background level. Asia's extinction rate of 34.62 E/MSY (95% CI: 23.08–46.15) is 105 times higher than natural background levels, while Africa, although least affected, still records a modern extinction rate of 13.92 E/MSY (95% CI: 6.60–21.23), a 42-fold increase.

The Bayesian mean estimates closely align with the above results: North America exhibited the highest rate at 719 E/MSY (95% CI: 630–815), followed by Europe at 688 E/MSY (95% CI: 570–814). Asia and Africa displayed lower rates at 98 E/MSY (95% CI: 85–113) and 51 E/MSY (95% CI: 39–65), respectively. These Bayesian credible intervals reinforce the pronounced regional disparities and confirm that extinction rates far exceed background levels, even when model uncertainty is explicitly incorporated.

3.4 | Global Drivers of Extinctions and Extinction Driver Synergies

Freshwater fish extinctions are primarily driven by four dominant extinction drivers: NSM, POL, INV, and BRU (Figure 4). Among these, NSM was the most frequent driver (27.47%), contributing to the extinction of 64 species. POL closely followed (23.61%), impacting 55 species. INV was linked to the extinction of 50 species (21.46%), while BRU accounted for the extinction of 31 species (13.30%). In contrast, AA and CLIM were reported as extinction drivers for only four species (1.72% of total reports) each. Finally, reports for 11 species (4.72% of total reports) fell under the UKN category.

Statistical analysis of extinction patterns revealed moderate-to-strong evidence for positive associations between extinction and the drivers NSM (mean = 0.7, SD = 0.2, CI: 0.5–1.0); POL (mean = 0.6, SD = 0.2, CI: 0.3–0.9); and INV (mean = 0.5, SD = 0.2, CI: 0.2–0.8), with NSM showing the largest effect size and the strongest link to extinctions (Table S4). In contrast, AA (mean = −2.1, SD = 0.6, CI: −2.9 to −0.5) and CLIM (mean = −2.1, SD = 0.6, CI: −2.9 to −1.5) showed consistently negative associations with extinction counts, suggesting either underreporting or limitations in attribution for species affected by these stressors. Similarly, categories such as OTH (mean = −1.2, SD = 0.4, CI: −1.6 to −0.7) and UKN (mean = −1.1, SD = 0.4, CI: −1.5 to −0.6) also showed negative trends, likely reflecting the diffuse or poorly defined nature of these labels, which may reduce their explanatory value.

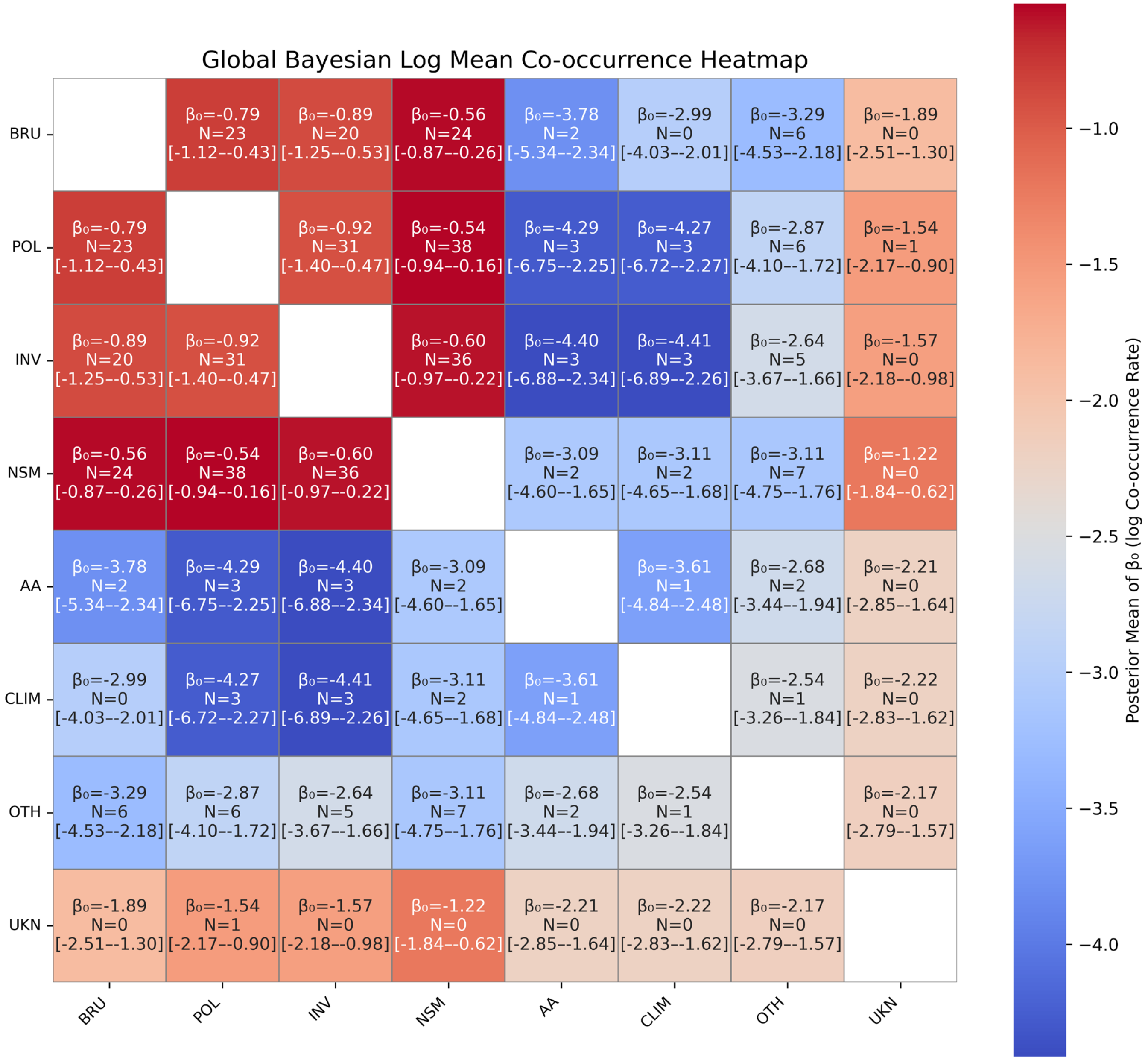

FIGURE 5 | Bayesian heatmap of log-mean co-occurrence among extinction driver pairs globally. Extinction drivers: Biological Resource Use (BRU), Pollution (POL), Invasive Non-Native/Alien Species and Diseases (INV), Natural System Modifications (NSM), Agriculture and Aquaculture (AA), Climate Change and Severe Weather (CLIM), "Unknown" (UKN), "Other" (OTH). Cell values represent the posterior mean log co-occurrence rate (β_0), the number of observed co-occurrences (N) for each driver pair and confidence intervals (95% CI). Color gradients indicate the strength of co-occurrence on a logarithmic scale, with red denoting higher co-occurrence (less negative β_0) and blue indicating lower co-occurrence (more negative β_0).

Many global species extinctions are believed to be the result of a complex interplay between multiple extinction drivers. The log-mean co-occurrence among extinction driver pairs confirmed a pronounced "synergy core" linking POL, NSM, INV, and BRU (Figure 5). The most common combination of drivers in the dataset was NSM and POL, which contributed to the extinction of 38 species, followed closely by the combination of NSM and INV, which led to 36 extinctions, and POL and INV responsible for 31 extinctions. Based on Bayesian modeling, NSM × BRU, NSM × POL, and NSM × INV exhibited the highest overlap, with similar mean values (Figure 5). Also, there was a secondary tier of moderate overlaps, that is, POL × BRU, INV × BRU, and INV × POL (Figure 5). By contrast, AA, CLIM, and OTH drivers yielded log-means ≤ -3.62 with very low raw counts ($N \leq 7$), signifying either broad-scale drivers under-reported at the species level or localized/idiosyncratic impacts.

Finally, 35 species extinctions were attributed to a single driver. Among these, NSM was the most frequent single driver, contributing to 12 extinctions, followed by POL with 8 extinctions and INV, which accounted for 5 extinctions, mirroring Bayesian modeling using the all species dataset that indicated a positive association of these three drivers with extinction counts. Extinctions with "Unknown" origins were overrepresented in the single-driver category, accounting for 10 extinctions.

