

CONSERVATION

Human impacts on global freshwater fish biodiversity

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Freshwater fish represent one-fourth of the world’s vertebrates and provide irreplaceable goods and services but are increasingly affected by human activities. A new index, Cumulative Change in Biodiversity Facets, revealed marked changes in biodiversity in >50% of the world’s rivers covering >40% of the world’s continental surface and >37% of the world’s river length, whereas <14% of the world’s surface and river length remain least impacted. Present-day rivers are more similar to each other and have more fish species with more diverse morphologies and longer evolutionary legacies. In temperate rivers, where the impact has been greatest, biodiversity changes were primarily due to river fragmentation and introduction of non-native species.

Rivers and lakes cover less than 1% of Earth’s surface but represent substantial biodiversity, including nearly 18,000 fish species that constitute one-fourth of global vertebrates (1–3). These freshwater fishes support the functioning and stability of ecosystems through their contribution to

biomass production and regulation of trophic networks and nutrient cycles (4). Freshwater fishes also contribute to human welfare as key food resources (5) and for recreational and cultural activities (2, 6).

For centuries, human populations have directly affected fish biodiversity (7) through

extraction and introduction of non-native species (8, 9). Human activities have also modified the natural environment by changing land uses, altering flow regimes, fragmenting rivers by dams, polluting soil and waters, and altering climate; such actions indirectly favor extinction of native species and/or establishment of non-native species (10–13). Consequently, these direct and indirect anthropogenic impacts have led to modification of local species compositions (8, 9). However, biodiversity is not restricted to purely taxonomic components but also includes functional and phylogenetic diversities. These two latter facets determine how organisms affect ecosystem functioning and stability (14–18) and are thus essential for conservation.

Here, we assess the extent to which six key facets of freshwater fish biodiversity—taxonomic, functional, and phylogenetic richness, plus the dissimilarity among river basins in each of these categories—have changed over the past two

