Dark fragmentation: daylighting hidden disconnections in river networks

Jingrui Sun[1,2,*], Damiano Baldan[3], Ellen Wohl[4], Yushan Tang[1], Julian D. Olden[5]

1. Yunnan Key Laboratory of International Rivers and Transboundary Eco-security, Institute of International Rivers and Eco-security, Yunnan University, Kunming, 650091, China.

2. Ministry of Education Key Laboratory for Transboundary Eco-Security of Southwest China, Yunnan University, Kunming, 650091, China

3. National Institute of Oceanography and Applied Geophysics (OGS), Trieste, Italy

4. *Department of Geosciences, Colorado State University, Fort Collins, Colorado, 80523-1482, USA*

5. *School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, 98195 USA*

* Correspondence; jingrui.sun@ynu.edu.cn

Abstract

River fragmentation is a central driver of freshwater biodiversity loss, yet its true extent is often underestimated due to incomplete barrier inventories, static river maps, and simplified assumptions about barrier passability. We propose dark fragmentation as the hidden component of river-network disconnection arising from three interacting dimensions: inventory darkness caused by unmapped barriers, functional darkness from poorly characterized barrier function, and hydrological darkness from under-documented hydrological interruptions. Together, these dimensions broader mismatch between mapped connectivity from realized ecological connectivity. Dark fragmentation provides a framework for identifying where conventional assessments overestimate river continuity and misguide conservation decisions. We outline how these hidden components can be estimated using improved barrier mapping, passability assessment, hydrological monitoring, and scenario-based connectivity modelling. Recognizing dark fragmentation can help target field surveys, reveal hidden bottlenecks that limit species from accessing required habitats, improve restoration prioritization, and support more realistic freshwater conservation targets.

In a nutshell

- Small barriers and dry river sections are often missing from maps and inventories, while the real effects of these are often oversimplified.
- ‘Dark fragmentation’ draws attention to hidden breaks that make rivers less connected than they appear.
- Recognizing dark fragmentation can improve field surveys, restoration planning, and decisions about where habitat reconnection matters most.

Introduction

Rivers are among the most fragmented ecosystems on Earth, yet the degree of fragmentation we report is still largely contingent on the barriers we have managed to record (Sun, Lucas, et al., 2025), their effect on fish populations (He et al., 2024), and the degree of hydrological alteration (Gou et al., 2025; Jaeger et al., 2014). Global and regional assessments of river fragmentation commonly rely on inventories of dams, weirs, sluices, culverts and other instream structures to estimate river connectivity, which are then used to identify free-flowing rivers and prioritize restoration action (Belletti et al., 2020; Grill et al., 2019). These inventories have improved substantially over the past decade, making it possible to quantify the number and location of large dams, reservoirs and many instream barriers at unprecedented scales (Lehner et al., 2024). However, it is well recognized that these assessments remain incomplete and geographically biased. Many small, obsolete, informal or locally managed barriers are missing, particularly in tributaries (Caskey et al., 2015), agricultural landscapes, urban streams and transboundary basins where infrastructure records are fragmented among agencies or countries (Baumgartner et al., 2022; Buchanan et al., 2022; Sun et al., 2024). Many recorded barriers also lack information on when they were built and attributes describing height, operation, seasonality, and biological passability (Sun et al., 2026). Further, fragmentation can arise also from the presence of other stressors not directly related to in-stream structures. For instance, point-pollution from wastewater treatment plants or mine effluents can isolate fish populations (Turner, 2022). Also, hydromorphological modifications such as river channelization can lead to increased fragmentation (Hayes et al., 2022). As a result, current assessments may underestimate the cumulative effects of small, poorly characterized, or less obvious barriers, whose ecological importance depends less on size alone than on position, density, passability and timing (Samia et al., 2015; Sun, Baldan, et al., 2025).

Hidden fragmentation can also arise from hydrological disconnection rather than physical structures alone. Many rivers are naturally intermittent, with seasonal flow contraction and expansion forming part of their ecological dynamics (Luo et al., 2026; Messager et al., 2021). Stream drying can result in highly fragmented river systems (e.g., Jaeger et al., 2014). However, ecological assessments may fail to represent the timing, frequency and spatial patterns of wet and dry phases, leading to river networks being treated as continuously connected even when aquatic organisms experience seasonal isolation into pools, disconnected reaches or dry channels (Palmer & Ruhi, 2019). Human activities can intensify this problem by converting naturally perennial reaches into intermittent or dewatered ones (Gou et al., 2025; Sarremejane et al., 2022) or by increasing the extent and duration of dry periods along intermittent rivers (Falke et al., 2011). In mountainous regions, diversion-type hydropower schemes may route water through canals, tunnels or pipes, leaving bypassed river sections with severely reduced flow (Chen et al., 2013; Couto et al., 2023). In some pumped-storage or peaking hydropower systems, water-level fluctuation and operational flow changes can also create periods of ecological disconnection (He et al., 2024; Poff & Zimmerman, 2010). These reaches may remain visible as river lines on maps while functioning as barriers to movement during critical seasons.

