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RESEARCH ARTICLE

Threats of dams to the persistence of the world's freshwater fishes

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Abstract

Habitat fragmentation due to dams is a well-known threat to freshwater fish. Yet, the global consequences of fragmentation for the viability of freshwater fish populations are unknown. Here, we provide the first global assessment of the threats of dams to the persistence of freshwater fish species. We developed a global macroecological relationship between freshwater fish range size and body size and used this relationship to assess whether isolated range fragments are too small to support a species. Our assessment includes 7369 freshwater fish species and considers the effects of 31,780 dams globally. Furthermore, we performed a more detailed analysis of the threats of dams in Brazil, the greater Mekong region and the United States, using complementary national and regional data sets. Globally, more than half of the species analysed face extirpation in a part of their geographic range, with an average potential range loss of 3.3% (95%-range: 0%–31.8%) across all species analysed. For 74 fish species, occurring in Brazil, China, India, the Mekong basin, the United States, South-Africa and the East Adriatic Coast, more than 50% of their range is potentially lost. This includes 18 species threatened with extinction across their whole range. Our complementary regional analysis revealed that the potentially lost range increases by a factor of 2–4 when considering both large and small dams compared with considering only large dams (≥15 m), highlighting the need to establish more comprehensive global dam inventories. Our novel approach and global analysis identifies species at risk of extirpation as well as geographic hotspots of extirpation threat by dams, which can aid in establishing more effective strategies for global hydropower development and barrier removal efforts to optimise the trade-offs between biodiversity conservation and the socio-economic benefits of dams.

KEYWORDS
biodiversity, extinction threat, freshwater fishes, habitat fragmentation, hydropower, isolation, river management

1 | INTRODUCTION

The number of dams worldwide has rapidly increased in the past decades (Lehner et al., 2011; Zhang & Gu, 2023). Between 1970 and 2000, dam construction peaked globally due to targeted investments to generate renewable energy (Couto & Olden, 2018). Especially, developing countries in Africa, Asia and South America have been witnessing a strong and ongoing increase in dam construction since the second half of the 20th century (Zhang & Gu, 2023). A global increase of up to 70% in installed capacity of hydropower is predicted by mid-century, mostly in developing regions with unused large hydroelectric potential (Zarfl et al., 2015). These include highly biodiverse regions such as the Amazon, Mekong and Congo (Latrubesse et al., 2017; Winemiller et al., 2016).

While dams provide clear societal benefits, damming of rivers is also one of the main threats to freshwater biodiversity, notably through the alteration of natural flow and inhibition of migration and dispersal of species (Barbarossa et al., 2020; Herbert & Gelwick, 2003; Reid et al., 2019). Of all rivers longer than 1000 km, only 37% remain free flowing through their entire reach (Grill et al., 2019). The Living Planet Index (LPI) of migratory freshwater fishes shows an average population decline of 76% between 1970 and 2016, with habitat loss and modifications, particularly by dams, as major threats to these species (WWF, 2022). Not only large dams contribute to the threat; the cumulative impact of many small barriers on fish can be even larger than the impact of a few large barriers (Athayde et al., 2019; Barbarossa et al., 2020; Consuegra et al., 2021). Besides forming barriers for migrating fish, dams divide freshwater habitats into multiple fragments. The fragmentation of a species geographic range can influence its survival potential, as fragmented ranges may contain (sub)populations too small to survive (Cardillo et al., 2008; Di Marco et al., 2015; IUCN Standards and Petitions Committee, 2022).

Several studies have quantified the threats of fragmentation by dams to freshwater fish species, using various approaches and indicators and at different scales. For example, the impact of dams on geographic range connectivity has been studied at both basin and global scales (e.g., Barbarossa et al., 2020; Rodeles et al., 2020; van Puijenbroek et al., 2019). Connectivity is typically quantified with metrics indicating how well a species' range is connected. However, geographic range connectivity is not directly indicative of the extent to which dams may threaten the persistence of a species. Quantifying extinction threat by dams requires identifying which range fragments are potentially lost because they are too small to support viable species populations. This approach has been applied to specific basins, including the Magdalena basin in Colombia (Carvajal-Quintero et al., 2017) and the six major Andean Amazon basins (primary headwater areas of the Amazon River; Herrera et al., 2020). These studies relied on a macroecological relationship between range size and body size to determine the minimum viable range size (MVRS) of species, which can be used to determine whether range fragments isolated by dams are too small to support viable populations (Gaston & Blackburn, 1996). Expanding this approach to the entire globe would allow for a more comprehensive assessment of the threats of isolation by dams to freshwater fish species, which is essential to understand the global magnitude of threat by dams and identify species and regions most affected. This in turn can inform global strategies and prioritisation efforts for further hydropower development or restoration efforts through dam removal or the implementation of fish passes.

