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Anthropogenic activities and environmental filtering have reshaped freshwater fish biodiversity patterns in China over the past 120 years

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1 **Anthropogenic activities and environmental filtering have reshaped freshwater**
2 **fish biodiversity patterns in China over the past 120 years**

3

4 **Abstract**

5 Over the past centuries, freshwater fish introductions and extinctions have been the
6 major environmental and ecological crises in various water bodies in China. However,
7 consequences of such crises on freshwater fish biodiversity in China remain only
8 partially or locally studied. Furthermore, identifications of relatively sensitive areas
9 along with stressors (i.e., environmental and anthropogenic drivers) influencing
10 freshwater fish biodiversity patterns are still pending. Taxonomic, functional, and
11 phylogenetic facets of biodiversity can well describe and evaluate the underlying
12 processes affecting freshwater fish biodiversity patterns under different
13 dimensionalities. Here we thus evaluated temporal changes in these facets of
14 freshwater fish biodiversity as well as a new developed biodiversity index,
15 multifaceted changes in fish biodiversity, for over a century at the basin level
16 throughout China using both alpha and beta diversity approaches. We also identified
17 the drivers influencing the changes in fish biodiversity patterns using random forest
18 models. The results showed that fish assemblages in Northwest and Southwest China
19 (e.g., Ili River basin, Tarim basin, and Erhai Lake basin) experienced extreme
20 temporal and multifaceted changes in the facets of biodiversity compared with other
21 regions, and environmental factors (e.g., net primary productivity, average annual
22 precipitation, and unit area) largely drove these changes. Since fish faunas in over 80%

23 of China's water bodies covering more than 80% of China's surface were currently
24 undergoing taxonomic, functional, and phylogenetic homogenization, targeted
25 conservation and management strategies should be proposed and implemented,
26 especially for the areas with relatively high changes in biodiversity.

27 **Keywords**

28 Fish extinctions; Fish introductions; Global changes; Biotic homogenization;
29 Multifaceted changes in fish biodiversity

30

31 **1. Introduction**

32 Global freshwater fish species, contributing a lot to various human livelihoods,
33 numerous ecosystem services, rich biological diversities, and so on (e.g., [Dudgeon et al., 2006](#);
34 [Naylor et al., 2021](#); [Stokes et al., 2021](#)), are capturing more and more
35 concerns from local governments and worldwide conservation groups and researchers
36 ([Zhang et al., 2020](#); [IUCN, 2021](#)). Nonetheless, there is growing evidence that many
37 fish species are currently undergoing a mass survival crisis, primarily due to
38 environmental changes and anthropogenic activities, such as climate change, habitat
39 destruction, pollution, overexploitation, and fish introductions ([Sax and Gaines, 2003](#);
40 [Dudgeon et al., 2006](#); [Barbarossa et al., 2021](#); [Su et al., 2021](#)). The most apparent
41 aftermath of this crisis is ongoing changes in compositions and richness of local fish
42 assemblages, i.e., some fish species are being extirpated from their native ranges
43 and/or colonizing novel areas ([Villéger et al., 2014](#); [Su et al., 2021](#)), which may cause
44 ecological, evolutionary, and economic impacts to varying degrees ([Cucherousset and](#)

45 [Olden, 2011; van der Veer and Nentwig, 2015](#)).

46 China, the world's most populous developing country ([National Bureau of Statistics,](#)
47 [2021](#)) and second largest economy ([Zhao et al., 2021](#)), as well as the one with a
48 megadiverse native fish fauna ([He et al., 2020; Xiang et al., 2021](#)), plays an oversized
49 role in the development of aquaculture, fisheries, aquariums, and relevant trades
50 around the world attributed to a large demand for fish proteins and growing spiritual
51 and cultural needs ([Cao et al., 2015; Xiong et al., 2015; Naylor et al., 2021](#)).

52 Meanwhile, China has to face a severe challenge by the imbalance between
53 high-speed economic development (e.g., urbanization, dam constructions, and fish
54 introductions for aquaculture) and inefficient freshwater biodiversity conservation
55 (e.g., spawning grounds degraded or destroyed by dams and functional niche of native
56 species undermined by non-natives) ([Xiong et al., 2015; Shuai et al., 2018; Zhang et](#)
57 [al., 2019; Mi et al., 2021](#)). Over the past centuries, at least 200 non-native freshwater
58 fish species have been introduced into the wild in China ([Xiang et al., 2021](#)) and 4
59 fishes have been declared to be extinct or extinct in the wild ([Liu et al., 2017](#)) mainly
60 owing to human-mediated disturbances. Such widespread fish introductions along
61 with a few fish extinctions in several areas have caused taxonomic homogenization of
62 China's freshwater fish faunas and loss of biological antiquity ([Liu et al., 2017](#)). This
63 biodiversity loss, however, is not only related to changes in the taxonomic facet of
64 biodiversity ([Marques et al., 2021](#)), since functional and phylogenetic facets of
65 biodiversity, which describe species' functional trait varieties and evolutionary history
66 breadth within the fish assemblage, respectively ([Kuczynski et al., 2018](#)), are also

67 strongly affected by both fish introductions and extinctions (Villéger et al., 2014;
68 Kuczynski et al., 2018; Su et al., 2021). For example, phylogenetic diversity provides
69 different and valuable information from taxonomic diversity when evaluating human
70 impacts on fish assemblages in the Lancang River in China (Zhang et al., 2018; 2019).
71 Further, even though there is no obvious change in local fish species richness of the
72 Pearl River in southern China which has been invaded by non-native fish species,
73 changes in some functional facets of biodiversity within the fish assemblage have
74 been detected (Shuai et al., 2018). These multiple facets of biodiversity which could
75 be helpful to better describe and evaluate the underlying processes affecting
76 freshwater fish biodiversity patterns (Jia et al., 2020) are thus increasingly applied for
77 fish conservation worldwide. Regrettably, consequences of fish introductions and/or
78 extinctions on the functional and phylogenetic facets as well as the taxonomic facet of
79 biodiversity in China remain only partially and locally studied, i.e., temporal changes
80 in the three facets at a national scale are incompletely understood (Liu et al., 2017; Su
81 et al., 2021). For instance, so far only in some Chinese rivers or isolated plateau lakes
82 have phylogenetic differentiation or homogenization of the fish faunas been found
83 (e.g., Jiang et al., 2019; Zhang et al., 2018; 2019), and just in some rivers, e.g., the
84 Yellow River, have temporal changes in the alpha and beta components of the three
85 facets of fish biodiversity in response to human disturbances been examined (e.g., Jia
86 et al., 2020). In addition, relevant studies on identifications of relatively sensitive
87 areas along with stressors (i.e., environmental and anthropogenic drivers) influencing
88 freshwater fish biodiversity patterns at the basin level in China, which can be a crucial