For fish and other river-dependent processes, this distinction is crucial. A species may not require continuously connected habitats, but may depend on connectivity during spawning migration, juvenile dispersal, recolonization after disturbance or seasonal movement to refuge habitats (Fullerton et al., 2010; Lucas & Baras, 2001). Dry river reaches can be as fragmenting as a physical barrier (J. S. Perkin et al., 2019). For metapopulations, intermittent disconnection can reduce recolonization after local extirpation. For sediment and organic matter, reduced flow or dewatered sections can interrupt transport pathways (Angelaki & Harbor, 1995; Bussi et al., 2021). The connectivity inferred from maps and existing inventories can therefore be more optimistic than the connectivity experienced by organisms and shaping ecological processes.

Defining dark fragmentation

Ecology has increasingly used “dark” concepts to daylight hidden environmental challenges and gaps in our scientific understanding. For instance, dark diversity refers to species absent from a site but belonging to its potential species pool (Pärtel et al., 2011), while dark extinction describes poorly documented species losses missing from formal extinction accounting (Boehm & Cronk, 2021). This logic can be extended to river networks by proposing dark fragmentation: the hidden component of river-network fragmentation that is absent from connectivity assessments because the full gamut of barrier types, from gray infrastructure to dry stream reaches are unmapped, undocumented or poorly characterized with respect to organisms seeking to circumvent them. Here, we focus primarily on longitudinal connectivity along river channels, while recognizing that hidden dimensions of lateral connectivity between channels and floodplains (Knox et al., 2022) and vertical connectivity between surface water and groundwater, also exist. The concept captures the gap between apparent connectivity inferred from existing maps and inventories and the realized connectivity experienced by organisms and ecological processes. Recognizing this gap is important because incomplete data on barriers, flow permanence and passability can cause conservation assessments to overestimate river connectivity and underestimate our understand of, and response to, ecological risk.

This definition is intentionally broader than “missing dams”. It recognizes that river fragmentation is not only caused by visible, permanent, concrete structures, but can also arise from hydrological disconnection caused by seasonal drying, water abstraction, from operational barriers such as sluices and temporary closures; and from structures whose passability remains unknown. A river channel may remain present on a map even when it becomes dry for several months. A dam may be present in a database but very often lacks information on whether, and if so with what likelihood, different fish can pass. A small irrigation structure may never appear in a national inventory but still disconnect river systems (Morden et al., 2022). These are all forms of hidden disconnection. A culvert may enhance flow velocity and cause vertical drops in the river bed, both of which can preclude passage by many aquatic organisms (Jones & Hale, 2020).

Given the different sources of uncertainty in the characterization of fragmentation highlighted above, we propose to separate dark fragmentation into three interacting dimensions. First, inventory darkness occurs when physical barriers exist but are absent from formal datasets. These may include small weirs, culverts, sluices, road crossings, other informal structures, or non-structural sources of fragmentation. Such barriers are often too small to be included in dam registries, too numerous for conventional field surveys, or managed by local agencies whose records are not integrated into national or global databases. Second, functional darkness occurs when barriers are mapped, but their ecological effects are unknown or highly uncertain. A barrier location alone does not reveal its passability. Height, slope, water depth, velocity, operation, fishway performance, seasonal closure and species-specific swimming ability all influence whether barrier passibility fragments a river (Sun et al., 2023). Treating mapped barriers as either fully passable or fully impassable can obscure this uncertainty. Third, hydrological darkness occurs when river channels are mapped as continuous, but flow conditions make them temporarily or persistently disconnected. Seasonal drying or drought, water abstraction, irrigation withdrawals, diversion of hydropower and some pumped-storage or peaking operations can create dry, reduced-flow or ecologically impassable reaches. These disconnections may not be visible in static hydrographic datasets, especially when maps represent the channel rather than the water actually present within it (Jaeger et al., 2014). Although such disconnections mainly refer to longitudinal movement, altered flow permanence and dewatered reaches can also reduce lateral exchange between rivers and adjacent floodplains, and modify vertical exchanges with hyporheic and groundwater systems. Together, these three dimensions shift the focus from barrier presence alone to the broader mismatch between mapped connectivity and realized ecological connectivity.