Here, we provide the first global assessment of the threats of river fragmentation to the persistence of freshwater fish species. We first developed a global macroecological relationship between freshwater fish range size and body size, conceptually building upon previous studies (e.g., Agosta & Bernardo, 2013; Brown & Maurer, 1987; Carvajal-Quintero et al., 2022). We then assessed for 7369 freshwater fish species whether isolated range fragments are too small to support the species, considering the effect of 31,780 existing dams derived from a global database (Zhang & Gu, 2023). As small dams are poorly represented in global georeferenced dam data sets (Couto & Olden, 2018), we also studied the additional impact of small dams compared with large dams using additional regional data sets from Brazil, the greater Mekong region and the United States. Our global species-level approach revealed species and regions most threatened by the isolation effects of river dams.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Species data

We retrieved data on extant geographic ranges referenced to HydroBASINS (customised with lakes, Pfafstetter level 8; Lehner & Grill, 2013) for 10,610 freshwater fish species from the International Union for the Conservation of Nature (IUCN, 2022). This represents 57% of the freshwater fish species currently known (~18,500; van der Laan, 2023). Regions best represented are Europe, Africa and many basins in North America, Southeast Asia and Oceania (Figure S1). As our analysis focusses on river dams, we selected species present in flowing water bodies. To this end, we classified each species as lentic (living in stagnant water bodies), lotic (living in flowing water bodies) or lenticlotic following the approach of Barbarossa et al. (2020). We labelled a species as lotic if the habitat description from the IUCN contained at least one of the words 'river', 'stream', 'creek', 'canal', 'channel', 'delta', 'estuaries', and as lentic if it contained 'lake', 'pool', 'bog', 'swamp' or 'pond'. If this information was not available, we flagged a species as lotic or lentic using habitat information from FishBase (Froese & Pauly, 2022), using the flags 'Streams' and 'Lakes', respectively. We then excluded species solely living in lentic environments. Based on species-specific information on habitat environment (freshwater, brackish, marine) and migration behaviour (we labelled a species flagged as diadromous using the flags 'amphidromous', 'amphidromous?', 'anadromous', 'catadromous' and 'diadromous') from FishBase, we further selected freshwater fish solely living in fresh waters, reasoning that the persistence of species migrating between marine and/or brackish waters and fresh water depends on the accessibility of their spawning grounds rather than range fragment size (Barbarossa et al., 2020). The data filtering steps resulted in a set of 8049 (partially or entirely) lotic fish species solely living in fresh waters with geographic range data available. Next, we retrieved species-specific information on maximum body length, required to establish a macroecological relationship for MVRS (see Section 2.2), from FishBase. We were able to obtain length data for 93% of the species remaining from the selection above, leaving 7457 species for further analysis (Figure S2). Taxonomic harmonisation across all databases was based on FishBase name validation.

2.1.2 | Dams data

For the global analysis, we retrieved location data of 31,780 dams worldwide from the Global Dam Tracker (GDAT; Zhang & Gu, 2023), which is the most comprehensive geo-referenced global dam database to date. Compared with other global dam data sets, GDAT shows improved coverage in Africa, Asia and South America (Zhang & Gu, 2023). It contains locations of about one-third of the large dams existing across the globe (ICOLD, 2020), and of 11,674 small dams (height <15 m). However, according to a global synthesis of energy policy, there are at least 82,891 small hydropower dams operating or under construction globally (Couto & Olden, 2018). This suggests that the global dam database is incomplete, especially for smaller dams.