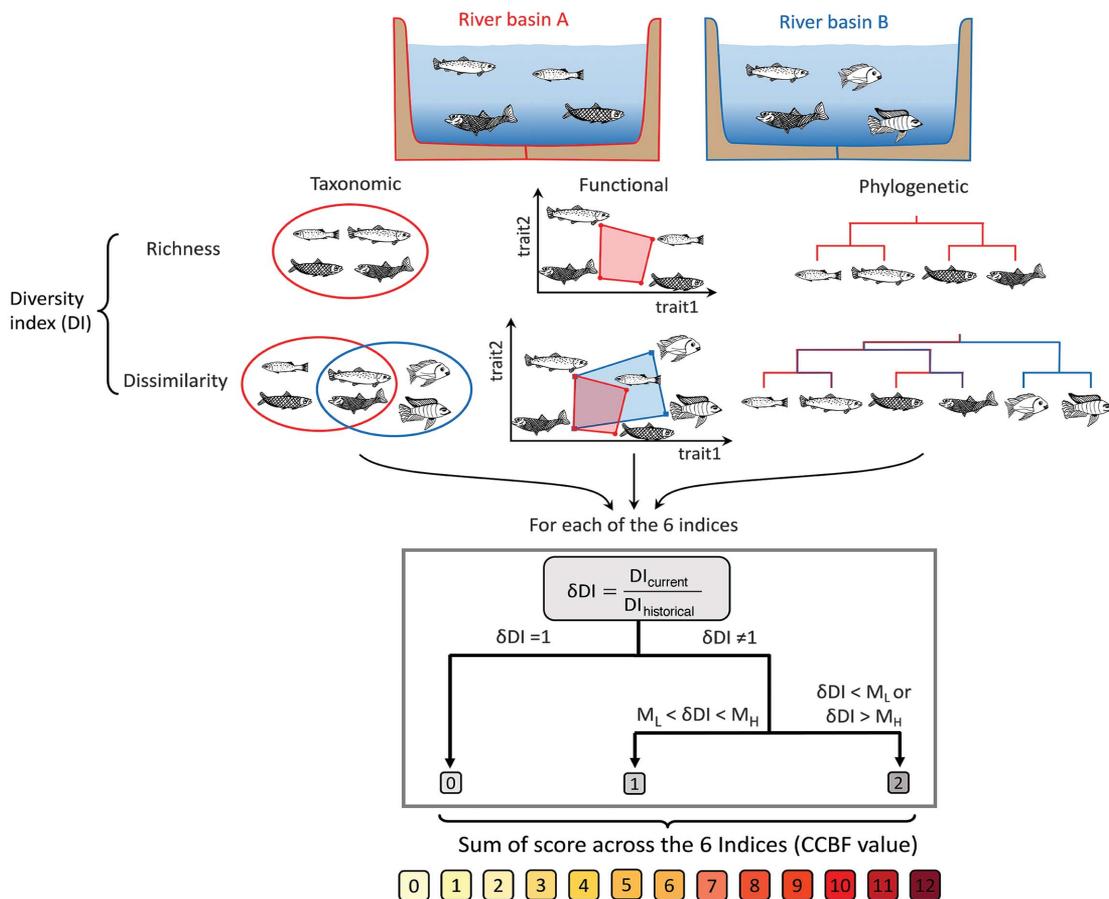


Fig. 1. Framework to measure the cumulative change in biodiversity facets (CCBF). δDI represents the change of a single diversity index among the six considered (taxonomic richness, functional richness, and phylogenetic richness within each river basin; taxonomic dissimilarity, functional dissimilarity, and phylogenetic dissimilarity between pairs of basins). M_L is the median of all the values lower than 1; M_H is the median of all the values higher than 1. The score is used to compute the CCBF index.

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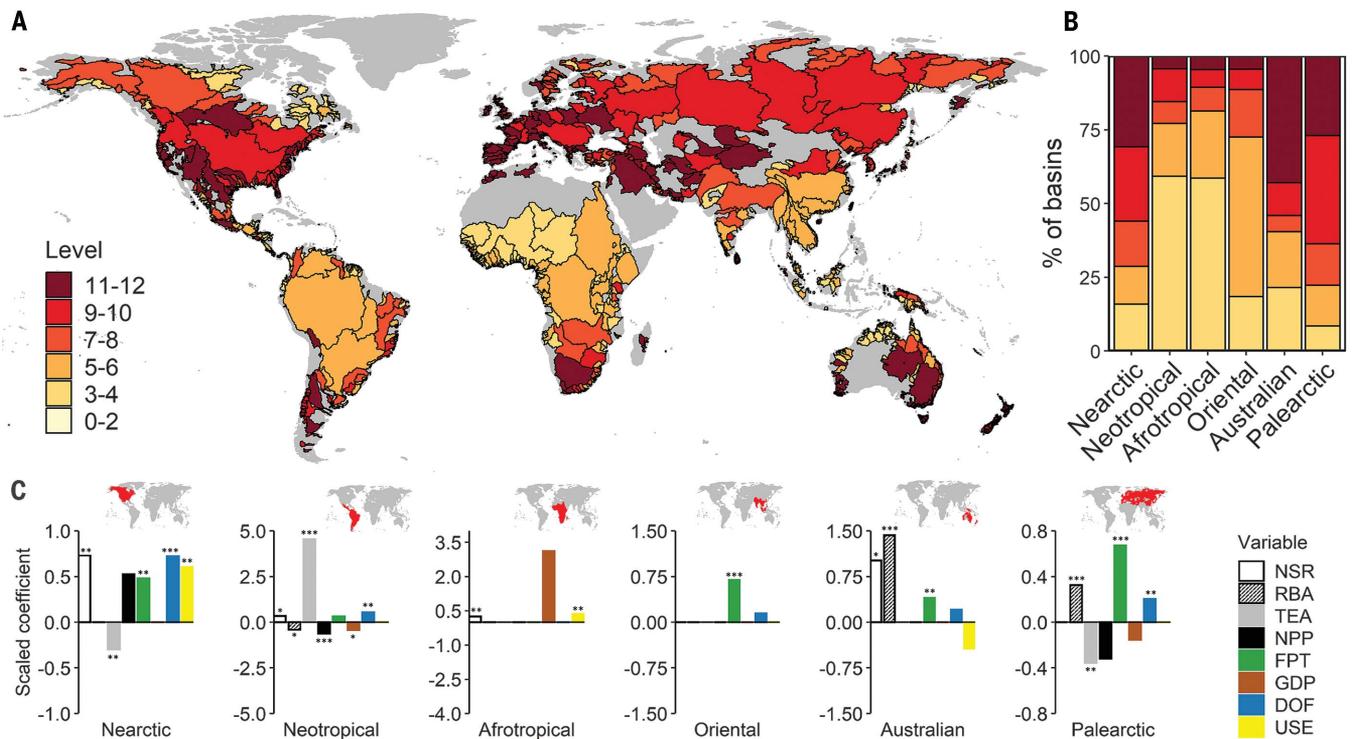