89 step forward for fish conservation efforts, are still pending and urgent.
90 Given that almost all documented introductions or extinctions of freshwater fish
91 species in China's wild habitats occurred after the 1900s (e.g., [Institute of Zoology,](#)
92 [Chinese Academy of Sciences et al., 1979](#); [Yue and Chen, 1998](#); [Xiang et al., 2021](#)),
93 the main objectives of this study were to (a) evaluate temporal changes in taxonomic,
94 functional, and phylogenetic facets of freshwater fish biodiversity for over a century
95 at the basin level throughout China using both alpha and beta diversity approaches
96 based on the most comprehensive freshwater fish database to date, (b) analyse
97 multifaceted changes in these facets of biodiversity to identify relatively sensitive
98 hydrological units as priority conservation zones, and (c) disentangle the relative
99 importance of environmental and anthropogenic drivers to temporal and multifaceted
100 changes in the facets of biodiversity. We believe that the present study, which
101 attempted to unveil China's freshwater fish biodiversity patterns, is essential for
102 fishery management and fish conservation, and call for further studies and concerns
103 on those sensitive zones identified.

104

105 **2. Materials and methods**

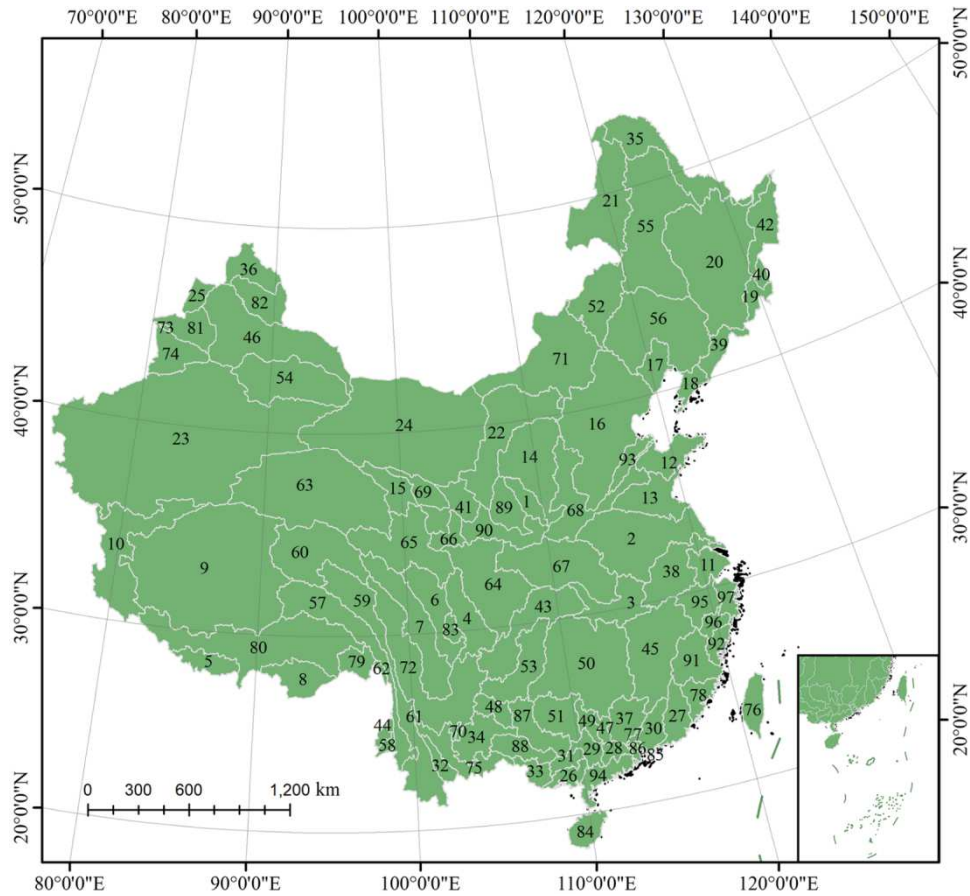
106 **2.1. Fish occurrences**

107 Based on previously reported basins or hydrological units for China's freshwater
108 fishes (e.g., [Lehner and Grill, 2013](#); [Liu et al., 2017](#); [He et al., 2020](#)) and the best
109 available fish distribution information, a total of 97 hydrological units throughout
110 China were divided ([Fig. 1](#)). Afterwards, China's freshwater fish species reported by

111 former works (e.g., [Xiang et al., 2021](#)) were assembled in each of these 97
112 hydrological units in historical (before the 1900s, i.e., before human-mediated species
113 introductions and extinctions) and current (after the 1900s) periods, respectively,
114 according to a comprehensive literature review, including peer-reviewed articles,
115 monographs, fish databases, and official survey reports. Each species in each
116 hydrological unit in the historical and/or current period was paired with a species
117 status, i.e., extant native, non-native, or extinct. Extant native species referred to
118 species which had been being present in a given unit ($n = 1,657$), while a species
119 present in the wild of a unit in China but not present originally in this unit before the
120 1900s was deemed as non-native to the matching unit, no matter it originated from
121 outside or within China ($n = 191$). Besides, species that were documented to be
122 extinct in their native units in China after the 1900s were considered as extinct ones (n
123 $= 6$) (e.g., [Yue and Chen, 1998](#); [IUCN, 2021](#)). Consequently, the fish occurrences of a
124 total of 1,742 species in the 97 hydrological units in historical (i.e., extant native
125 species + extinct species) and current (i.e., extant native species + non-native species)
126 periods were obtained.