To better understand the threats due to small dams, we selected three regions with more detailed national or regional data available, that is, the United States, Brazil and the greater Mekong region. For the United States, we retrieved 91,609 dams from the National Inventory of Dams (NID; USACE, 2023). We excluded dams with the purpose of fire protection, stock, small fishpond, debris control or tailings, as these are likely located off-stream. The remaining 74,310 dams include 68,185 small dams. For Brazil, we retrieved data on 498 large dams and 2076 small hydropower dams from the Brazilian energy agency ANEEL (2020). For the greater Mekong region (Mekong-Irrawaddy-Salween hydrologic basins), we retrieved data on 1005 dams from Open Development Mekong (2020). From these, we selected existing dams or dams under construction, resulting in 229 large and 543 small dams. We merged the data sets for each of these three regions with the GDAT data for the same region and then split the three resulting dam data sets into small and large dams, based on a height threshold of 15 m (ICOLD, 2020).

Following the approach of Barbarossa et al. (2020) to identify fragments separated by dams, we referenced dams to the downstream boundary of the encompassing HydroBASINS subbasin (Pfafstetter level 12). This ensures that duplicate dams, which may arise after merging the regional and GDAT data, are translated into a single barrier.

2.2 | Determining MVRS

Following previous studies (Agosta & Bernardo, 2013; Carvajal-Quintero et al., 2022), we determined the MVRS of species based on a macroecological relationship between range size and body size. The lower bound of this relationship represents MVRS as a function of body size, below which species have heightened extinction risk (Gaston & Blackburn, 1996). This lower limit may contain a break point around the modal ('optimal') body size, as revealed by Agosta and Bernardo (2013). For species smaller than the mode, MVRS decreases with body size, while for species larger than the mode, MVRS increases with body size. The breakpoint reflects a transition in the energetics of body size (Agosta & Bernardo, 2013; Brown & Maurer, 1989). More specifically, the negative relationship between MVRS and body size for species smaller than the modal body size reflects that smaller species have higher mass-specific energy demands and are limited by the rate of resource acquisition for reproduction, meaning they require larger areas to persist. On the right side of the modal body size, the relationship is positive because larger species have larger absolute energy requirements and the rate of conversion of resources into viable offspring is limiting. They therefore need larger areas to persist. The trade-off between the two constraints of energy acquisition and conversion mechanisms results in an optimal body size around the mode, where space requirements are minimised (Brown et al., 1993; Brown & Maurer, 1989).

For our assessment, we established a novel global macroecological relationship between MVRS and body size for freshwater fish species by relating the species' range size within a hydrological basin, that is, part of land draining to the ocean or an internal sink, to the species body length. We based our relationship on the range size per hydrological basin, assuming exchange of individuals between subbasins but not between hydrological basins. Thus, we assume that the hydrological basin boundary acts as a physical space constraint, and that fragmentation by dams occurs within a hydrological basin. We do not account for natural barriers or discontinuities like waterfalls as physical constraints as these features develop over evolutionary timescales. Therefore, we assume a species to be either adapted to the feature or have undergone allopatric speciation resulting in different species on either side of the feature (Barbarossa et al., 2020; Kano et al., 2012). If a species occurs in multiple hydrological basins, we assume that the mean geographic range size across the basins is a representative global estimate of the species' basin-level range size, averaging out intra-species differences in basin-level range size due to inter-basin variability in ecological and evolutionary processes influencing geographic range size (Fine, 2015).

To derive the relationship between basin-level range size and body size, we excluded species classified as data-deficient and threatened by IUCN's Red List, as their current ranges may not adequately reflect the species' area needs (Carvajal-Quintero et al., 2022). Specifically, threatened species are characterised by declines or extreme fluctuations in distribution or abundance (IUCN Standards and Petitions Committee, 2022), indicating that their current extent of occurrence is not viable. Furthermore, we excluded hydrological basins defined as 'Coastal' by HydroBASINS, as for these basins the true physical boundary (of the species range) is uncertain as it changes with Pfafstetter level (i.e., depending on level, small coastal basins draining between large watersheds may or may not be lumped together; Lehner & Grill, 2013). We calculated the geographic range size of each fish species per hydrological basin only including species-basin combinations as confirmed by Tedesco et al. (2017), to prevent spatial or taxonomic errors in the IUCN data to bias the basin-level range size estimates. We further excluded species-basin combinations if a species was identified as non-native or extinct in that basin, according to Tedesco et al. (2017) and Su et al. (2021). This filtering resulted in the initial removal of 505 species as they did not occur in the Tedesco et al. (2017) data. The filtered data for retrieving the MVRS-body size relationship includes 4162 species (Figure S2), occurring across 1736 hydrological basins (area median = 3332 km^2, interquartile range = 13,343 km^2).

