

<https://doi.org/10.1038/s43247-025-02467-y>

Widespread and strong impacts of river fragmentation by anthropogenic barriers on fishes in the Mekong River Basin



Jingrui Sun ^{1,2}✉, Damiano Baldan³, Martyn C. Lucas⁴, Jie Wang¹, Amaia A. Rodeles ⁵, Shams M. Galib ⁶, Juan Tao^{1,2}, Mingbo Li¹, Daming He¹ & Chengzhi Ding^{1,2}

The Mekong River, a global freshwater biodiversity hotspot, has suffered from intensive barrier construction, resulting in major challenges in safeguarding its fauna. Here, we provide a comprehensive evaluation of the impacts of river barriers on the distribution of 952 fish species in the Mekong River Basin. Our analysis revealed that 93% of Mekong fish species analysed suffer from habitat fragmentation, and species with larger habitat range requirements experienced higher river fragmentation impacts. Sub-basins along the main channel in the Lower Mekong had high values of species richness but relatively high barrier impacts. Across all migration types, freshwater-resident migratory (potamodromous) fishes were affected by the greatest levels of habitat fragmentation (Fragmentation Index, 42.45 [95% confidence interval, 38.61–46.62]). Among all International Union for Conservation of Nature conservation status categories, Critically Endangered species experienced the highest habitat fragmentation index (34.48 [19.46–53.52]). Among all barrier types in the Mekong, small dams and sluice gates contributed more to habitat fragmentation than large dams. While the effects of existing individual large dams on habitat fragmentation and fish distribution in the Mekong Basin are greater than for small barriers, the cumulative impacts of small barriers are greater; hence, basin-wide connectivity planning is needed for more effective conservation.

Freshwater systems occupy a small fraction of the Earth's surface but contribute disproportionately to global biodiversity due to the high number of species they host¹. Such biodiversity is threatened by several interacting pressures (e.g. land use change, climate change, flow alterations, loss of connectivity), resulting in strong declines worldwide^{2–6}. The loss of longitudinal connectivity in rivers, due to the construction of barriers, is a particularly relevant pressure^{7,8}. The dendritic structure of rivers renders them especially sensitive to habitat connectivity losses, as even a single barrier can isolate entire sections of the river network^{9–11}. When multiple barriers are placed on a river system, the result is a sequence of isolated sections where the movement of water, sediments, energy and organisms is impeded¹². Fragmented rivers are widespread^{7,13}, and are expected to further increase in the future due to the global proliferation of dams under construction and planned^{14,15}.

Riverscape fragmentation impacts the geographic distribution of fish biodiversity. Due to the presence of barriers, potamodromous and diadromous species may be prevented from reaching habitats that are necessary for the completion of their life cycles^{16–19}. Even non-migratory fish species are exposed to local extinctions if they occupy isolated river fragments which do not offer enough habitat to support viable populations and prevent rescue effects from neighboring populations^{15,20}. As a result, river habitat fragmentation impacts the structure of freshwater fish communities^{21–24}, with cascading socioeconomic effects, for instance concerning fisheries declines^{25,26}. Such impacts are expected to increase in the future, given the projected increases in river fragmentation worldwide¹⁵. Comprehensive, spatially explicit assessments of fish habitat fragmentation are urgently needed in large river basins to facilitate future fish habitat management and protection²⁷.

¹Yunnan Key Laboratory of International Rivers and Transboundary Eco-security, Institute of International Rivers and Eco-security, Yunnan University, Kunming, 650091, China. ²Ministry of Education Key Laboratory for Transboundary Eco-Security of Southwest China, Yunnan University, Kunming, 650091, China. ³National Institute of Oceanography and Applied Geophysics – OGS, Trieste, Italy. ⁴Department of Biosciences, University of Durham, Durham, DH1 3LE, UK. ⁵Centro de Investigación Marítima, Universidade de Vigo, 36310 Vigo, Spain. ⁶Department of Fisheries, University of Rajshahi, Rajshahi, 6205, Bangladesh.

✉ e-mail: jingrui.sun@ynu.edu.cn

The Mekong River lies within the Indo-Burma biodiversity hotspot, supporting the highest fish diversity in Asia, with more than 1,000 freshwater fish species, hundreds of which are endemic²⁸. The Mekong basin is also the largest inland fishery in the world, with an estimated mean annual catch of 2.1 million tonnes, about 15% of the world's total inland fish catch²⁹. The river suffers from intensive anthropogenic pressures including river barrier construction, overexploitation, pollution, water abstraction, and habitat destruction^{28,30–32}. Among all anthropogenic threats, barrier construction is the most concerning due to its profound impacts on flow regimes, sediment transportation and freshwater biodiversity and its rapid projected growth in the near future^{32–35}. Existing analyses conducted using global datasets of georeferenced dams highlighted the poor connectivity status of the upper Mekong³³, and have warned about the detrimental effect of future hydropower development on connectivity³⁶. However, there is ongoing debate over whether few large dams or numerous small barriers are more detrimental to habitat connectivity and consequently, biodiversity^{15,20}.

Existing analyses of habitat fragmentation effects in the world's largest river basins^{15,20,33,36,37}, including the Mekong, employed global databases or regional databases where barrier data had poor completeness and/or resolution. In particular, these studies used datasets describing large dams located in the main river channel and larger tributaries. While large dams are more likely to occur in the main channel, other barriers like small dams, weirs, and sluice gates are likely to be located in low-order streams and are more likely to be unreported^{13,38}. Estimating the impact of barriers in more distal regions of river networks is also relevant because, while generally having fewer aquatic species, these sites usually host more distinct communities due to their more isolated position in the river network^{21,39,40}. Recent developments in AI-assisted identification of barriers in the Mekong Basin has led to the compilation of a comprehensive dataset with more than 13,000 barriers that also include smaller barriers, such as small dams and sluice gates⁴¹. Although small barriers can have major impacts on fish distribution^{42,43}, the impacts of such structures on fragmentation of fish populations in the Mekong basin have not been investigated so far.

Based on the highlighted knowledge gaps, in this paper, we used a comprehensive barriers dataset to investigate the spatial distribution of fragmentation and its link with fish population longitudinal connectivity status in the Mekong Basin. We first reconstructed the potential distribution range of all fish species in the Mekong Basin by overlaying fish dispersal abilities on a fish occurrence database^{28,44}. We then assessed all species' habitat fragmentation status using the most complete barrier database available to calculate a Population Connectivity index (PCI) and compared the differences in connectivity reduction between migration types and conservation status at the species level. Subsequently, we evaluated which types of barriers contributed most to the degradation of river connectivity by using a Fragmentation Index (FI) that compares the population connectivity with and without barriers, and its normalized version \wedge FI, that accounts for the mean contribution of a single barrier. With this approach, we identified fish species and regions most threatened by the construction of river barriers in the Mekong Basin, to support future management plans including connectivity restoration and habitat conservation.

Results

Fish distribution within the Mekong Basin

Fish species richness differed between seven ecological regions (i.e., Himalaya, Upper Mekong, Middle Mekong, Chi-Mun, 3S [the Sesan, Sre Pok, and Sekong rivers], Tonle Sap and Delta^{30,33}) of the Mekong Basin (Kruskal-Wallis H test, $\chi^2(6) = 521.9$, $P < 0.001$), reducing with increasing elevation. Two species were found in the upper reaches of the Himalaya region whereas 413 occurred in sub-basins near the boundary between the Tonle Sap and Delta region (Fig. 1). On the other hand, the Upper Mekong exhibited the most unique communities, as measured by the local contribution to beta diversity index (LCBD), higher than other ecological regions except the Delta (Kruskal-Wallis H test, $\chi^2(6) = 332.7$, $P < 0.001$).

Sub-basins near the confluence of the Mun River (outlet of the Chi-Mun Region) and the Mekong main channel exhibited the highest fish

species richness (157–385 species per sub-basin) as well as the highest river barrier density (8–215 per 100 km; Fig. 2). The 'betweenness centrality', which measures the structural importance of sub-basins within the river network, was high within the Middle Mekong region (mean BC and 95% CI, 2974.5 [2172.8–3776.3]; Supplementary Data 1). This basin also exhibited high species richness (42–385 species per sub-basin) and moderate barrier densities (1–8 per 100 km). The Tonle Sap region also exhibited high species richness (86–345 species per sub-basin) but lowest mean BC (233.2 [156.8–309.7]). The Upper Mekong exhibited relatively low species richness (20–240 species per sub-basin) but high mean BC (2909.6 [2079.4–3739.8]); a few areas in this region had relatively high barrier densities (Fig. 2).

Potamodromous species ($n = 135$, see Supplementary Data 2), undertaking migrations solely in freshwater, were found to mostly inhabit the main channel in the Middle Mekong, the Tonle Sap, and the Chi-Mun regions. Within the distribution ranges of potamodromous species, high barrier density mostly occurred in the Chi-Mun region, and moderate barrier density was found in sub-basins along the main Mekong channel. Diadromous species ($n = 125$), which migrate between freshwater and the sea, were mainly found in the Lower Mekong between the 3S (i.e., the Sesan, Sre Pok, and Sekong rivers) confluence and the Delta. Barrier densities were moderate, covering much of the Mekong Delta and reduced further upstream. The listed threatened species (vulnerable [$n = 42$], endangered [$n = 25$], and critically endangered [$n = 13$]) mostly inhabit the main channel between the middle and lower Mekong, the Tonle Sap Lake, and sub-basins next to them (Fig. 3). Similarly, high and moderate barrier densities along the main channel pose threats to those species.

