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1 **Title: Human activities have disrupted freshwater fish biodiversity**

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17 **Abstract:** Freshwater fish represent one fourth of the world's vertebrates and provide
18 irreplaceable goods and services to humans, while being increasingly affected by human
19 activities. A new index, Cumulative Change in Biodiversity Facets, revealed marked changes
20 in biodiversity in >50% of the world's rivers covering >40% of the world's continental surface
21 and >37% of the world's river length, whereas <14% of the world's surface and river length
22 remain least impacted. Current rivers are more similar to each other, have more fish species
23 with more diverse morphologies and longer evolutionary legacies. Temperate rivers have been
24 the most impacted, and biodiversity changes were primarily due to river fragmentation and
25 introduction of non-native species.

26 **One Sentence Summary:** Introduction of non-native species and modification of water flow
27 have changed richness and similarity of fish faunas in most of the world rivers

28 **Main Text:**

29 Rivers and lakes cover less than 1% of the Earth's surface but they host large levels of
30 biodiversity, including near 18,000 fish species that represent one quarter of global vertebrates
31 (1-3). These freshwater fishes support the functioning and stability of ecosystems through their
32 contribution to biomass production and regulation of trophic networks and nutrient cycles (4).
33 Freshwater fishes also contribute to human welfare as key food resources (5), and for recreative
34 and cultural activities (2, 6).

35 For centuries human populations have directly affected fish biodiversity (7) through extraction
36 and introduction of non-native species (8, 9). Human activities have also modified the natural
37 environment by changing land uses, altering flow regimes, fragmenting rivers by dams,
38 polluting soil and waters and altering climate, actions that indirectly favor extinction of native
39 species and/or establishment of non-native species (10-13). Consequently, these direct and
40 indirect anthropogenic impacts have led to modification of local species compositions (8, 9).
41 However, biodiversity is not restricted to purely taxonomic components but also includes
42 functional and phylogenetic diversities. These two latter facets determine how organisms affect
43 ecosystem functioning and stability (14-18) and are thus essential for conservation.

44 Here, we assess the extent to which six key facets of freshwater fish biodiversity (taxonomic,
45 functional and phylogenetic richness and corresponding dissimilarities between river basins)
46 have changed over the last two centuries in 2,456 river basins, covering almost the entire

47 continental surface of the Earth (excluding deserts and poles) and hosting >14,000 species (>
48 80% of the global freshwater fish pool) (19). We computed an index of cumulative change in
49 biodiversity facets (CCBF) which ranges from 0 to 12 with higher scores depicting stronger
50 changes across more biodiversity facets. A score higher than 6 indicates either changes in all
51 the six facets, or changes higher than median in more than three biodiversity facets (Fig. 1) (20).
52 We further unravel the natural and anthropogenic drivers that have led to the observed changes
53 across the main regions of the world.

54 More than half of the river basins (52.8%, 1,297 rivers covering 40.2% of the world continental
55 surface and 37.3% of the world river length) show CCBF scores higher than 6 (Fig. 2), revealing
56 deep and spatially distributed anthropogenic impacts on fish biodiversity. In contrast, one third
57 of the river basins (35.7%, 878 rivers) did not experience changes in local richness but only
58 changes in dissimilarity with assemblages from the same realm (Fig. S1). Those least impacted
59 river basins are mostly small-sized and occupy only 13.4% of the world river basin surface and
60 support 3,876 species, only 21.7% of the world fish fauna. Moreover, the least impacted rivers
61 are overrepresented in Afrotropical and Australian regions, whereas the Neotropics, although
62 being the richest in species, functional and phylogenetic diversity (21, 22) account for less than
63 6% of the "least impacted" category (Fig. S1).

64 Fish assemblages from the temperate regions of Nearctic, Palearctic and Australian realms
65 experienced the largest biodiversity changes, with more than 60% of the rivers reaching a CCBF
66 score higher than 6 (Fig. 2 a,b). Overall biodiversity changes in temperate regions (CCBF = 8.6
67 \pm 0.1, mean \pm standard error) were higher than in tropical rivers (CCBF = 5.1 \pm 0.1). For

68 instance, large temperate rivers such as the Mississippi, Danube, or Murray-Darling show
69 CCBF scores higher than 8, whereas large tropical rivers, such as the Amazon, Congo or
70 Mekong were less impacted (CCBF = 6, Fig. S2). Such a spatial pattern is consistent with
71 previous studies on changes in taxonomic richness and dissimilarity of freshwater fishes (8, 9),
72 and with historical reports on anthropogenic degradation of ecosystems (23), but contrasts with
73 changes observed in other taxa for which changes in biodiversity were the highest in tropical
74 regions [e.g., for marine biome (24), forest (25)].

75 Mapping the patterns of changes across the six diversity components revealed discrepancies
76 between richness facets (Fig. 3). Except for a few rivers in the northern part of the Palearctic
77 and Nearctic realms, fish biodiversity did not decline in most of the rivers (Fig. 3 a,b,c). This
78 markedly differs from recent results documenting the decline in freshwater living resources at
79 the local scale (i.e. over 1-10 km of river stretch) within some of these river basins (12, 26).
80 Interestingly, we report an inverse trend in freshwater fish for local taxonomic, functional and
81 phylogenetic richness in more than half of the world rivers (Fig. 3 a,b,c, Fig. 4). This increase
82 in local diversity is primarily explained by anthropogenic species introductions that compensate
83 for or even exceed extinctions in most rivers (27). 170 fish species went extinct in a river basin
84 but this number might be underestimated due to time lag between effective extinction and
85 published extinction reports (28). In addition, 23% of freshwater fish species are currently
86 considered as threatened (29), which might turn to increase extinctions in the near future (26).
87 In addition to the overall increase in richness of fish assemblages in river basins, a general
88 declining trend in biological dissimilarity between river basins, that is biotic homogenization,

89 appears pervasive throughout the world's rivers (Fig. 3 d,e,f). Functional dissimilarity was the
90 most impacted facet with a decrease in 84.6% of the rivers while taxonomic dissimilarity and
91 phylogenetic dissimilarity decreased in only 58% and 35% of the rivers (Fig. 3 d,e,f). The
92 discrepancy between change in functional diversity and changes in taxonomic and phylogenetic
93 diversity (Fig. 4) primarily stems from the origin of non-native species introduced in rivers.
94 Species translocated from a river to nearby basins promote losses of dissimilarity because they
95 often already occur as natives in many rivers of the realm and are often functionally and
96 phylogenetically close to other native species (9, 30). In contrast, exotic species (i.e. originating
97 from other realms) are less frequently introduced and their divergent evolutionary history with
98 native species led to increase phylogenetic dissimilarity of their recipient rivers (30). For
99 instance, the exotic species introduced in only a few rivers of Europe (e.g., the mosquitofish,
100 *Gambusia affinis*, established in south-western Europe or the brook trout, *Salvelinus fontinalis*,
101 established in cold-water ecosystems) (30), markedly enhanced the phylogenetic dissimilarity
102 between those rivers. However, exotic species even from distinct evolutionary lineages could
103 share functional traits with some native species, hence leading to increase phylogenetic
104 dissimilarity but decrease functional dissimilarity (Fig. 3). For instance, European trout, *Salmo*
105 *trutta* and Pacific Salmon, *Oncorhynchus mykiss*, belong to an order (Salmoniformes) absent
106 from the Australian realm but those exotic salmonids are functionally similar to some native
107 Australian fishes such as the spotted mountain trout, *Galaxias truttaceus* (Osmeriformes) (31).

108 The CCBF score was positively linked to human activities related to the industrialization and
109 economic development, such as human footprint [FPT, (23)], with an increase of biodiversity
110 changes with the FPT in all the industrialized and populated realms. River fragmentation by

111 dams, represented by the degree of fragmentation index [DOF, (32)], was also a widespread
112 disturbance in the Nearctic and Palearctic realms (Fig. 2c) that experienced intensive damming
113 for more than a century (33). Fragmentation by dams was also a significant driver of
114 biodiversity change in the Neotropics, probably due to the rise of hydropower dam construction
115 in this realm (34). Higher DOF values were reached in small or medium sized rivers, whereas
116 the largest and most diverse rivers such as the Amazon, Orinoco or Congo remain mostly free
117 flowing (32), but the current rise of dam construction on those rivers (35, 36) will constitute a
118 major threat to their biodiversity. Apart from river fragmentation, consumptive water use for
119 agriculture and industry [USE, (32)] was a significant driver of CCBF increase in the Nearctic
120 realm, where water withdrawal for agriculture is intense (32, 37) and act in synergy with
121 increasing DOF. In the Afrotropics, USE was the only significant human driver of CCBF, due
122 to marked consumptive water use in regions with marked seasonal aridity (32, 37). In addition,
123 the CCBF score was positively correlated to the richness in native species in most of the realms,
124 indicating that the most speciose rivers are also the most impacted by biodiversity changes.
125 Moreover, no negative associations between the species richness and the CCBF were observed,
126 providing little support to the hypothesis of biotic resistance that assumes a higher resistance of
127 species-rich assemblages against disturbances (38-40).