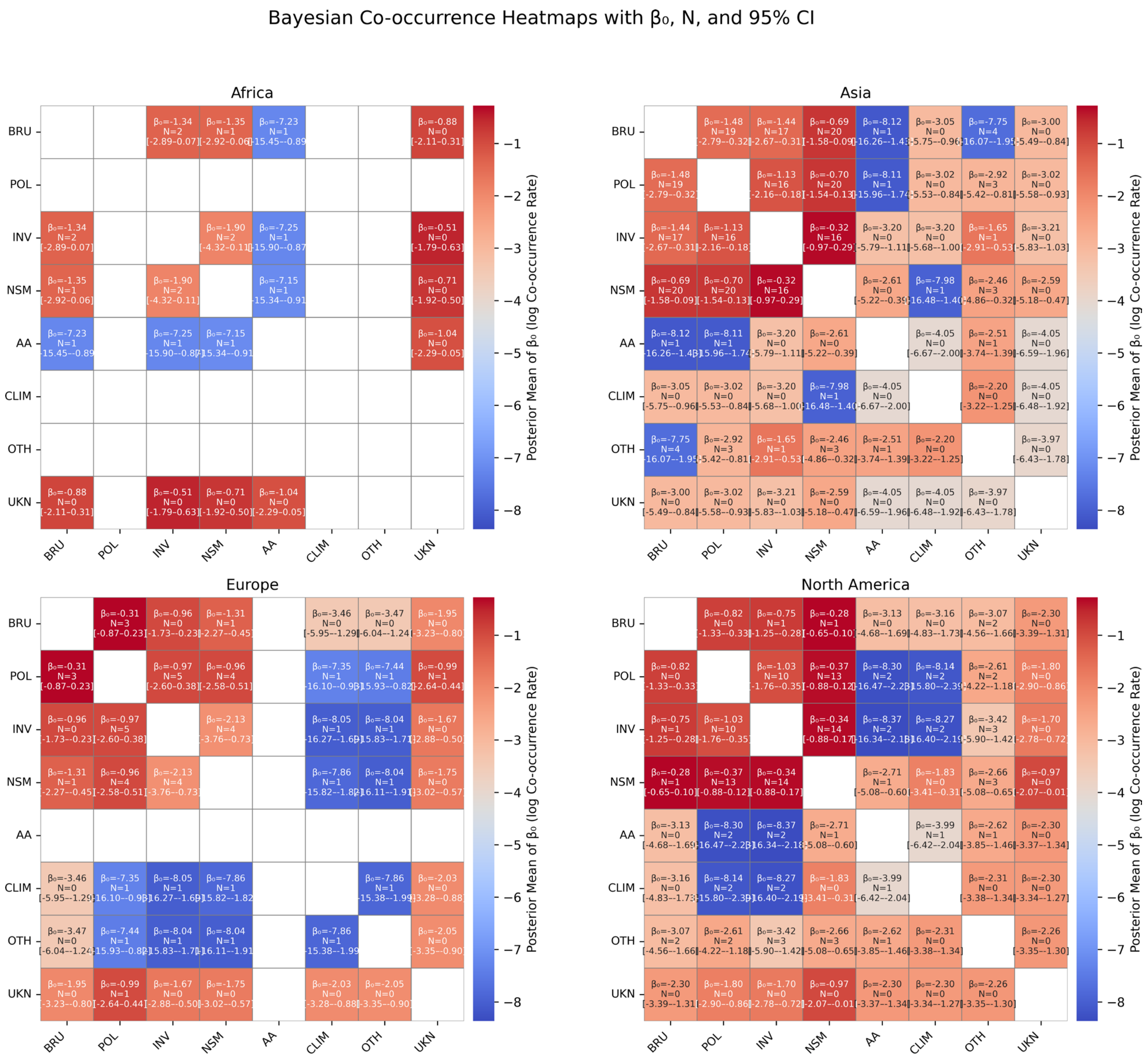

FIGURE 6 | Bayesian heatmap of log-mean co-occurrence among extinction driver pairs at the continental level. Extinction drivers: Biological Resource Use (BRU), Pollution (POL), Invasive Non-Native/Alien Species and Diseases (INV), Natural System Modifications (NSM), Agriculture and Aquaculture (AA), Climate Change and Severe Weather (CLIM), "Unknown" (UKN), "Other" (OTH Cell values represent the posterior mean log co-occurrence rate (β_0), the number of observed co-occurrences (N) for each driver pair and confidence intervals (95% CI). Color gradients indicate the strength of co-occurrence on a logarithmic scale, with red denoting higher co-occurrence (less negative β_0) and blue indicating lower co-occurrence (more negative β_0).

3.5 | Continental Patterns of Extinction Drivers and Extinction Driver Synergies

The distribution of extinction drivers across continents reveals notable regional differences in the patterns of species loss. In North America, where 37 species have gone extinct, most extinctions were driven by more than one driver (only 14 species extinctions were due to a single driver, with NSM being the predominant cause). Specifically, the combination of NSM and INV contributed to the extinction of 14 species, while NSM and POL together drove 13 species extinctions (Figure 6). Bayesian modeling also indicated high co-occurrence in North America, for NSM × INV and NSM × BRU, followed by NSM × POL (Figure 6).

In Asia, with 34 recorded extinctions, the pattern similarly reflects multiple extinction drivers, with NSM paired with POL (21 species), BRU (21 species) or INV (16 species) (Figure 6). Bayesian modeling indicated that NSM × INV in Asia had the highest log-mean co-occurrence, followed closely by NSM × POL and NSM × BRU, compared to the other continents, indicating their strong synergy in Asian species extinctions. Only eight species in Asia had single-driver extinctions, attributed to NSM or INV alone.

Europe exhibited a hybrid pattern, with both single and multiple driver extinctions. Pollution emerged as the dominant single driver in Europe, causing the extinction of almost half of the extinct species (eight species); the extinction of the remaining 12 species was attributed to multiple drivers, most commonly combinations of POL and INV (five species), or POL and NSM (four species). Bayesian modeling indicated that extinction drivers in Europe display uniformly low co-occurrence, with the "least negative" pairs—hence the most frequent—being BRU × POL, BRU × INV, INV × POL, and NSM × POL indicating rare synergistic interactions of drivers in European freshwater environments (Figure 6).

In Africa, with a total of eight species extinctions, five were due to single drivers, with most classified as UKN. The remaining three extinctions were driven by multiple factors, primarily INV combined with other drivers. Bayesian modeling indicated that among African freshwater taxa, the two threat combinations exhibiting the highest co-occurrence rates are INV × UKN and NSM × UKN with low synergy of these drivers (Figure 6).

3.6 | Global Temporal Patterns of Extinction Drivers

The pattern of freshwater fish extinctions shows a marked shift in the mid-20th century, with a notable increase in species losses. Up until the 1940s, cumulative extinctions were relatively low and largely attributed to pollution (Figure 6). However, beginning in the 1950s and 1960s, a significant acceleration in extinctions occurred, with NSM, POL, and INV emerging as the dominant drivers. To a lesser extent, BRU also played a role. This accelerating trend continued into the 1980s and beyond, with NSM-driven extinctions showing the sharpest rise, while BRU-driven extinctions stabilized (Figure 7).

3.7 | Habitat and Species Traits Patterns of Extinctions

Across climate zones, all regions exhibited negative mean coefficients, suggesting a generally reduced association with high-risk extinction drivers compared to the baseline (Table S5). However, species from tropical climates exhibited the higher (less negative) coefficient (mean = −0.6, SD = 0.2), possibly indicating a greater likelihood of being linked to major extinction drivers compared to other zones. Subtropical and temperate zones displayed lower mean coefficients (mean = −1.2 each, SD = 0.2), consistent with a more moderate connection to extinction patterns.

Statistical analysis did not reveal any strong association between habitat type and extinction risk (see River, Lake, and Wetland in Table S5). In terms of fish traits, preference for lotic habitats showed a moderate positive effect on extinction counts (mean = 0.9, SD = 1.2, 90% CI: −0.4 to 2.5), though with high uncertainty, while preference for lentic habitats showed a weaker positive effect (mean = 0.4, SD = 3.6) (Table S5). Finally, analysis indicated that the extinction probability is independent of fish position in the water column and body size (Table S5).