Habitat fragmentation of Mekong fishes

Across all 952 fish species for which data was available, 881 (92.5%) of them suffered from decreased population connectivity (PCI_F) comparing with their barrier-free population connectivity (PCI_O , see methods). When considering barriers, the Population Connectivity Index (PCI) pooled for all the fish species significantly decreased from 4.35 [3.81–5.02] (median and 95% CI, natural status) to 3.70 [3.06–4.21] (moderate passage status). The Fragmentation Index (FI, modeled under moderate barrier passability) ranged from 0.01 to 76.20, with a median value of 19.37, and was positively related to available fish habitat length (Spearman's correlation, $r = 0.566$, $P < 0.001$; Fig. S1). Among all fish families (for circumstances where there were more than five species present), the Pangasiidae ($n = 19$) experienced the most serious habitat fragmentation (average Fragmentation Index, FI = 51.91), followed by Notopteridae ($n = 5$; average FI = 51.27) and Channidae ($n = 10$; average FI = 48.84, Supplementary Data 2). Among all species, *Bagarius suchus* (Near Threatened conservation status) suffered from the most profound habitat fragmentation level (FI = 76.20), followed by *Wallago attu* (Vulnerable conservation status; FI = 74.43) and *Phalacrodonotus micronemus* (Least Concern conservation status; FI = 74.37).

Significant differences were found in FI between different migration types (Fig. 4, Kruskal-Wallis H test, $\chi^2(5) = 143.9$, $P < 0.001$). Potamodromous fish had the worst FI (42.45 [38.61–46.62]), significantly higher than anadromous fish (14.55 [2.18–27.29]), amphidromous fish (7.30 [5.98–10.45]), and species with unknown migration type (18.13 [16.64–19.92]) (pairwise post hoc, $P < 0.05$ in all cases). Significant differences in \wedge FI were also observed (Kruskal-Wallis H test, $\chi^2(5) = 19.42$, $P < 0.001$), with potamodromous fish (0.09 [0.06–0.10]) and unknown migration type (0.12 [0.11–0.14]) significantly lower than catadromous fish (0.67 [0.52–1.16]) (pairwise post hoc, $P < 0.05$ in both cases). The FI exhibited a statistically significant positive relationship with mean habitat betweenness centrality (Spearman's correlation, $r = 0.183$, $P < 0.001$); however, the effect size suggests a practically negligible monotonic association.

Significant differences in FI occurred across IUCN categories (Fig. 4, Kruskal-Wallis H test, $\chi^2(5) = 30.13$, $P < 0.001$). Critically Endangered species experienced the greatest FI (34.48 [19.46–53.52]). The FI status of Least Concern species was higher than Not Evaluated and Data Deficient (combined) species (pairwise post hoc, $P < 0.001$). Significant differences in

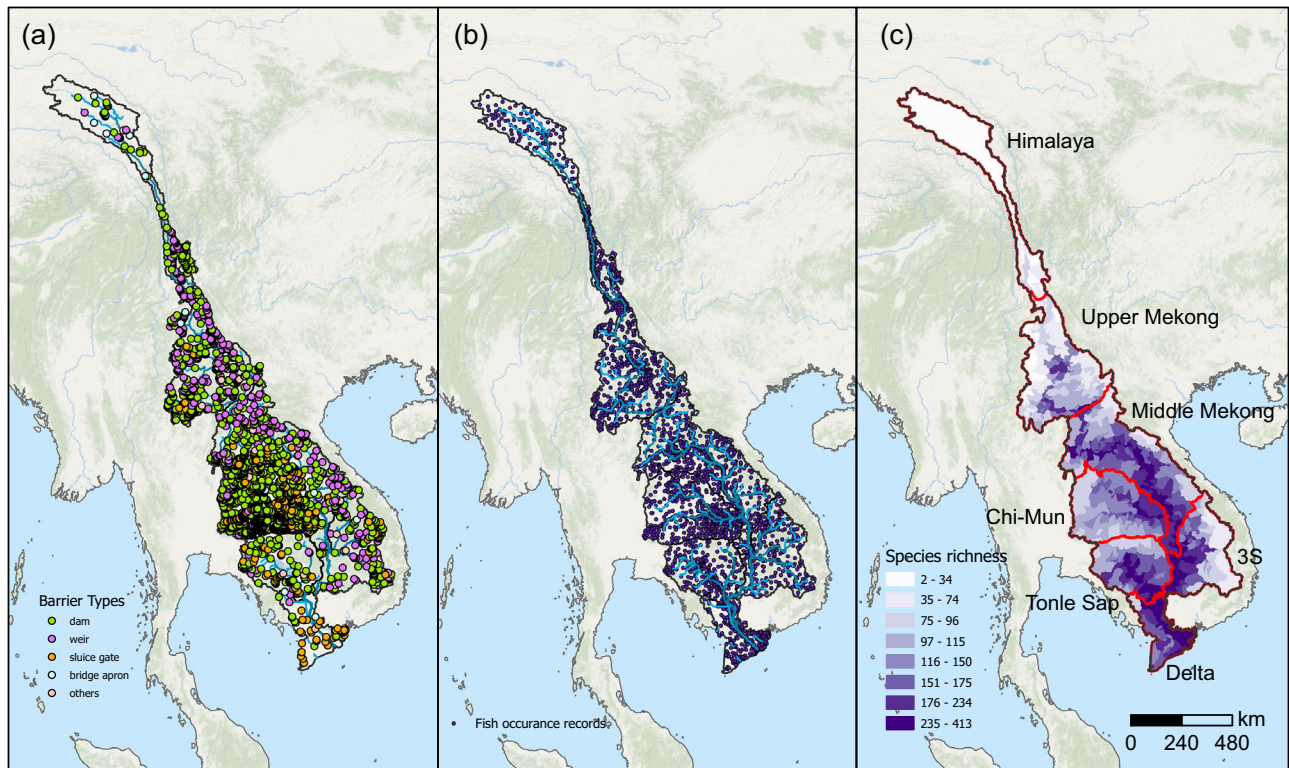


Fig. 1 | Distribution of river barriers, fish occurrence, and species richness across the Mekong Basin. The main channel barriers **a**, fish occurrence records **b**, and cumulative fish species richness in each sub-basin and the location of seven

ecological regions (i.e., Himalaya, Upper Mekong, Middle Mekong, Chi-Mun, 3S, Tonle Sap and Delta) of the Mekong Basin **c**.

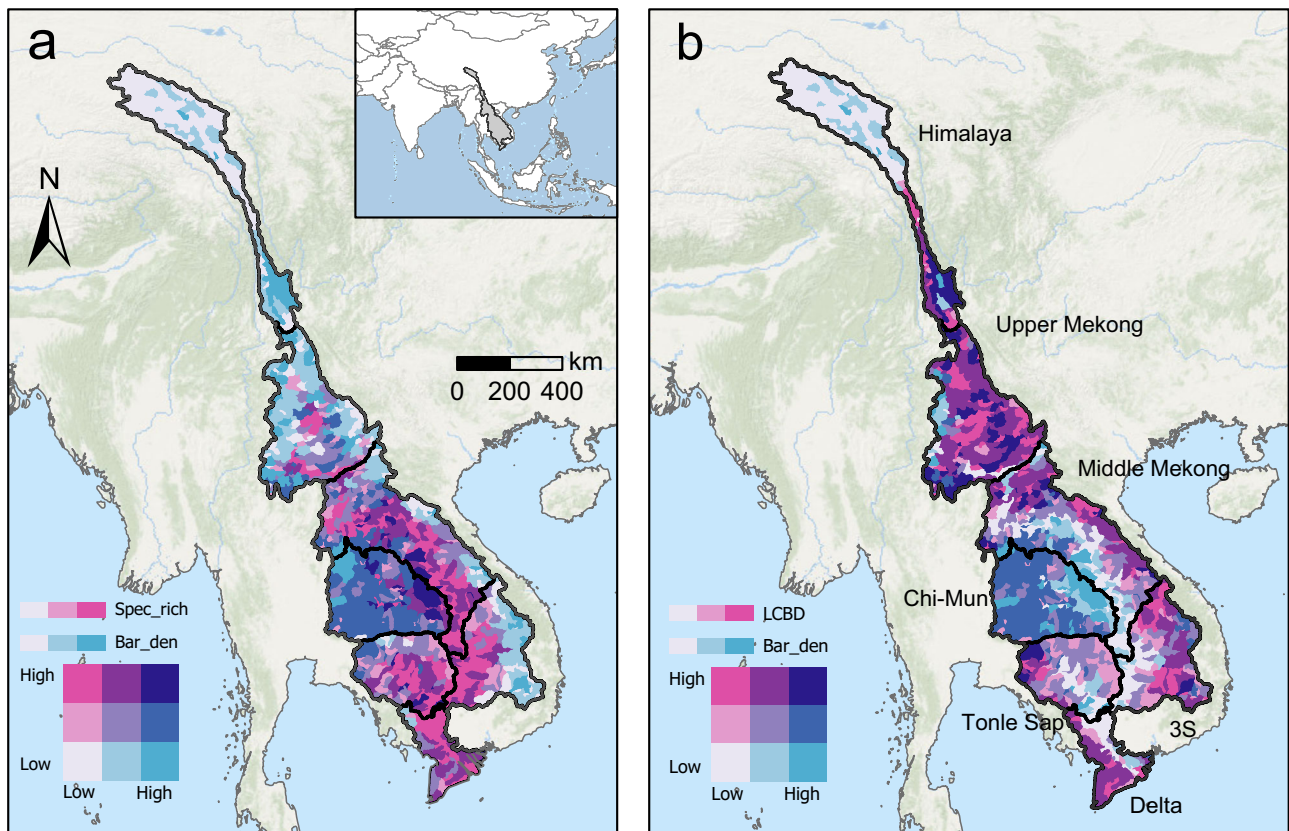


Fig. 2 | Relationship between river barrier density and biodiversity patterns in the Mekong Basin. Bivariate choropleth plot showing the relationship between barrier density (ranged from 0–2.2 per km) and total species richness (ranged from 0–952 species; **a**), and local contributions to beta diversity (LCBD) **b**.