To define the macroecological relationship, we averaged the basin-specific range size estimates per species and related these mean values to the species body length. Following the procedure suggested by Blackburn et al. (1992) and used by Agosta and Bernardo (2013), we divided the data over equally sized body size bins, took the minimum geographic range size for each bin and fitted a least squares regression through these data on either side of the modal body length (6 cm). Because of the different number of observations and total body size range on either side of the mode, we set the bin width of small animals (length ≤ mode) to log 10[0.05] (16 size classes) and the bin width of large animals (length ≥mode) to log10[0.1] (17 size classes). Using the least square regression outcomes, we calculated the MVRS of each of the 7457 fish species with length data available.

2.3 | Impact of dams

To identify range fragments separated by dams, we used the approach of Barbarossa et al. (2020). First, we referenced the species range data to subbasins at the finest HydroBASINS resolution (Pfafstetter level 12; area median = 135 km^2, interquartile range = 64 km^2), which are nested within the subbasins of the original resolution (Pfafstetter level 8). Then, we determine isolated fragments of geographic ranges in the area upstream of a dam or the outlet/internal sink, connecting subbasins until the next upstream dam or hydrological basin boundary. Because information on passability, that is, whether a dam is equipped with infrastructure that allows (partial) up- or downstream movement, was typically unavailable, we considered all dams fully impassable.

To evaluate the extirpation threat of dams (i.e., whether isolated range fragments are too small to sustain a viable fish population), we compared the sizes of the species' range fragments to the MVRS of the species. Prior to the analysis, we excluded species ranges already smaller than the MVRS estimate without considering the effect of dams. This resulted in the exclusion of 88 species from the analysis, leaving 7369 species for the impact assessment (Figure S2). To summarise our results, we calculated the size (km^2) and proportion (%) of potentially lost range (PLR) for each species. Additionally, we calculated per subbasin the potentially affected fraction (PAF) of species to highlight hotspots of threat. Further, per hydrological basin we calculated the relative cumulative range loss (CRL, in %) as

$$\mathrm{CRL} = \frac{\sum_{i=1}^{n} \mathrm{PLR}\left(\mathrm{km}^2\right)}{\sum_{i=1}^{n} \mathrm{BGRS}\left(\mathrm{km}^2\right)} \times 100,$$

where n is equal to the number of species occurring in the basin, PLR is a species' potentially lost range within the basin, and BGRS is a species' geographic range size within the basin. We also assessed the number of species of which the entire range within that hydrological basin is potentially lost (PLR = 100% for the species' range within the basin of interest). Finally, to study the additional impact of small dams compared to large dams, we followed the same steps as for the global evaluation and compared the results when considering only large dams (height ≥15 m) to considering both large and small dams in Brazil, the greater Mekong region and the United States.

3 | RESULTS

3.1 | Body size—Range size relationship

Our analysis of the relationship between minimum basin-level range size and body size revealed that the regression lines on either side of the modal body length converge at the breakpoint (Figure 1), suggesting that the modal body size indeed represents a transition in rate-limiting processes from energy acquisition to energy conversion. For species larger than the modal body size, we observe a positive relationship between MVRS and body size. Thus, the larger the species, the more area needed to sustain a viable population. For species smaller than the mode we see the opposite pattern: the smaller the species the more area needed to sustain a viable population. Both relationships are significant ($p < .001$); the negative slope for small species is steeper (−1.98, 95% CI: [−2.99, −0.97]) than the positive slope for large species (1.42, 95% CI: [1.05, 1.79]).

3.2 | Potentially lost range

Of the 7369 species analysed, 72% (n = 5305) experience range fragmentation by the 31,780 dams considered. Of all species analysed, 53% (n = 3923) face local extinction in a part of their range due to range fragments not meeting the MVRS. On average across all species,