4 | Discussion

This study represents the first global-scale assessment quantifying extinction rates among extinct freshwater fish species, despite growing concerns over unnoticed extinctions, particularly in regions with limited surveying efforts such as South America and Africa (Darwall and Freyhof 2016). It complements the recent Sayer et al. (2025) study, a multi-taxon global freshwater fauna extinction risk assessment of threatened freshwater organisms as various as fish, crustaceans and odonates, to identify prevalent extinction drivers for taxa inhabiting freshwater

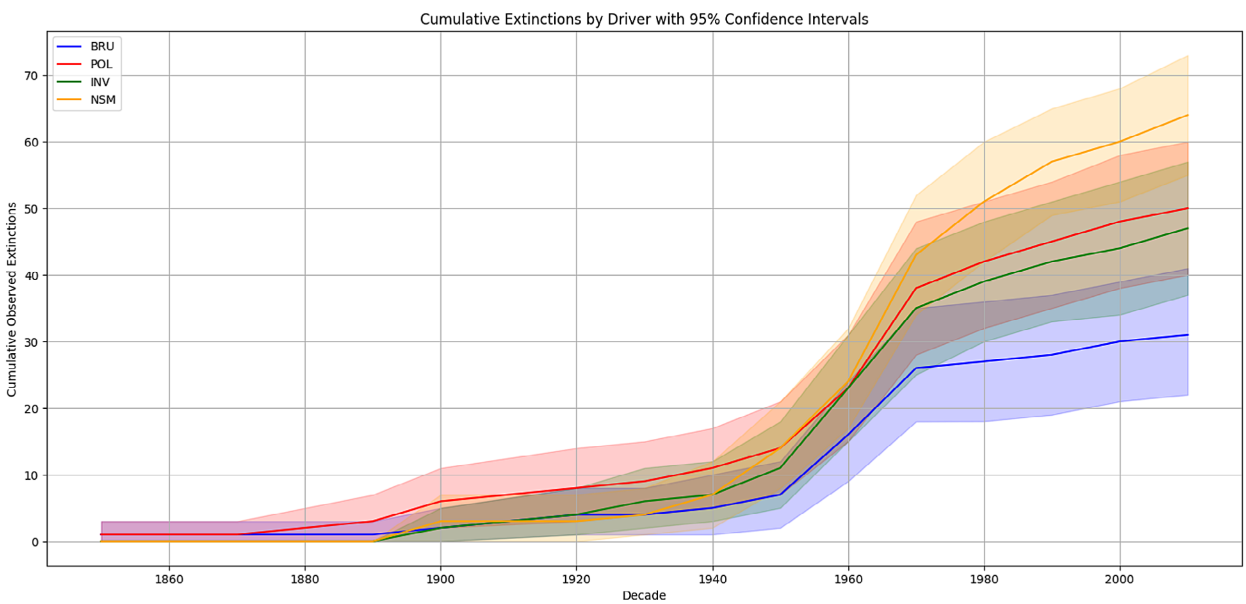

FIGURE 7 | Temporal pattern in freshwater fish extinctions per major driver with confidence intervals (95% CI). Extinction drivers: BRU, Biological Resource Use; INV, Invasive Non-Native/Alien Species and Diseases; NSM, Natural System Modifications; POL, Pollution.

environments. The current study focuses on the extinction drivers, habitats and ecology of extinct fishes, enabling a more taxon-specific analysis, as it explores critical patterns and provides insights regarding the spatio-temporal, trait-related, ecosystem-based, and anthropogenic drivers that contribute to extinction events in the freshwater fish taxonomic group. With 100 recorded extinctions, representing less than 1% of the estimated freshwater fish species worldwide (Fricke et al. 2025), this study emphasizes that the observed losses, though relatively small in percentage, may serve as an indicator of broader, yet-to-be documented biodiversity declines. The results contribute to a better understanding of the drivers of extinction and their synergies but also lay a foundational groundwork for future research in conservation biology and freshwater fish conservation planning. Rather than concluding with a sense of finality, this "obituary" serves as a stepping stone for deeper investigation into the preservation of freshwater ecosystems and the species that depend on them, ensuring that more attention is paid to those species that remain under threat but have not yet been documented as extinct.

The persistent decline in freshwater fish biodiversity during the Anthropocene shows no clear signs of slowing down, despite increased environmental awareness and improved conservation efforts in some regions. This ongoing crisis is largely driven by direct human-generated impacts, as demonstrated in this study, within the broader context of an accelerating climate emergency. The intensifying demands for water, food, energy, and land are placing increasing pressure on freshwater ecosystems, exacerbating biodiversity loss (D'Odorico et al. 2018). Using conservative assumptions of background and modern extinction rates based on IUCN Red List EX and EW species, it is evident that contemporary freshwater fish extinctions are occurring at rates far exceeding background levels that prevailed over tens of millions of years. These rates are particularly high in North America, Europe, and Asia (considering also the total number of freshwater fish species per continent), and consistent with previous estimates suggesting that modern extinction rates for North American freshwater fishes are nearly 800 times greater than background levels (Burkhead 2012). The observed trajectory of freshwater fish extinctions has sharply accelerated since the mid-20th century, mirroring trends seen in mammals and other vertebrates and confirming the rapid loss of biodiversity associated with the ongoing sixth mass extinction (Ceballos et al. 2010, 2015, 2020). This divergence between background extinction rates and current trends highlights the substantial impact of anthropogenic pressures on freshwater ecosystems, since natural extinction rates alone cannot account for the observed loss of biodiversity.

Many additional freshwater fish species, which are already at a "point of nearly improbable return" due to persistent and emerging anthropogenic pressures, are objectively expected to be added to the extinction list in the near future (Reid et al. 2019; Sayer et al. 2025). This includes species currently classified as data deficient (DD) or possibly extinct, reflecting critical knowledge gaps that hinder effective conservation efforts. The uncertainty surrounding these classifications emphasizes the need for comprehensive surveys and improved assessment methodologies to better understand species' true conservation statuses. Conversely, some species previously declared extinct—such as the Constance deepwater charr (*Salvelinus profundus*) in Europe (Ford 2024)—may yet be rediscovered in their historical habitats or in newly identified locations. Such cases, often resulting from incomplete distributional data or taxonomic reevaluations, reinforce the importance of continued monitoring and genetic studies to clarify species status. Each documented extinction, along with the trends identified in this study, offers valuable insights for the conservation of freshwater fish species currently at risk of extinction. Understanding the drivers behind past extinctions can help refine conservation priorities and strategies, ensuring that threatened species receive the targeted protections necessary to prevent further losses (Darwall and Freyhof 2016; Sayer et al. 2025).

4.1 | Taxonomic Patterns

Three major drivers of freshwater fish extinctions—NSM, POL, and INV—have independently or synergistically contributed to the loss of species within the most extinction-affected families included in the IUCN Red List, that is, Cyprinidae, Leuciscidae, and Salmonidae. Cyprinidae and Leuciscidae, the two largest and most diverse freshwater fish families, have experienced significant extinction events, largely due to INV, often in conjunction with NSM or POL. Cyprinidae species, with a native distribution spanning most of the world except Central and South America, Madagascar, Australia, and New Zealand (Nelson et al. 2016), have been particularly vulnerable to the introduction of invasive species and habitat alterations. Similarly, Leuciscidae, which are native to Europe, North America, and Asia, have faced extinction pressures primarily from INV, often exacerbated by changes in hydrological regimes and pollution. In contrast, extinctions within Salmonidae—including whitefishes, trout, and char—have been predominantly driven by habitat degradation linked to POL, with additional pressures from overfishing and the effects of INV.

4.2 | Spatial Patterns

Modern freshwater fish extinctions are disproportionately higher in North America and Asia followed by Europe, emphasizing the significant impact of anthropogenic pressures on global freshwater biodiversity. The apparent lack of documented extinctions in South America and the relatively lower rate and extinctions in Africa likely reflect insufficient ichthyological research rather than a true absence of species loss. Limited taxonomic assessments, coupled with lower international funding for freshwater biodiversity studies and conservation efforts (Palacio et al. 2023) contribute to significant knowledge gaps. In Africa, the possible extinction of 45 *Haplochromis* cichlid species in Lake Victoria—if formally classified as extinct—would significantly increase the continent's cumulative extinctions and rates. Conversely, the lower recorded extinctions (one species) in Oceania may be attributed to its naturally depauperate freshwater fish fauna, which has fewer endemic species vulnerable to extinction (Stiassny 1996; Gillespie et al. 2008; Reis et al. 2016; Dudgeon and Strayer 2025). Nevertheless, recent studies suggest that most vertebrates on the brink of extinction—species with fewer than 1,000 individuals—are found in South America, followed by Oceania, Asia, and Africa (Ceballos et al. 2020). These regions, notably underrepresented in the IUCN extinction list, may be experiencing a hidden biodiversity crisis, highlighting the urgent need for expanded research and targeted conservation efforts.