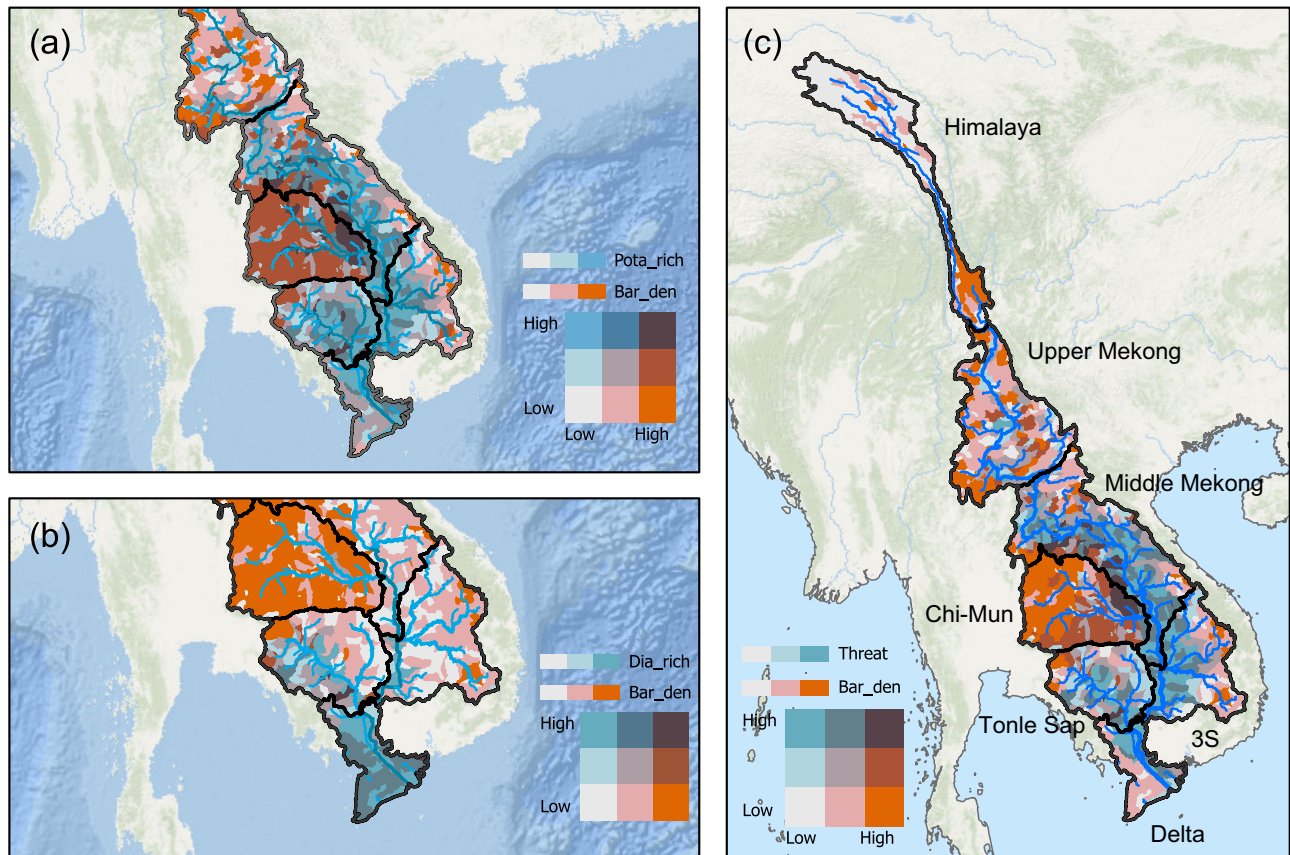


Fig. 3 | Relationships between river barrier density and fish species richness across migration and threatened categories in the Mekong Basin. Bivariate choropleth plots showing the relationship between barrier density and potamodromous species richness (ranged from 0–135 species; **a**, diadromous migrant fish

species richness (ranged from 0–125 species; **b** threatened fish species richness (IUCN status: Vulnerable (low threat), Endangered (moderate threat), and Critically Endangered (highest threat) **c**, in each sub-basin of the Mekong River.

Δ FI were observed among conservation status (Kruskal-Wallis H test, $\chi^2(5) = 28.1$, $P < 0.001$); CR species had higher Δ FI (0.33 [0.18–3.13]) than LC species (0.10 [0.08–0.11]).

Contribution of different barrier types to fragmentation

Across four major types of barriers, small dams and sluice gates cumulatively contributed most significantly to habitat fragmentation as measured by FI for all fish species – more than weirs and large dams (ANOVA, $F(3, 3804) = 42.6$, $P < 0.001$; pairwise post hoc, $P < 0.001$ in all cases; Fig. 5) under all passability values (modeled passability ranged between 0.1 and 0.9). A similar pattern was observed for all tested passability values, here only values for passability = 0.3 are presented. This pattern was evident for potamodromous species, where small dams and sluice gates had a profound impact on habitat fragmentation compared to weirs and large dams (ANOVA, $F(3, 536) = 43.1$, $P < 0.001$). For diadromous species, the impact of sluice gates on habitat fragmentation was significantly greater than that for other barrier types (ANOVA, $F(3, 496) = 57.4$, $P < 0.001$). For non-migratory species, no significant differences were found across the four types of barriers (ANOVA, $P > 0.05$). For species with unknown migratory status, small dams contributed more to habitat fragmentation than the other barrier types under all passability values (ANOVA, $F(3, 2720) = 10.6$, $P < 0.001$).

In comparison, large dams individually contributed more to habitat fragmentation as measured by Δ FI, compared to other barrier types, were observed when considering all fish species (ANOVA, $F(3, 3804) = 4.14$, $P = 0.006$) and unknown migration types (ANOVA, $F(3, 2720) = 4.7$, $P = 0.003$) species (Fig. 5), suggesting a single large dam can have a large impact on such migration life history categories. For potamodromous

(ANOVA, $P > 0.05$), diadromous (ANOVA, $F(3, 496) = 1.5$, $P = 0.004$), and non-migratory species (ANOVA, $P > 0.05$), sluice gates and small dams contributed more to Δ FI, indicating that these barrier types have a greater localized impact on fragmentation for these groups.

Discussion

By utilizing the most complete fish occurrence database alongside the most comprehensive basin-scale barrier database, the impacts of various barrier types on habitat fragmentation for all fish species in the Mekong Basin have been assessed for the first time. Our results demonstrate that high species richness predominantly occurs in the middle and lower Mekong Basin along the main channel, which is also the region where a high number of barriers have been constructed²⁸. On the other hand, sub-basins with a high ecological uniqueness, as measured by the local contribution to beta diversity (LCBD) were identified in the upper Mekong where the Chinese cascade dams are located. Across the entire basin, the most fragmented region appears to be the Chi-Mun sub-basin, characterized by the highest numbers of small dams and sluice gates⁴⁵. In contrast, the Mekong headwaters and most of the upper regions were relatively less fragmented and still provide accessible habitats for certain highland fish species. Nevertheless, among all fish species, 93% were affected by barrier construction, strongly suggesting that most Mekong fish species are already threatened by habitat fragmentation.

Relationships between life history traits and habitat fragmentation

Since the start of the Anthropocene, many migratory fish species have experienced reductions in habitat range⁴⁶. According to the Living Planet

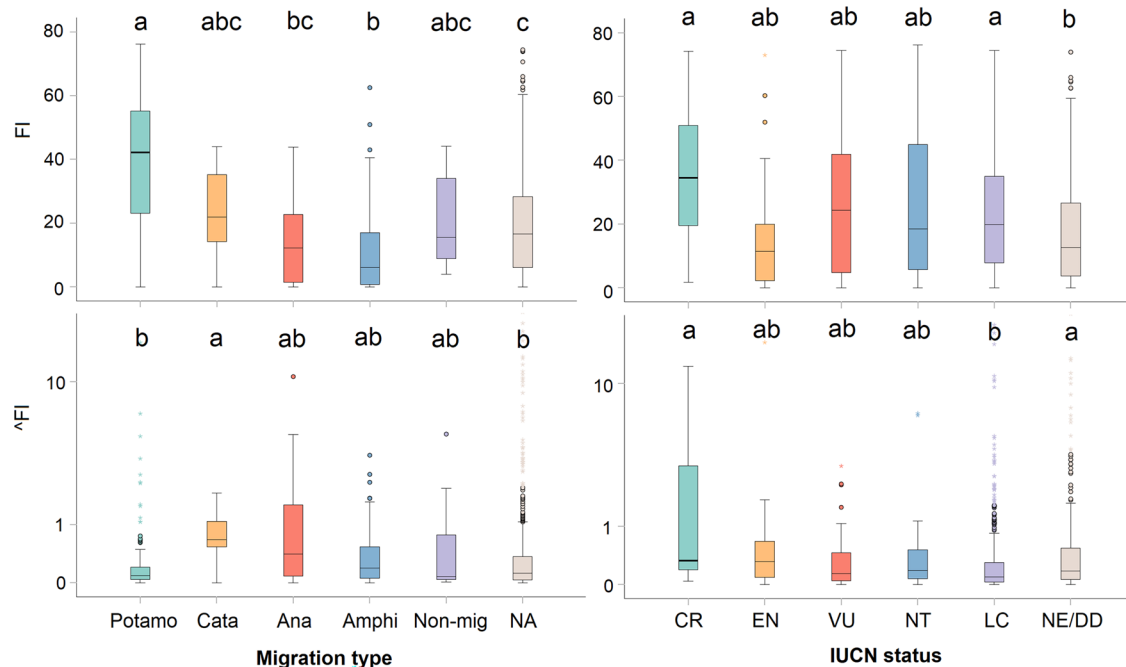


Fig. 4 | Variation in fragmentation index across fish migration types and conservation statuses. Boxplots showing the fragmentation index (FI) and mean fragmentation index caused per barrier (ΔFI) across different migration types (potamodromous, catadromous, anadromous, amphidromous, non-migratory, and

unknown [NA]) and conservation status (Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT], Least Concern [LC], Not Evaluated [NE], and Data Deficient [DD]). Letters above each box (e.g., “a”, “b”, “c”) denote statistical groupings based on post-hoc comparisons.