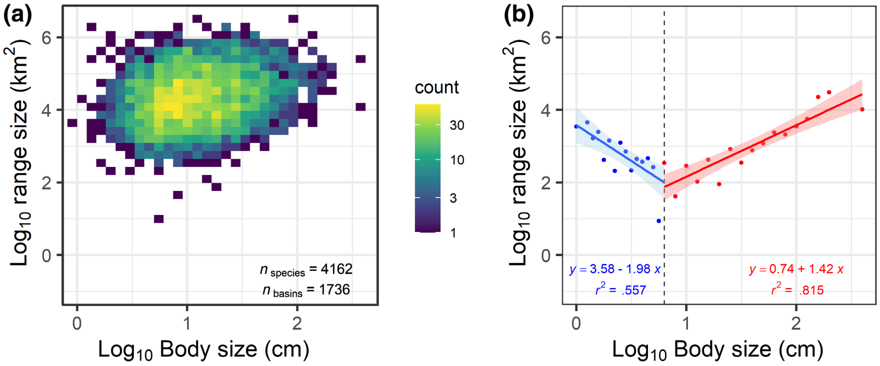

FIGURE 1 Empirical relationship between body size and range size. (a) Density plot of the observations. (b) The minimum observed range size in each body size class on either side of the modal body size (6 cm, dashed line). In blue species smaller than the mode, in red larger than the mode. Lines are lines-of-best-fit from ordinary least-squares regression with 95% CIs. Formula and r^2 of the regression lines are shown.

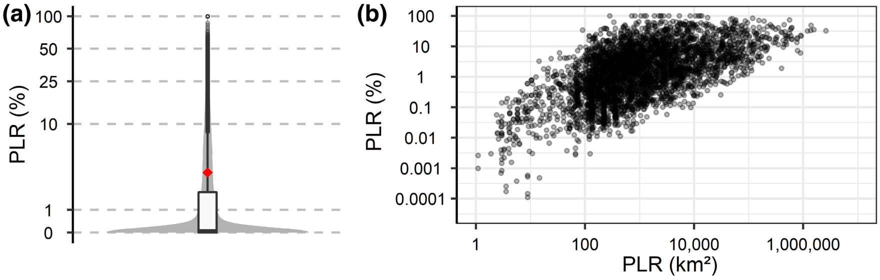

FIGURE 2 Potentially lost range (PLR) of freshwater fish species due to isolation by dams. (a) PLR relative to the total range across species (n = 7369). Box represents the interquartile range and the median, and whiskers the 95% interval. Dots show outliers. Red diamond represents the mean. Grey violin shows the values distribution. (b) Relative (%) versus absolute (km^2) PLR for the freshwater fish species with PLR >0 (n = 3923).

the PLR is 3.3% (95%-range: 0%–31.8%), corresponding with 8139 km^2 (95%-range: 0–58,971 km^2; Figure 2a). For 74 species, more than half of their range is threatened. These species occur in Brazil, China, India, the Mekong basin, the United States, South-Africa, Austria, France and the East Adriatic Coast. Among those are 18 species threatened with extinction across their entire range. These species occur in Brazil, India, China, South-Africa and Austria. We found a positive relationship between relative PLR and absolute PLR (Figure 2b), yet with a considerable spread, reflecting that a given relative PLR corresponds with a range in absolute PLR. Species with large absolute losses (>1,000,000 km^2, n = 5) occur in Southern Asia (*Channa marulius*, *Sperata aor* and *Cirrhinus mrigala*) and North America (*Pylodictis olivaris* and *Micropterus salmoides*). In some hydrological basins in Brazil, Europe, India, North America and South Africa more than half of the cumulative freshwater fish range in the basins is potentially lost (CRL >50%; Figure 3). In basins across the world, species are threatened with extinction (species PLR = 100% within that basin; Figure S3).

3.3 | Additional effect of small dams

To study the additional impact of small dams compared with large dams, we quantified fragmentation threats in Brazil, the greater Mekong region and the United States using only large dams (≥15 m) or both large and small dams (Figure 4).

In Brazil, the addition of small dams leads to an increase in PLR from 3.7% to 8.3%, corresponding with 1730–4232 km^2, on average across species (n = 1497). Particularly small dams in the Central-West, upstream in the Amazon, Tocantins and Parana river basins, contribute to this increase (Figures S4 and S5). The addition of small dams causes extra PLR for half of the species (n = 716) and more than doubles PLR for a third of the species (n = 520). For 19 species, small dams cause an extra potential range loss representing more than half of their total range. The addition of small dams causes potential extinction of six species (*Glanidium catharinensis*, *Cnesterodon omorgmatos*, *Hemiancistrus megalopteryx*, *Melanorivulus pinima*, *Hypostomus kuarup* and *Characidium satoi*) locally occurring in this region (total range size <1500 km^2).