Fig. 2. Cumulative change in biodiversity of freshwater fish faunas. A cumulative index accounts for the sum of the changes in the six diversity indices: three facets (taxonomic, functional, and phylogenetic) measured at two scales (local and regional). **(A)** Map of the changes in 2456 river basins. **(B)** Percentage of river basins for six intensities of change in each biogeographic realm. **(C)** Scaled coefficient of the eight drivers of biodiversity change in an autoregressive

error model in each realm (NSR, native species richness; RBA, river basin area; TEA, temperature anomaly since the last glacial maximum; NPP, net primary productivity; FPT, human footprint; GDP, gross domestic product; DOF, degree of fragmentation; USE, consumptive water use). Number of river basins used in the models: Afrotropical, $n = 198$; Australian, $n = 525$; Nearctic, $n = 241$; Neotropical, $n = 350$; Oriental, $n = 292$; Palearctic, $n = 729$. $***P < 0.001$, $**P < 0.01$, $*P < 0.05$.

centuries in 2456 river basins, covering almost the entire continental surface of Earth (excluding deserts and poles) and hosting >14,000 species (>80% of the global freshwater fish pool) (19). We computed an index of Cumulative Change in Biodiversity Facets (CCBF), which ranges from 0 to 12, with higher scores depicting stronger changes across more facets. A score higher than 6 indicates either changes in all six biodiversity facets or changes higher than the median in more than three facets (Fig. 1) (20).

More than half of the river basins (52.8%; 1297 basins representing 40.2% of the world continental surface and 37.3% of the world river length) had CCBF scores higher than 6 (Fig. 2), revealing deep and spatially distributed anthropogenic impacts on fish biodiversity. In contrast, one-third of the river basins (35.7%; 878 rivers) did not experience changes in local richness but only changes in dissimilarity relative to assemblages from the same realm (fig. S1). Those least-impacted river basins were mostly small-sized, occupying only 13.4% of the world river basin surface, and supported 3876 species, or only 21.7% of the world fish fauna. Moreover, the least-impacted rivers were over-represented in Afrotropical and Australian

regions, whereas the Neotropics, although being the richest in species, functional, and phylogenetic diversity (21, 22), accounted for less than 6% of the “least impacted” category (fig. S1).

Fish assemblages from the temperate regions of Nearctic, Palearctic, and Australian realms experienced the largest biodiversity changes, with more than 60% of the rivers reaching a CCBF score higher than 6 (Fig. 2, A and B). Overall biodiversity changes in temperate regions (CCBF = 8.6 ± 0.1 , mean \pm SE) were higher than in tropical rivers (CCBF = 5.1 ± 0.1). For instance, large temperate rivers such as the Mississippi, Danube, or Murray-Darling had CCBF scores higher than 8, whereas large tropical rivers, such as the Amazon, Congo, or Mekong, were less impacted (CCBF = 6, fig. S2). Such a spatial pattern is consistent with previous studies on changes in taxonomic richness and dissimilarity of freshwater fishes (8, 9) and with historical reports on anthropogenic degradation of ecosystems (23) but is not consistent with changes observed in other taxa, for which changes in biodiversity were the highest in tropical regions [e.g., for marine biome (24) and forest (25)].

Mapping the patterns of changes across the six diversity components revealed discrepan-

cies between richness facets (Fig. 3). Except for a few rivers in the northern part of the Palearctic and Nearctic realms, fish biodiversity did not decline in most of the rivers (Fig. 3, A to C). This markedly differs from recent results documenting the decline in freshwater living resources at the local scale (i.e., >1 to 10 km of river stretch) within some of these river basins (12, 26). Interestingly, we report an inverse trend in freshwater fish for local taxonomic, functional, and phylogenetic richness in more than half of the world's rivers (Fig. 3, A to C, and Fig. 4). This increase in local diversity is primarily explained by anthropogenic species introductions that compensate for or even exceed extinctions in most rivers (27). Among the 10,682 fish species considered, 170 fish species went extinct in a river basin, but this number might be underestimated because of the time lag between effective extinction and published extinction reports (28). In addition, 23% of freshwater fish species are currently considered to be threatened (29), and some of these might become extinct in the near future (26).