Index method, among 184 monitored freshwater migratory fish species globally, 81% exhibited a decreasing abundance trend between 1970 and 2020^{47,48}. When migratory fish traverse multiple sub-basins containing various habitats, they encounter a broader array of anthropogenic threats including a higher number of constructed barriers⁴⁹. Habitat loss due to barriers constructed at key locations (e.g., stopover sub-basins, spawning and foraging habitat) may contribute to population decline by limiting migration success^{50,51}. On the other hand, when larger areas of habitat are fragmented into smaller, less accessible patches of river channel, fish populations become more isolated, therefore making it more difficult to maintain meta-populations⁴². This results in decreased rates of immigration and emigration, hindering gene flow⁴⁹.

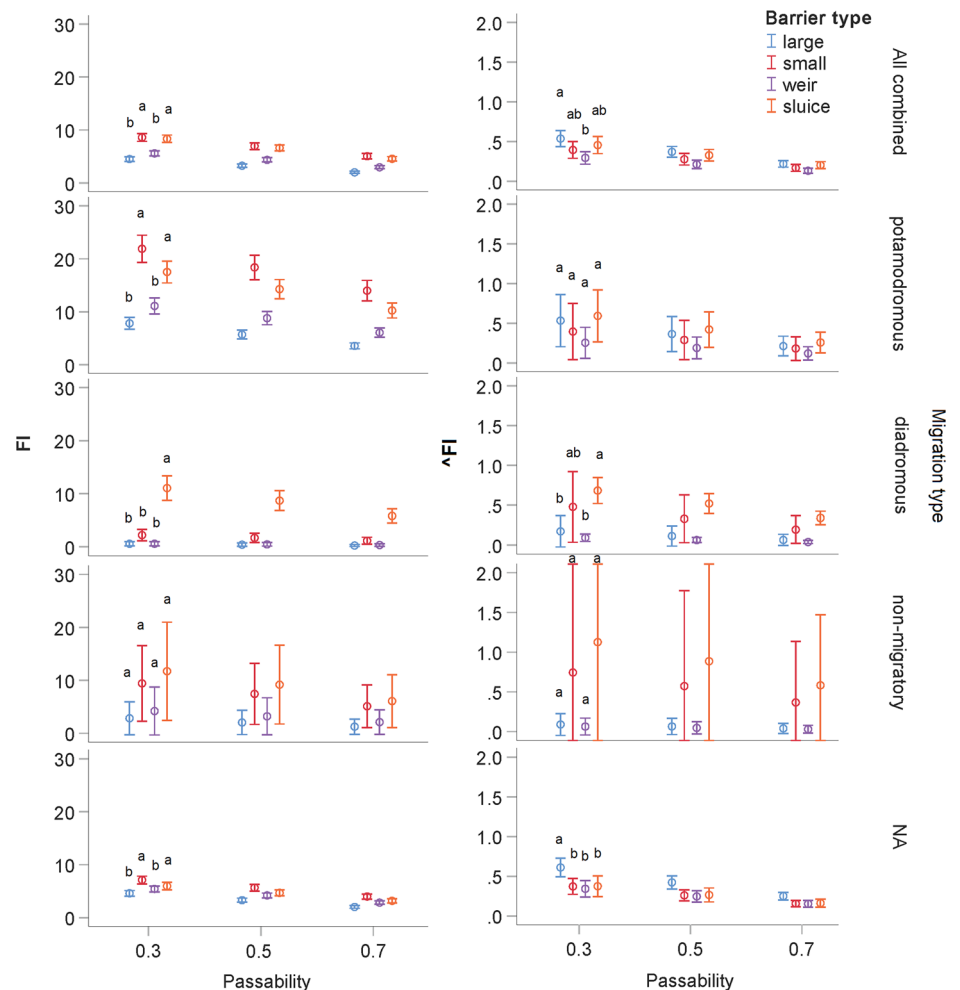
In the Mekong Basin, we found that migratory species with larger habitat range and longer dispersal distances suffered more profound habitat fragmentation compared to species with narrower habitat ranges and limited dispersal ability. The greater dispersal distance, the higher the likelihood that species would encounter more barriers during movement^{49,52}, and result in reduced population exchange. The habitat connectivity status of potamodromous species was significantly worse compared to other migration types, particularly for the middle and lower parts of the main Mekong channel and major sub-basins linked to it (e.g., the 3S, Chi-Mun, and Xe Don [located at the bottom of the Middle Mekong region] sub-basins). Small barriers such as sluice gates and small earthen dams were found to have particularly strong impacts on potamodromous species in the Chi-Mun and Middle Mekong regions⁵³. Although certain sluice gates (e.g., the Pak Mun Dam [located at the outlet of the Mun River]) in the Chi-Mun region are regulated to open during the rainy season, which could provide temporal passage for migratory species such as *Helicophagus waandersii*⁵⁴, thousands of other sluice gates are managed by various authorities, with unclear operational regimes. Further evaluation is needed to quantify their effects on fish migration dynamics.

Diadromous fish species such as *Pangasius krempfi*, *Arius maculatus* and *Osteogobius militaris*, depend on seasonal migrations between freshwater, estuarine, and marine habitats for their life cycles⁵⁵. However, increasing development of tidal barriers in the Mekong Delta has

significantly disrupted these migration routes. Otolith microchemistry studies have revealed complex and diverse migration patterns in these species, which are now at risk due to physical barriers that block or delay upstream and downstream movements⁵⁶. These disruptions pose serious threats to the sustainability of diadromous fish populations in the Mekong and underscore the urgent need for integrated river management strategies that account for their full migratory range.

Among the taxa exhibiting greatest habitat fragmentation risks, the Osteoglossiformes contains many highly threatened species according to the IUCN Red List, including the Endangered Asian bony-tongue *Scleropages formosus*, the Near Threatened royal featherback *Chitala blanci*, and the now Extinct giant featherback *Chitala lopis*. The population of *S. formosus* has experienced a significant decline over the past decades due to multiple human disturbance, with catch statistics indicating a 90% reduction in Cambodia and Thailand since 2010⁵⁷. In the Mekong, the freshwater habitats of the aforementioned species are evaluated as under pressure due to dam construction⁵⁷ according to the IUCN Red List, and their conservation status could be further worsened when considering all proposed barriers as well as those omitted from existing databases⁵⁸. With regard to fish families of particular concern, the most impacted Pangasiidae includes many flagship and megafauna freshwater species, such as the Critically Endangered Mekong giant catfish *Pangasianodon gigas*, Giant pangasius *Pangasius sanitwongsei* and Endangered striped catfish *Pangasianodon hypophthalmus*, all of which are ecologically and economically important. This family mostly consists of potamodromous species that undertake long-distance migrations along the main channel of the middle and lower Mekong, which suffers from main channel dams and sluice gates⁵⁹. The population of *P. gigas* has declined by 80% over the past two decades in the Mekong River, with annual catches dropping from 40–50 individuals in the early 1900s to just 1–2 individuals in recent years⁶⁰. The population of *Pangasius sanitwongsei* has undergone a drastic decline; annual catches of this species have dropped from around 100 individuals in the late 1980s to just 5–20 individuals by the late 1990s, with the species virtually disappearing from local fisheries thereafter⁵⁹. Further research is urgently needed to re-assess the conservation status of all these threatened species

Fig. 5 | Contribution of different barrier types to habitat fragmentation across fish migration categories and barrier passability levels. Comparison of habitat fragmentation by barrier type across different fish migration categories (potamodromous, diadromous, non-migratory, and unknown [NA]) and passability scenarios. This set of graphs displays the Fragmentation Index (FI) and average fragmentation index (Δ FI) for four barrier types (large dam, small dam, weir, and sluice gate) across various passability values, stratified by migratory behavior of fish species. Each point represents the mean FI, and the error bars indicate the 95% confidence interval (CI). Letters above each box (e.g., “a”, “b”) denote statistical groupings based on post-hoc comparisons, shown at 0.3 passability only, as patterns across all modeled passability levels were similar.



within the Mekong, using the complete barrier database⁵⁸. Additionally, the passability of most Mekong fish species at semi-passable barriers (barriers including weirs or sluice gates that allow fish to pass under certain conditions) remains unclear due to the lack of monitoring and performance standards. Future studies are required to address these gaps and to develop highly efficient bidirectional fish passes.

Large vs small barriers: which causes greater habitat fragmentation?

Our analysis revealed that, across all species, the cumulative effect of small dams and sluice gates nearly doubled the habitat fragmentation compared to large dams at all modeled levels of passability. This finding aligns with previous research suggesting that the cumulative impacts of small-sized barriers are comparable to those of large dams^{15,20,61}. Although the relationship between the fragmentation index (FI) and mean habitat betweenness centrality was statistically significant, the weak effect size suggests that tributary-dwelling species may experience fragmentation levels comparable to those in the mainstem, highlighting the need for greater attention to connectivity in tributary habitats. Such results underscore the importance of maintaining an openly accessible comprehensive barrier database to support ecological conservation and management efforts⁴¹, and highlight the need for standardized comprehensive databases at the river basin scale or, even, global scale.