128 Conserving freshwater fish diversity in the least impacted rivers (accounting for 13.4 % of the
129 world basin surface) will remain under the target to protect at least 30% of the Earth's surface
130 by 2030, proposed by a broad coalition of environmental organizations (41, 42). This result
131 suggests that reaching the freshwater fish target must involve consideration of not only the least
132 impacted rivers, but also areas where biodiversity has already been eroded by human activities.

133 Moreover, conservation has moved toward systematically identifying regions in need of
134 protection (43). The discrepancy in biodiversity erosion we report between freshwater and
135 marine and terrestrial ecosystems (24, 25) demonstrates that current measures of biodiversity
136 erosion, derived from marine and terrestrial organisms, do not apply to freshwaters, and thus
137 underlines the need to develop freshwater-focused conservation priorities. In addition, the
138 mismatches between changes in taxonomic, functional and phylogenetic dissimilarities among
139 the world freshwater fish fauna highlight the risk of evaluation based on change in a single facet
140 as a surrogate of the changes in other facets. More importantly, our results highlight the need to
141 consider the cumulative and synergistic effects of multiple human activities on the
142 complementary facets of biodiversity. The CCBF index we propose presents a holistic measure
143 of multiple measures of biodiversity change and offers potential for prioritizing and informing
144 adaptive management and global conservation targets. Future studies and planning need to
145 expand the focus from simple loss of species to integrated changes in facets of biodiversity
146 resulting from interactions between synergetic human activities.

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334 coding in R. All authors led to revising the paper and preparing and approving it for publication.
335 **Competing interests:** The authors declare no competing interests. **Data and materials**
336 **availability:** Data and materials availability: All data needed to evaluate the conclusions in the
337 paper are present in the paper and/or the Supplementary Materials. Additional data, scripts and
338 files related to this paper are available at <https://figshare.com/s/5fadc2c14cbb1f39c25c>.

339 **Supplementary Materials:**

340 Materials and Methods

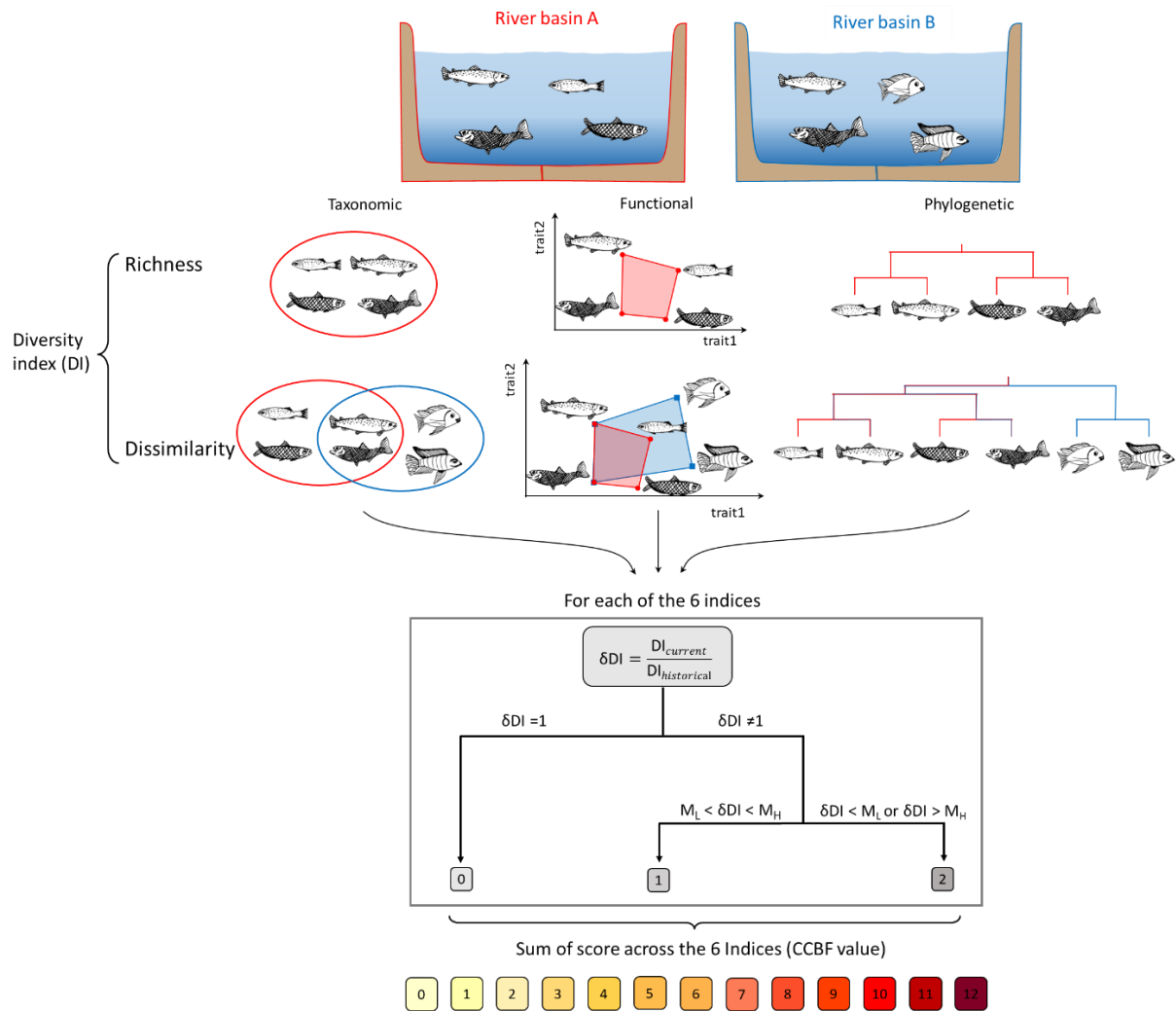
341 Figs. S1-S4

342 Table S1

343 References (44-81)

344 Table S2 (separate file)

345 Table S3 (separate file)



346

347 **Fig. 1. Framework to measure the cumulative change in biodiversity facets (CCBF).** δDI