In addition to the overall increase in richness of fish assemblages in river basins, biotic homogenization—a general declining trend

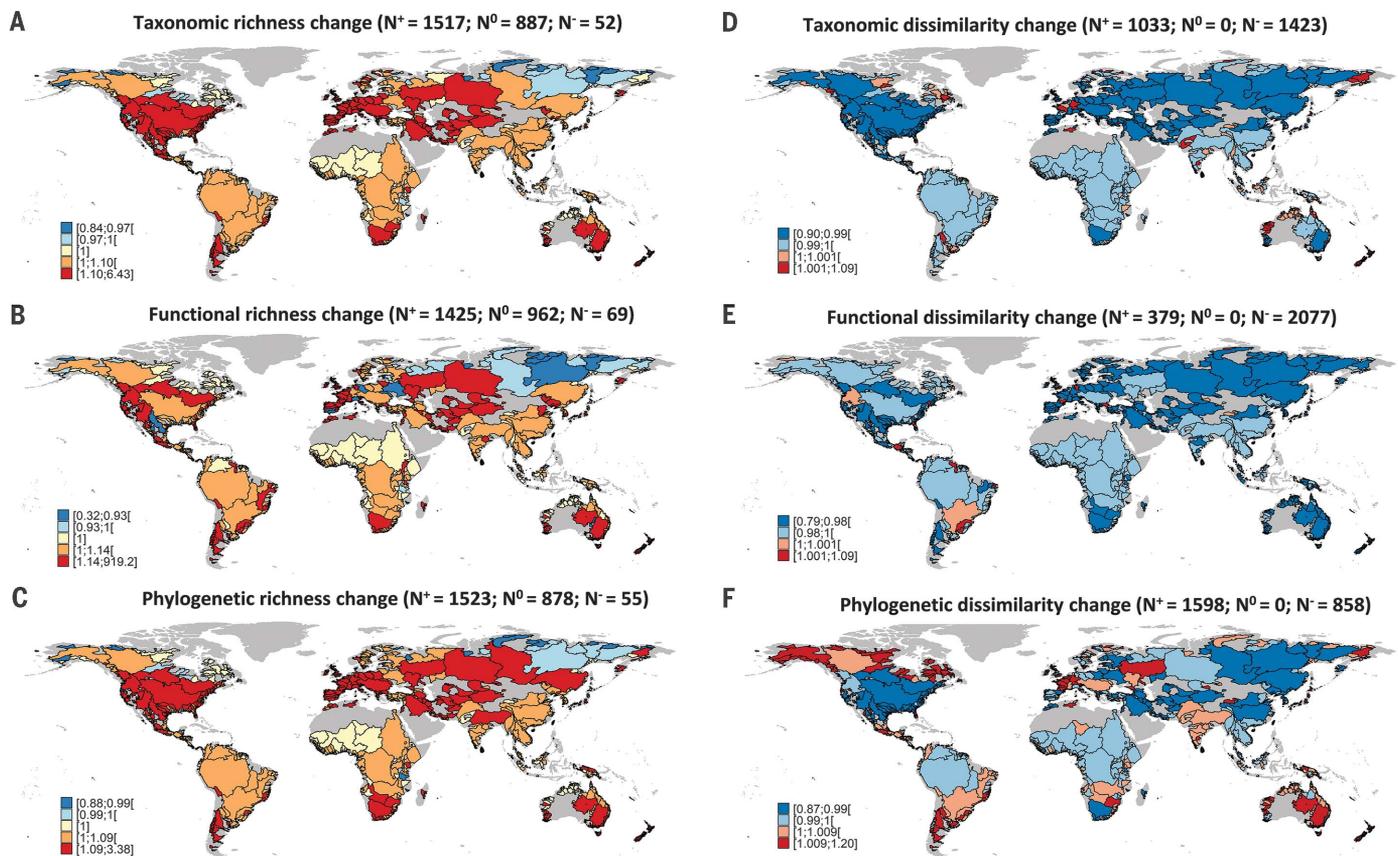


Fig. 3. Changes in each of the six biodiversity indices for the world freshwater fish assemblages (2456 river basins). (A) Taxonomic richness change; (B) functional richness change; (C) phylogenetic richness change; (D) taxonomic dissimilarity change; (E) functional dissimilarity change;