A conceptual framework for assessing dark fragmentation

Dark fragmentation could be conceptualized as the difference between the available connectivity estimates (inferred from the available knowledge of barriers distribution, functional attributes and hydrological patterns) and the true connectivity that would be obtained if the full barrier population, true passability, and actual hydrological connectivity regime were known. For any selected connectivity metric C, this can be conceptualized as:

$$DF = C(B_{mapped}, P_{default}, H_{static}) - C(B_{true}, P_{true}, H_{actual})$$

Where, B_{mapped} represents the barriers recorded in existing inventories; $P_{default}$ represents default assumptions about barrier passability; and H_{static} represents the static hydrological condition usually implied by mapped river networks. In contrast, B_{true} denotes the complete barrier population, P_{true} denotes the true (dynamic) passability of those barriers for the organisms or processes of interest. Such passability information can be obtained from telemetry, mark–recapture studies, fishway monitoring, or assessments linking barrier hydraulics to species-specific swimming capacity. H_{actual} denotes the actual hydrological connectivity regime, including seasonal drying, dewatered reaches, and other flow discontinuities.

In practice, however, B_{true}, P_{true}, and H_{actual} are rarely fully known. If the complete barrier distribution, true passability regime, and actual hydrological connectivity regime are unknown, then $C(B_{true}, P_{true}, H_{actual})$ cannot be calculated and total dark fragmentation cannot be directly measured. Conversely, if these components were known perfectly, the hidden component would no longer be “dark”, because it would already be incorporated into the connectivity assessment. Thus, dark fragmentation is best understood not as a single directly measurable value, but as a hidden component that can be progressively revealed, bounded or inferred. Operationally, the concept should therefore be assessed through evidence, uncertainty and ecological mismatch. We identify three approaches to support the quantification of dark diversity.

First, detection-based assessment uses existing and newly added data to reveal specific hidden disconnections. For example, hidden barriers can be estimated using multiple evidence sources, including high-resolution satellite imagery, deep-learning object detection, historical maps, local infrastructure records, field surveys, and citizen-science observations (Allen et al., 2019; Morden et al., 2022; Sun, Lucas, et al., 2025). Hydrological disconnection can be incorporated using stream gauges, surface-water remote sensing, hydrological models, environmental-flow records or local observations, so that connectivity models represent when and where flow is sufficient for ecological movement. This approach quantifies the portion of dark fragmentation revealed by additional information, while recognizing that remaining hidden components may persist. Once detected and validated, these previously hidden disconnections should be incorporated into future baseline inventories and connectivity assessments, thereby reducing the remaining dark-fragmentation component.

Second, uncertainty-based assessment evaluates how sensitive connectivity estimates are to plausible but unverified assumptions. Instead of requiring complete knowledge of true passability or all unrecorded barriers, this approach compares scenarios such as high versus low passability, wet-season versus dry-season connectivity, or alternative densities of unmapped barriers (Kowal et al., 2024). If connectivity estimates, free-flowing river classifications or restoration rankings change substantially while exploring such uncertainties, the river network is highly exposed to dark-fragmentation uncertainty. Passability should be treated as uncertain and species-specific (Panagiotopoulos et al., 2024; Samia et al., 2015). A barrier may be passable for large-bodied strong swimmers during high flows but impassable for juveniles, small-bodied species or benthic fishes and crayfishes (Bourne et al., 2011). Similarly, a dry reach may block fish movement during one season while remaining less relevant to other organisms, processes or periods. Dark fragmentation should therefore be evaluated relative to focal organisms, ecological processes and seasons. Rather than reporting a single connectivity value, assessments should compare scenarios based on known barriers, likely additional barriers, alternative passability assumptions and seasonal-flow conditions. Scenario-based assessments can also compare fragmentation estimates with and without fish-passage structures or other mitigation measures. Treating barriers as unmitigated provides a conservative baseline, whereas incorporating known fish passes and their species-specific effectiveness can estimate how much connectivity is actually restored. This approach can highlight geographic gaps in fish-passage provision, identifying basins or barrier clusters where barriers remain abundant but mitigation infrastructure is absent, poorly documented or concentrated in only a few regions. Overall, it can identify where management conclusions are robust and where additional data would most improve decision-making.

Third, inference-based assessment mirrors the logic of dark diversity by comparing expected ecological connectivity with observed ecological outcomes (Pärtel et al., 2011). If a river reach is environmentally suitable, has no clear evidence of habitat degradation, water pollution, fishing pressure, other anthropogenic disturbance or sampling insufficiency, and appears accessible according to existing barrier inventory and river-network data, but the target species is repeatedly absent or unexpectedly isolated, this mismatch can provide evidence of potential dark fragmentation (Wegscheider et al., 2024). In such cases, the absence or isolation may indicate unrecognized connectivity constraints, and this inference should then guide targeted field surveys, passability assessment or hydrological validation.