A major pattern in freshwater fish extinctions involves multiple, localized extinctions (regional extinction hotspots) within genera that exhibit high speciation rates, often confined to a single watershed. One such case is the extinction of 15 species from the genus *Barbodes*, native (or near native) to Lake Lanao in the Philippines (surface area approx. 340 km^2). These species, which underwent rapid evolutionary diversification, were last recorded before the early 1990s. Their extinction resulted from a multifactorial process involving the introduction of invasive species, overharvesting, and destructive fishing practices, particularly dynamite fishing (Torres et al. 2020). Additional contributing factors included water abstraction, illegal logging leading to soil erosion, and the resultant influx of nutrients and pollutants (Metillo and Garcia-Hansel 2016). Another instance of multiple, localized extinctions in the wild is seen in four Mexican pupfishes of the genus *Cyprinodon* (*C. ceciliae, C. immemoriam, C. longidorsalis*, and *C. veronicae*), endemic to La Presa Springs. These springs dried up due to overabstraction, with aridity and desertification exacerbating their extinction risk (Contreras-Balderas et al. 2002; Lozano-Vilano and De La Maza-Benignos 2017). A separate extinction pattern involves single species localized extinctions such as those observed in Anatolia (Turkey), where endemic species were lost due to the introduction of invasive predators. The Beyşehir bleak (*Alburnus akili*), endemic to Lake Beyşehir, and the Eğirdir minnow (*Pseudophoxinus handlirschi*), endemic to Lake Eğirdir, were both driven to extinction by the introduction of the predatory Eurasian pikeperch (*Sander lucioperca*) (Giannetto and Innal 2021). A similar pattern of extinctions has occurred in European lakes, particularly among endemic whitefish species (*Coregonus* spp.) that became extinct primarily due to nutrient pollution (Vonlanthen et al. 2012). These cases highlight the vulnerability of freshwater fish species confined to small, isolated ecosystems.

A less common pattern involves larger-scale extinctions of a single or a small number of related, often commercially-valuable, species over a broad geographic range, such as the ciscos of the Great Lakes in North America. The Longjaw cisco (*Coregonus alpenae*) and the Deepwater cisco (*Coregonus johannae*) were extirpated primarily due to overfishing, coupled with the invasion of the parasitic Sea lamprey (*Petromyzon marinus*) in the early 19th century (Miller et al. 1989). Similar large-scale extinctions have affected large-bodied chinese endemics, such as the anadromous Chinese paddlefish (*P. gladius*). This species was driven to extinction by fragmentation caused by mega-dam construction and overfishing. Likewise, Dabry's sturgeon (*A. dabryanus*), a commercially important species, faced extinction due to overexploitation (Zhang et al. 2020; Cao et al. 2024).

4.3 | Drivers and Fish Traits

Despite evidence that larger species, particularly apex predators with naturally low population densities even in undisturbed ecosystems (Winemiller et al. 2016), are more vulnerable to extinction, our analysis indicates that extinction probability is independent of body size. This result may be influenced by our categorization into only two size classes (<15 cm and ≥ 15 cm) or by limitations in the completeness of available body size data. Nonetheless, our findings align with those of Olden et al. (2007) who reported no major differences in body size distributions among threatened freshwater species across various threat categories, which broadly correspond to our identified extinction drivers. However, Olden et al. (2007) showed that larger-bodied freshwater fishes that are also important to commercial or subsistence fisheries are at greater risk of extinction compared to non-fisheries species. These findings offer valuable insights for managing biodiversity loss across different extinction drivers and inform conservation strategies tailored to specific traits and regions. However, further research is needed to explore additional ecological factors, such as species-specific traits or genetic factors, that may contribute to observed fish extinction patterns. Long-term ecological studies that account for temporal variation in extinction drivers and trophic interactions could also provide a more nuanced understanding of how specific threats impact fish species at different stages of ecological succession.

4.4 | Variation in Modern Extinction Rates Through Time

Human activities have drastically altered ecosystems, threatening aquatic biodiversity and human well-being (Lee et al. 2023). This is starkly manifested in species' extinction acceleration, since the mid-20th century, closely linked to population growth and resource consumption (Myers 1990), with freshwater fish extinctions mirroring these broader socioeconomic shifts.

During the early industrial era (1851–1890s: The Early "Lag-Phase") rapid urbanization, agriculture expansion, and the development of transportation infrastructure, exerted increased pressure on freshwater ecosystems. Minimal environmental regulations, largely limited to fisheries management, combined with the widespread introduction of non-native species, exacerbated ecological imbalances. This period saw an average extinction rate of 0.2 species/per year, foreshadowing future biodiversity losses.

The 20th century (1890s–1970s: Exponential Increase) witnessed an explosion in global population, mirroring agricultural and industrial expansion that profoundly impacted freshwater habitats, notably accelerated by the Green Revolution (Ramankutty et al. 2002; Pisani 2003; Tudi et al. 2021). Post-1950 industrialization accelerated species loss through chemical pollution, overfishing, and invasive species introductions (Hulme 2009); the latter exploding through global trade, aquaculture, recreational fisheries, and the ornamental fish trade, in an environment of poor biosecurity and nascent public awareness. By the 1970s, 62 freshwater fish species had gone extinct, with extinction rates rising to 0.69 per year.

The turn of the century (1970s–2016: Misleading Deceleration) was marked by a growing environmental awareness, leading to conservation initiatives and regulations, such as the Ramsar Convention (1971), the US Clean Water Act (1972), the Convention on Biological Diversity (CBD, 1992), and the EU Water Framework Directive (2000) to mitigate anthropogenic impacts on the environment (Haase et al. 2023). However, industrialization in emerging economies and climate change posed new challenges. Thus, the apparent slowdown in this period (rate: 0.55 species per year) may be misleading, as there are probably "extinction debts" to be paid, with species bound to be lost due to our past actions (Dudgeon and Strayer 2025).

4.5 | IUCN Red List Issues

To evaluate the accuracy and relevance of the IUCN's extinct fish dataset, an additional post-analysis comprehensive literature survey was carried out in December 2024 to track any updates in the conservation status of species since their initial assessment. This aimed to identify potential rediscoveries or reclassifications that would reflect changes in the latest data available for these species. One prominent example of this dynamic process is the rediscovery of the Giant featherback (*Chitala lopis*), which was found at its type locality in Java, with morphological and genetic evidence revealing that the species is more widespread across Java, Sumatra, and Borneo than previously believed (Wibowo et al. 2023). Another case in point involves the Maryland darter (*Etheostoma sellare*), which the IUCN has classified as extinct, but the United States Fish and Wildlife Service has retained the species on the Endangered Species List, citing insufficient evidence to confirm extinction. This uncertainty arises from the difficulty in detecting the species, underlining the challenges of monitoring species that may be rare or cryptic (Kilian et al. 2010). These examples emphasize the importance of resolving taxonomic uncertainties and the need for advanced genetic techniques (Hebert and Gregory 2005; Taberlet et al. 2018). Additionally, emerging technologies like environmental DNA sampling can provide novel tools for confirming species presence or absence with greater precision.

Given these complexities, revising a species' IUCN Red List status—whether "uplisting" or "downlisting,"—requires careful consideration. This process may need to incorporate criteria beyond the standard IUCN Red List metrics (Grace 2023). One such initiative is the "Green status" assessment, which aims to complement the Red List by evaluating species' conservation dependence (i.e., the potential for decline in the absence of conservation efforts) and their recovery potential (Grace et al. 2021; Grace 2023). Furthermore, some researchers advocate for a more comprehensive approach to conservation, challenging the species-centric focus that has historically dominated the field. These researchers propose an integrative strategy that considers various facets of biodiversity, such as taxonomic, phylogenetic, as well as importantly, functional diversity (Su et al. 2021). This more holistic framework may better capture the complexities of biodiversity loss and inform conservation strategies that promote ecosystem resilience across multiple scales.