127 Meanwhile, we further divided non-native fish species into exotic species originating
128 from outside China ($n = 81$) and translocated species originating from within China (n
129 $= 110$) to distinguish the introduction effects on beta diversity, i.e., the current fish
130 assemblages for the exotic species introduction pattern assumed only exotic species
131 had been introduced (i.e., extant native species + exotic species) and current fish
132 assemblages for the translocated species introduction pattern assumed only

133 translocated species had been introduced (i.e., extant native species + translocated
134 species).
135



136
137 **Fig. 1.** Sketch map of China at the basin level. The map showed 97 hydrological units
138 within the whole country, among which 95 units were defined for the subsequent
139 analysis. Unit 8 (Xibaxiaqu River basin) and 73 (Sayram Lake basin) were excluded
140 from the following functional diversity calculation due to fewer than five fish species
141 in each unit.
142

143 2.2. Phylogeny

144 ‘FishPhyloMaker’ package, which can automatically insert in and prune fish species

145 from the most comprehensive phylogenetic tree (Rabosky et al., 2018) for the
146 provided species following their taxonomic hierarchy, was used to generate
147 phylogenies for describing phylogenetic diversity of China's freshwater fish species
148 (Nakamura et al., 2021).

149 **2.3. Functional traits**

150 Ten morphological traits associated with food acquisition and locomotion which are
151 widely considered in functional diversity of freshwater fish species (e.g., Toussaint et
152 al., 2016; Su et al., 2021) were adopted to describe China's freshwater fish species
153 (Fig. S1; Table S1). Except for maximum body lengths describing fish size taken from
154 FishBase (Froese and Pauly, 2019) and related literature, the remaining 9
155 morphological traits are ratios of 11 morphological measurements measured on at
156 least one scientific side-view drawing or good-quality picture of an entire adult animal
157 (Fig. S1) collected from various fish databases (e.g., FishBase and Global
158 Biodiversity Information Facility (GBIF; <https://www.gbif.org/>; retrieved in
159 December 2020)) and literature using ImageJ software (<https://imagej.nih.gov/ij/>). All
160 measurement rules of the 11 morphological measurements were detailed in Toussaint
161 et al. (2016) and Xiang et al. (2021), and the morphological trait data were available
162 for the 1,742 species with 16,077 traits (92.29%) in this study. For the missing
163 morphological traits (7.71%), the 'Rphylopars' package, which can be used for
164 phylogenetic imputation of missing data and estimation of trait covariance across
165 species and within species, was applied (Bruggeman et al., 2009; Goolsby et al.,
166 2017). Furthermore, it's worth mentioning that the 10 traits turned out to be hardly

167 correlated to each other (the absolute values of Spearman's rho for all the 45 pairwise
168 comparisons ranged from 0.005 to 0.648 with an average of 0.211) after filling the
169 missing values. Then, a principal coordinates analysis (PCoA) using the
170 morphological trait-based distances was carried out to generate a multidimensional
171 space (Mouillot et al., 2013). Considering a trade-off between the quality of
172 PCoA-based multidimensional space and time cost (Maire et al., 2015), we selected
173 the first four PCoA axes (the mean absolute deviation was equal to 0.013) to compute
174 functional diversity indices.

175 **2.4. Environmental and anthropogenic drivers**

176 A total of 10 representative drivers encompassing various geo-morphological,
177 hydrological, climatic, social, and economic features, which are widely adopted in
178 fish invasion ecology and conservation management research (e.g., Kuczynski et al.,
179 2018; Lin et al., 2021; Su et al., 2021), were selected to describe China's hydrological
180 units: (a) unit area (UAR), (b) elevation (ELE), (c) average annual temperature (AAT),
181 (d) average annual precipitation (AAP), (e) net primary productivity (NPP), (f) river
182 fragmentation (RFR), (g) human footprint (HFP), (h) consumptive water loss (CWL),
183 (i) aquaculture pressure (APR), and (j) fishing pressure (FPR) (Table S2). We then
184 calculated the mean value of the cells within each hydrological unit for all drivers so
185 as to apportion the attribute values of each stressor to corresponding units.

186 **2.5. Diversity indices**

187 Here, we adopted six diversity indices, including three alpha diversity indices (i.e.,
188 taxonomic richness (TRic), functional richness (FRic), and phylogenetic richness

189 (PRic)) and three beta diversity indices (i.e., Jaccard-index for taxonomic
190 dissimilarity (TDis), beta-FRic for functional dissimilarity (FDis), and UniFrac for
191 phylogenetic dissimilarity (PDis)), to measure for fish assemblages in China's
192 hydrological units in the historical and current periods, respectively. These indices are
193 the most often applied in assessing multiple facets of freshwater fish biodiversity (e.g.,
194 [Villéger et al., 2014](#); [Kuczynski et al., 2018](#); [Su et al., 2021](#)). Notably, the two units
195 (Xibaxiaqu River basin and Sayram Lake basin) with fewer than five fish species
196 were excluded from the functional diversity calculation as four functional dimensions
197 were kept. Among the three alpha diversity indices, TRic referred to the total number
198 of species in one hydrological unit, FRic was estimated as the volume of the
199 minimum convex hull shaping all the species from one hydrological unit in the
200 4-dimensional functional space ([Cornwell et al., 2006](#); [Villéger et al., 2008](#)), and PRic
201 was measured as the sum of the branch lengths connecting all species present in one
202 hydrological unit within the phylogenetic tree ([Faith, 1992](#)). For the three beta
203 diversity indices, TDis was measured using the percentage of dissimilarity in species
204 composition between each pair of fish assemblages present in hydrological units
205 ([Jaccard, 1912](#); [Baselga, 2012](#); [Villéger et al., 2013](#)), FDis was measured as the
206 non-shared fraction of total functional space volume between each pair of fish
207 assemblages ([Villéger et al., 2011a](#); [2013](#)), and PDis was measured as the unique
208 fraction of total phylogenetic diversity between each pair of fish assemblages
209 ([Lozupone and Knight, 2005](#); [Lozupone et al., 2006](#)). Considering China's topography,
210 e.g., the sizeable east-west and north-south span, we therefore adopted the inverse of