All river barriers should be considered both individually, and in terms of cumulative effects when planning and conducting ecological impact and restoration activities^{6,62}. For example, our analysis suggests that small dams and sluice gates are the main reason for habitat fragmentation of potamodromous fish species, which suffered from the most significant habitat

fragmentation among all migration types. By contrast, large dams, which have generally received more attention in previous studies, contribute less to habitat fragmentation for potamodromous species compared with other barrier types. So, impacts of small-sized barriers should be carefully evaluated during connectivity impact assessment and restoration processes⁶². In comparison, the habitat of diadromous species in the Mekong is largely fragmented due to the construction of sluice gates^{56,63}. As a large number of tidal gates and flaps have been built in the Mekong estuary region in the last 50 years to support regional agriculture⁴⁵, these have blocked routes between the freshwater environments and the South China Sea⁴⁵, necessitating increased connectivity restoration in the near future. For non-migratory species (resident fish), all types of barriers contributed equally to the fragmentation effects. Although the impacts of barriers on fish dispersal may be less severe for these species, their short distance movements between metapopulations, as well as egg and larvae drifting phases, still require protection^{64,65}.

While small and semi-passable barriers contribute significantly to habitat fragmentation in the Mekong Basin, the impacts of large dams should never be underestimated, and particularly for dams located in sub-basins hosting unique fish communities, such as those identified by high LCBD in our analysis. For example, a new large hydropower station is set to be constructed at Ganlanba (in the lower reaches of the Lancang River), where the highest LCBD within the basin has been observed. Long-term monitoring will be essential to assess its ongoing impacts and guide adaptive management efforts to minimize ecological impacts. Together, these findings emphasize the need for integrated management strategies that account for both the type and spatial context of barriers to effectively safeguard freshwater biodiversity.

Strategic restoration plan needed to mitigate barrier impacts

River management decisions to prioritize passability improvement of a large dam or remove multiple small barriers must carefully balance ecological benefits, economic costs, and the presence of key species^{66,67}. Large dams, while having the potential to cause widespread flow modification and ecological disruption, are often critical for power generation and regional development. Installing fish passes or bypass channels at such dams can reconnect migratory routes and mitigate some ecological impacts but is often difficult or ineffective at large dams in the tropics⁶⁸. These solutions can be expensive, with installation and maintenance costs running into millions of dollars, and their effectiveness is site- and species-dependent. For example, species with limited swimming ability may still struggle to navigate even well-designed fish passes⁶⁹. Moreover, fish passage measures cannot address broader impacts such as habitat degradation (transformation of lotic to lentic habitats), modified sediment transport, altered flow regimes, and degraded water quality⁶⁷.

In contrast, small barriers often have lower socioeconomical benefits but are numerous and cumulatively can cause extensive habitat fragmentation, especially in areas located in remote tributary sections far from the main channel where high fish community differentiation might occur^{9,40,53}. Removing multiple small barriers can significantly restore connectivity across a broad spatial scale, benefiting a wide range of aquatic species and enhancing ecosystem functions⁷⁰. However, this approach involves substantial logistical and financial challenges, as the costs of identifying, assessing, and dismantling barriers across an entire basin, or multiple sub-basins, can be high. Moreover, some small barriers serve local needs, such as irrigation or flood control, which complicates their removal due to stakeholder opposition⁷¹. In such contexts, where resources are limited, a low-cost method for prioritizing barrier remediation, such as those developed from a fish passage perspective in previous studies can offer a practical solution for guiding restoration efforts^{70,72}.

The presence of species with specific ecological requirements further complicates the decision regarding the optimal management strategy for mitigating impacts of habitat fragmentation from anthropogenic river barriers⁶⁷. For instance, if a region or sub-basin supports a flagship or economically significant migratory species that requires access to upstream habitats, improving the passability of a large dam might be the most effective action when the ΔFI value is high. On the other hand, for sub-basins with diverse, localized species (i.e., regions with high LCBF values) that depend on interconnected habitats, removing small barriers may yield greater cumulative benefits (for species with high FI and relative lower ΔFI values).

A cost-effective and ecologically sound river management strategy often requires an integrated approach³⁷. This may involve improving fish passage at key large dams to benefit migratory species while systematically prioritizing and removing small barriers to restore the dendritic structure of the river network²¹. Decisions should be guided by ecological modeling, cost-benefit analyses, and species-specific data, ensuring that investments align with ecological priorities and stakeholder needs, while minimizing unnecessary expenses³⁷.

Limitations in current study and future direction

Several limitations in current study deserve consideration. First, our analysis is based on modeling approaches. We made assumptions regarding barrier passability in the model, which were informed by previous studies and expert knowledge (see Methods). However, properly assessing the passability of individual barriers requires fish tagging and monitoring experiments at key sites under the range of environmental conditions, particularly flow, that are commonly experienced⁶⁹. Future validation work should aim to compare model outputs with observed species distributions and movement patterns across selected locations. Additionally, the uneven spatial distribution of barriers across the basin (as shown in Fig. 1) may result in region-specific impacts on fish populations. This spatial bias highlights the need for further investigation into how fish species distributions have changed in response to localized high barrier densities, as reductions in richness and connectivity may be strongly dependent on regional contexts³². Such validation would

enhance the robustness of the methodology and support the application of these tools in conservation planning and policy development. In the present study, all fish species occurrence data were used collectively to reconstruct potential distribution ranges, without separating records by time periods. However, historical records of species presence in localities within watersheds can serve as valuable baselines for assessing the impacts of river barrier construction^{31,73}. When combined with information on barrier age, location, and restoration time (if applicable), such records allow for inference of connectivity loss and recovery over time, identification of range contractions, and estimation of species' pristine dispersal potential, offering useful benchmarks for guiding barrier removal or mitigation strategies⁷⁴.

Second, many fish species in the Middle Mekong require lateral dispersal during the high flow period (June–October) to complete their life cycle, particularly to access inundated floodplains, wetlands, and off-channel habitats for spawning, feeding, and juvenile development⁷². They also need to be able to return to main channels or survive in isolated lentic waters as floodwaters recede. Yet lateral connectivity onto the Mekong floodplain is increasingly threatened by different types of barriers such as levees, embankments, and pumping stations^{53,65,72}. While our current study focused on longitudinal connectivity, future research should also assess the impacts of such structures on lateral movement of fishes and other aquatic biota. Incorporating lateral connectivity into fragmentation assessments will be essential for capturing the full ecological consequences of river infrastructure development and for designing effective conservation and restoration strategies.

Last, while the present study focuses primarily on barriers as physical impediments to fish movement, we recognize that their ecological consequences often extend beyond fragmentation alone. River barriers, especially larger ones, also modify natural flow regimes and local habitat conditions^{75–77}, which can disrupt critical ecological processes such as fish spawning, hatching, and juvenile development^{19,53,78}. For example, many fish species in the Mekong floodplains spawn at the beginning of the flood season⁵³. The flow-regime-adapted spawning behavior can be easily disturbed when dams or sluice gates are operational, potentially delaying migratory or spawning timings^{4,78}. Additionally, many species depend on the drifting of eggs (e.g., *Bagarius sp.*), larvae, and juvenile stages to downstream nursery and feeding areas to complete their life cycles⁷⁹, but elevated flow velocity is seldom maintained in impounded regions, and the minimum flow speed required to keep larval fish in the water column is rarely met. Although these factors were not directly addressed in this study, they represent critical dimensions for future research in the Mekong Basin. Furthermore, barrier construction derived habitat modifications may facilitate the invasion of non-native species⁸⁰, further exacerbating conservation challenges. To advance effective management strategies in the Mekong Basin, future assessments should incorporate a broader suite of hydrological, geomorphological, and ecological variables, such as flow regimes, seasonal hydrological variability, and barrier characteristics¹⁹.

Conclusion

We demonstrate that while the effects of individual large dams on habitat fragmentation and fish distribution in the Mekong Basin are greater than for small barriers, the large number of small barriers potentially causes greater cumulative impacts on fragmentation and resultant risks for effective conservation especially for non-migratory fish. We showcase the importance of using complete databases with small, as well as large, river barriers for evaluating conservation risks for barrier development and connectivity restoration in large river basins. We encourage the development of thorough barrier and faunal databases in other large, biodiverse river basins and the application of similar analyses of the ecological impacts of existing and projected barrier distributions.

Materials and methods

River barrier data processing

River barrier data of the Mekong Basin were gathered from the Mekong River Barrier Database⁴¹. This database comprises 13,054 barriers classified

into five types following standardized terminology (dam, sluice gate, weir, bridge apron, and others) given in that publication⁷⁰. Ninety seven percent of the barriers in this database were previously unreported in the Mekong Basin compared with other openly accessible databases. To analyse the impact of barrier distribution on fish dispersal across sub-basins, we first extracted all main channel networks (i.e. the section of a river network that links sub-basins to each other), then manually reviewed all barriers in associated Google Earth satellite (Landsat, NASA-USGS) images, and retained barriers that were located in the main river channel, resulting in 3066 barriers including 1648 dams, 488 sluice gates, 840 weirs, 42 bridge aprons, and 48 'other' type barriers (e.g. ramps, bamboo/wooden fences, Fig. 1). Among the 1,130 sub-basins in the Mekong Basin (HydroBASIN level 8), 604 have barriers constructed along their main channels. Dam were categorized into large dam (≥ 10 m) and small dam (< 10 m) based on available information from the Mekong dam database⁸¹. While this database provides detailed information on dams, it lacks records for other types of barriers⁸¹. The main channel barrier density for each sub-basin was calculated by dividing barrier numbers by main channel length.