A critical limitation of the IUCN Red List's threat classification scheme (version 3.3, December 2022) lies in its broad categorization. These categories, which are largely based on expert judgment, introduce a degree of subjectivity, creating potential uncertainties in the assessment. This broad approach can obscure the specific anthropogenic pressures that are driving species extinctions and, at the same time, may underrepresent the overarching role of climate change, which exacerbates virtually all abiotic and biotic pressures. Climate change-related factors are particularly challenging to attribute directly and specifically to species declines, which further complicates their representation in the current system. Although additional information can be recorded for each identified threat—such as timing (i.e., whether the threat is past, ongoing, or future), scope (i.e., the extent of the population affected), and severity (i.e., the level of impact)—only the timing element is required by the minimum documentation standards, while scope and severity remain optional. Prior to the 2022-2 Red List update, IUCN applied a scoring system to quantify these variables and report their impacts. However, due to concerns about the scientific robustness of these scores, IUCN suspended their use, pending a review of the methodology for assigning threats and calculating their effects. As a result, the current classification lacks a standardized approach to assess the severity of different threats/extinction drivers, further limiting its utility in guiding conservation strategies. This lack of precision in assigning causality hinders the development of targeted conservation interventions. Without clear and consistent threat classifications, it becomes difficult to design effective, species-specific conservation actions that directly address the most impactful drivers of extinction. To improve the situation, it is essential to refine the classification of extinction drivers through more sophisticated, data-driven approaches. This could involve species-specific threat modeling, standardized threat assessment metrics, and a deeper integration of ecological and socioeconomic data (Jarić et al. 2019). Such advancements would allow for better-tailored conservation strategies that can more effectively mitigate the primary threats contributing to freshwater fish extinctions at regional and global levels (Palacio et al. 2023).

4.6 | Conservation Lessons Learned

This study, which focuses on EX and EW freshwater fish species, emphasizes the complex and multifaceted nature of extinction processes in freshwater ecosystems. It emphasizes the importance of adopting integrated conservation strategies that can effectively address the multiple, interconnected threats that contribute to species loss. The overrepresentation of NSM, POL, and INV as both primary and combined drivers highlights the severe, ongoing impacts that these human-induced factors have on freshwater biodiversity (Su et al. 2021; Sayer et al. 2025). Given the significant role that these threats play, conservation efforts must focus on proactively mitigating their impacts. This includes tackling habitat degradation, reducing pollution, and controlling the spread of invasive species. At the same time, it is critical to prepare for emerging risks, such as those driven by climate change and the introduction of new pollutants, which could exacerbate the pressures on already vulnerable freshwater species (Reid et al. 2019; Tickner et al. 2020; Dudgeon and Strayer 2025).

The ongoing declines and extinctions of freshwater fishes during the Anthropocene necessitate a global, hybrid approach to freshwater system management, bringing together experts from various fields of freshwater biodiversity and conservation (Darwall et al. 2018). This approach requires managing freshwater ecosystems not only as providers of essential services—such as sustainable agriculture and fisheries—but also as critical biodiversity hotspots that need to be preserved for future generations.

Effective conservation strategies must include a combination of approaches, that is, environmental flow regulations (Arthington et al. 2018) essential for maintaining the ecological balance and health of freshwater habitats and habitat restoration efforts (Bellmore et al. 2017; Reid et al. 2019; Bănăduc et al. 2022; Piczak et al. 2023) helping rebuild ecosystems that have been damaged by human activities. Furthermore, better-designed and more effectively implemented protected areas should specifically include freshwater ecosystems, ensuring long-term conservation and fostering biodiversity resilience (Moberg et al. 2024).

Addressing the global loss of freshwater biodiversity requires the development of more robust international agreements and policies that facilitate coordinated action across nations and regions. These efforts should prioritize the strict protection of relatively pristine freshwater habitats, while also implementing aggressive restoration interventions that target threatened species, critical habitats and even entire ecosystems. Conservation translocations and reintroductions, guided by strict scientific protocols, along with ex situ breeding programs, must become urgent priorities for species in rapid decline. Moreover, bold initiatives for habitat restoration employing an ecosystemic approach are essential for restoring both the biotic and abiotic integrity of freshwater ecosystems. This comprehensive restoration effort may be one of the few viable paths to reversing the trend of global freshwater biodiversity loss and "bending the curve" of extinction (Tickner et al. 2020; Dudgeon and Strayer 2025). To support such large-scale initiatives, there is also a crucial need for enhanced funding strategies. Thus, innovative financial mechanisms must be developed to support effective biodiversity conservation initiatives, ensuring that these efforts are not solely reliant on resources like the IUCN Red List (Palacio et al. 2023). Additionally, such strategies can provide direction to governmental bodies and help them implement policies that align with global conservation goals (Maasri et al. 2022).

There are several significant obstacles that could hinder future efforts to reverse biodiversity loss in freshwater ecosystems (Arthington et al. 2018; Piczak et al. 2023; Dudgeon and Strayer 2025). One of the primary challenges is the lack of sufficient data or the inaccessibility of existing data. This issue can be addressed, albeit partially, by tools that incorporate uncertainty into decision-making, highlighting the need for greater investment in quantitative research and the continuous monitoring of freshwater species (López-Gamero et al. 2011; Tydecks et al. 2019; Hemming et al. 2022). Additionally, the integration of artificial intelligence tools could accelerate data mining and assessments, enabling faster analysis and supporting more holistic approaches to freshwater conservation. Life Cycle Assessment tools could also provide valuable insights by measuring the comparative environmental footprint of various sectors and activities impacting freshwater diversity.

Another critical challenge is the underfunding of freshwater efforts, a problem that is particularly pronounced in this sector (Birnie-Gauvin et al. 2023), often compounded by conflicting priorities among different agencies and stakeholders. To address it, future conservation interventions must incorporate socioeconomic factors and foster a close collaboration between scientists, managers, and local communities. Engaging local stakeholders in decision-making processes is essential for ensuring that conservation schemes are equitable and locally relevant. In addition, political barriers present a major obstacle, as economic development often takes precedence over environmental conservation, with both policymakers and the general public lacking sufficient awareness of the threats facing freshwater biodiversity (Cooke et al. 2013). Increasing exposure to the value of freshwater ecosystems through diverse communication channels is a promising approach toward raising public awareness and appreciation for these habitats. This, in turn, can build the political will needed to implement and enforce appropriate conservation policies (He et al. 2021; Cooke et al. 2013). Enhanced public understanding and political engagement can also catalyze a shift in governance frameworks, recognizing freshwater ecosystems as unique and critical components of global environmental governance, which have historically been sidelined in comparison to terrestrial and marine ecosystems (Tickner et al. 2020; but see Cooke et al. 2023).

A final critical issue worth addressing involves some challenging questions that a devil's advocate might raise. For instance, one could ask: "*Why should we care about the extinction of freshwater fishes? Do all species have the same ecological importance, or are some extinctions more harmful than others? Could freshwater ecosystem services be substituted by replacing native species with non-native ones for fisheries?*" Moreover, *is it realistic to focus on freshwater fish conservation when there are other urgent global issues, such as food security, health crises and climate change?"* Indeed, the devil's advocate position raises important questions, but when examined closely, these arguments fail to account for the deep ecological, ethical, and socioeconomic consequences of species loss. The idea that freshwater fish extinctions do not matter, or that non-native species can simply replace the lost ones, overlooks critical elements of ecosystem functioning and the broader implications for human societies. From an ecological standpoint, each species plays a unique and essential role in maintaining ecosystem balance. The extinction of even one species can have cascading effects that disrupt the entire system (Dudgeon et al. 2006; Closs et al. 2016; Lee et al. 2023). Ethically, the intrinsic value of species cannot be ignored. Every species has a right to exist, regardless of its direct utility to humans. This ethical standpoint asserts that species should not be valued only based on their short-term economic or functional benefit but also for their place in the broader web of life. Even from a utilitarian perspective, the loss of species is a costly affair. Each extinction eliminates a potential genetic resource and an irreplaceable part of biodiversity that could have provided invaluable insights into medicine, biotechnology, or ecosystem resilience (Foret et al. 2008). The genetic diversity within species forms the foundation of long-term ecological adaptability, which is increasingly crucial in the face of climate change and other environmental stressors. The argument that non-native species can replace native species for fisheries is not only ecologically misguided but also economically hazardous. While it is true that certain non-native species, like the Nile perch (*Lates niloticus*) in Lake Victoria, may offer short-term economic benefits, their introduction often leads to severe long-term ecological disruptions. The Nile perch's introduction to Lake Victoria, for example, led to the decimation of numerous endemic fish species, destabilizing the ecosystem and ultimately threatening the very fisheries it was supposed to enhance (Aloo et al. 2017). Thus, non-native species may initially appear to provide a functional substitute, but they often become invasive, outcompeting native species and degrading habitats. Their population booms can destabilize ecosystems, and their sudden crashes often lead to the collapse of fisheries, leaving communities dependent on these resources worse off.