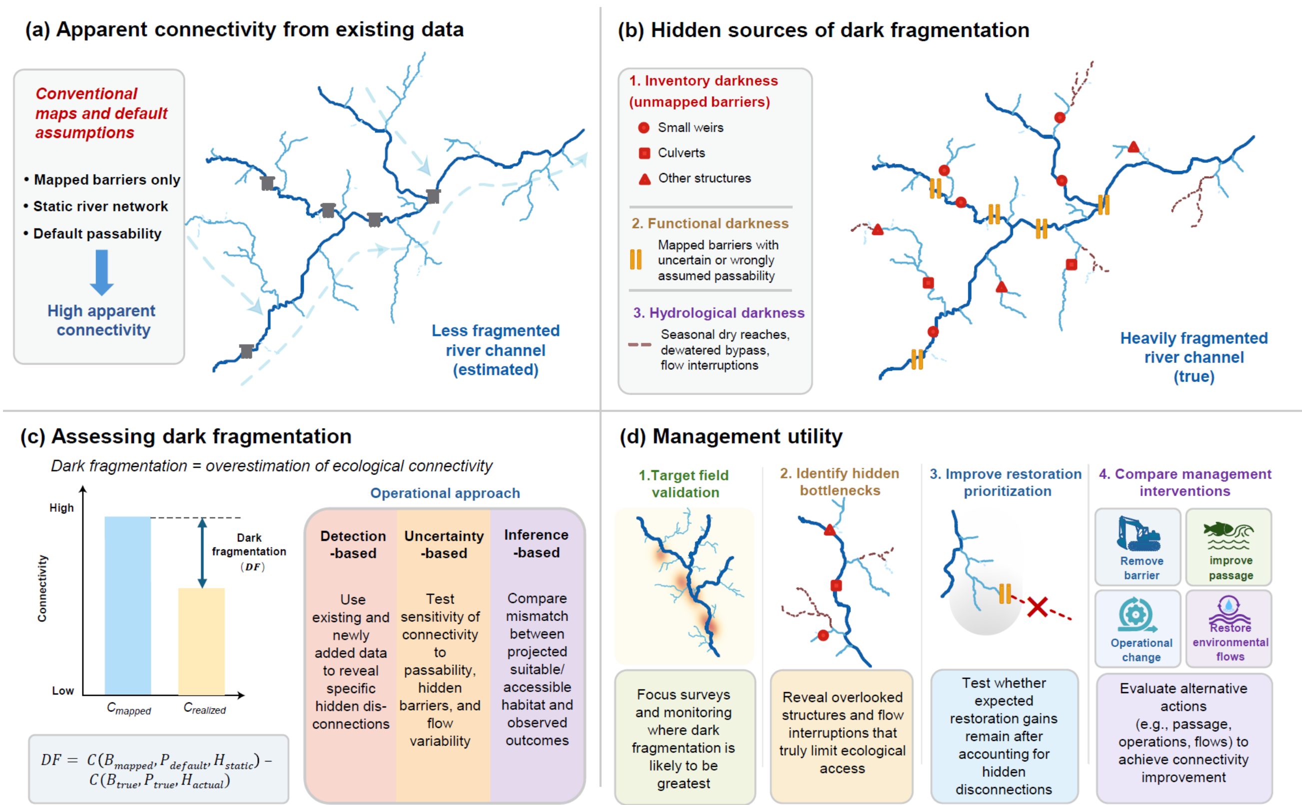

Figure 1. Conceptual framework for dark fragmentation in river networks. (a) Conventional connectivity assessments often rely on mapped barriers, static river networks and default passability assumptions, which can produce high apparent connectivity and underestimate river fragmentation. (b) Dark fragmentation arises when hidden sources of disconnection are absent from, or poorly represented in, existing assessments. These include inventory darkness from unmapped barriers such as small weirs and culverts; functional darkness from mapped barriers with uncertain or wrongly assumed passability; and hydrological darkness from seasonal dry reaches, dewatered bypasses or flow interruptions. (c) Dark fragmentation can be conceptualized as the overestimation of ecological connectivity, expressed as the gap between mapped connectivity and realized connectivity. (d) Assessing dark fragmentation can support river management by targeting field validation, improving restoration prioritization, identifying overlooked barriers or flow interruptions that limit ecological access, and comparing interventions such as barrier removal, fish-passage improvement, operational changes and environmental-flow restoration.