Across the 617 species assessed in the greater Mekong region, average PLR increases from 2.7% to 5.6% of a species' range, corresponding with 5271–11,069 km^2, when including small dams. This is mostly due to small dams in the lower Mekong basin (Figures S6 and S7). The increase in PLR is highest in the Mekong basin (factor 2.3), followed by the Salween basin (factor 2.0) and the Irrawaddy basin (factor 1.4). For 394 species PLR increases, including 305 for which PLR more than doubles. *Probarbus labeamajor*, an endangered

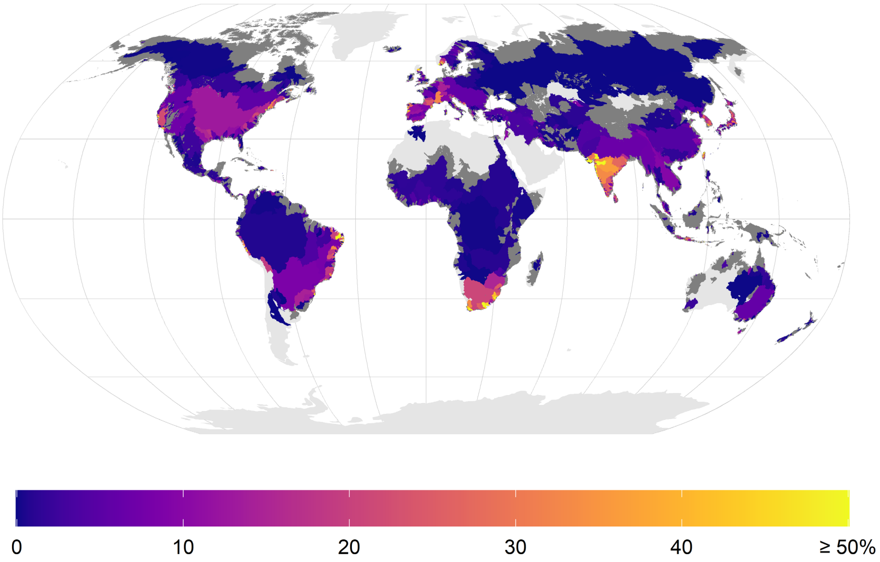

FIGURE 3 Cumulative range loss (CRL) due to isolation by dams. Basins without dams data in dark grey. Basins without species data in light grey.

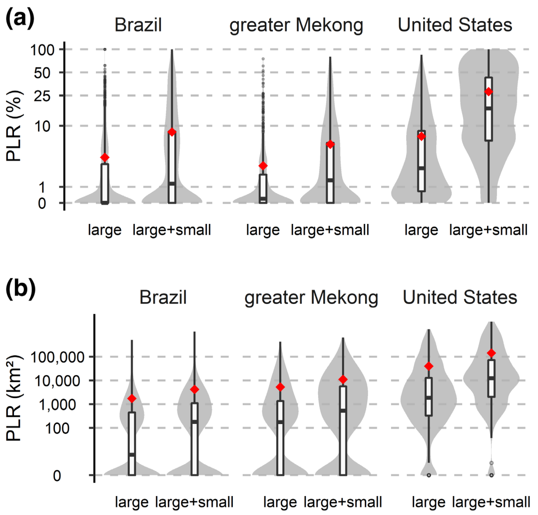

FIGURE 4 Additional effect of small dams, compared to only large dams, on potentially lost range (PLR) of freshwater fish in Brazil, the greater Mekong region and the United States. PLR is given in percentage of a species' range (a) or area (b). For each region, the comparison is made by considering only large dams (left) or both small and large dams (right). Box represents the interquartile range and the median, and whiskers the 95% interval. Dots show outliers. Red diamond represents the mean. Grey violin shows the values distribution.

fish species occurring in the Mekong, and *C. marulius*, a species of commercial importance, are affected most by the addition of small dams. They show highest relative (30%–55%) and absolute (430,453–640,226 km^2) increase in PLR, respectively, when including small dams.