Furthermore, dismissing the significance of even a small percentage of species extinctions, such as the argument that "*0.5% of freshwater species extinctions can be ignored since 99.5% have survived*" is a dangerous oversimplification. The sheer number of extinctions may seem small in a quantitative sense, but the impact on ecosystem health is disproportionately large. Freshwater fish species are often highly specialized, and their loss can have far-reaching consequences for ecosystem function and resilience. Moreover, the timeline of extinction—just 165 years—highlights the alarming speed at which biodiversity is being lost, something that is unprecedented in evolutionary terms.

In conclusion, the devil's advocate argument dismisses the complexity of freshwater biodiversity loss and its profound implications for ecosystems and human societies. The loss of freshwater fish species is not just a matter of numbers or economic considerations; it is an urgent ecological, ethical, and socioeconomic issue. To ignore this loss is to risk further destabilization of vital ecosystem services that humans rely on, such as clean water, food security, and climate regulation. Thus, addressing freshwater biodiversity loss must remain a priority, and any arguments that attempt to trivialize or dismiss this issue are ultimately flawed and shortsighted.

Author Contributions

Leonidas Vardakas: conceptualization, data curation, formal analysis, investigation, methodology, supervision, validation, visualization, writing – original draft, writing – review and editing. **Costas Perdikaris:** conceptualization, investigation, writing – original draft, writing – review and editing. **Jörg Freyhof:** validation, writing – review and editing. **Brian Zimmerman:** validation, writing – review and editing. **Matthew Ford:** data curation, validation, writing – original draft, writing – review and editing. **Konstantinos Vlachopoulos:** formal analysis, methodology, visualization, writing – review and editing. **Nicholas Koutsikos:** data curation, investigation, methodology, writing – review and editing. **Ioannis Karaouzas:** validation, writing – review and editing. **Maria Chamoglou:** data curation, investigation, methodology, validation, writing – review and editing. **Eleni Kalogianni:** conceptualization, methodology, supervision, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15342655 (Dataset) and https://doi.org/10.5281/zenodo.15343457 (Model). Species extinction status, anthropogenic pressures, and spatial range data were primarily obtained from the IUCN Red List of Threatened Species at https://www.iucnredlist.org. Habitat classification followed the IUCN Habitats Classification Scheme, Version 3.1 at https://www.iucnredlist.org/resources/habitat-classification-scheme. Supplementary species-level trait data were obtained from FishBase at https://www.fishbase.org.

References

Aloo, P. A., J. Njiru, J. S. Balirwa, and C. S. Nyamweya. 2017. "Impacts of Nile Perch, *Lates Niloticus*, Introduction on the Ecology, Economy and Conservation of Lake Victoria, East Africa." *Lakes & Reservoirs: Research and Management* 22: 320–333. https://doi.org/10.1111/lre.12192.

Arthington, A. H., A. Bhaduri, S. E. Bunn, et al. 2018. "The Brisbane Declaration and Global Action Agenda on Environmental Flows (2018)." *Frontiers in Environmental Science* 6: 45. https://doi.org/10.3389/fenvs.2018.00045.

Bănăduc, D., V. Simić, K. Cianfaglione, et al. 2022. "Freshwater as a Sustainable Resource and Generator of Secondary Resources in the 21st Century: Stressors, Threats, Risks, Management and Protection Strategies, and Conservation Approaches." *International Journal of Environmental Research and Public Health* 19, no. 24: 16570. https://doi.org/10.3390/ijerph192416570.

Barnosky, A. D., N. Matzke, S. Tomiya, et al. 2011. "Has the Earth's Sixth Mass Extinction Already Arrived?" *Nature* 471, no. 7336: 51–57. https://doi.org/10.1038/nature09678.

Bellmore, J. R., J. J. Duda, L. S. Craig, et al. 2017. "Status and Trends of Dam Removal Research in the United States." *Wiley Interdisciplinary Reviews: Water* 4, no. 2: e1164. https://doi.org/10.1002/wat2.1164.

Birnie-Gauvin, K., A. J. Lynch, P. A. Franklin, et al. 2023. "The RACE for Freshwater Biodiversity: Essential Actions to Create the Social Context for Meaningful Conservation." *Conservation Science and Practice* 5, no. 4: e12911. https://doi.org/10.1111/csp2.12911.

Bocchi, F., A. Bokulich, L. C. Brache, G. Grand-Pierre, and A. Watkins. 2022. "Are we in a Sixth Mass Extinction? The Challenges of Answering and Value of Asking." *British Journal for the Philosophy of Science*. https://doi.org/10.1086/722107.

Burkhead, N. M. 2012. "Extinction Rates in North American Freshwater Fishes, 1900–2010." *Bioscience* 62, no. 9: 798–808. https://doi.org/10.1525/bio.2012.62.9.5.

Cao, L., W. H. Shao, W. J. Yi, and E. Zhang. 2024. "A Review of Conservation Status of Freshwater Fish Diversity in China." *Journal of Fish Biology* 104, no. 2: 345–364. https://doi.org/10.1111/jfb.15606.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. "Accelerated Modern Human–Induced Species Losses: Entering the Sixth Mass Extinction." *Science Advances* 1, no. 5: e1400253. https://doi.org/10.1126/sciadv.1400253.

Ceballos, G., P. R. Ehrlich, and P. H. Raven. 2020. "Vertebrates on the Brink as Indicators of Biological Annihilation and the Sixth Mass Extinction." *Proceedings of the National Academy of Sciences* 117, no. 24: 13596–13602. https://doi.org/10.1073/pnas.1922686117.

Ceballos, G., A. García, and P. R. Ehrlich. 2010. "The Sixth Extinction Crisis: Loss of Animal Populations and Species." *Journal of Cosmology* 8, no. 1821: 31.

Chichorro, F., A. Juslén, and P. Cardoso. 2019. "A Review of the Relation Between Species Traits and Extinction Risk." *Biological Conservation* 237: 220–229. https://doi.org/10.1016/j.biocon.2019.07.001.

Closs, G. P., P. L. Angermeier, W. R. Darwall, and S. R. Balcombe. 2016. "Why Are Freshwater Fish So Threatened?" In *Conservation of Freshwater Fishes. Conservation Biology*, edited by G. P. Closs, M. Krkosek, and J. D. Olden, vol. 2015, 37–75. Cambridge University Press. https://doi.org/10.1017/CBO9781139627085.

Contreras-Balderas, S., P. Almada-Villela, M. de Lourdes Lozano-Vilano, and M. García-Ramírez. 2002. "Freshwater Fish at Risk or Extinct in Mexico." *Reviews in Fish Biology and Fisheries* 12: 241–251. https://doi.org/10.1023/A:1025053001155.

Cooke, S. J., N. W. R. Lapointe, E. G. Martins, et al. 2013. "Failure to Engage the Public in Issues Related to Inland Fishes and Fisheries: Strategies for Building Public and Political Will to Promote Meaningful

Conservationa." *Journal of Fish Biology* 83, no. 4: 997–1018. https://doi.org/10.1111/jfb.12222.

Cooke, S. J., M. L. Piczak, E. A. Nyboer, et al. 2023. "Managing Exploitation of Freshwater Species and Aggregates to Protect and Restore Freshwater Biodiversity." *Environmental Reviews* 32, no. 3: 414–437. https://doi.org/10.1139/er-2022-0118.