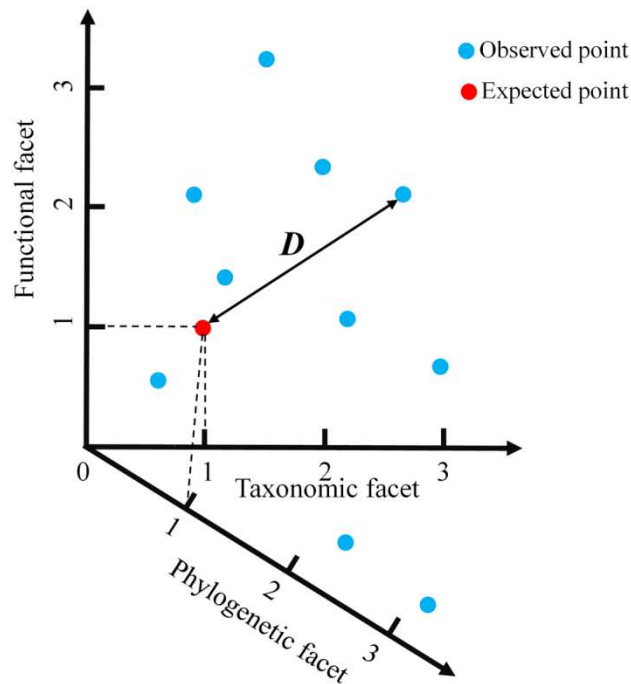
211 geographical distance between focal units as weights (Villéger et al., 2013). Each beta
212 diversity index for every hydrological unit was then calculated using the weighted
213 average value of the pairwise comparisons between the fish assemblage in the target
214 unit and all the other assemblages in corresponding units.

215 **2.6. Statistical analyses**

216 Each of the six current diversity indices for every hydrological unit was divided by
217 their corresponding historical counterpart, which can be treated as a metric of
218 temporal change (i.e., $Diversity_{current} / Diversity_{historical}$). We then innovatively
219 projected the six ratios for the 95 hydrological units into a six-dimensional Cartesian
220 coordinate system, where taxonomic, functional, and phylogenetic richness and
221 dissimilarity were set as corresponding axes (Fig. 2). In the six-dimensional Cartesian
222 coordinate system, $(r_1, r_2, r_3, r_4, r_5, r_6)$ (i.e., six ratios for each hydrological unit) was
223 deemed as an observed point, while $(1, 1, 1, 1, 1, 1)$ was regarded as the expected
224 point. The Euclidean distance between an observed point and the expected point,
225 which was considered as multifaceted changes in the biodiversity facets in a unit, was
226 calculated as follows:

$$227 \quad D = \sqrt{\sum_{i=1}^6 (r_i - 1)^2}$$

228 where, r_i is the above-mentioned ratio for each unit. Further, we used the quartile
229 method to divide the 95 temporal changes for each diversity index as well as the
230 multifaceted changes into different groups, and then we defined outlier changes (if
231 existed) as extreme ones.



233

234 **Fig. 2.** Sketch of the three(six)-dimensional Cartesian coordinate system. D referred
 235 to the Euclidean distance between an observed point and the expected point.

236

237 Afterwards, in order to identify the potential drivers affecting the temporal and
 238 multifaceted changes in biodiversity facets, random forest models which show less
 239 sensitivity to the issues of multicollinearity and spatial autocorrelation and play a
 240 good performance in analysing a very large number of independent variables without
 241 screening (Breiman, 2001a; 2011b) were applied. In the random forest models, the 10
 242 drivers and temporal and multifaceted changes ($\log_{10}(X)$ -transformed if the
 243 distributions were not Gaussian) were considered as the explanatory and response
 244 variables, respectively. We employed 5,000 decision trees in the random forest models,
 245 and the percentage increase in mean squared error (%IncMSE) and total decrease in

246 node impurities from splitting on the variable, averaged over all trees (IncNodePurity),
247 were used to measure the importance of the drivers. Finally, partial dependence plots
248 were adopted to visualize the relationships between relatively important drivers
249 identified by the random forest models and the temporal and multifaceted changes
250 (Friedman, 2001).

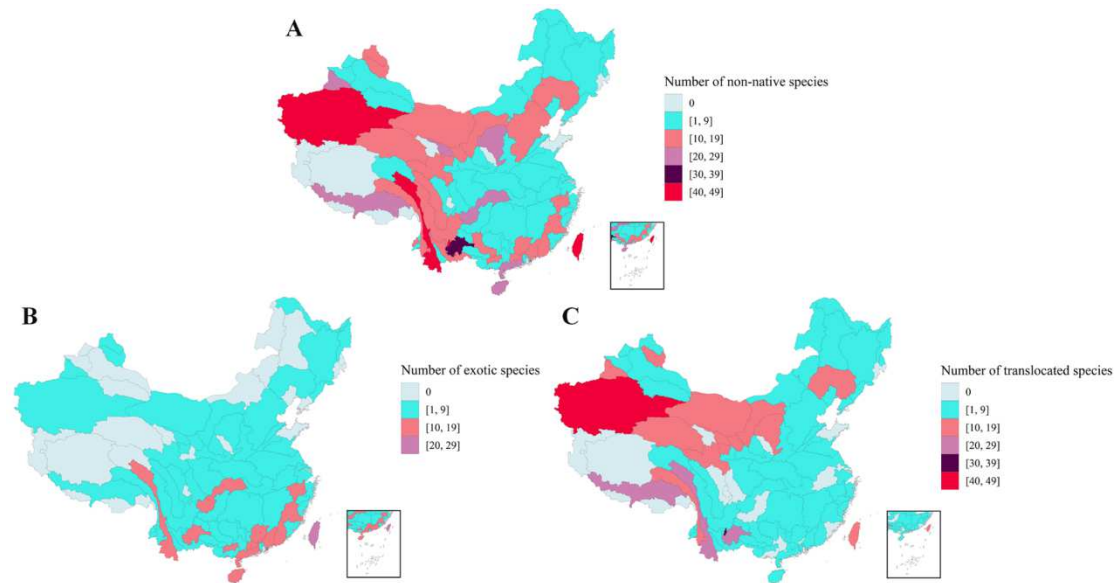
251 All statistical analyses were performed with R software version 4.0.5 (R Core Team,
252 2021) using the packages FishPhyloMaker, picante, Rphylopars, mFD, rfPermute, and
253 randomForest.