For the United States, the addition of small dams leads to an increase in PLR from 7.2% to 28.1%, corresponding with 40,187–143,313 km^2, on average across the species ($n = 615$). The additional impact of small dams is mainly visible across the Mississippi basin, where the CRL triples (from 14% to 46%) when including small dams, and across basins in the South-West (Figures S8 and S9). Of all 615 species analysed, 590 experience additional PLR by small dams. For 76 species, the additional impact comprises more than half of their range. *Erimyzon tenuis* and *Ameiurus natalis* experience the highest relative (7%–94% PLR) and absolute (941,121–3,011,248 km^2 PLR) additional threat by small dams, respectively.

4 | DISCUSSION

In this study, we assessed the threat of river dams to the persistence of 7369 non-diadromous riverine fish species. We developed a novel global macroecological relationship between MVRS and body size for freshwater fishes and we used this relationship to provide the first global and species-level assessment of dam-related threats to freshwater fish persistence. Furthermore, we studied the additional impact of small dams compared with only large dams in Brazil, the greater Mekong region and the United States, capitalising on the availability of more detailed dam data sets for these regions.

Our novel global macroecological relationship showed a decrease in MVRS with body size for species smaller than the modal body size (slope: −1.98), and an increase in MVRS with body size for species larger than the mode (slope: 1.42; Figure 1). Such triangular relationships between minimum range size and body size have been uncovered across various geographic scales and taxonomic groups (Agosta & Bernardo, 2013; Brown & Maurer, 1987; Newsome et al., 2020), including fish (Carvajal-Quintero et al., 2017, 2022; Le Feuvre et al., 2016). For terrestrial mammals, Agosta and Bernardo (2013) also found a steeper slope for small species (−3.33) compared to large species (1.24). A similar positive slope (~1–1.5) for the lower bound was also found in Le Feuvre et al. (2016) studying Australian freshwater fish, and Carvajal-Quintero et al. (2022) studying freshwater fish from Nearctic, Palearctic and Australian realms. Intercepts may vary between studies due to differences in geographic scale. For example, our MVRS estimates are generally lower than those reported by Carvajal-Quintero et al. (2022), as we accounted for the hydrological basin as physical space constraint.

The accuracy of our MVRS estimates depends on the accuracy of the underlying data as well as underlying assumptions. Regarding the former, we acknowledge that our macroecological relationship is based on a minority of the freshwater fish species (4162 of ~18,500 species). If we assume that more abundant hence better-known species have larger ranges (Brown, 1984), this could imply that our relationship overestimates MVRS hence threats by dams. Considering the entire range within the basin rather than only the habitable part may also cause overestimation of MVRS (Ramesh et al., 2017). On the other hand, the basin-level range size estimates underlying our relationship might be smaller than viable, causing an underestimation of the MVRS. Finally, we note that if we fit the macroecological relationship without excluding non-native, introduced or extinct species, we find lower MVRS estimates for species larger than 6 cm and smaller than 2 cm (Figure 1; Figure S10). This may be due to the inclusion of possible inaccuracies in the IUCN data or be due to more small hydrological basins being included (8257 hydrological basins; area median = 1056 km^2, interquartile range = 2260 km^2). However, impact estimates based on this alternative relationship showed similar patterns (Figures S11 and S12).

Apart from data issues, we note that the accuracy of our MVRS estimates depends on the assumption that the minimum of mean basin-level range sizes for a given body size is indicative of the MVRS. Our global relationship between range size and body size may overestimate the MVRS in small basins where ecological and evolutionary processes may have led to a smaller MVRS or underestimate the MVRS in large basins. Furthermore, we acknowledge that river volume is likely more representative of the minimum space requirement of fish species than geographic range area. Future research may employ river volume instead of range area, though this is challenging as river volume varies through time and would need to be estimated at the spatial grain of the species data (HydroBASINS subbasins).

We found particularly large threats by dams to the fish diversity in basins in Brazil, India, China, South-Africa, the Mekong basin, the United States and parts of Europe. These regions harbour species with high relative and absolute potential range loss. Furthermore, more than half of the cumulative freshwater fish range is potentially lost in basins in these regions. We acknowledge that these findings are contingent on the data available on both freshwater fish species ranges and dams, hence include only a subset of all species and dams occurring in the basin (Figure S1). Nevertheless, our results point at relatively large threats of extirpation of freshwater fish species in these regions, which may increase by expected future dam construction (Moran et al., 2018; Zhang & Gu, 2023). Overall, the smaller the fragments created by damming, the higher the PAF of species (Figure S13; Carvajal-Quintero et al., 2017), highlighting the importance of strategic dam placement.