Cowie, R. H., P. Bouchet, and B. Fontaine. 2022. "The Sixth Mass Extinction: Fact, Fiction or Speculation?" *Biological Reviews* 97, no. 2: 640–663. https://doi.org/10.1111/brv.12816.

Danet, A., X. Giam, J. D. Olden, and L. Comte. 2024. "Past and Recent Anthropogenic Pressures Drive Rapid Changes in Riverine Fish Communities." *Nature Ecology & Evolution* 8, no. 3: 442–453. https://doi.org/10.1038/s41559-023-02271-x.

Darwall, W., V. Bremerich, A. De Wever, et al. 2018. "The Alliance for Freshwater Life: A Global Call to Unite Efforts for Freshwater Biodiversity Science and Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 1015–1022. https://doi.org/10.1002/aqc.2958.

Darwall, W. R. T., and J. Freyhof. 2016. "Lost Fishes, Who Is Counting? The Extent of the Threat to Freshwater Fish Biodiversity." In *Conservation of Freshwater Fishes*, edited by G. P. Closs, M. Krkosek, and J. D. Olden, 1–36. Cambridge University Press.

Davies, R. G., C. D. L. Orme, V. Olson, et al. 2006. "Human Impacts and the Global Distribution of Extinction Risk." *Proceedings of the Royal Society B: Biological Sciences* 273, no. 1598: 2127–2133. https://doi.org/10.1098/rspb.2006.3551.

del Monte-Luna, P., M. Nakamura, A. Vicente, et al. 2023. "A Review of Recent and Future Marine Extinctions." *Cambridge Prisms: Extinction* 1: e13. https://doi.org/10.1017/ext.2023.11.

Dias, M. S., P. A. Tedesco, B. Hugueny, et al. 2017. "Anthropogenic Stressors and Riverine Fish Extinctions." *Ecological Indicators* 79: 37–46. https://doi.org/10.1016/j.ecolind.2017.03.053.

D'Odorico, P., K. F. Davis, L. Rosa, et al. 2018. "The Global Food-Energy-Water Nexus." *Reviews of Geophysics* 56, no. 3: 456–531. https://doi.org/10.1029/2017RG000591.

Dudgeon, D. 2019. "Multiple Threats Imperil Freshwater Biodiversity in the Anthropocene." *Current Biology* 29, no. 19: R960–R967. https://doi.org/10.1016/j.cub.2019.08.002.

Dudgeon, D., A. H. Arthington, M. O. Gessner, et al. 2006. "Freshwater Biodiversity: Importance, Threats, Status and Conservation Challenges." *Biological Reviews* 81, no. 2: 163–182. https://doi.org/10.1017/s1464793105006950.

Dudgeon, D., and D. L. Strayer. 2025. "Bending the Curve of Global Freshwater Biodiversity Loss: What Are the Prospects?" *Biological Reviews* 100, no. 1: 205–226. https://doi.org/10.1111/brv.13137.

Ford, M. 2024. "Salvelinus Profundus. The IUCN Red List of Threatened Species 2024: e.T135539A137333942." https://doi.org/10.2305/IUCN.UK.2024-2.RLTS.T135539A137333942.en.

Foret, E., B. Chapelet, Y. Vitasse, M. Tilquin, B. Touzard, and R. Michalet. 2008. "The Relative Importance of Disturbance and Environmental Stress at Local and Regional Scales in French Coastal Sand Dunes." *Journal of Vegetation Science* 19, no. 4: 493–502. https://doi.org/10.3170/2008-8-18392.

Fricke, R., W. N. Eschmeyer, and J. D. Fong. 2025. "Species by Family/Subfamily." Accessed January 7, 2025. http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp.

Funge-Smith, S., and A. Bennett. 2019. "A Fresh Look at Inland Fisheries and Their Role in Food Security and Livelihoods." *Fish and Fisheries* 20, no. 6: 1176–1195. https://doi.org/10.1111/faf.12403.

Giannetto, D., and D. Innal. 2021. "Status of Endemic Freshwater Fish Fauna Inhabiting Major Lakes of Turkey Under the Threats of Climate Change and Anthropogenic Disturbances: A Review." *Watermark* 13, no. 11: 1534. https://doi.org/10.3390/w13111534.

Gillespie, R. G., E. M. Claridge, and S. L. Goodacre. 2008. "Biogeography of the Fauna of French Polynesia: Diversification Within and Between a Series of Hot Spot Archipelagos." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 363, no. 1508: 3335–3346. https://doi.org/10.1098/rstb.2008.0124.

Grace, M. 2023. "Assessing Species Conservation Status: The IUCN Red List and Green Status of Species." In *The Living Planet: The State of the World's Wildlife*, edited by N. Maclean, 333–348. Cambridge University Press. https://doi.org/10.1017/9781108758826.019.

Grace, M. K., H. R. Akçakaya, E. L. Bennett, et al. 2021. "Testing a Global Standard for Quantifying Species Recovery and Assessing Conservation Impact." *Conservation Biology* 35, no. 6: 1833–1849. https://doi.org/10.1111/cobi.13756.

Haase, P., D. E. Bowler, N. J. Baker, et al. 2023. "The Recovery of European Freshwater Biodiversity Has Come to a Halt." *Nature* 620, no. 7974: 582–588. https://doi.org/10.1038/s41586-023-06400-1.

He, F., S. C. Jähnig, A. Wetzig, and S. D. Langhans. 2021. "More Exposure Opportunities for Promoting Freshwater Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 31, no. 12: 3626–3635. https://doi.org/10.1002/aqc.3725.

Hebert, P. D., and T. R. Gregory. 2005. "The Promise of DNA Barcoding for Taxonomy." *Systematic Biology* 54, no. 5: 852–859. https://doi.org/10.1080/10635150500354886.

Hemming, V., A. E. Camaclang, M. S. Adams, et al. 2022. "An Introduction to Decision Science for Conservation." *Conservation Biology* 36, no. 1: e13868. https://doi.org/10.1111/cobi.13868.

Holmlund, C. M., and M. Hammer. 1999. "Ecosystem Services Generated by Fish Populations." *Ecological Economics* 29, no. 2: 253–268. https://doi.org/10.1016/S0921-8009(99)00015-4.

Hulme, P. E. 2009. "Trade, Transport and Trouble: Managing Invasive Species Pathways in an Era of Globalization." *Journal of Applied Ecology* 46: 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x.

Hutchings, J. A., R. A. Myers, V. B. García, L. O. Lucifora, and A. Kuparinen. 2012. "Life-History Correlates of Extinction Risk and Recovery Potential." *Ecological Applications* 22, no. 4: 1061–1067. https://doi.org/10.1890/11-1313.1.

Irwin, A., A. Geschke, T. M. Brooks, J. Siikamaki, L. Mair, and B. B. N. Strassburg. 2022. "Quantifying and Categorising National Extinction-Risk Footprints." *Scientific Reports* 12: 5861. https://doi.org/10.1038/s41598-022-09827-0.

Jarić, I., R. J. Lennox, G. Kalinkat, G. Cvijanović, and J. Radinger. 2019. "Susceptibility of European Freshwater Fish to Climate Change: Species Profiling Based on Life-History and Environmental Characteristics." *Global Change Biology* 25: 448–458. https://doi.org/10.1111/gcb.14518.

Kilian, J., R. Raesly, T. Jones, and A. Moser. 2010. *Surveys for the Endangered Maryland Darter (August 2008–September 2010)*. Final report submitted to US Fish and Wildlife Service, Chesapeake Field Office.

Lee, M., Y. Kim, D. Nam, and K. Cho. 2023. "Impacts of the Accumulated Extinction of Endangered Species on Stream Food Webs." *Global Ecology and Conservation* 48: e02747. https://doi.org/10.1016/j.gecco.2023.e02747.

López-Gamero, M. D., J. F. Molina-Azorin, and E. Claver-Cortés. 2011. "Environmental Uncertainty and Environmental Management Perception: A Multiple Case Study." *Journal of Business Research* 64, no. 4: 427–435. https://doi.org/10.1016/j.jbusres.2010.11.009.

Lozano-Vilano, M. L., and M. De La Maza-Benignos. 2017. "Diversity and Status of Mexican Killifishes." *Journal of Fish Biology* 90, no. 1: 3–38. https://doi.org/10.1111/jfb.13186.