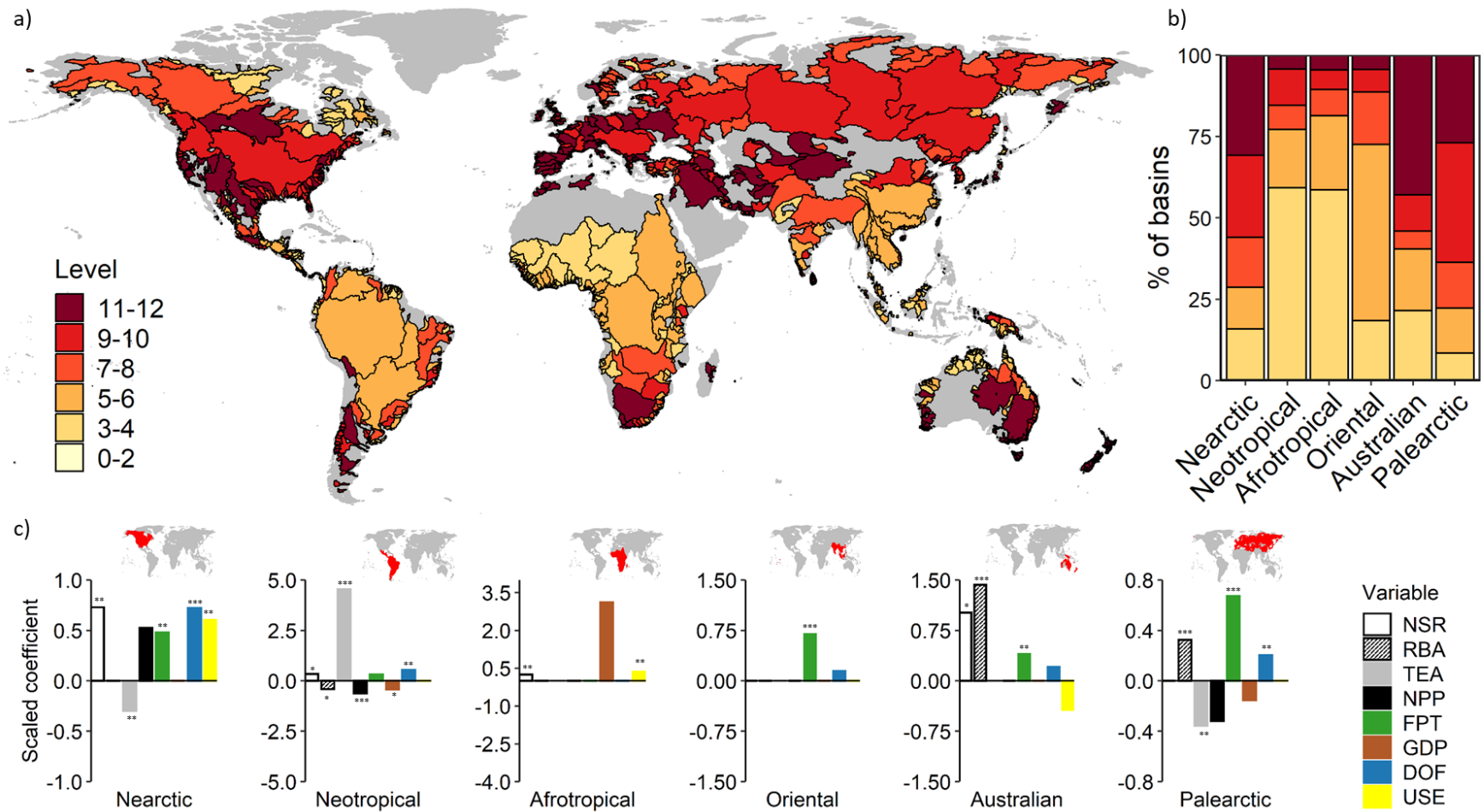
348 represents the change of a single diversity index among the six considered (Taxonomic richness,

349 Functional richness, and Phylogenetic richness within each river basin and Taxonomic

350 dissimilarity, Functional dissimilarity and Phylogenetic dissimilarity between pairs of basins);

351 M_L is the median of all the values lower than 1, M_H is the median of all the values higher than

352 1. Score is used to compute the CCBF index.

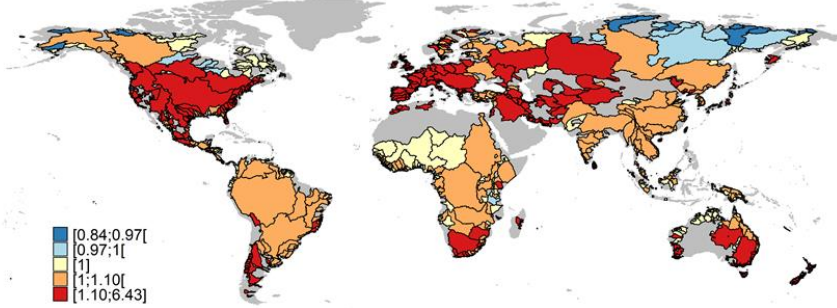


353

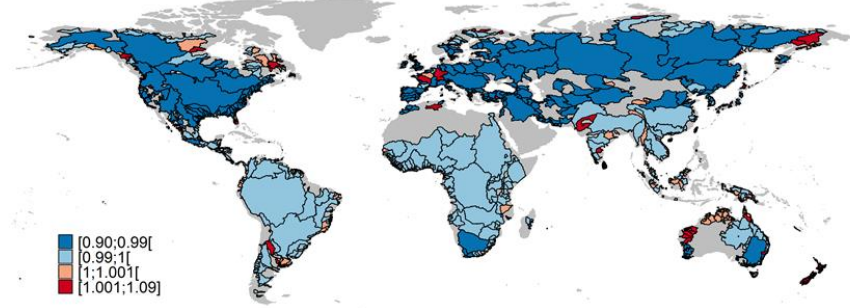
354 **Fig. 2. Cumulative change in biodiversity of freshwater fish faunas.** Cumulative index accounts for the sum of the changes in the six diversity
 355 indices: three facets (taxonomic, functional and phylogenetic) measured at two scales (local and regional). **a)** Map of the changes in 2,456 river

356 basins; **b**) percentage of river basins for six intensities of change in each biogeographic realm; **c**) scaled coefficient of the eight drivers of biodiversity
357 change in autoregressive error model in each realm. (NSR: native species richness; RBA: river basin area; TEA: temperature anomaly since the last
358 glacial maximum; NPP: net primary productivity; FPT: human footprint; GDP: gross domestic product; DOF: degree of fragmentation; USE:
359 consumptive water use). Number of river basins used in the models: Afrotropical, n=198; Australian, n=525; Nearctic, n=241; Neotropical, n=350;
360 Oriental, n=292; Palearctic, n=729. (***) $P < 0.001$; ** $P < 0.01$; * $P < 0.05$)

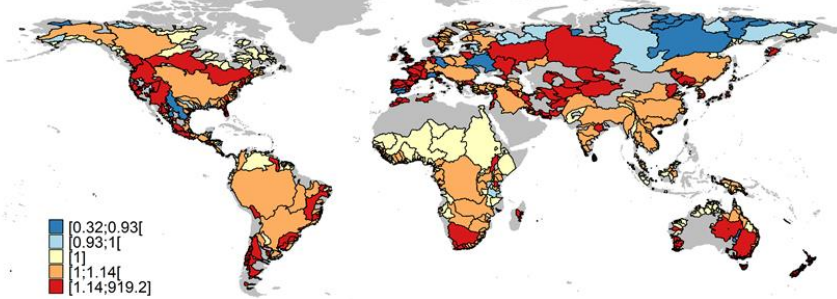
a) Taxonomic richness change ($N^+ = 1517$; $N^0 = 887$; $N^- = 52$)



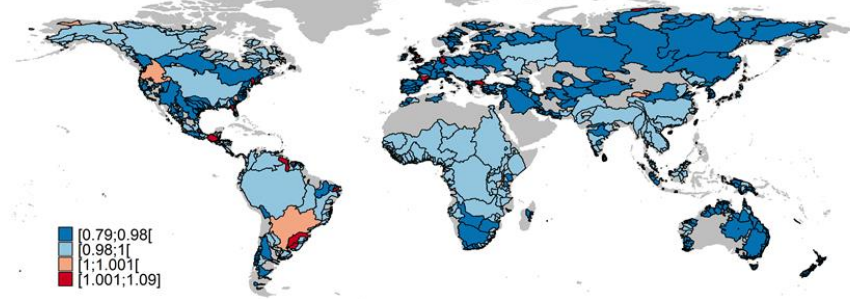
d) Taxonomic dissimilarity change ($N^+ = 1033$; $N^0 = 0$; $N^- = 1423$)



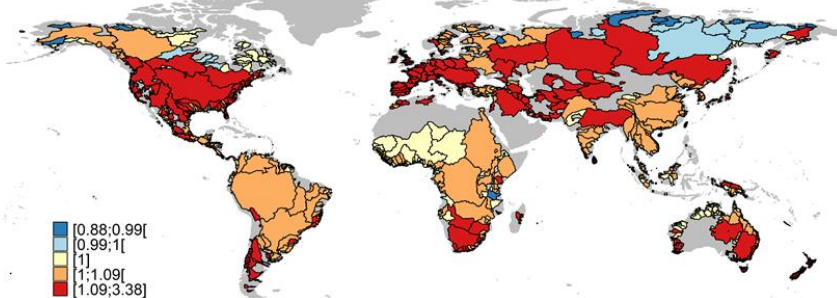
b) Functional richness change ($N^+ = 1425$; $N^0 = 962$; $N^- = 69$)