Fish species data processing

Fish occurrence data for the Mekong Basin were gathered from a published systematic database^{28,82}, that compiles all fish occurrence data by combining long-term field sampling data and data gathered from all existing books, peer-reviewed articles, gray literature, and online databases via literature review (covering the time period from 1970s to 2020 s). Non-native fish species, farmed species, and species without occurrence descriptions were excluded from the original database, which resulted in the final database comprising a total of 164,878 occurrence points from 1032 species (Fig. 1). The migration type of each species was gathered from FishBase⁸³ and published literature. Each species was categorized into one of six migration types: potamodromous, catadromous, anadromous, amphidromous, non-migratory, and unknown (defined according to Lucas & Baras⁸⁴; see Supplementary Data 2). Each species was categorized into one of eight conservation status categories according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (<https://www.iucnredlist.org/>): Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Extinct (EX). To analyze the spatial patterns of fish distribution, the cumulative fish species richness of each category was calculated at sub-basin level (HydroBASIN level 8^{85,86}) and compared across seven ecological regions^{30,33} (i.e., Himalaya, Upper Mekong, Middle Mekong, Chi-Mun, 3S, Tonle Sap and Delta; see Supplementary Notes for details). The HydroBASINS level 8 was adopted to align with the resolution used in previous studies^{61,87}.

To reconstruct the potential distribution range of each species, the dispersal distance of each species was calculated⁸⁸. Total fish length, aspect ratio of the caudal fin, stream order inhabited, and timescale allowed for dispersal were employed in this model^{88,89}. Species-specific fish length and aspect ratio of the caudal fin for each species were measured based on figures from published articles or gathered from FishBase. The highest stream order that each species inhabits was gathered using the HydroRIVERS dataset⁸⁵. A time window of 10 years was used in the model, as appropriate to long-term population level dispersal^{89,90}. The estimated dispersal distance was used as a radius to create buffer zones for each occurrence point^{44,91}. Then, sub-basins (HydroBASIN level 8) that overlapped with buffer zones of all occurrence points were considered as the predicted distribution for that species^{31,92}. The predicted distribution of each species was further refined by cropping to its native sub-basins to exclude predictions that were out of range, based on the occurrence points and expert opinion⁴⁴. For example, if one species only moves along the main channel of the Mekong and does not inhabit tributaries according to published literature, when the buffered regions fell within some tributaries, then those overlapped sub-basins were removed during this manual refinement step. Furthermore, if a potential sub-basin was linked with valid habitat only through land rather than river channel, then it was removed during the manual process.

To express the compositional uniqueness of each subbasin, and thus to identify unique biodiversity hotspots within the Mekong basin, we calculated the local contributions to beta diversity (LCBD)⁹³. We calculated the LCBDs based on the beta diversity distance matrix calculated using Sørensen-based indices of the Podani family ('BAT' package)⁹⁴.

Fish habitat fragmentation level assessment

To assess the species' habitat connectivity, we used the Population Connectivity Index (PCI)⁹⁵, which considers structural connectivity (spatial arrangement of the sub-basins and the barriers) and functional connectivity (fish dispersal ability), distribution range (habitat length), and the passability between sub-basins. The PCI considers that a fish population inhabits multiple sub-basin:

$$PCI = \sum_{i=1}^n \sum_{j=1}^n B_{ij} c_{ij} \frac{l_i l_j}{L L} \delta_i \delta_j \quad (1)$$

Where n is the number of sub-basins, B_{ij} measures the dispersal capacity of the given fish species between sub-basin i and sub-basin j , c_{ij} is the total cumulative passability of river barriers between sub-basins i and j , and l_i and l_j represent the total length of the river network in sub-basin i and j , which are inhabited by the specific species; δ_i and δ_j represent the presence of a species in subcatchments i and j (0 if species is absent, 1 if present); L represents the total river length of all populations in the basin. Since the PCI is a network-based index, we generated a spatial network accounting for the geographic distribution of subbasins. We used the 1,130 HydroBASINS level 8 sub-basins as nodes of the network, where outlets/entrances between sub-basins are links.

We defined the cumulative passability c_{ij} between sub-basins i and j as:

$$c_{ij} = \prod_{m=1}^M p_m \quad (2)$$

Where p_m is the passability of the sub-basin m , defined as:

$$p_m = \prod_k p_k^{n_k} \quad (3)$$

Where p_k is the passability of each barrier type k , where $k = 1$ for large dams, $k = 2$ for small dams, $k = 3$ for sluice gates, $k = 4$ for weirs; n_k is the number of k -th fragmentation item in the main channel of sub-basin m .

The dispersal capacity B_{ij} is defined as follows:

$$B_{ij} = PD^{d_{ij}} \quad (4)$$

Where the probability of dispersal (PD) is based on fish size and swimming capability⁸⁸, and the distance (d_{ij}) is the main channel length between two populations located in sub-basins i and j . The dispersal distance of each species was estimated using the 'fishmove' R package⁸⁸. Next, we defined seven classes of dispersal distance of all species of the entire fish community, by setting the quantiles at 0%, 14.3%, 28.6%, 42.9%, 57.1%, 71.4%, 85.7%, and 100%⁹⁵. Dispersal distance that fell within the quantile ranges was then categorized into one of the seven class boundaries, ranging from PD = 0.3 to PD = 0.9, which represent fish species' dispersal probability from low to high⁹⁵. As this index is applicable to species that occupy two or more sub-basins, species that inhabit only one sub-basin ($n = 80$) were excluded from further analysis, resulting in a total of 952 fish species for which PCI was calculated using the 'riverconn' package⁹⁶.

We calculated PCI for each species and scenario (i.e., different barrier passability status). We defined the fragmentation index (FI) as the percentage decrease of PCI when barriers are considered. While PCI describes the fragmentation status of populations that is due to barriers and isolation, FI describes the effect of barriers on the geographic range occupied

by the species.

$$FI = \frac{(PCI_o - PCI_F)}{PCI_o} \times 100 \quad (5)$$

Where, PCI_o is the population connectivity index calculated when no barrier is present within the species' distribution range (i.e. calculating PCI by setting $c_{ij} = 1$). PCI_F represents the fragmented status (i.e. all the barriers are considered). When calculating the PCI_F , p_k for dams (both large and small) was set to 0 in all circumstances²⁰. For semi-passable barriers such as weirs, p_k was set to 0.5, representing moderate fish passability²¹. The FI values range from 0 to 100. When fish populations are located in connected (neighboring) sub-basins with no barriers, or barriers are only located at the edge of the fish's distribution range such that they do not affect the internal dispersal, FI = 0. Conversely, if the species' range is greatly fragmented by barriers, preventing fish from freely moving from one sub-basin to another, the FI value would approach 100. The FI integrates both structural connectivity and functional connectivity into a species-specific, quantitative measure that reflects the percentage loss of connectivity due to barriers. Unlike structural and functional connectivity alone, FI provides a direct assessment of fragmentation impacts on fish populations by comparing with ideal connectivity scenarios.

We also calculated the average fragmentation index (ΔFI) as the ratio between FI and the number of barriers considered in PCI_F . ΔFI represents the average fragmentation caused by one barrier and is useful when comparing scenarios where different numbers of barriers are considered. ΔFI is calculated by dividing total FI by the number of barriers within a given species' distribution range, making it useful for comparing scenarios with varying barrier counts.

Additionally, as a metric of network centrality, based on the graph used to calculate PCI, we calculated also the betweenness centrality (BC) for each sub-basin (HydroBASIN level 8) using the 'igraph' R package⁹⁷. BC quantifies the structural importance of sub-basins within a network by measuring their role as intermediary pathways between other nodes. High betweenness sub-basins, serving as pivotal pathways for ecological processes (e.g., fish dispersal and migration), are critical to network resilience and are prioritized in conservation planning due to their disproportionate vulnerability to fragmentation. BC differentiates between central and isolated sites and was shown to be a strong predictor of fish alpha and beta diversity in undisturbed river systems^{21,40,98}. Sites with high BC are located in the main channel, while sites with low BC are located in the tributaries. To assess whether habitat fragmentation differs between tributary-dwelling and mainstream-dwelling species, we calculated the mean BC for each species based on their occupied habitats. We then assessed the relationship between mean habitat BC and the associated fragmentation index (FI).

Contribution of different types of barriers to habitat fragmentation

To assess how different types of barriers affect species with different migration types, and which type of barrier contributed most to habitat fragmentation, four major type barriers: large dam (≥ 10 m), small dam (< 10 m), weir, and sluice gate were selected. Then, the FI for each species was calculated at nine different passability status values (from 0.1, 0.2, 0.3 to 0.9), assuming only one type of barrier is present in each occasion¹⁷. After that, the difference between $FI_{\text{large-dam}}$, $FI_{\text{small-dam}}$, FI_{weir} and FI_{sluice} among all migration types of fish was evaluated.

Data analysis

Spearman's correlation was used to identify the relationship between fish habitat range and its associated fragmentation index (FI), as well as the relationship between mean habitat betweenness centrality (BC) and FI. Kruskal-Wallis H tests were used to identify if there were significant differences in fragmentation index (FI and ΔFI) between different migration types and IUCN conservation status⁹⁹ (<https://www.iucnredlist.org/>), followed by a Bonferroni post-hoc test to identify the significantly different

groups. ANOVA followed by a Turkey post-hoc test were used to assess the difference in fragmentation status (FI and ΔFI) contributed by different types of barriers across migration types.

Data availability

Supplementary Files include two tables cited as Supplementary Data in the text. Supplementary Data 1 provides a summary of barrier types and fish diversity metrics for each sub-basin in the Mekong River Basin. Supplementary Data 2 contains species information used in the analysis, including taxonomic classification, migratory type, and IUCN conservation status. The river barrier data used in this study are available at Zenodo [<https://doi.org/10.5281/zenodo.10141668>]. The fish distribution data, and shapefiles used in this study have been deposited in Zenodo [<https://doi.org/10.5281/zenodo.15273072>]. The dimension information of basin dams can be found at Dataverse [<https://doi.org/10.21979/N9/ACZIJN>].