254

255 **3. Results**

256 The number of extant native and non-native species per hydrological unit ranged from
257 0 to 243 with an average of 84.97 and from 0 to 47 with an average of 10.47,
258 respectively (Fig. 3). Further, the number of exotic and translocated species per unit
259 ranged from 0 to 29 with an average of 4.52 and from 0 to 42 with an average of 5.96,
260 respectively (Fig. 3). Compared with fish introductions, fish extinctions were far less
261 frequent, with six species extirpated in only four units including Unit 15 (Qinghai
262 Lake basin), 34 (Nanpanjiang River basin), 36 (Irtys River basin), and 85 (Hong
263 Kong).

264



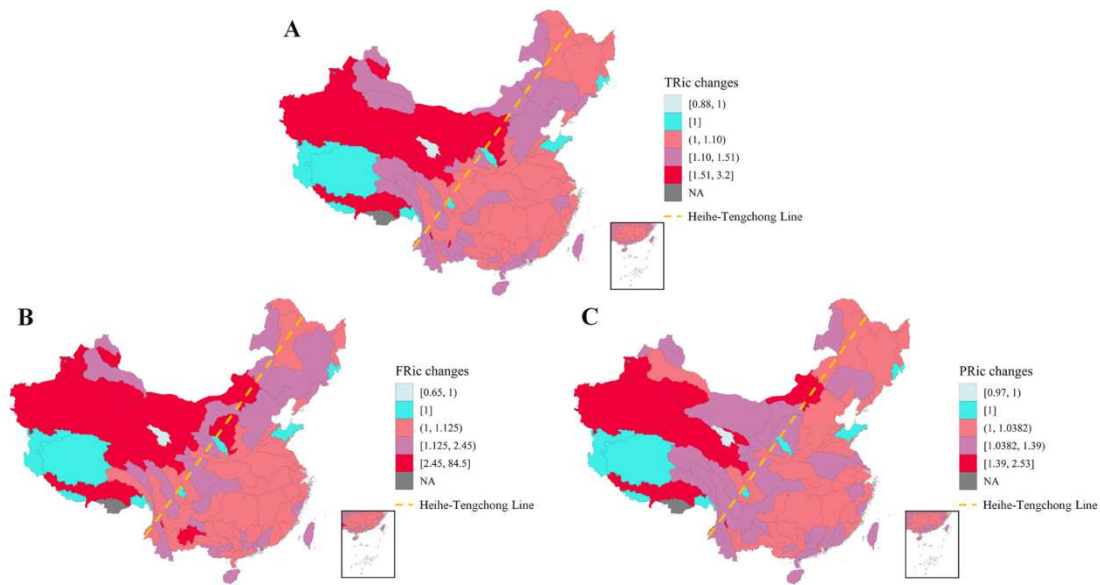
265

266 **Fig. 3.** Number of (A) non-native (i.e., exotic + translocated), (B) exotic, and (C)
 267 translocated species in China's hydrological units.

268

269 3.1. Temporal changes in alpha diversity

270 Overall, TRic, FRic, and PRic in China's hydrological units all increased by 11.99%,
 271 16.71%, and 9.43% on average from the historical to the current period, respectively,
 272 and the trends of the temporal changes predominantly showed positive longitudinal
 273 gradients from southeast to northwest (Fig. 4). However, among these units, the three
 274 facets of alpha diversity declined in Unit 15 (Qinghai Lake basin) located in
 275 Northwest China, and had no changes in another 9 units (9.69% of China's surface)
 276 mainly located in Southwest China (Fig. 4). Besides, extreme increases in the three
 277 facets of alpha diversity mostly occurred in Northwest and Southwest China, e.g.,
 278 Unit 74 (Ili River basin; 3.18-fold, 84.48-fold, and 1.94-fold increases in TRic, FRic,
 279 and PRic, respectively), Unit 63 (Qaidam basin; 1.82, 53.90, and 2.46) and Unit 61
 280 (Erhai Lake basin; 2.32, 4.00, and 1.47) (Fig. 4; Fig. S2).



282

283 **Fig. 4.** Temporal changes in (A) TRic, (B) FRic, and (C) PRic of freshwater fish
 284 assemblages in China's hydrological units. TRic: taxonomic richness; FRic:
 285 functional richness; PRic: phylogenetic richness. The Heihe-Tengchong Line is an
 286 important geographical dividing line related to populations, environments, economy,
 287 and so on in China.

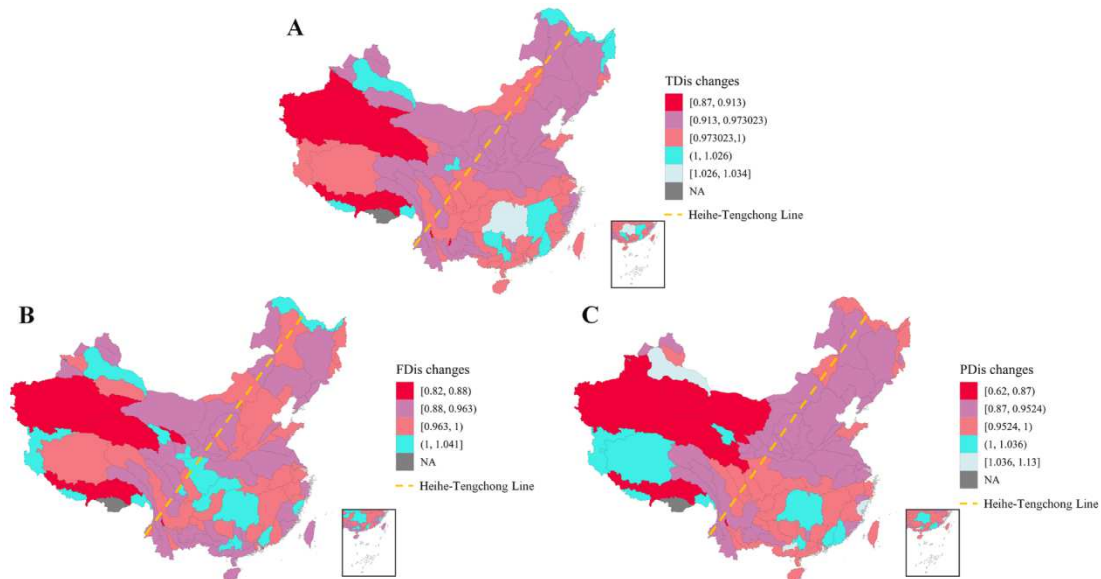
288

289 3.2. Temporal changes in beta diversity

290 Overall, fish assemblages in the 95 hydrological units showed a trend towards biotic
 291 homogenization, i.e., the three facets of beta diversity decreased by 3.20% (TDis),
 292 4.00% (FDis) and 5.76% (PDis) on average, respectively, and the trends of the
 293 temporal changes predominantly showed negative longitudinal gradients from
 294 southeast to northwest (Fig. 5). More specifically, fish assemblages in 86.60% (88.52%
 295 of China's surface), 81.44% (85.86%) and 83.51% (84.03%) of the units showed a
 296 trend towards taxonomic, functional, and phylogenetic homogenization, respectively,

297 and extreme decreases mostly occurred in Northwest and Southwest China (Fig. 5;
298 Fig. S3).