Utility of dark fragmentation assessment

Dark fragmentation has practical consequences for conservation science and policy. First, it can inflate estimates of free-flowing river extent. A river may be classified as free-flowing or weakly fragmented if only large dams are considered, while numerous small barriers, culverts or dry reaches remain unrecorded (Sun, Lucas, et al., 2025). This is especially likely in low-order streams, where many barriers are small but ecologically consequential. Second, dark fragmentation can mislead restoration prioritization. Barrier-removal planning often estimates the amount of habitat that would be reconnected by removing a specific structure. If unmapped barriers remain upstream, or if the restored reach becomes seasonally dry, expected gains may be overestimated (Ioannidou et al., 2023). Conversely, a small unmapped structure or dewatered reach may be the actual bottleneck preventing access to high-value habitat. Third, dark fragmentation may bias biodiversity models. Species-distribution models, population-connectivity analyses and conservation-priority maps often assume that river networks represent available pathways and rarely consider connectivity as a driver of species distribution (but see Felin et al., 2025 for an example). If hidden barriers or dis-connected reaches are omitted, models may overestimate dispersal, gene flow and habitat accessibility (Wegscheider et al., 2024). This can be particularly problematic for migratory fishes, headwater specialists, floodplain-dependent species and species with limited swimming capacity.

Dark fragmentation assessment is useful for river management because it identifies where conventional connectivity estimates are most likely to misinform decision-making. First, it may guide field validation by highlighting reaches where missing barriers, uncertain passability or hydrological disconnection are most likely to alter connectivity estimates (Sun, Lucas, et al., 2025). Second, it can improve restoration prioritization by testing whether the expected connectivity gains from removing a mapped barrier would remain after accounting for unmapped upstream or downstream barriers, uncertain passability, and seasonal flow gaps (King & O'Hanley, 2016). Third, because dark fragmentation can be partitioned into inventory, functional and hydrological components, it can help managers compare alternative interventions, including barrier removal, fish-passage improvement, operational changes and environmental-flow restoration (Thieme et al., 2023).

Although we focus on river networks, the logic of dark fragmentation is transferable to other ecosystems where apparent structural connectivity differs from realized ecological connectivity. In terrestrial landscapes, for example, linear infrastructure such as roads and fences creates physical barriers that restrict movement directly (Boone & Hobbs, 2004), while land-use change or artificial lighting can create functional barriers through habitat avoidance that may not be represented by habitat maps. In marine ecosystems, ocean currents, thermal fronts, hypoxic zones, shipping lanes, underwater noise, fishing pressure or coastal infrastructure may restrict fish larval dispersal, migration routes or population exchange despite the apparent continuity of open water (Cooke et al., 2024). In aerial systems, species may experience hidden fragmentation through artificial light at night, wind farms, collision risk, habitat loss at stopover sites, atmospheric conditions or other disturbance along flyways (E. K. Perkin et al., 2011). The broader value of dark fragmentation is therefore to encourage conservation assessments to distinguish mapped or apparent connectivity from functional connectivity experienced by organisms and ecological processes.

The concept of dark fragmentation should be applied carefully. Not every unmapped barrier or dry reach causes major ecological fragmentation, and natural intermittency can be an important feature of river ecosystems to which some species are adapted. Similarly, hydropower systems differ in their effects: some create physical barriers, some alter flow timing, and others dewater bypassed reaches or generate rapid flow fluctuations (He et al., 2024). The key issue is therefore not whether a river is always wet or connected, but whether current assessments accurately capture the connectivity conditions that matter for the organisms and processes being evaluated. Dark fragmentation is not a criticism of existing barrier inventories, which remain essential, but a call to use them more transparently as incomplete and uncertain representations of river connectivity that should be complemented with a much richer set of information. More broadly, dark fragmentation assessment shifts connectivity planning from static maps of barriers and channels toward dynamic evaluations of whether organisms and ecological processes can actually move through river networks under relevant seasonal, hydrological and operational conditions (Palmer & Ruhi, 2019). Advances in remote sensing, surface-water mapping, object detection and field validation now make this shift increasingly feasible.

Importantly, dark fragmentation should not be interpreted as a technical deficiency that can be fully overcome simply by improving datasets or applying new monitoring technologies. Some hidden disconnections will remain difficult to detect, quantify or generalize because barrier passability is species-specific, hydrological connectivity is seasonally dynamic, and ecological responses often depend on life stage, timing and local context. The aim of dark fragmentation assessment is to make this uncertainty explicit, spatially interpretable, and relevant to decision-making. In this sense, dark fragmentation marks the boundary between what current connectivity assessments can represent and what organisms and ecological processes may actually experience. Recognizing this boundary can help avoid false confidence in apparently connected river networks, encourage more cautious interpretation of free-flowing river estimates and restoration benefits, and identify where additional evidence would most improve management decisions.

Conclusion

We propose the concept of dark fragmentation to shed light on hidden disconnections in river networks caused by incomplete and/or uncertain knowledge of the number, type, distribution, and passability of riverine barriers. The concept does not replace existing barrier inventories or river-network datasets, but encourages their use as incomplete and uncertain representations of dynamic river systems. By identifying where connectivity is most likely to be overestimated, dark-fragmentation assessment can help improve barrier mapping, guide field validation, refine restoration priorities, evaluate protected-area effectiveness, and support more realistic river-conservation targets. Its practical value lies in turning hidden uncertainty into explicit evidence for decision-making, so that freshwater conservation is based not only on the rivers we can map, but also on the disconnections we have yet to see.