Code availability

The Population Connectivity index was calculated using the R 'riverconn' package⁹⁶. The local contributions to beta diversity was calculated using the R 'BAT' package⁹⁴. The dispersal distance of fish species was calculated using the R 'fishmove' package⁸⁸. The betweenness centrality for each sub-basin was calculated using the R 'igraph' package⁹⁷. All R codes used in this study have been deposited in Zenodo [<https://doi.org/10.5281/zenodo.15273072>].

Received: 5 February 2025; Accepted: 10 June 2025;

Published online: 07 July 2025

References

- Dudgeon, D. et al. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* **81**, 163–182 (2006).
- He, F. et al. The global decline of freshwater megafauna. *Glob. Chang. Biol.* **25**, 3883–3892 (2019).
- Reid, A. J. et al. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **94**, 849–873 (2019).
- He, F. et al. Hydropower impacts on riverine biodiversity. *Nat. Rev. Earth Environ.* **5**, 755–772 (2024).
- Sayer, C. A. et al. One-quarter of freshwater fauna threatened with extinction. *Nature* <https://doi.org/10.1038/s41586-024-08375-z> (2025).
- Harper, M. et al. Twenty-five essential research questions to inform the protection and restoration of freshwater biodiversity. *Aquat. Conserv.* **31**, 2632–2653 (2021).
- Grill, G. et al. Mapping the world's free-flowing rivers. *Nature* **569**, 215–221 (2019).
- WWF. *Living Planet Report 2020 - Bending the Curve of Biodiversity Loss*. (WWF, Gland, Switzerland, 2020).
- Altermatt, F. Diversity in riverine metacommunities: a network perspective. *Aquat. Ecol.* **47**, 365–377 (2013).
- Fagan, W. F. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**, 3243–3249 (2002).
- Larsen, S. et al. The geography of metapopulation synchrony in dendritic river networks. *Ecol. Lett.* **24**, 791–801 (2021).
- Jumani, S. et al. River fragmentation and flow alteration metrics: a review of methods and directions for future research. *Environ. Res. Lett.* **15**, 123009 (2020).
- Belletti, B. et al. More than one million barriers fragment Europe's rivers. *Nature* **588**, 436–441 (2020).
- Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L. & Tockner, K. A global boom in hydropower dam construction. *Aquat. Sci.* **77**, 161–170 (2015).
- Barbarossa, V. et al. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proc. Natl. Acad. Sci.* **117**, 3648–3655 (2020).
- Katano, O., Nakamura, T., Abe, S., Yamamoto, S. & Baba, Y. Comparison of fish communities between above- and below-dam

- sections of small streams; barrier effect to diadromous fishes. *J. Fish Biol.* **68**, 767–782 (2006).
17. Kowal, J. L. et al. River continuum disruptions in a highly altered system: The perspective of potamodromous fish. *Ecol. Indic.* **164**, 112130 (2024).
 18. Waldman, J. R. & Quinn, T. P. North American diadromous fishes: Drivers of decline and potential for recovery in the Anthropocene. *Sci. Adv.* **8**, eabl5486 (2022).
 19. de Visser, S., Barbarossa, V., Keijzer, T., Verones, F. & Dorber, M. Characterizing dam fragmentation impacts on freshwater fish within life cycle impact assessment. *Environ. Impact Assess. Rev.* **114**, 107929 (2025).
 20. Keijzer, T. et al. Threats of dams to the persistence of the world's freshwater fishes. *Glob. Chang. Biol.* **30**, e17166 (2024).
 21. Baldan, D. et al. The effects of longitudinal fragmentation on riverine beta diversity are modulated by fragmentation intensity. *Sci. Total Environ.* **903**, 166703 (2023).
 22. Díaz, G. et al. The longest fragment drives fish beta diversity in fragmented river networks: Implications for river management and conservation. *Sci. Total Environ.* **766**, 144323 (2021).
 23. Mahlum, S., Kehler, D., Cote, D., Wiersma, Y. F. & Stanfield, L. Assessing the biological relevance of aquatic connectivity to stream fish communities. *Can. J. Fish Aquat. Sci.* **71**, 1852–1863 (2014).
 24. Perkin, J. S. & Gido, K. B. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecol. Appl.* **22**, 2176–2187 (2012).
 25. Arantes, C. C., Fitzgerald, D. B., Hoeinghaus, D. J. & Winemiller, K. O. Impacts of hydroelectric dams on fishes and fisheries in tropical rivers through the lens of functional traits. *Curr. Opin. Environ. Sustain* **37**, 28–40 (2019).
 26. Campbell, I. & Barlow, C. Hydropower development and the loss of fisheries in the Mekong River basin. *Front. Environ. Sci.* **8**, 566509 (2020).
 27. Mulligan, M. et al. Global Dam Watch: curated data and tools for management and decision making. *Environ. Res. Infrastruct. Sustain* **1**, 033003 (2021).
 28. Sun, J. et al. Research status of the Lancang-Mekong River Basin: fish and environmental stressors. *Rev. Fish Biol. Fish* **33**, 89 (2023).
 29. Ainsworth, R. F., Cowx, I. G. & Funge-Smith, S. J. Putting the fish into inland fisheries – A global allocation of historic inland fish catch. *Fish Fish* **24**, 263–278 (2023).
 30. Kang, B. & Huang, X. Mekong fishes: biogeography, migration, resources, threats, and conservation. *Rev. Fisher. Sci. Aquac.* 1–38 <https://doi.org/10.1080/23308249.2021.1906843> (2021).
 31. Sun, J. et al. River fragmentation and barrier impacts on fishes have been greatly underestimated in the upper Mekong River. *J. Environ. Manag.* **327**, 116817 (2023).
 32. Ziv, G., Baran, E., Nam, S., Rodriguez-Iturbe, I. & Levin, S. A. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proc. Natl. Acad. Sci.* **109**, 5609–5614 (2012).
 33. Grill, G., Ouellet Dallaire, C., Fluet Chouinard, E., Sindorf, N. & Lehner, B. Development of new indicators to evaluate river fragmentation and flow regulation at large scales: a case study for the Mekong River Basin. *Ecol. Indic.* **45**, 148–159 (2014).
 34. Kondolf, G. M., Rubin, Z. K. & Minear, J. T. Dams on the Mekong: Cumulative sediment starvation. *Water Resour. Res.* **50**, 5158–5169 (2014).
 35. Sor, R. et al. Fish biodiversity declines with dam development in the Lower Mekong Basin. *Sci. Rep.* **13**, 8571 (2023).
 36. Shaad, K., Souter, N. J., Farrell, T., Vollmer, D. & Regan, H. M. Evaluating the sensitivity of dendritic connectivity to fish pass efficiency for the Sesan, Srepok and Sekong tributaries of the Lower Mekong. *Ecol. Indic.* **91**, 570–574 (2018).
 37. Barbarossa, V. & Schmitt, R. J. P. Strategic restoration-development mitigates tradeoffs between hydropower and fish habitat fragmentation in the Mekong. *One Earth* **7**, 1096–1107 (2024).
 38. Jones, J. et al. A comprehensive assessment of stream fragmentation in Great Britain. *Sci. Total Environ.* **673**, 756–762 (2019).
 39. Edge, C. B. et al. Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities. *Landsc. Ecol.* **32**, 647–662 (2017).
 40. Henriques-Silva, R. et al. A comprehensive examination of the network position hypothesis across multiple river metacommunities. *Ecography* **42**, 284–294 (2019).
 41. Sun, J. et al. Convolutional Neural Networks Facilitate River Barrier Detection and Evidence Severe Habitat Fragmentation in the Mekong River Biodiversity Hotspot. *Water Resour. Res.* **60**, e2022WR034375 (2024).
 42. Jones, P. E. et al. Selective effects of small barriers on river-resident fish. *J. Appl. Ecol.* **58**, 1487–1498 (2021).
 43. Lucas, M. C., Bubbs, D. H., Jang, M.-H., Ha, K. & Masters, J. E. G. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshw. Biol.* **54**, 621–634 (2009).
 44. Tao, J. et al. Boosting freshwater fish conservation with high-resolution distribution mapping across a large territory. *Conserv. Biol.* **37**, e14036 (2023).
 45. Li, M. et al. Human barriers fragment three-quarters of all rivers in the Mekong basin. *Renew Sustain Energy Rev.* **210**, 115158 (2025).
 46. Hardesty-Moore, M. et al. Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. *Philos. Trans. R. Soc. B. Biol. Sci.* **373**, 20170017 (2018).
 47. Deinet, S. et al. The Living Planet Index (LPI) for migratory freshwater fish - Technical Report. https://worldfishmigrationfoundation.com/wp-content/uploads/2024/05/LPI_migratory-freshwater-fishes-2024_Technical-report.pdf (World Fish Migration Foundation, Netherlands, 2020).
 48. Tickner, D. et al. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *Bioscience* **70**, 330–342 (2020).
 49. Cooke, S. J. et al. Animal migration in the Anthropocene: threats and mitigation options. *Biol. Rev.* **99**, 1242–1260 (2024).
 50. Galib, S. M., Lucas, M. C., Chaki, N., Fahad, F. H. & Mohsin, A. B. M. Is current floodplain management a cause for concern for fish and bird conservation in Bangladesh's largest wetland?. *Aquat. Conserv.* **28**, 98–114 (2018).
 51. Sun, J., Galib, S. M. & Lucas, M. C. Rapid response of fish and aquatic habitat to removal of a tidal barrier. *Aquat. Conserv.* **31**, (2021).
 52. Saunders, S. P. et al. Multispecies migratory connectivity indicates hemispheric-scale risk to bird populations from global change. *Nat. Ecol. Evol.* **9**, 491–504 (2025).
 53. Cowx, I. G. et al. Understanding the threats to fish migration: applying the global swimways concept to the lower mekong. *Revi. Fisheries. Sci. Aquac.* 1–29 <https://doi.org/10.1080/23308249.2024.2401018> (2024).
 54. Jutagate, T., Thapanand, T. & Tabthipwan, P. Is sluice gate management beneficial for spawning migrations? The case of the shark catfish (*Helicophagus waandersii*) in the Mun River below the Pak Mun Dam, Thailand. *River Res. Appl.* **23**, 87–97 (2007).
 55. Vu, A. V. et al. Variability in water chemistry in the Lower Mekong Basin: Considerations for fish life history reconstruction. *Estuar. Coast. Shelf Sci.* **255**, 107355 (2021).
 56. Vu, A. V. et al. Diverse migration strategies of ariid catfishes along a salinity gradient in the Mekong River. *Fish Res.* **279**, 107133 (2024).
 57. Larson, H. & Vidthayanon, C. *Sclerophages formosus*. *IUCN Red List Threatened Species* **2019**, e.T152320185A89797267 (2019).