299



300

301 **Fig. 5.** Temporal changes in (A) TDis, (B) FDis, and (C) PDis of freshwater fish
302 assemblages in China's hydrological units. TDis: taxonomic dissimilarity; FDis:
303 functional dissimilarity; PDis: phylogenetic dissimilarity.

304

305 The exotic species introduction pattern resulted in slight trends towards taxonomic
306 (0.21%), functional (0.06%), and phylogenetic (0.49%) differentiation. More
307 specifically, exotic introductions induced taxonomic, functional, and phylogenetic
308 differentiation of fish assemblages in 58.76% (56.54% of China's surface), 42.27%
309 (34.34%), and 64.95% (57.48%) of the units, respectively. The translocated species
310 introduction pattern resulted in more pronounced trends towards taxonomic (3.53%),
311 functional (4.44%), and phylogenetic (7.46%) homogenization. More specifically,
312 translocations induced taxonomic, functional, and phylogenetic homogenization of

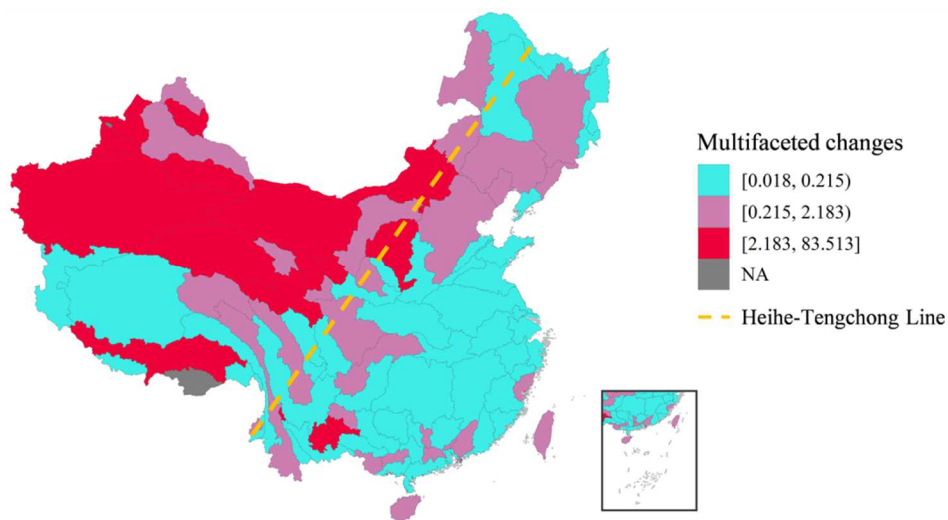
313 fish assemblages in 87.63% (89.16% of China's surface), 86.60% (87.98%), and
314 88.66% (85.34%) of the units, respectively.

315

316 **3.3. Multifaceted changes in biodiversity facets**

317 Multifaceted changes experienced by fish assemblages showed a clear spatial pattern,
318 with a positive gradient from southeast to northwest (Fig. 6; Fig. S4). The greatest
319 multifaceted change took place in Unit 74 (Ili River basin; $D = 83.51$), followed by
320 another 16 relatively extreme situations mainly occurring in Northwest, Southwest,
321 and North China, e.g., Unit 69 (Huangshui River basin; $D = 71.43$), 63 (Qaidam basin;
322 $D = 52.93$), and 23 (Tarim basin; $D = 13.35$), which held 31.36% of China's surface
323 and supported 336, 23, and 82 extant native, exotic, and translocated species,
324 respectively (Fig. 6).

325



326

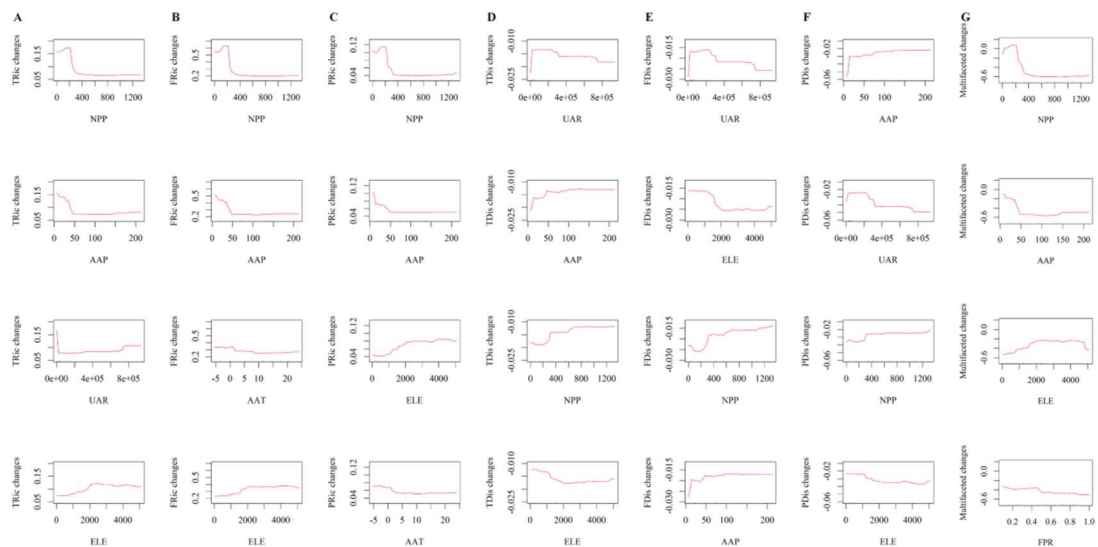
327 **Fig. 6.** Multifaceted changes in biodiversity of freshwater fish assemblages in China's
328 hydrological units.