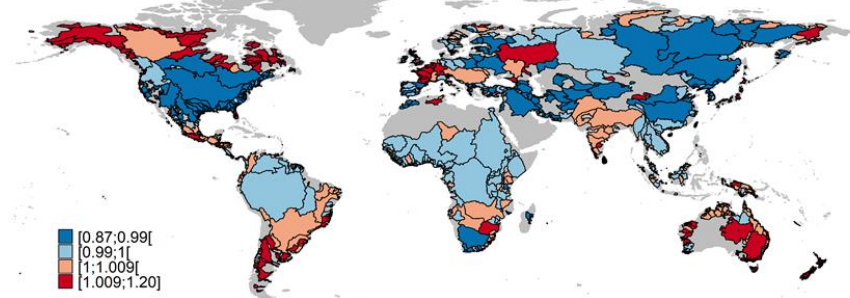
e) Functional dissimilarity change ($N^+ = 379$; $N^0 = 0$; $N^- = 2077$)



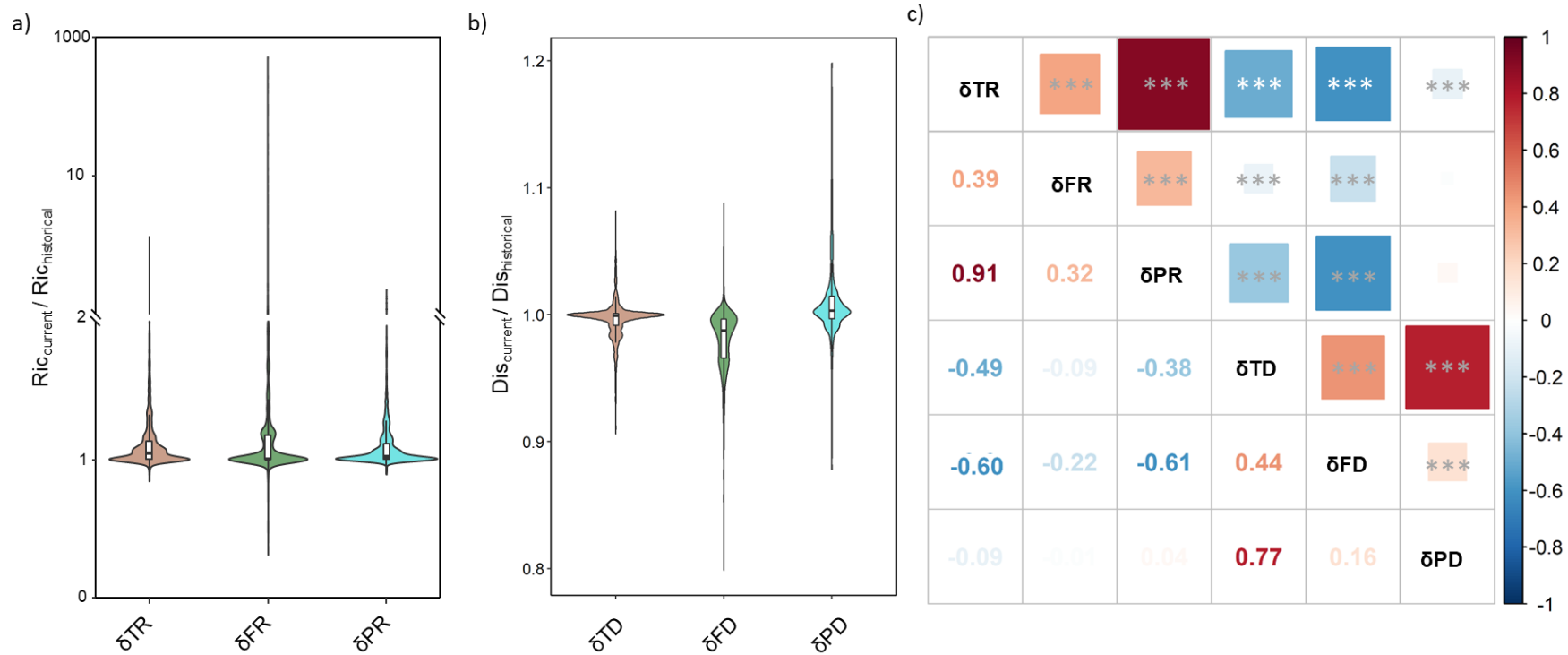
c) Phylogenetic richness change ($N^+ = 1523$; $N^0 = 878$; $N^- = 55$)



f) Phylogenetic dissimilarity change ($N^+ = 1598$; $N^0 = 0$; $N^- = 858$)



362 **Fig. 3. Changes in each of the six biodiversity indices for the world freshwater fish assemblages (2,456 river basins).** a) Taxonomic richness
363 change; b) Functional richness change; c) Phylogenetic richness change; d) Taxonomic dissimilarity change; e) Functional dissimilarity change; f)
364 Phylogenetic dissimilarity change. Legend values are the original ratio $DI_{\text{current}}/DI_{\text{historical}}$. Number of basins where fish diversity increased (N^+),
365 remained unchanged (N^0) or decreased (N^-) are provided at the top of each panel.



367

368 **Fig. 4. Changes in biodiversity from historical to current period. a)** Violin plots show the distribution of the three richness change indices values.

369 **b)** Violin plots show the distribution of the three dissimilarity change indices values. **c)** Pearson correlation between the changes in diversity indices.

370 (River basin number = 2,456, *** $P < 0.001$)

371

372

Supplementary Materials for

373

Human activities have disrupted freshwater fish biodiversity

374

375

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This word file includes:

379

Materials and Methods

380

Figs. S1-S4

381

Table S1

382

References 44-81

383

Other Supplementary Materials for this manuscript include the following:

384

Table S2

385

Table S3

386 **Materials and methods**

387 **Occurrence data:** We used the most comprehensive database of freshwater fish species
388 distributions across the world [(19) available at <http://data.freshwaterbiodiversity.eu>]. The fish
389 occurrence database gathers the occurrence of 14,953 species (more than 83% of the freshwater
390 fish species) in 3,119 drainage basins, covering more than 80% of the Earth's surface (19). Fish
391 occurrence in each river basin accounts for all the freshwater fish species inhabiting the entire
392 river network of each basin, from 1st order streams to the sea. Each occurrence is paired with a
393 status, either native or non-native established if the species was not historically present in the
394 river basin. Each river basin was assigned to one of the six terrestrial biogeographic realms [i.e.,
395 Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palearctic]
396 according to Lévêque et al. (44) and Brosse et al. (45). Historical fish assemblages composition
397 in the river basins refers to only native species, and thus roughly corresponds to the preindustrial
398 period (i.e., before the 18th century), from when industrialization began and fish introductions
399 for aquaculture, fishing, and ornamental purposes sharply increased (8, 46, 47). Similarly, the
400 current sixth mass extinction rises from the beginning of the industrial period (48). Therefore,
401 despite a few human mediated species introductions and extinctions occurred before the 18th
402 century (e.g., common carp, *Cyprinus carpio*, introduction in Western Europe), most are more
403 recent. Current fish assemblages composition refers to the non-native species and excludes the
404 local extirpated or extinct native ones. Extirpations refer to the extinction of a fish species within
405 a river basin and data were extracted from the literature reviews of Brosse et al. (45) and Diaz
406 et al. (49). We then updated these data using IUCN Red lists (29). Species with "extinct" or
407 "extinct in the wild" status in the IUCN Red list were thus considered as extinct in their native

408 river basins (Table S2). Although species extirpations/extinctions are probably underestimated
409 for a number of reasons such as the time lag between local report of species extinction and
410 validation of extinction over an entire river basin, we here used the most comprehensive and
411 updated information on fish extinction at the river basin scale.