References

Allen, D. C., Kopp, D. A., Costigan, K. H., Datry, T., Hugueny, B., Turner, D. S., Bodner, G. S., & Flood, T. J. (2019). Citizen scientists document long-term streamflow declines in intermittent rivers of the desert southwest, USA. *Freshwater Science*, *38*(2), 244–256. https://doi.org/10.1086/701483

Angelaki, V., & Harbor, J. M. (1995). IMPACTS OF FLOW DIVERSION FOR SMALL HYDROELECTRIC POWER PLANTS ON SEDIMENT TRANSPORT, NORTHWEST WASHINGTON. *Physical Geography*, *16*(5), 432–443. https://doi.org/10.1080/02723646.1995.10642564

Baumgartner, L. J., Marsden, T., Duffy, D., Horta, A., & Ning, N. (2022). Optimizing efforts to restore aquatic ecosystem connectivity requires thinking beyond large dams. *Environmental Research Letters*, *17*(1), 014008. https://doi.org/10.1088/1748-9326/ac40b0

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436–441. https://doi.org/10.1038/s41586-020-3005-2

Boehm, M. M. A., & Cronk, Q. C. B. (2021). Dark extinction: the problem of unknown historical extinctions. *Biology Letters*, *17*(3), rsbl.2021.0007. https://doi.org/10.1098/rsbl.2021.0007

Boone, R. B., & Hobbs, N. T. (2004). Lines around fragments: effects of fencing on large herbivores. *African Journal of Range & Forage Science*, *21*(3), 147–158. https://doi.org/10.2989/10220110409485847

Bourne, C. M., Kehler, D. G., Wiersma, Y. F., & Cote, D. (2011). Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. *Aquatic Ecology*, *45*(3), 389–403. https://doi.org/10.1007/s10452-011-9362-z

Buchanan, B. P., Sethi, S. A., Cuppett, S., Lung, M., Jackman, G., Zarri, L., Duvall, E., Dietrich, J., Sullivan, P., Dominitz, A., Archibald, J. A., Flecker, A., & Rahm, B. G. (2022). A machine learning approach to identify barriers in stream networks demonstrates high prevalence of unmapped riverine dams. *Journal of Environmental Management*, *302*, 113952. https://doi.org/10.1016/j.jenvman.2021.113952

Bussi, G., Darby, S. E., Whitehead, P. G., Jin, L., Dadson, S. J., Voepel, H. E., Vasilopoulos, G., Hackney, C. R., Hutton, C., Berchoux, T., Parsons, D. R., & Nicholas, A. (2021). Impact of dams and climate change on suspended sediment flux to the Mekong delta. *Science of The Total Environment*, *755*, 142468. https://doi.org/10.1016/j.scitotenv.2020.142468

Caskey, S. T., Blaschak, T. S., Wohl, E., Schnackenberg, E., Merritt, D. M., & Dwire, K. A. (2015). Downstream effects of stream flow diversion on channel characteristics and riparian vegetation in the Colorado Rocky Mountains, USA. *Earth Surface Processes and Landforms*, *40*(5), 586–598. https://doi.org/10.1002/esp.3651

Chen, Q., Chen, D., Li, R., Ma, J., & Blanckaert, K. (2013). Adapting the operation of two cascaded reservoirs for ecological flow requirement of a de-watered river channel due to diversion-type hydropower stations. *Ecological Modelling*, *252*, 266–272. https://doi.org/10.1016/j.ecolmodel.2012.03.008

Cooke, S. J., Piczak, M. L., Singh, N. J., Åkesson, S., Ford, A. T., Chowdhury, S., Mitchell, G. W., Norris, D. R., Hardesty-Moore, M., McCauley, D., Hammerschlag, N., Tucker, M. A., Horns, J. J., Reisinger, R. R., Kubelka, V., & Lennox, R. J. (2024). Animal migration in the Anthropocene: threats and mitigation options. *Biological Reviews*, *99*(4), 1242–1260. https://doi.org/10.1111/brv.13066

Couto, T. B. A., Rezende, R. S., de Aquino, P. P. U., Costa-Pereira, R., de Campos, G. L., Occhi, T.