(F) phylogenetic dissimilarity change. Legend values are the original ratio $D_{I_{current}}/D_{I_{historical}}$. Numbers of basins where fish diversity increased (N^+), remained unchanged (N^0), or decreased (N^-) are shown at the top of each panel.

in biological dissimilarity between river basins—appears pervasive throughout the world's rivers (Fig. 3, D to F). Functional dissimilarity was the most impacted facet, with a decrease in 84.6% of the rivers, whereas taxonomic dissimilarity and phylogenetic dissimilarity decreased in only 58% and 35% of the rivers, respectively (Fig. 3, D to F). The discrepancy between change in functional diversity and changes in taxonomic and phylogenetic diversity (Fig. 4) primarily stems from the origin of non-native species introduced into rivers. Species translocated from a river to nearby basins promote losses of dissimilarity because they often already occur as natives in many rivers of the realm and are often functionally and phylogenetically close to other native species (9, 30). In contrast, exotic species (i.e., originating from other realms) are less frequently introduced, and their divergent evolutionary history with native species led to increased phylogenetic dissimilarity of their recipient rivers (30). For instance, the exotic species introduced in only a few rivers of Europe (e.g., the mosquitofish, *Gambusia affinis*, established in southwestern Europe, or the

brook trout, *Salvelinus fontinalis*, established in cold-water ecosystems) (30), markedly enhanced the phylogenetic dissimilarity between those rivers. However, exotic species even from distinct evolutionary lineages could share functional traits with some native species, thereby leading to increased phylogenetic dissimilarity but decreased functional dissimilarity (Fig. 3). For instance, European trout (*Salmo trutta*) and Pacific salmon (*Oncorhynchus mykiss*) belong to an order (Salmoniformes) absent from the Australian realm, but those exotic salmonids are functionally similar to some native Australian fishes such as the spotted mountain trout (*Galaxias truttaceus*; Osmeriformes) (31).

The CCBF score was positively linked to human activities related to industrialization and economic development, such as human footprint [FPT (23)], with an increase of biodiversity changes with increased FPT in all the industrialized and populated realms. River fragmentation by dams, represented by the degree of fragmentation [DOF (32)] index, was also a widespread disturbance in the Nearctic and Palearctic realms (Fig. 2C) that experienced intensive damming for more

than a century (33). Fragmentation by dams was also a significant driver of biodiversity change in the Neotropics, probably due to the rise of hydropower dam construction in this realm (34). Higher DOF values were reached in small- or medium-sized rivers, whereas the largest and most diverse rivers such as the Amazon, Orinoco, or Congo remain mostly free-flowing (32), although the current rise of dam construction on those rivers (35, 36) will constitute a major threat to their biodiversity. Apart from river fragmentation, consumptive water use for agriculture and industry [USE (32)] was a significant driver of CCBF increase in the Nearctic realm, where water withdrawal for agriculture is intense (32, 37) and acts in synergy with increasing DOF. In the Afrotropics, USE was the only significant human driver of CCBF, due to marked consumptive water use in regions with marked seasonal aridity (32, 37). In addition, the CCBF score was positively correlated to richness in native species in most of the realms, indicating that the most speciose rivers are also the most impacted by biodiversity changes. Moreover, no negative associations between species richness and the CCBF were