329

330 **3.4. Determinants of the temporal and multifaceted changes in biodiversity facets**

331 The random forest models with all 10 drivers for temporal and multifaceted changes
 332 explained 36.60% (TRic changes), 21.61% (FRic changes), 19.92% (PRic changes),
 333 20.86% (TDis changes), 2.89% (FDis changes), 8.22% (PDis changes), and 28.51%
 334 (Multifaceted changes) of the total variances, respectively. Environmental factors (e.g.,
 335 NPP, ELE, UAR, AAT, and AAP) were the main drivers explaining the temporal
 336 changes of the six diversity indices and multifaceted changes (Fig. S5). Partial
 337 dependence plots showed negative responses of the temporal changes of alpha
 338 diversity and multifaceted changes to NPP and AAP, and positive responses to ELE.
 339 On the contrary, the temporal changes of beta diversity showed positive responses to
 340 NPP and AAP, and negative responses to UAR and ELE (Fig. 7).

341



342

343 **Fig. 7.** Partial dependence plots for the four most important drivers (based on

344 IncNodePurity) for temporal and multifaceted changes (log-transformed) in

345 biodiversity facets through the random forest models (for the remaining drivers, see

346 [Fig. S6](#)). The y-axis in each plot referred to log-transformed changes in biodiversity
347 facets: (A) TRic changes, (B) FRic changes, (C) PRic changes, (D) TDis changes, (E)
348 FDis changes, (F) PDis changes, and (G) multifaceted changes. NPP: net primary
349 productivity; AAP: average annual precipitation; UAR: unit area; ELE: elevation;
350 AAT: average annual temperature; FPR: fishing pressure.

351

352 **4. Discussion**

353 Fish introductions to various inland water bodies across China inevitably caused
354 overall increases in TRic, FRic, and PRic even though fish extinctions happened in
355 several areas. Additionally, fish assemblages in most of China's water bodies had
356 experienced homogenization in the three biodiversity facets, which are consistent with
357 previous studies documenting the current biodiversity crisis across the world ([Villéger
358 et al., 2011b](#); [Villéger et al., 2014](#); [Su et al., 2021](#)).

359 A high increase in species richness is generally accompanied by relatively high
360 increases in FRic and PRic but at different rates ([Toussaint et al., 2018](#); [Zhang et al.,
361 2018](#)). Among the three facets, the functional facet increased by 16.71% on average
362 and appeared to be the most sensitive facet for detecting changes in alpha diversity,
363 followed by taxonomic (11.99%) and phylogenetic (9.43%) facets. FRic is greatly
364 affected by TRic ([Su et al., 2022](#)), however, tremendous alterations might happen in
365 FRic even though little changes in TRic ([Toussaint et al., 2018](#)). The typical example
366 occurred in Qaidam basin possessing low species richness but highly distinctive
367 species (i.e., *Triplophysa*, *Schizopygopsis*, and *Gymnocypris* spp.) (e.g., [Tedesco et al.,](#)

2017), which experienced the lower change in TRic (1.82 folds vs 2.32 folds) but a far higher change in FRic (53.90 folds vs 4.00 folds) compared with Erhai Lake basin with a more diverse native fish fauna (at least 10 genera) (e.g., Tang et al., 2013). The discrepancy in the huge change in FRic mainly stemmed from a relatively rich native fish fauna with more diverse morphological traits in Erhai Lake basin though more species were introduced, while non-native species (e.g., *Misgurnus*, *Megalobrama*, and *Hypophthalmichthys* spp.) (Tang and He, 2015) with more extreme traits than native species in Qaidam basin were introduced there. Compared with the global situation, China's hydrological units tended to hold non-native species with more similar morphological traits to its natives as the increase in FRic (16.71%) was far less than the global average (150%) even though the magnitude of increase in TRic (11.99%) in China got close to the global average (15%) (Toussaint et al., 2018). Nevertheless, extreme increases in FRic in some units located in Northwest China revealed profound biodiversity changes (Toussaint et al., 2018; Jia et al., 2020), which deserve more attention. For beta diversity, the phylogenetic facet (decreasing in 83.51% of the units) was the greatest (an overall decrease of 5.76%) in the extent of biotic homogenization in China, followed by the functional (decreasing in 81.44% of the units with an overall decrease of 4.00%) and taxonomic (86.60%; 3.20%) facets. These situations indicated that fish assemblages in most of China's water bodies had been more extensively altered in beta diversity compared with those in global rivers (PDis, FDis, and TDis with a decrease in only 35%, 84.6%, and 58% of the global rivers, respectively) (Su et al., 2021). In view of the far higher frequency of fish

390 introductions than extinctions, biotic homogenization in China's water bodies was
391 largely owing to fish introductions. To be more specific, translocated species are
392 functionally and phylogenetically more similar to other native species than exotic
393 species considering they were historically already present in similar ecosystems as
394 natives (Villéger et al., 2014; Su et al., 2021), which tend to result in biotic
395 homogenization. Our results also confirmed this point as translocated species
396 introductions led to a far larger degree of homogenization in the three biodiversity
397 facets than exotic species introductions which mostly induced mild biotic
398 differentiation. Compared with exotic species, translocated species were more often
399 introduced in China's hydrological units. Less frequent introductions of functionally
400 and phylogenetically distinct exotic species thus cannot compensate for the effects of
401 more frequent introductions of functionally and phylogenetically more similar
402 translocated species resulting in the homogenization of recipient units (Su et al., 2021).
403 Massive losses of taxonomic, functional, and phylogenetic distinctiveness
404 predominantly caused by translocated species may weaken the resilience or resistance
405 for these homogenized communities in China to external disturbances (Olden et al.,
406 2004; Villéger et al., 2011b; Jiang et al., 2019; Jia et al., 2020). Translocated species
407 introductions should thus be treated more prudently, especially in Northwest China
408 where highest biotic homogenization mostly occurred.

409 Without doubt, human activities (e.g., aquaculture, capture fisheries, and hydraulic
410 constructions) can bring about fish introductions and extinctions which would alter
411 local fish compositions (Villéger et al., 2011b; Xiong et al., 2015; Su et al., 2021).