412 **Functional traits:** Among the 14,953 species present in the occurrence database, 10,705
413 species were morphologically described using pictures and drawings from textbooks and
414 scientific websites. Morphology was assessed using ten traits describing the size and shape of
415 body parts involved in food acquisition and locomotion (19, 21). The fish size was described
416 using the maximum body length (Max. Body Length) taken from (50). Those maximum body
417 lengths were carefully reviewed, and irrelevant measures have been corrected according to
418 appropriate literature. In addition to size, 11 morphological measures were assessed on side
419 view pictures (Fig. S4a) collected during an extensive literature review including our field data
420 and scientific literature sources made of peer-reviewed articles, books, and scientific websites.
421 We collected at least one picture (photograph or scientific drawing) per species. Only good
422 quality pictures and scientific side view drawings of entire adult animals, with confirmed
423 species identification, were kept. For species with marked sexual dimorphism, we considered
424 male morphology, as female pictures are scarce for most species (especially for Perciformes
425 and Cyprinodontiformes). Intraspecific morphological traits variability was not considered in
426 this study as it hardly affects functional diversity at the large spatial resolution considered (27).
427 The nine unitless traits describing the morphology of the fish head (including mouth and eye),
428 body, pectoral and caudal fins (Fig. S4b) were computed as ratios between 11 morphological
429 measures done using ImageJ software (<http://rsb.info.nih.gov/ij/index.html>). The 10

430 morphological traits (9 unitless ratios and body size) selected are commonly used in assessment
431 of fish functional diversity [e.g., (21, 51-53)] and are linked to the feeding and locomotion
432 functions of fish that themselves determine their contribution to key ecosystem processes such
433 as controlling food webs and nutrient cycles (4) (Fig. S4b). The 10 traits were not markedly
434 correlated to each other (Spearman's correlation coefficient, $|\rho| < 0.45$ for all the 45 pairwise
435 comparisons). Functional traits not measurable on side pictures, such as gut length, oral gape
436 area and shape, were not included because they are currently only available for a few species
437 in public databases.

438 Some species have unusual morphologies (species without tails, flatfishes) that prevent from
439 measuring some morphological traits. We thus applied conventions as mentioned in Su et al.
440 (51), Toussaint et al. (21) and Villéger et al. (53) for these few exceptions. Due to the lesion of
441 body parts or the quality of fish pictures, some traits have not been measured for some species.
442 Overall, 24.1% of the values were missing in the raw morphological traits dataset (from 6.9%
443 for maximum body length to 31.4% for relative maxillary length). Those missing values were
444 filled using a phylogenetic generalized linear model (54, 55). We then computed a principal
445 component analysis (PCA) using values of the 10 morphological traits for all the species. We
446 selected the first four PCA axes, which explained 68.2% of the total variance among the world's
447 fish functions, to compute the functional diversity indices.

448 **Phylogenetic diversity:** Phylogenetic distances between all species were computed on the tree
449 from Rabosky et al. (56), including 31,526 marine and freshwater ray-finned fishes. This dataset
450 is based on 11,638 species whose position was estimated from genetic data; the remaining
451 19,888 species were placed in the tree using stochastic polytomy resolution (56).

452 **Environmental and Anthropogenic variables:** We selected four environmental and four
453 anthropogenic variables as proxies of the main processes responsible from native biodiversity
454 and impacts of human activities on freshwater ecosystems: (i) NSR: native species richness. (ii)
455 RBA: river basin area; (iii) NPP: net primary productivity; (iv) TEA: temperature anomaly from
456 the Last Glacial Maximum to the present; (v) DOF: degree of fragmentation; (vi) FPT: human
457 footprint; (vii) GDP: gross domestic product; and (viii) USE: consumptive water use. These 8
458 metrics were overall independent of each other ($|\text{Pearson's } r| < 0.5$), to the exception of NSR
459 and RBA (Fig. S3).

460 NSR accounts for the biotic resistance hypothesis, which assumes a higher resistance of
461 species rich assemblages against disturbances (40). RBA, NPP and TEA were from Tedesco et
462 al. (19), and account for the three main hypotheses explaining biodiversity, namely the species-
463 area hypothesis that predicts a positive relationship between river basin area and biodiversity;
464 the species-energy hypothesis that predicts higher biodiversity in energy rich areas, and the
465 historical contingency, which has largely been influenced by the last glacial events in freshwater
466 fish (57-60).

467 FPT is a comprehensive representation of anthropogenic threats to biodiversity, which
468 cumulatively accounts for eight human pressures—built environments, croplands, pasture lands,
469 human population density, night lights, railways, major roadways and navigable waterways (23).
470 FPT dataset (resolution: 1 km²) was taken from Venter et al. (23). GDP measures the size of the
471 economy and is defined as the market value of all final goods and services produced within a
472 region in a given period (61, 62). GDP dataset (1 square degree resolution) was taken from
473 Nordhaus & Chen (61).

474 DOF accounts for the degree to which river networks are fragmented longitudinally by
475 infrastructure, such as hydropower and irrigation dams (32). DOF dataset (resolution: 500 m²)
476 was taken from Grill et al. (32).

477 USE accounts for water consumption for irrigation, industry, municipal uses and water
478 transfer to other river systems. USE (resolution: 1 km²) for each river basin was calculated by
479 using $100 \cdot (d_{\text{nat}} - d_{\text{ant}}) / d_{\text{nat}}$, where d_{nat} represents the total amount of long-term discharge without
480 human influences in each river basin and d_{ant} represents the total amount of average long-term
481 discharge after human extractions and use in each river basin. d_{ant} and d_{nat} were both taken from
482 the WaterGAP model (32, 63).

483 We mapped FTP, GDP, DOF and USE by their relative resolution grid data over the basin-
484 scale map and then calculated the mean value of all the cells covered by each basin. Here we
485 considered the 2,335 river basins (out of the 3,119) with available values for both CCBF (see
486 below) and the eight environmental and anthropogenic variables.

487 **Measuring temporal changes in biodiversity of freshwater fishes:** Among the 3,119 river
488 basins with fish occurrence data, diversity indices were measured for all basins with more than
489 5 fish species to meet the requirements of functional diversity calculation, leading to consider
490 a total of 2,456 river basins. 10,682 species were obtained after matching the occurrence,
491 functional and phylogenetic databases. We assessed the 6 facets of biodiversity (Fig. 1) for fish
492 assemblage inhabiting each of the 2,456 river basins for the current and historical period:
493 taxonomic richness (TR) measured as the number of species, functional richness (FR) measured
494 as the volume of the functional space occupied by an assemblage [i.e., the volume of the
495 minimum convex hull in the functional space which includes all the species in the assemblage,

496 (64)], and phylogenetic richness (PR) as the total length of branches linking all species from
497 the assemblage on the phylogenetic tree (65). In addition to these indices describing diversity
498 within each assemblage (i.e., alpha-diversity), we also accounted for the dissimilarity among
499 assemblages (i.e., beta-diversity). More specifically, we quantified taxonomic, functional and
500 phylogenetic dissimilarity between each pair of fish assemblages from the same realm as the
501 proportion of total richness in the pair that is not shared by the assemblages, [i.e., Jaccard-index
502 for taxonomic dissimilarity (66), beta-FR_{ic} for functional dissimilarity (64) and UniFrac for
503 phylogenetic dissimilarity (67)]. Then the average value of dissimilarity between a fish
504 assemblage and all the other assemblages from the same realm was computed to get for each
505 river basin values of taxonomic dissimilarity (TD), functional dissimilarity (FD), and
506 phylogenetic dissimilarity (PD).