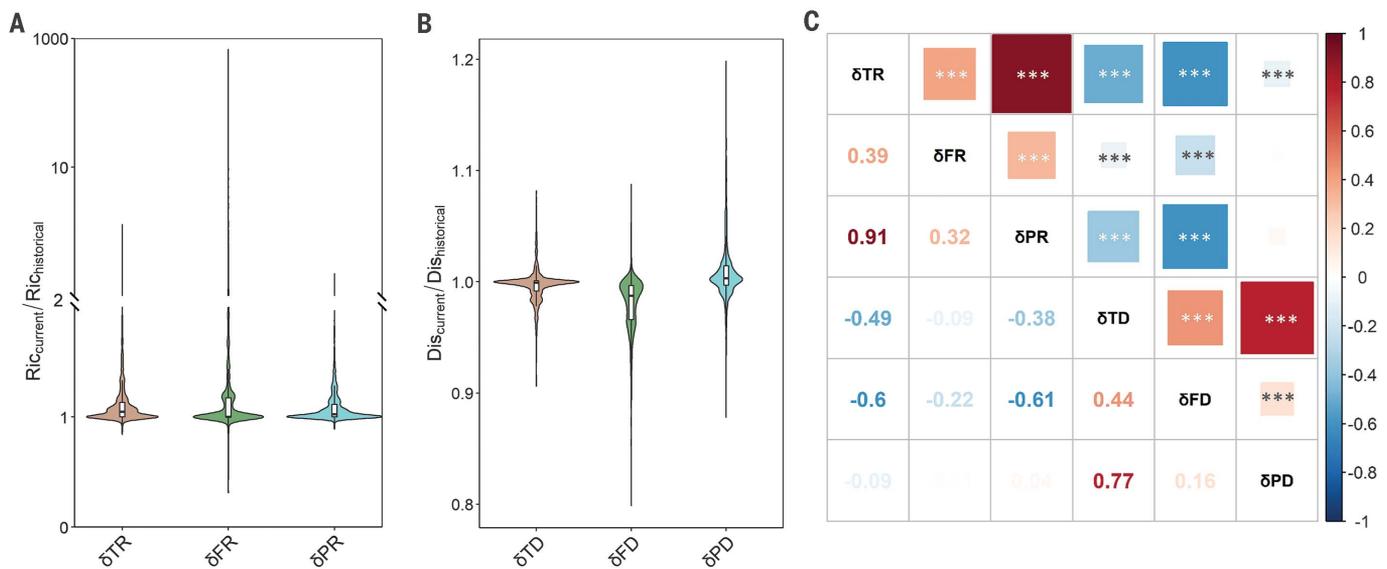


Fig. 4. Changes in biodiversity from historical period to current period. (A and B) Violin plots show the distribution of values of the three richness change indices (A) and the three dissimilarity change indices (B). (C) Pearson correlation between the changes in diversity indices (river basin number = 2456, *** $P < 0.001$).

observed, providing little support for the hypothesis of biotic resistance that assumes a higher resistance of species-rich assemblages against disturbances (38–40).

Conserving freshwater fish diversity in the least-impacted rivers (accounting for 13.4% of the world basin surface) will remain below the target to protect at least 30% of Earth's surface by 2030, as proposed by a broad coalition of environmental organizations (41, 42). This result suggests that reaching the freshwater fish target must involve consideration of not only the least impacted rivers but also areas where biodiversity has already been eroded by human activity. Moreover, conservation has moved toward systematically identifying regions in need of protection (43). The discrepancy in biodiversity erosion we report between freshwater ecosystems and marine and terrestrial ecosystems (24, 25) demonstrates that current measures of biodiversity erosion, derived from marine and terrestrial organisms, do not apply to freshwaters, and thus underscores the need to develop freshwater-focused conservation priorities. In addition, the mismatches between changes in taxonomic, functional, and phylogenetic dissimilarities among the world freshwater fish fauna highlight the risk of evaluation based on change in a single facet as a surrogate of the changes in other facets. More important, our results highlight the need to consider the cumulative and synergistic effects of multiple human activities on the complementary facets of biodiversity. The CCBF index we propose presents a holistic measure of multiple measures of biodiversity change and offers potential for prioritizing and informing adaptive management and global conservation targets. Future studies and plan-

ning need to expand the focus from simple loss of species to integrated changes in facets of biodiversity resulting from interactions between synergetic human activities.