V. T., Vitule, J. R. S., Espírito-Santo, H. M. V., Soares, Y. F. F., & Olden, J. D. (2023). Effects of small hydropower dams on macroinvertebrate and fish assemblages in southern Brazil. *Freshwater Biology*, *68*(6), 956–971. https://doi.org/10.1111/fwb.14078

Falke, J. A., Fausch, K. D., Magelky, R., Aldred, A., Durnford, D. S., Riley, L. K., & Oad, R. (2011). The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecohydrology*, *4*(5), 682–697. https://doi.org/10.1002/eco.158

Felin, S., Belliard, J., Grenouillet, G., Moatar, F., Le Pichon, C., Thieu, V., Thirel, G., & Jeliazkov, A. (2025). The role of river connectivity in the distribution of fish in an anthropized watershed. *Science of The Total Environment*, *959*, 178204. https://doi.org/10.1016/j.scitotenv.2024.178204

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G. R., Feist, B. E., Torgersen, C. E., Miller, D. J., & Sanderson, B. L. (2010). Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology*, *55*(11), 2215–2237. https://doi.org/10.1111/j.1365-2427.2010.02448.x

Gou, J., Miao, C., Ni, J., Sorooshian, S., Duan, Q., Yan, D., Slater, L., Xu, Z., Borthwick, A. G. L., Su, L., Zhang, Q., & Wada, Y. (2025). Warming climate and water withdrawals threaten river flow connectivity in China. *Proceedings of the National Academy of Sciences*, *122*(34). https://doi.org/10.1073/pnas.2421046122

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*(7755), 215–221. https://doi.org/10.1038/s41586-019-1111-9

Hayes, D. S., Schaufler, G., Schmutz, S., Unfer, G., Führer, S., Auer, S., & Seliger, C. (2022). Hydro-morphological stressors reduce distribution range and affect population status of cyprinid fishes in Austria. *Frontiers in Environmental Science*, *10*. https://doi.org/10.3389/fenvs.2022.991722

He, F., Zarfl, C., Tockner, K., Olden, J. D., Campos, Z., Muniz, F., Svenning, J.-C., & Jähnig, S. C. (2024). Hydropower impacts on riverine biodiversity. *Nature Reviews Earth & Environment*, *5*, 755–772. https://doi.org/10.1038/s43017-024-00596-0

Ioannidou, C. T., Neeson, T. M., & O'Hanley, J. R. (2023). Boosting large-scale river connectivity restoration by planning for the presence of unrecorded barriers. *Conservation Biology*, *37*(3), e14093. https://doi.org/10.1111/cobi.14093

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894–13899. https://doi.org/10.1073/pnas.1320890111

Jones, M. J., & Hale, R. (2020). Using knowledge of behaviour and optic physiology to improve fish passage through culverts. *Fish and Fisheries*, *21*(3), 557–569. https://doi.org/10.1111/faf.12446

King, S., & O'Hanley, J. R. (2016). Optimal fish passage barrier removal-revisited. *River Research and Applications*, *32*(3), 418–428. https://doi.org/10.1002/rra.2859

Knox, R. L., Morrison, R. R., & Wohl, E. E. (2022). Identification of Artificial Levees in the Contiguous United States. *Water Resources Research*, *58*(4). https://doi.org/10.1029/2021WR031308

Kowal, J. L., Funk, A., Unfer, G., Baldan, D., Haidvogl, G., Hauer, C., Ferreira, M. T., Branco, P., Schinegger, R., & Hein, T. (2024). River continuum disruptions in a highly altered system: The perspective of potamodromous fish. *Ecological Indicators*, *164*, 112130. https://doi.org/10.1016/j.ecolind.2024.112130

Lehner, B., Beames, P., Mulligan, M., Zarfl, C., De Felice, L., van Soesbergen, A., Thieme, M., Garcia de Leaniz, C., Anand, M., Belletti, B., Brauman, K. A., Januchowski-Hartley, S. R., Lyon, K., Mandle, L., Mazany-Wright, N., Messager, M. L., Pavelsky, T., Pekel, J.-F., Wang, J., … Higgins, J. (2024). The Global Dam Watch database of river barrier and reservoir information for large-scale applications. *Scientific Data*, *11*(1), 1069. https://doi.org/10.1038/s41597-024-03752-9

Lucas, M. C., & Baras, E. (2001). *Migration of Freshwater Fishes*. Blackwell Science Ltd. https://doi.org/10.1002/9780470999653

Luo, Q., Feng, L., Park, E., Walling, D. E., Huang, L., Wang, M., Woolway, R. I., Fang, H., & Gong, J. (2026). Global net increase in surface water connectivity in river–floodplain systems. *Nature Geoscience*, *19*(5), 556–564. https://doi.org/10.1038/s41561-026-01953-y

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391–397. https://doi.org/10.1038/s41586-021-03565-5

Morden, R., Horne, A., Bond, N. R., Nathan, R., & Olden, J. D. (2022). Small artificial impoundments have big implications for hydrology and freshwater biodiversity. *Frontiers in Ecology and the Environment*, *20*(3), 141–146. https://doi.org/10.1002/fee.2454