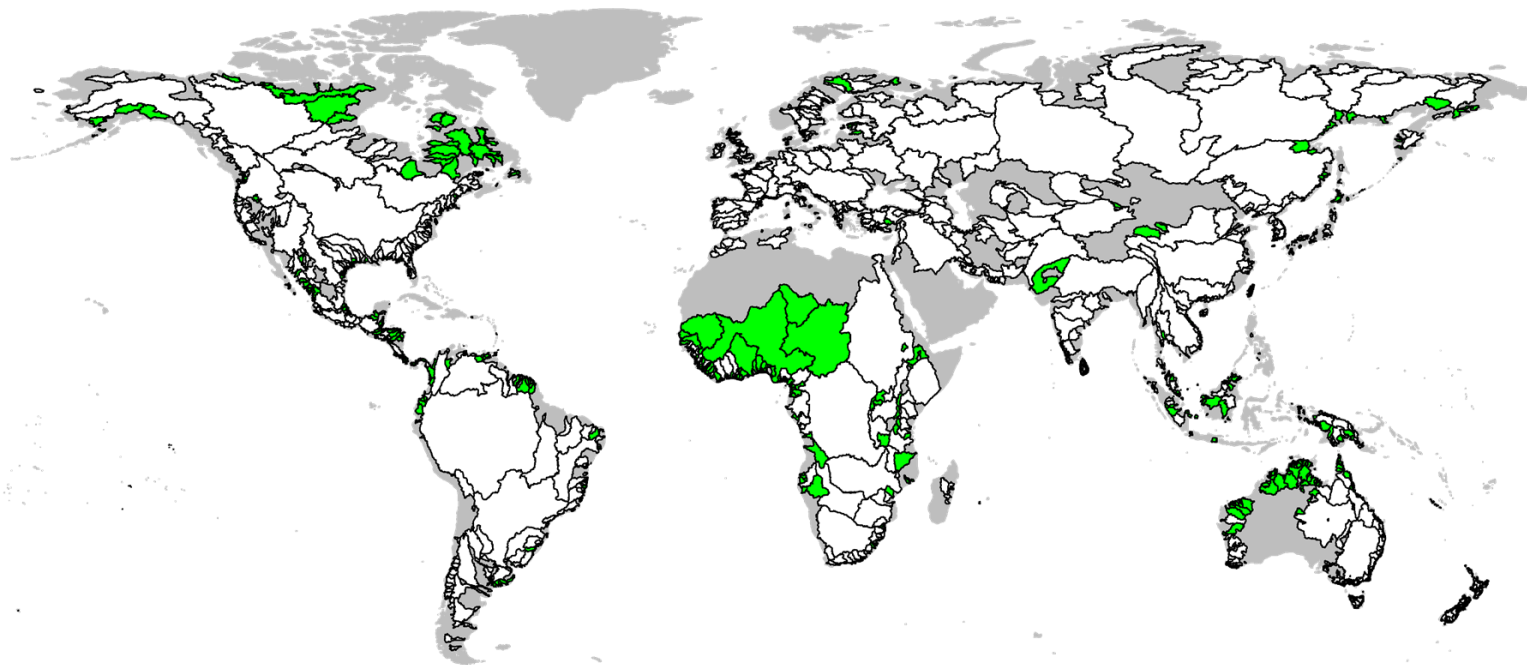
507 We then calculated for each of these six diversity indices the temporal change (δ DI) as the
508 ratio: $DI_{\text{current}} / DI_{\text{historical}}$. We then computed score for each δ DI according to its values: If δ DI
509 = 1, it scores 0; if δ DI is higher than the median of all the values lower than 1 and lower than
510 the median of all the values higher than 1, it scores 1; and if δ DI is lower than the median of all
511 the values lower than 1 or higher than the median of all the values higher than 1, it scores 2.
512 Then we sum up the scores of the six δ DI for each basin to get the index of cumulative changes
513 in biodiversity facets which ranges from 0 to 12 (CCBF, Fig. 1).

514 Thus, our cumulative index accounts for all marked changes in biodiversity facets, not only
515 species loss. Null values are possible only if taxonomic, functional and phylogenetic
516 composition of all assemblages from a realm remained unchanged because otherwise all
517 dissimilarity indices are changed. CCBF scores from 0 to 6 account for moderate changes in

518 biodiversity for all the six facets (all the 6 facets scoring 0 or 1) or strong changes for no more
519 than half of the facets (no more than 3 facets scoring 2). Such CCBF values are considered as
520 moderate changes in biodiversity. CCBF scores from 7 to 12 account for strong changes in
521 biodiversity with all 6 facets changes or more than half of the facets scoring 2. See table S3 for
522 the six diversity indices and CCBF scores for the 2,456 basins.

523 **Statistical analyses:** To assess how environmental processes and human activities contributed
524 to the observed change in biodiversity in each realm, we quantified the relative contribution of
525 NSR, RBA, TEA, NPP, FPT, GDP, DOF and USE to the CCBF values of the 2,335 river basins
526 for which all variables were available, using spatial simultaneous autoregressive error models
527 (SAR_{error}). These eight variables were previously scaled to a zero mean and unit variance to
528 ensure equal weighting in the models. We first ran the null model (intercept-only) with none of
529 the variables as a reference. Then we used stepwise regression to select the best models by AIC
530 (Akaike's Information Criterion). We eventually selected the model with the lowest AIC (68)
531 (Table S2). We used Nagelkerke's R^2 (69) as the pseudo R-squared to qualify the final models'
532 performance. After model fitting, we checked for broad spatial autocorrelation in model
533 residuals by computing the Moran's I statistic (70).

534 All statistical analyses were performed with the R software environment version 3.3 (*R Core*
535 *Team*), including the library 'RPhylopars' (55) for filling the missing values in the trait database,
536 'betapart' for computing dissimilarity indices (71, 72), 'spatialreg' and 'spdep' for developing
537 SAR_{error} models (73) and performing Moran's I tests (74).



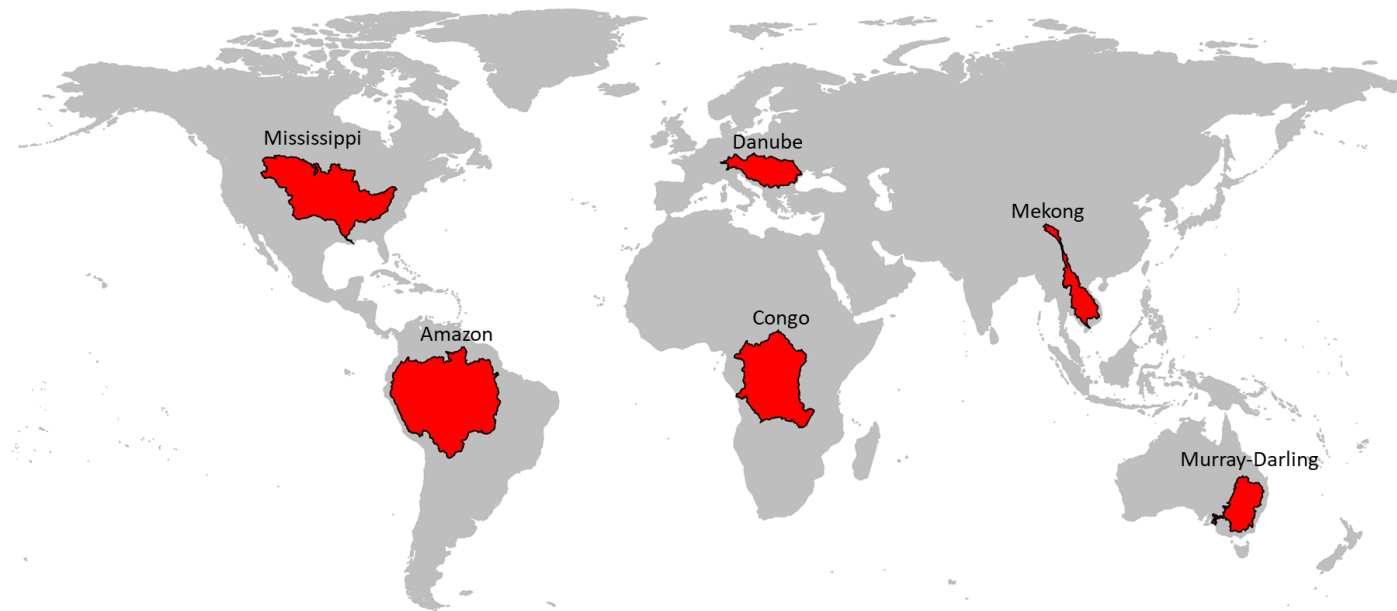
538

| | Nearctic | Neotropical | Afrotropical | Oriental | Australian | Palaearctic | World |
|---|----------|-------------|--------------|----------|------------|-------------|-------|
| Number of basin without changes in richness | 76 | 225 | 116 | 97 | 198 | 166 | 878 |
| Percentage of basin number (%) | 31.54 | 60 | 57.43 | 28.87 | 37.08 | 21.61 | 35.75 |
| Percentage of basin area (%) | 11.45 | 5.6 | 34.9 | 10.06 | 26.65 | 1.94 | 13.4 |
| Percentage of river length (%) | 12.77 | 6.02 | 34.7 | 11.15 | 27.21 | 2.05 | 13.42 |

539

540 **Fig. S1.**

541 River basins (green color) where the three richness diversity facets remained unchanged from historical to current period.