REFERENCES AND NOTES

- G. H. Allen, T. M. Pavelsky, *Science* **361**, 585–588 (2018).
- D. Dudgeon *et al.*, *Biol. Rev. Camb. Philos. Soc.* **81**, 163–182 (2006).
- R. van der Laan, *Freshwater Fish List* (Almere, Netherlands, ed. 30, 2020).
- S. Villéger, S. Brosse, M. Mouchet, D. Mouillot, M. J. Vanni, *Aquat. Sci.* **79**, 783–801 (2017).
- R. Hassan, R. Scholes, N. Ash, *Ecosystems and Human Well-Being: Current State and Trends* (Island, 2005).
- R. Arlinghaus *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **116**, 5209–5213 (2019).
- R. C. Hoffmann, *Am. Hist. Rev.* **101**, 631–669 (1996).
- F. Leprieux, O. Beauchard, S. Blanchet, T. Oberdorff, S. Brosse, *PLoS Biol.* **6**, e28 (2008).
- S. Villéger, S. Blanchet, O. Beauchard, T. Oberdorff, S. Brosse, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 18003–18008 (2011).
- H. M. Pereira *et al.*, *Science* **330**, 1496–1501 (2010).
- C. J. Vorösmarty *et al.*, *Nature* **467**, 555–561 (2010).
- A. J. Reid *et al.*, *Biol. Rev. Camb. Philos. Soc.* **94**, 849–873 (2019).
- D. Tickner *et al.*, *Bioscience* **70**, 330–342 (2020).
- D. Mouillot, N. A. Graham, S. Villéger, N. W. Mason, D. R. Bellwood, *Trends Ecol. Evol.* **28**, 167–177 (2013).
- S. Naeem, J. E. Duffy, E. Zavaleta, *Science* **336**, 1401–1406 (2012).
- D. Craven *et al.*, *Nat. Ecol. Evol.* **2**, 1579–1587 (2018).
- P. Brun *et al.*, *Nat. Commun.* **10**, 5691 (2019).
- C. Pimiento *et al.*, *Sci. Adv.* **6**, eaay7650 (2020).
- P. A. Tedesco *et al.*, *Sci. Data* **4**, 170141 (2017).
- See supplementary materials.
- A. Toussaint, N. Charpin, S. Brosse, S. Villéger, *Sci. Rep.* **6**, 22125 (2016).
- D. L. Rabosky, *J. Biogeogr.* **47**, 1207–1217 (2020).
- O. Venter *et al.*, *Sci. Data* **3**, 160067 (2016).
- S. A. Blowes *et al.*, *Science* **366**, 339–345 (2019).
- M. C. Hansen *et al.*, *Science* **342**, 850–853 (2013).
- J. S. Albert *et al.*, *Ambio* **50**, 85–94 (2021).
- A. Toussaint *et al.*, *Ecol. Lett.* **21**, 1649–1659 (2018).
- S. T. Jackson, D. F. Sax, *Trends Ecol. Evol.* **25**, 153–160 (2010).
- IUCN, *The IUCN Red List of Threatened Species Version 2017-3* (2018); www.iucnredlist.org.
- S. Villéger, G. Grenouillet, S. Brosse, *Glob. Ecol. Biogeogr.* **23**, 1450–1460 (2014).

- S. Burgin, *Sustainability* **9**, 280 (2017).
- G. Grill *et al.*, *Nature* **569**, 215–221 (2019).
- B. Lehner *et al.*, *Front. Ecol. Environ.* **9**, 494–502 (2011).
- C. Zarfl, A. E. Lumsdon, J. Berlekamp, L. Tydecks, K. Tockner, *Aquat. Sci.* **77**, 161–170 (2015).
- E. P. Anderson *et al.*, *Sci. Adv.* **4**, eaal642 (2018).
- K. O. Winemiller *et al.*, *Science* **351**, 128–129 (2016).
- P. Döll, K. Fiedler, J. Zhang, *Hydro. Earth Syst. Sci.* **13**, 2413–2432 (2009).
- J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6230–6235 (2016).
- M. Loreau *et al.*, *Science* **294**, 804–808 (2001).
- J. M. Levine, *Science* **288**, 852–854 (2000).
- E. Dinerstein *et al.*, *Sci. Adv.* **5**, eaaw2869 (2019).
- S. L. Pimm, C. N. Jenkins, B. V. Li, *Sci. Adv.* **4**, eaat2616 (2018).
- C. R. Margules, R. L. Pressey, *Nature* **405**, 243–253 (2000).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S4
Tables S1 to S3
References (44–81)

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No waters left untouched

We are increasingly aware of human impacts on biodiversity across our planet, especially in terrestrial and marine systems. We know less about fresh waters, including large rivers. Su *et al.* looked across such systems globally, focusing on several key measures of fish biodiversity. They found that half of all river systems have been heavily affected by human activities, with only very large tropical river basins receiving the lowest levels of change. Fragmentation and non-native species have also led to the homogenization of rivers, with many now containing similar species and fewer specialized lineages.

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