Luck, G. W., T. H. Ricketts, G. C. Daily, and M. Imhoff. 2004. "Alleviating Spatial Conflict Between People and Biodiversity." *Proceedings of the National Academy of Sciences* 101, no. 1: 182–186. https://doi.org/10.1073/pnas.2237148100.

Lynch, A. J., S. J. Cooke, A. M. Deines, et al. 2016. "The Social, Economic, and Environmental Importance of Inland Fish and Fisheries." *Environmental Reviews* 24, no. 2: 115–121. https://doi.org/10.1139/er-2015-0064.

Maasri, A., S. C. Jähnig, M. C. Adamescu, et al. 2022. "A Global Agenda for Advancing Freshwater Biodiversity Research." *Ecology Letters* 25, no. 2: 255–263. https://doi.org/10.1111/ele.13931.

McIntyre, P. B., C. A. Reidy Liermann, and C. Revenga. 2016. "Linking Freshwater Fishery Management to Global Food Security and Biodiversity Conservation." *Proceedings of the National Academy of Sciences* 113, no. 45: 12880–12885. https://doi.org/10.1073/pnas.1521540113.

Metillo, E. B., and C. O. Garcia-Hansel. 2016. "A Review on the Ecology and Biodiversity of Lake Lanao (Mindanao Is., The Philippines)." *IAMURE International Journal of Ecology and Conservation* 18, no. 1: 17–66. https://doi.org/10.7718/ijec.v18i1.1110.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. "Extinctions of North American Fishes During the Past Century." *Fisheries* 14, no. 6: 22–38. https://doi.org/10.1577/1548-8446(1989)014%3C0022:EONAFD%3E2.0.CO;2.

Moberg, T., R. Abell, N. Dudley, et al. 2024. *Designing and Managing Protected and Conserved Areas to Support Inland Water Ecosystems and Biodiversity*. IUCN. IUCN WCPA Technical Report Series No. 8. https://doi.org/10.2305/ZOKC6253.

Myers, N. 1990. "Mass Extinctions: What can the Past Tell us About the Present and the Future?" *Palaeogeography, Palaeoclimatology, Palaeoecology* 82, no. 1–2: 175–185. https://doi.org/10.1016/S0031-0182(12)80031-9.

Nelson, J. S., T. C. Grande, and M. V. H. Wilson. 2016. *Fishes of the World*. 5th ed. John Wiley and Sons. https://doi.org/10.1002/9781119174844.

Olden, J. D., Z. S. Hogan, and M. J. V. Zanden. 2007. "Small Fish, Big Fish, Red Fish, Blue Fish: Size-Biased Extinction Risk of the World's Freshwater and Marine Fishes." *Global Ecology and Biogeography* 16, no. 6: 694–701. https://doi.org/10.1111/j.1466-8238.2007.00337.x.

Palacio, R. D., M. Abarca, D. Armenteras, et al. 2023. "The Global Influence of the IUCN Red List can Hinder Species Conservation Efforts." *Authorea*. https://doi.org/10.22541/au.169945445.50394320/v1.

Piczak, M. L., D. Perry, S. J. Cooke, et al. 2023. "Protecting and Restoring Habitats to Benefit Freshwater Biodiversity." *Environmental Reviews* 32, no. 3: 438–456. https://doi.org/10.1139/er-2023-0034.

Pimm, S. L., C. N. Jenkins, R. Abell, et al. 2014. "The Biodiversity of Species and Their Rates of Extinction, Distribution, and Protection." *Science* 344, no. 6187: 1246752. https://www.science.org/doi/10.1126/science.1246752.

Pisani, D. J. 2003. "Federal Reclamation and the American West in the Twentieth Century." *Agricultural History* 77, no. 3: 391–419. http://www.jstor.org/stable/3745040.

Ramankutty, N., J. A. Foley, and N. J. Olejniczak. 2002. "People on the Land: Changes in Global Population and Croplands During the 20th Century." *Ambio: A Journal of the Human Environment* 31, no. 3: 251–257. https://doi.org/10.1579/0044-7447-31.3.251.

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94, no. 3: 849–873. https://doi.org/10.1111/brv.12480.

Reis, R. E., J. S. Albert, F. Di Dario, M. M. Mincarone, P. Petry, and L. A. Rocha. 2016. "Fish Biodiversity and Conservation in South America." *Journal of Fish Biology* 89, no. 1: 12–47. https://doi.org/10.1111/jfb.13016.

Ricciardi, A., and J. B. Rasmussen. 1999. "Extinction Rates of North American Freshwater Fauna." *Conservation Biology* 13, no. 5: 1220–1222. https://doi.org/10.1046/j.1523-1739.1999.98380.x.

Sayer, C. A., E. Fernando, R. R. Jimenez, et al. 2025. "One-Quarter of Freshwater Fauna Threatened With Extinction." *Nature* 638: 1–8. https://doi.org/10.1038/s41586-024-08375-z.

Stiassny, M. L. 1996. "An Overview of Freshwater Biodiversity: With Some Lessons From African Fishes." *Fisheries* 21, no. 9: 7–13. https://doi.org/10.1577/15488446(1996)021<0007:AOOFB>2.0.CO;2.

Su, G., M. Logez, J. Xu, S. Tao, S. Villéger, and S. Brosse. 2021. "Human Impacts on Global Freshwater Fish Biodiversity." *Science* 371, no. 6531: 835–838. https://doi.org/10.1126/science.abd3369.

Taberlet, P., A. Bonin, L. Zinger, and E. Coissac. 2018. *Environmental DNA: For Biodiversity Research and Monitoring*. Oxford University Press. https://doi.org/10.1093/oso/9780198767220.001.0001.

Taylor, W. W., D. M. Bartley, C. I. Goddard, N. J. Leonard, and R. Welcomme. 2016. *Freshwater, Fish and the Future: Proceedings of the Global Cross-Sectoral Conference*. Food and Agriculture Organization of the United Nations, Rome; Michigan State University, East Lansing; American Fisheries Society ISBN 978–92–5-109263-7.

Tedesco, P. A., T. Oberdorff, J. F. Cornu, et al. 2013. "A Scenario for Impacts of Water Availability Loss due to Climate Change on Riverine Fish Extinction Rates." *Journal of Applied Ecology* 50, no. 5: 1105–1115. https://doi.org/10.1111/1365-2664.12125.

Tickner, D., J. J. Opperman, R. Abell, et al. 2020. "Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan." *Bioscience* 70, no. 4: 330–342. https://doi.org/10.1093/biosci/biaa002.

Torres, A. G., R. D. I. I. Guerrero, S. S. Nacua, et al. 2020. "*Barbodes lanaoensis*. The IUCN Red List of Threatened Species 2020: e.T18892A90996974." https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T18892A90996974.en.

Tudi, M., H. Daniel Ruan, L. Wang, et al. 2021. "Agriculture Development, Pesticide Application and Its Impact on the Environment." *International Journal of Environmental Research and Public Health* 18, no. 3: 1112. https://doi.org/10.3390/ijerph18031112.

Tydecks, L., B. W. Ibelings, and K. Tockner. 2019. "A Global Survey of Freshwater Biological Field Stations." *River Research and Applications* 35, no. 8: 1314–1324. https://doi.org/10.1002/rra.3476.

Vonlanthen, P., D. Bittner, A. G. Hudson, et al. 2012. "Eutrophication Causes Speciation Reversal in Whitefish Adaptive Radiations." *Nature* 482, no. 7385: 357–363. https://doi.org/10.1038/nature10824.

Wibowo, A., H. Haryono, K. Kurniawan, et al. 2023. "Rediscovery of the Giant Featherback *Chitala Lopis* (Notopteridae) in Its Type Locality Resolves Decades of Taxonomic Confusion." *Endangered Species Research* 52: 285–301. https://doi.org/10.3354/esr01281.

Winemiller, K. O., P. A. U. L. Humphries, and B. J. Pusey. 2016. "Protecting Apex Predators. Conservation of Freshwater Fishes, 361-398." https://doi.org/10.1017/CBO9781139627085.013.

WWF. 2024. *Living Planet Report 2024 – A System in Peril*. WWF.

Zhang, H., M. Kang, L. Shen, et al. 2020. "Rapid Change in Yangtze Fisheries and Its Implications for Global Freshwater Ecosystem Management." *Fish and Fisheries* 21, no. 3: 601–620. https://doi.org/10.1111/faf.12449.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.