542

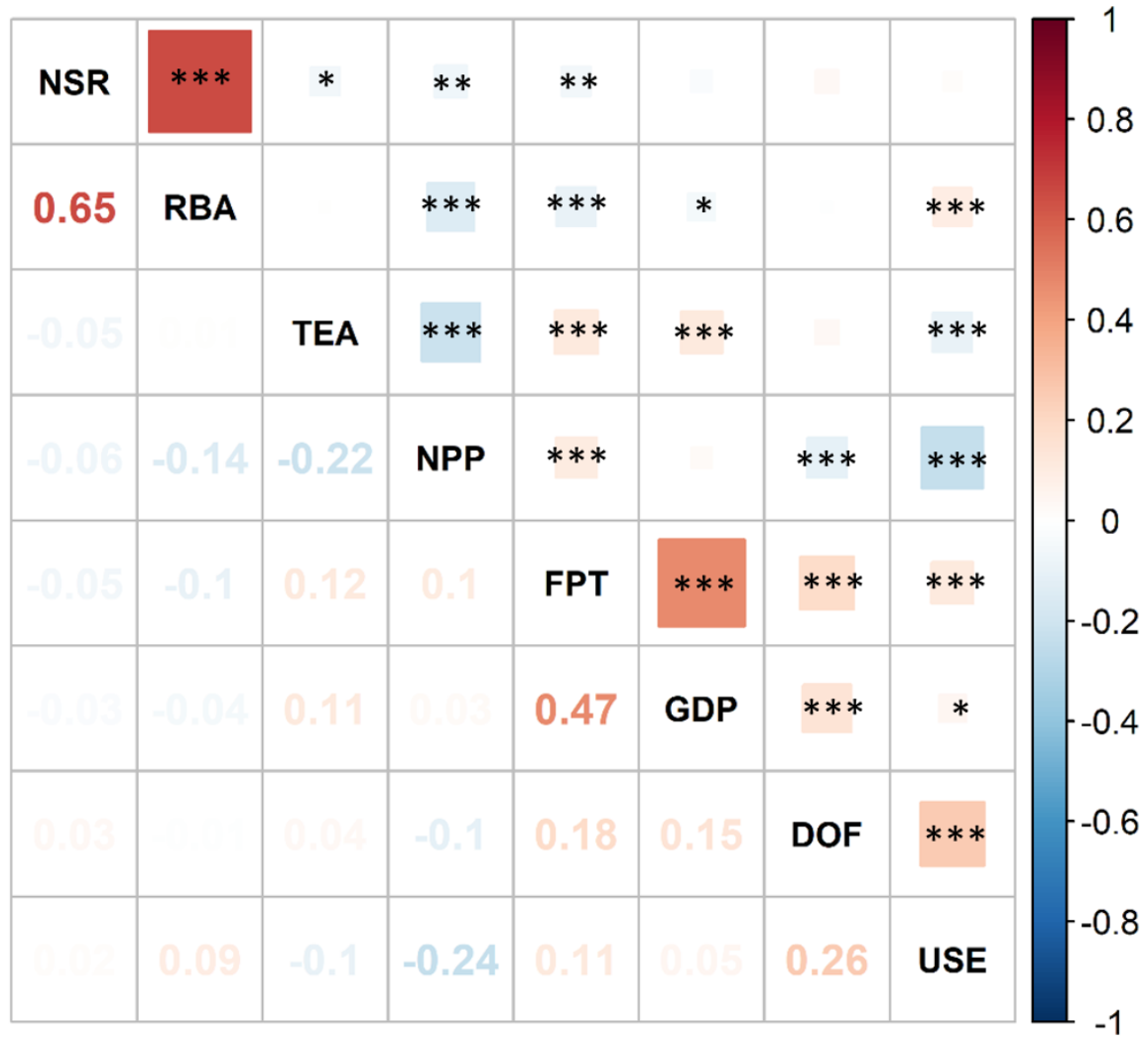
| Basin names | δ TR | δ FR | δ PR | δ TD | δ FD | δ PD | CCBF |
|----------------|-------------|-------------|-------------|-------------|-------------|-------------|------|
| Amazon | 1.0026 | 1.0003 | 1.0036 | 0.9997 | 0.9980 | 0.9991 | 6 |
| Congo | 1.0073 | 1.0061 | 1.0122 | 0.9991 | 0.9952 | 0.9989 | 6 |
| Mekong | 1.0346 | 1.0061 | 1.0394 | 0.9977 | 0.9958 | 0.9973 | 6 |
| Danube | 1.2247 | 1.1238 | 1.1865 | 0.9797 | 0.9937 | 1.0051 | 9 |
| Mississippi | 1.1523 | 1.0727 | 1.1863 | 0.9802 | 0.9955 | 0.9885 | 10 |
| Murray-Darling | 1.2642 | 1.1458 | 1.2800 | 0.9906 | 0.9714 | 1.0189 | 11 |

543

544 **Fig. S2.**

545 Changes in freshwater fish biodiversity for 6 representative river basins over the world. δ TR: taxonomic richness change; δ FR: functional richness

546 change; δ PR: phylogenetic richness change; δ TD: taxonomic dissimilarity change; δ FD: functional dissimilarity change; δ PD: phylogenetic
547 dissimilarity change. CCBF is the index of cumulative change in biodiversity facets.

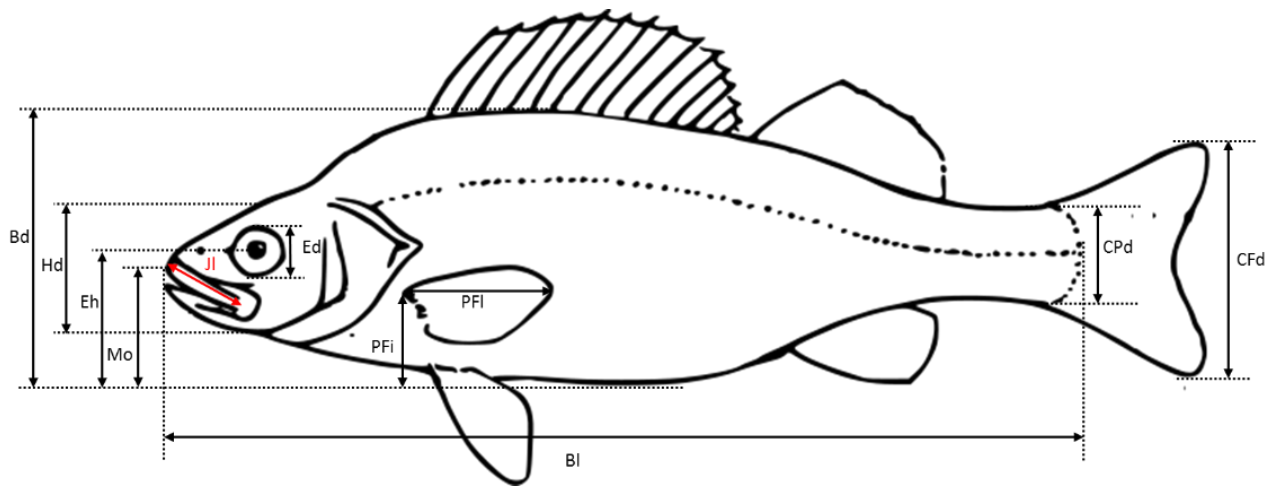


548

549 **Fig. S3.**

550 Pearson correlation between the eight environmental and human activity variables of the world
 551 river basins (n = 2,335). NSR: native species richness; RBA: river basin area; TEA: temperature
 552 anomaly since the last glacial maximum; NPP: net primary productivity; FPT: human footprint;
 553 GDP: gross domestic product; DOF: degree of fragmentation; USE: consumptive water use.