412 Nevertheless, mounting evidence shows that it is not anthropogenic pressures but
413 environmental factors that play predominant roles in structuring fish assemblage
414 patterns (e.g., [Brucet et al., 2013](#); [Kuczynski et al., 2018](#)). For example,
415 environmental variables (e.g., temperature anomaly since the last glacial maximum
416 and river basin area) contribute a lot to the multifaceted changes in biodiversity of fish
417 assemblages from the Neotropical and Australian realms ([Su et al., 2021](#)). Consistent
418 with this phenomenon, our study also demonstrated that environmental, not
419 anthropogenic factors, e.g., net primary productivity, elevation, and precipitation
420 strongly drove temporal and multifaceted changes in China's three biodiversity facets.
421 In general, species tend to distribute in the most suitable habitats ([Kang et al., 2014](#)).
422 Therefore, whether non-native species introduced to various water bodies for human
423 purposes can establish and spread well at initial entry points partially depends on
424 various environmental conditions, e.g., temperature, precipitation, and duration of
425 drought season ([Lin et al., 2015](#); [Trochine et al., 2018](#); [Lin et al., 2021](#)). For instance,
426 several species (e.g., *Hypophthalmichthys nobilis* (Richardson, 1845)) released into
427 Lahunshui Reservoir, lower Yellow River basin cannot survive well because of local
428 insufficient plankton net primary productivity resulting from low precipitation since
429 1998 ([Guo, 2004](#)). As for extinct species, the extinction of both *Anabarilius*
430 *macrolepis* Yih & Wu, 1964 and *Cyprinus yilongensis* Yang et al., 1977 in Yilonghu
431 Lake, Nanpanjiang River basin is directly due to the complete drought in 1981
432 ([Darwall and Freyhof, 2016](#)), which heightened the environmental filtering hypothesis
433 ([Kraft et al., 2015](#); [Lin et al., 2021](#)). Except positive relationships between the

434 changes in biodiversity facets (i.e., the multifaceted changes, temporal changes of
435 alpha diversity, and extent of biotic homogenization) and elevation, negative
436 relationships were detected between the aforementioned changes and net primary
437 productivity and average annual precipitation. Multifaceted changes, temporal
438 changes in alpha diversity, and extent of biotic homogenization across China were
439 almost differentiated along the Heihe-Tengchong Line with relatively high altitude
440 and low vegetation cover and precipitation in its west side compared with its east side
441 (Wang et al., 2014; Liu et al., 2021; Zheng et al., 2021). Coincidentally, since the
442 1900s, a large number of non-native fish species including translocated species (e.g.,
443 Chinese carps) originating from China's eastern basins and exotic species (e.g.,
444 *Oncorhynchus* and *Piaractus* spp.) originating from outside China have been
445 introduced to western basins in this country, many of which now contribute
446 significantly to the production of local fisheries enhancement and aquaculture (e.g.,
447 Walker and Yang, 1999), and have established populations in various water bodies of
448 recipient areas. Compared with fish faunas in the east side, those in the west side of
449 the Heihe-Tengchong Line (e.g., Tarim basin, Qaidam basin, Hexi Corridor basin, and
450 Middle Inner Mongolia basin) were more distinct and specialized (e.g., *Triplophysa*,
451 *Schizothorax*, *Hedinichthys*, and *Gymnocypris* spp.) but poorer, which were chiefly
452 attributed to the local environmental conditions including unique river systems,
453 geographic situations, and/or climate (Yan, 2003; Kang et al., 2014). Such sizable
454 regions only holding relatively low richness of native species with periodic life
455 history strategies provided abounding divergent water bodies and vacant niche

456 opportunities for non-native species with opportunistic strategies (e.g., a great range
457 of ecological traits and tremendous variation in morphology and genetics) ([Kang et al.,](#)
458 [2014](#); [Xing et al., 2016](#); [Liu et al., 2017](#)), where they can find suitable habitats that
459 may be inhospitable to natives ([Wei et al., 2021](#)). Compared with other units in the
460 west side of the Heihe-Tengchong Line, striking exceptions mostly occurred in Unit 9
461 (Changtang basin) and 10 (Shiquan River basin), where fish assemblages experienced
462 very mild multifaceted changes in biodiversity along with minor changes in
463 dissimilarity but no changes in alpha diversity. Such a situation primarily resulted
464 from local traditions and harsh environments of the areas which prevented many
465 anthropogenic activities including aquaculture and fisheries ([Zhang and Xing, 1996](#);
466 [Zhang et al., 2020](#)), which caused relatively little chance for non-native species to
467 spread and establish.

468 In conclusion, China's freshwater fish faunas were currently undergoing taxonomic,
469 functional, and phylogenetic homogenization which is now considered one of the
470 most prominent components of the biodiversity crisis worldwide. Predictably, fish
471 assemblages in China's water bodies would continue to experience biotic
472 homogenization in light of the rapid development of hydro projects, aquaculture, and
473 aquarium trades ([Jia, 2016](#); [Liu et al., 2017](#); [Gu et al., 2022](#)), as well as challenges in
474 the eradication of non-native species ([Britton et al., 2011](#)). Targeted conservation and
475 management strategies should be urgent, especially for hydrological units with
476 relatively high multifaceted changes in biodiversity, because almost all fish
477 introductions and extinctions were accelerated by human activities, including

478 facilitating biotic exchange among areas and altering habitats. More specifically,
479 certain focused strategies can be implemented: (a) formulate stricter legislation and
480 policies to conserve fish resources; (b) strengthen regulatory efforts for artificial fish
481 propagation and release to prevent non-native fish species from entering novel areas;
482 (c) establish detection and monitoring systems for non-native fish species; (d) provide
483 scientific training for relevant practitioners to enhance their knowledge and awareness
484 of fish invasions and conservation; and (e) reduce anthropogenic disturbances and
485 establish aquatic reserves in vulnerable areas (i.e., areas with relatively high
486 multifaceted changes in biodiversity demonstrated by this study).

487

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495

496 **Data availability**

497 Literature and relevant databases adopted for constructing the datasets of China’s
498 freshwater fish species (e.g., morphological data and fish occurrences) can be found
499 in the Supplementary data. The complete biological database is available from T.X.

500 upon request.

501

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