In general, our assessment may overestimate impacts by assuming dams are fully impassable. However, the mitigation effect of potentially present fish passes is selective for specific species and may even be harmful for some (Birnie-Gauvin et al., 2019; Silva et al., 2018). For many species, the effectiveness is unknown due to lack of monitoring and performance standards (O'Connor et al., 2022; Silva et al., 2018), pointing at a need for further investigations of the benefits of fish passes. On the other hand, incompleteness of the dam data set may lead to an underestimation of the threats. Comparison of our results with IUCN threat data highlights this issue, as 147 species in our analysis are threatened by dams according to the IUCN, yet occur exclusively in basins without dams according to our global dam dataset (Figure S14). Though GDAT is the most comprehensive global dam dataset to date, a comparison with other global dam datasets by Zhang and Gu (2023) revealed a substantial gap in each dataset. This highlights the need for a globally consistent and comprehensive dam database.

Our analyses for Brazil, the greater Mekong region and the United States revealed that the inclusion of small dams in addition to large dams in the analysis leads to an increase of the PLR of freshwater fish species by a factor 2–4 on average (Figure 4). Although our global analysis includes 11,674 small dams (height <15 m), a global synthesis revealed that there are at least 82,891 small hydropower dams operating or under construction (Couto & Olden, 2018). Small dams are thus underrepresented as georeferenced data is often lacking (Couto & Olden, 2018; Grill et al., 2019; Zhang & Gu, 2023). These findings further stress the importance of identifying and georeferencing dams, especially in regions with a potential massive increase in small dams for hydropower, such as Russia, China, India, and South America (Couto & Olden, 2018).

Fragmentation by dams can also be expressed in loss of connectivity between patches. Comparing the results of our analysis with species-specific connectivity index values from Barbarossa et al. (2020) reveals a moderate correlation (Figure S15; Spearman's rank correlation = −0.59, n = 4873). However, for some species, one indicator may indicate a large threat of dams while the other indicates small to no threat (Figure S15). Thus, species facing no threat of range loss due to fragmentation, might still be impacted by the loss of connectivity, particularly if this prevents migration to spawning grounds. Future refinements in our approach may include temporal access to habitats and temporal range shifts including migration within freshwaters of certain fish species, as this can influence the accessibility and suitability of range area, respectively. Furthermore, species may be threatened by additional and indirect impacts caused by dams, such as the alteration of flow and thermal regimes, and sediment and nutrient supply, which may all put additional pressure on freshwater species (Agostinho et al., 2008; Jellyman & Harding, 2012; Keppeler et al., 2022; Poff et al., 1997; Poff & Schmidt, 2016). These additional impact pathways may explain why 201 species without PLR in our study are indicated as threatened by large dams or dams of unknown size by the IUCN (Figure S14).

Our species-specific and high spatial resolution assessment (subbasin units of ~100 km^2) provides first hand insights into one of the fundamental negative effects of dams on (non-diadromous) freshwater fishes, i.e., potential extirpation due to the isolation of populations. The results of our global assessment can inform actors at the global science-policy interface on climate and biodiversity (e.g., via IPCC and IPBES). Our study further provides a scalable approach to assess the threats of dams to freshwater fish species persistence in any region of interest. For applications at national or regional scale, we recommend using the best dams data available, as illustrated by our applications to Brazil, the greater Mekong region, and the United States. Our approach identifies species most threatened by dams and geographic hotspots of extirpation threat, which can help freshwater biodiversity researchers, spatial planners and decision-makers evaluating the trade-offs between freshwater biodiversity conservation and the socio-economic benefits of dams. This, in turn, can aid in designing strategies for both hydropower development and barrier removal efforts (de Leaniz & O'Hanley, 2022).

AUTHOR CONTRIBUTIONS

Tamara Keijzer: Data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Valerio Barbarossa:** Conceptualization; methodology; supervision; writing – review and editing. **Alexandra Marques:** Methodology; supervision; writing – review and editing. **Juan D. Carvajal-Quintero:** Methodology; writing – review and editing. **Mark A. J. Huijbregts:** Methodology; supervision; writing – review and editing. **Aafke M. Schipper:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.24981228. The code used to perform the analyses described by this article is openly available in Zenodo at http://doi.org/10.5281/zenodo.10489590.

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

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