554 (***) $P < 0.001$, ** $P < 0.01$, * $P < 0.05$)



555

a. Morphological measurements

| Code | Name | Protocol for measurement |
|-------|-----------------------|---|
| Blmax | Maximum Body length | Maximum adult length |
| Bl | Body length | Standard length (snout to caudal fin basis) |
| Bd | Body depth | Maximum body depth |
| Hd | Head depth | Head depth at the vertical of eye |
| CPd | Caudal peduncle depth | Minimum depth of the caudal peduncle |
| CFd | Caudal fin depth | Maximum depth of the caudal fin |
| Ed | Eye diameter | Vertical diameter of the eye |
| Eh | Eye position | Vertical distance between the centre of the eye to the bottom of the body |
| Mo | Oral gape position | Vertical distance from the top of the mouth to the bottom of the body |
| JI | Maxillary jaw length | Length from snout to the corner of the mouth |
| PFI | Pectoral fin length | Length of the longest ray of the pectoral fin |
| PFi | Pectoral fin position | Vertical distance between the upper insertion of the pectoral fin to the bottom of the body |

All measurements were made on pictures except Blmax values, which were downloaded from Fishbase.org

556

b. Morphological traits

| Morphological traits | Formula | Potential link with fish functions | References |
|--------------------------------|-------------------|---|------------|
| Maximum body length | BLmax | Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling | (21) |
| Body elongation | $\frac{Bl}{Bd}$ | Hydrodynamism | (75) |
| Eye vertical position | $\frac{Eh}{Bd}$ | Position of fish and/or of its prey in the water column | (76) |
| Relative eye size | $\frac{Ed}{Hd}$ | Visual acuity | (77) |
| Oral gape position | $\frac{Mo}{Bd}$ | Feeding position in the water column | (78, 79) |
| Relative maxillary length | $\frac{Jl}{Hd}$ | Size of mouth and strength of jaw | (21) |
| Body lateral shape | $\frac{Hd}{Bd}$ | Hydrodynamism and head size | (21) |
| Pectoral fin vertical position | $\frac{Pfi}{Bd}$ | Pectoral fin use for swimming | (78) |
| Pectoral fin size | $\frac{Pfl}{Bl}$ | Pectoral fin use for swimming | (80) |
| Caudal peduncle throttling | $\frac{CFd}{CPd}$ | Caudal propulsion efficiency through reduction of drag | (81) |

557 **Fig. S4.**

558 Morphological measurements (a) and morphological traits (b) measured on each fish species.

559 For each morphological trait, the potential link with food acquisition and locomotion and

560 associated references are provided.

561 **Table S1.**

562 Results of the spatial simultaneous autoregressive error models (SAR_{error}) showing the
 563 coefficients of the selected optimal model in each realm. Model with the lowest AIC was
 564 selected for each realm. (NSR: native species richness; RBA: river basin area; TEA:
 565 temperature anomaly since the last glacial maximum; NPP: net primary productivity; FPT:
 566 human footprint; GDP: gross domestic product; DOF: degree of fragmentation; USE:
 567 consumptive water use; AIC: Akaike’s Information Criterion). The Moran’s *I* value represents
 568 the remaining autocorrelation on the residuals of the model for the first distance class (i.e.,
 569 neighbor drainages) in each realm.

Nearctic (n=241)

| NULL Model | | | AIC = 1416.66 |
|--|------------------|---------|----------------------|
| Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE | | | AIC = 1116.66 |
| Optimal Model: NSR+TEA+NPP+FPT+DOF+USE | | | AIC = 1113.68 |
| Statistics in Optimal Model | coefficient (SE) | z-value | <i>P</i> |
| NSR | 0.73(0.3) | 2.433 | 0.015 |
| TEA | -0.297(0.139) | -2.139 | 0.0325 |
| NPP | 0.526(0.297) | 1.769 | 0.0768 |
| FPT | 0.482(0.187) | 2.581 | 0.0099 |
| DOF | 0.722(0.197) | 3.667 | 0.0002 |
| USE | 0.604(0.196) | 3.077 | 0.0021 |
| Nagelkerke's R2 | 0.353 | | |
| Moran's I | -0.006 | | n.s. |

Neotropical (n=350)

| NULL Model | | | AIC = 1578.34 |
|---|------------------|---------|----------------------|
| Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE | | | AIC = 1546.92 |
| Optimal Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF | | | AIC = 1544.92 |
| Statistics in Optimal Model | coefficient (SE) | z-value | <i>P</i> |
| NSR | 0.344(0.142) | 2.421 | 0.0155 |
| RBA | -0.412(0.168) | -2.45 | 0.0143 |
| TEA | 4.54(1.166) | 3.893 | 0.0001 |
| NPP | -0.63(0.189) | -3.331 | 0.0009 |
| FPT | 0.32(0.189) | 1.692 | 0.0907 |
| GDP | -0.434(0.192) | -2.265 | 0.0235 |
| DOF | 0.535(0.203) | 2.632 | 0.0085 |
| Nagelkerke's R2 | 0.336 | | |
| Moran's I | -0.03 | | n.s. |

570

Afrotropical (n=198)

| NULL Model | | | AIC = 831.50 |
|--|------------------|---------|---------------------|
| Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE | | | AIC = 827.53 |
| Optimal Model: NSR+GDP+USE | | | AIC = 821.11 |
| Statistics in Optimal Model | coefficient (SE) | z-value | <i>P</i> |
| NSR | 0.247(0.09) | 2.749 | 0.006 |
| GDP | 3.108(1.598) | 1.945 | 0.0518 |
| USE | 0.355(0.127) | 2.799 | 0.0051 |
| Nagelkerke's R2 | 0.444 | | |
| Moran's I | -0.044 | | n.s. |

571

Oriental (n=292)

| NULL Model | | | AIC = 1154.37 |
|--|------------------|---------|----------------------|
| Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE | | | AIC = 1146.19 |
| Optimal Model: FPT+DOF | | | AIC = 1137.89 |
| Statistics in Optimal Model | coefficient (SE) | z-value | <i>P</i> |
| FPT | 0.695(0.149) | 4.675 | <0.0001 |
| DOF | 0.144(0.083) | 1.739 | 0.082 |
| Nagelkerke's R2 | 0.246 | | |
| Moran's I | -0.003 | | n.s. |

572

Australian (n=525)

NULL Model AIC = 2382.61

Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE AIC = 2361.76

Optimal Model: NSR+RBA+FPT+DOF+USE **AIC = 2357.49**

| Statistics in Optimal Model | coefficient (SE) | z-value | <i>P</i> |
|-----------------------------|------------------|---------|----------|
|-----------------------------|------------------|---------|----------|

| | | | |
|-----|--------------|-------|---------------|
| NSR | 1.015(0.474) | 2.143 | 0.0321 |
|-----|--------------|-------|---------------|

| | | | |
|-----|-------------|-------|-------------------|
| RBA | 1.43(0.328) | 4.365 | <0.0001 |
|-----|-------------|-------|-------------------|

| | | | |
|-----|------------|-------|---------------|
| FPT | 0.4(0.182) | 2.194 | 0.0282 |
|-----|------------|-------|---------------|

| | | | |
|-----|--------------|-------|--------|
| DOF | 0.208(0.122) | 1.701 | 0.0889 |
|-----|--------------|-------|--------|

| | | | |
|-----|--------------|--------|--------|
| USE | -0.43(0.289) | -1.489 | 0.1366 |
|-----|--------------|--------|--------|

| | | | |
|------------------------|-------|--|--|
| Nagelkerke's R2 | 0.529 | | |
|------------------------|-------|--|--|

| | | | |
|------------------|-------|--|------|
| Moran's I | -0.12 | | n.s. |
|------------------|-------|--|------|

Palearctic (n=729)

NULL Model AIC = 3161.83

Initial Model: NSR+RBA+TEA+NPP+FPT+GDP+DOF+USE AIC = 3101.15

Optimal Model: RBA+TEA+NPP+FPT+GDP+DOF AIC = 3097.47

| Statistics in Optimal Model | coefficient (SE) | z-value | P |
|-----------------------------|------------------|---------|-------------------|
| RBA | 0.324(0.069) | 4.673 | <0.0001 |
| TEA | -0.356(0.126) | -2.835 | 0.0046 |
| NPP | -0.319(0.181) | -1.761 | 0.0783 |
| FPT | 0.671(0.112) | 5.999 | <0.0001 |
| GDP | -0.155(0.086) | -1.808 | 0.0706 |
| DOF | 0.206(0.063) | 3.28 | 0.001 |
| Nagelkerke's R2 | 0.38 | | |
| Moran's I | -0.047 | | n.s. |

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661 **Table S2. (separate file)**

662 Species extirpations/extinctions and introductions in each of the 2456 river basins.

663 **Table S3. (separate file)**

664 The changes in the six diversity indices and the index of cumulative change in biodiversity

665 facets for the fish faunas in 2,456 basins. δ TR: change in taxonomic richness; δ FR: change in

666 functional richness; δ PR: change in phylogenetic richness; δ TD: change in taxonomic

667 dissimilarity; δ FD: change in functional dissimilarity; δ PD: change in phylogenetic

668 dissimilarity; CCBF: index of cumulative change in biodiversity facets.

669 Tables S2 and S3 are also provided in a public online repository (figshare.com). Here is the

670 private link: <https://figshare.com/s/5fadc2c14cbb1f39c25c>.