Palmer, M., & Ruhi, A. (2019). Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. *Science*, *365*(6459). https://doi.org/10.1126/science.aaw2087

Panagiotopoulos, P., Buijse, A. D., Winter, H. V., & Nagelkerke, L. A. J. (2024). A large-scale passage evaluation for multiple fish species: Lessons from 82 fishways in lowland rivers and brooks. *Ecological Engineering*, *199*, 107158. https://doi.org/10.1016/j.ecoleng.2023.107158

Pärtel, M., Szava-Kovats, R., & Zobel, M. (2011). Dark diversity: shedding light on absent species. *Trends in Ecology & Evolution*, *26*(3), 124–128. https://doi.org/10.1016/j.tree.2010.12.004

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere*, *2*(11), art122. https://doi.org/10.1890/ES11-00241.1

Perkin, J. S., Starks, T. A., Pennock, C. A., Gido, K. B., Hopper, G. W., & Hedden, S. C. (2019). Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecohydrology*, *12*(6). https://doi.org/10.1002/eco.2120

Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*(1), 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Samia, Y., Lutscher, F., & Hastings, A. (2015). Connectivity, passability and heterogeneity interact to determine fish population persistence in river networks. *Journal of The Royal Society Interface*, *12*(110), 20150435. https://doi.org/10.1098/rsif.2015.0435

Sarremejane, R., Messager, M. L., & Datry, T. (2022). Drought in intermittent river and ephemeral stream networks. *Ecohydrology*, *15*(5). https://doi.org/10.1002/eco.2390

Sun, J., Baldan, D., Lucas, M. C., Wang, J., Rodeles, A. A., Galib, S. M., Tao, J., Li, M., He, D., & Ding, C. (2025). Widespread and strong impacts of river fragmentation by anthropogenic barriers on fishes in the Mekong River Basin. *Communications Earth & Environment*, *6*(1), 534. https://doi.org/10.1038/s43247-025-02467-y

Sun, J., Ding, C., Lucas, M. C., Tao, J., Cheng, H., Chen, J., Li, M., Ding, L., Ji, X., Wang, Y., & He, D. (2024). Convolutional Neural Networks Facilitate River Barrier Detection and Evidence Severe Habitat Fragmentation in the Mekong River Biodiversity Hotspot. *Water Resources Research*, *60*(1), e2022WR034375. https://doi.org/10.1029/2022WR034375

Sun, J., Lucas, M. C., Olden, J. D., Couto, T. B. A., Ning, N., Duffy, D., & Baumgartner, L. J. (2025). Towards a comprehensive river barrier mapping solution to support environmental management. *Nature Water*, *3*, 38–48. https://doi.org/10.1038/s44221-024-00364-w

Sun, J., Lucas, M. C., Olden, J. D., & He, D. (2026). Closing Data Gaps to Improve River Barrier Management in South and Southeast Asia. *WIREs Water*, *13*(1). https://doi.org/10.1002/wat2.70055

Sun, J., Tan, J., Zhang, Q., Shen, Y., Shi, J., Zhang, H., & Shi, X. (2023). Attraction and passage efficiency for salmonids and non-salmonids based on fishway: A meta-analysis approach. *River Research and Applications*, *39*(10), 1933–1949. https://doi.org/10.1002/rra.4194

Thieme, M., Birnie-Gauvin, K., Opperman, J. J., Franklin, P. A., Richter, H., Baumgartner, L., Ning, N., Vu, A. V., Brink, K., Sakala, M., O'Brien, G. C., Petersen, R., Tongchai, P., & Cooke, S. J. (2023). Measures to safeguard and restore river connectivity. *Environmental Reviews*. https://doi.org/10.1139/er-2023-0019

Turner, A. M. (2022). Chemical fragmentation of stream systems and fish species richness: The upstream effects of water pollution. *Freshwater Science*, *41*(4), 615–625. https://doi.org/10.1086/722102

Wegscheider, B., Waldock, C., Calegari, B. B., Josi, D., Brodersen, J., & Seehausen, O. (2024). Neglecting biodiversity baselines in longitudinal river connectivity restoration impacts priority setting. *Science of The Total Environment*, *954*, 175167.

https://doi.org/10.1016/j.scitotenv.2024.175167

ACKNOWLEDGEMENTS

The study was funded by the National Natural Science Foundation of China (42301064).

Author Contributions Statement

JS and DB contributed to the conceptualization and discussion of the content. JS and DB led the writing of the draft manuscript. YT and JS contributed to visualization and figure preparation. All authors (JS, DB, EW, YT, and JDO) reviewed and edited the manuscript before submission.

Financial and Non-Financial Competing Interest statement

The authors declare no competing interests.