58. Vidthayanon, C. Chitala blanci (errata version published in 2020). *IUCN Red List Threatened Species* **2011**, e.T4694A174778090 (2011).
59. Jenkins, A., Kullander, F. F. & Tan, H. H. Pangasius sanitwongsei. *IUCN Red List Threatened Species* **2009**, e.T15945A5324983 (2009).
60. Hogan, Z. Pangasianodon gigas. The IUCN Red List of Threatened Species 2011: e.T15944A5324699. 2011 <https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T15944A5324699.en> (2011).
61. Couto, T. B. A., Messenger, M. L. & Olden, J. D. Safeguarding migratory fish via strategic planning of future small hydropower in Brazil. *Nat. Sustain* **4**, 409–416 (2021).
62. Baumgartner, L. J., Marsden, T., Duffy, D., Horta, A. & Ning, N. Optimizing efforts to restore aquatic ecosystem connectivity requires thinking beyond large dams. *Environ. Res. Lett.* **17**, 014008 (2022).
63. Vu, A. V. et al. Diverse migration tactics of fishes within the large tropical Mekong River system. *Fish Manag. Ecol.* **29**, 708–723 (2022).
64. Cowx, I. G. et al. *Larval and Juvenile Fish Communities of the Lower Mekong Basin. MRC Technical Paper No. 49. Phnom Penh, Cambodia: Mekong River Commission.* (2015).
65. Baumgartner, L. J. et al. Using an experimental in situ fishway to provide key design criteria for lateral fish passage in tropical rivers: a case study from the mekong river, central Lao PDR. *River Res. Appl.* **28**, 1217–1229 (2012).
66. Thieme, M. L. et al. Navigating trade-offs between dams and river conservation. *Glob. Sustain* **4**, e17 (2021).
67. Thieme, M. et al. Measures to safeguard and restore river connectivity. *Environ. Rev.* <https://doi.org/10.1139/er-2023-0019> (2023).
68. Pelicice, F. M. & Agostinho, A. A. Fish-passage facilities as ecological traps in large neotropical rivers. *Conserv. Biol.* **22**, 180–188 (2008).
69. Silva, A. T. et al. The future of fish passage science, engineering, and practice. *Fish Fish* **19**, 340–362 (2018).
70. Sun, J. et al. Towards a comprehensive river barrier mapping solution to support environmental management. *Nat. Water* **3**, 38–48 (2025).
71. Birnie-Gauvin, K., Tummers, J. S., Lucas, M. C. & Aarestrup, K. Adaptive management in the context of barriers in European freshwater ecosystems. *J. Environ. Manag.* **204**, 436–441 (2017).
72. Marsden, T., Baumgartner, L. J., Duffy, D., Horta, A. & Ning, N. Evaluation of a new practical low-cost method for prioritising the remediation of fish passage barriers in resource-deficient settings. *Ecol. Eng.* **194**, 107024 (2023).
73. Kowal, J. L. et al. Over 100 years of longitudinal connectivity changes from the perspective of a migratory fish species. *Ecol. Indic.* **175**, 113436 (2025).
74. Vasconcelos, L. P., Alves, D. C. & Gomes, L. C. Fish reproductive guilds downstream of dams. *J. Fish Biol.* **85**, 1489–1506 (2014).
75. Rao, S., Krishnaswamy, J. & Bhalla, R. S. Linking flow alteration with fish assemblage structure in a river regulated by a small hydropower project in the Western Ghats of Karnataka, India. *River Res. Appl.* **38**, 138–151 (2022).
76. Atkore, V., Kelkar, N., Badiger, S., Shanker, K. & Krishnaswamy, J. Multiscale investigation of water chemistry effects on fish guild species richness in regulated and nonregulated rivers of India's Western Ghats: implications for restoration. *Trans. Am Fish Soc.* **149**, 298–319 (2020).
77. Jumani, S. et al. Fish community responses to stream flow alterations and habitat modifications by small hydropower projects in the Western Ghats biodiversity hotspot, India. *Aquat. Conserv.* **28**, 979–993 (2018).
78. Ding, C. et al. Flow and thermal regimes altered by a dam caused failure of fish recruitment in the upper Mekong River. *Freshw. Biol.* **68**, 1319–1329 (2023).
79. Chhuoy, S. et al. Declines in the Mekong's megadiverse larval fish assemblages: implications for sustainable development. *Sustainability* **15**, 13535 (2023).
80. Havel, J. E., Lee, C. E. & Vander Zanden, J. M. Do reservoirs facilitate invasions into landscapes? *Bioscience* **55**, 518–525 (2005).
81. Ang, W. J., Park, E., Pokhrel, Y., Tran, D. D. & Loc, H. H. Dams in the Mekong: a comprehensive database, spatiotemporal distribution, and hydropower potentials. *Earth. Syst. Sci. Data* **16**, 1209–1228 (2024).
82. Wang, J., Tao, J., Heino, J., Huang, M. & Ding, C. Geodiversity as a surrogate to inform freshwater fish diversity conservation and management. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.70057> (2025).
83. Froese, R. & Pauly, D. FishBase. *World Wide Web electronic publication* <https://www.fishbase.in/search.php> (2024).
84. Lucas, M. C. & Baras, E. *Migration of Freshwater Fishes.* (Blackwell Science Ltd, Oxford, UK, 2001). <https://doi.org/10.1002/9780470999653>.
85. Lehner, B. & Grill, G. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. *Hydrol Process* **27**, 2171–2186 (2013).
86. Linke, S. et al. Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. *Sci. Data* **6**, 283 (2019).
87. Zarfl, C. et al. Future large hydropower dams impact global freshwater megafauna. *Sci. Rep.* **9**, 18531 (2019).
88. Radinger, J. & Wolter, C. Patterns and predictors of fish dispersal in rivers. *Fish Fish* **15**, 456–473 (2014).
89. Radinger, J. et al. The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Glob. Chang. Biol.* **23**, 4970–4986 (2017).
90. Herrera-R, G. A. et al. The combined effects of climate change and river fragmentation on the distribution of Andean Amazon fishes. *Glob. Chang. Biol.* **26**, 5509–5523 (2020).
91. Cassemiro, F. A. S. et al. Landscape dynamics and diversification of the megadiverse South American freshwater fish fauna. *Proc. Natl. Acad. Sci.* **120**, e2211974120 (2023).
92. Wang, J. et al. Analysing spatio-temporal patterns of non-native fish in a biodiversity hotspot across decades. *Divers Distrib.* **29**, 1492–1507 (2023).
93. Legendre, P. & De Cáceres, M. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* **16**, 951–963 (2013).
94. Legendre, P. Interpreting the replacement and richness difference components of beta diversity. *Glob. Ecol. Biogeogr.* **23**, 1324–1334 (2014).
95. Rodeles, A. A., Galicia, D. & Miranda, R. A simple method to assess the fragmentation of freshwater fish meta-populations: Implications for river management and conservation. *Ecol. Indic.* **125**, 107557 (2021).
96. Baldan, D., Cunillera-Montcusí, D., Funk, A. & Hein, T. Introducing 'riverconn': an R package to assess river connectivity indices. *Environ. Model Softw.* **156**, 105470 (2022).
97. Csárdi, G. et al. Package 'igraph'. *CRAN: Contributed Packages* <https://doi.org/10.32614/CRAN.package.igraph> (2025).
98. Borthagaray, A. I. et al. Community isolation drives lower fish biomass and species richness, but higher functional evenness, in a river metacommunity. *Freshw. Biol.* **65**, 2081–2095 (2020).
99. IUCN. The IUCN Red List of Threatened Species. Version 2024-2. <https://www.iucnredlist.org> (2024).

Acknowledgements

The study was funded by the National Natural Science Foundation of China (42301064), and the Yunnan Scientist Workstation on International River Research of Daming He (K264202011220).

Author contributions

J.S., M.C.L., and C.D. planned the project. J.S., J.W., and M.L. prepared the data. J.S. and D.B. performed the connectivity analysis and the statistical analysis. J.S., M.C.L., and D.B. wrote the original draft. All authors (J.S., D.B., M.C.L., J.W., A.R., S.G., J.T., M.L., D.H., and C.D.) commented and

improved the manuscript and agreed on the final version. J.S. supervised this work.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s43247-025-02467-y>.

Correspondence and requests for materials should be addressed to Jingrui Sun.

Peer review information *Communications Earth and Environment* thanks Vidyadhar Atkore and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editor: Alice Drinkwater. A peer review file is available.

Reprints and permissions information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025