Research article

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

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ABSTRACT

Over the past centuries, freshwater fish introductions and extinctions have been the major environmental and ecological crises in various water bodies in China. However, consequences of such crises on freshwater fish biodiversity in China remain only partially or locally studied. Furthermore, identifications of relatively sensitive areas along with stressors (i.e., environmental and anthropogenic drivers) influencing freshwater fish biodiversity patterns are still pending. Taxonomic, functional, and phylogenetic facets of biodiversity can well describe and evaluate the underlying processes affecting freshwater fish biodiversity patterns under different dimensionalities. Here we thus evaluated temporal changes in these facets of freshwater fish biodiversity as well as a new developed biodiversity index, multifaceted changes in fish biodiversity, for over a century at the basin level throughout China using both alpha and beta diversity approaches. We also identified the drivers influencing the changes in fish biodiversity patterns using random forest models. The results showed that fish assemblages in Northwest and Southwest China (e.g., Ili River basin, Tarim basin, and Erhai Lake basin) experienced extreme temporal and multifaceted changes in the facets of biodiversity compared with other regions, and environmental factors (e.g., net primary productivity, average annual precipitation, and unit area) largely drove these changes. Since fish faunas in over 80% of China's water bodies covering more than 80% of China's surface were currently undergoing taxonomic, functional, and phylogenetic homogenization, targeted conservation and management strategies should be proposed and implemented, especially for the areas with relatively high changes in biodiversity.

Credit author statement

T.X.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Visualization, Original draft, Review & editing. X.H.D.: Conceptualization, Formal analysis, Funding acquisition, Methodology, Software, Visualization, Review & editing. G.G.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Review & editing. T.J.: Review & editing. L.S.: Review & editing.

1. Introduction

Global freshwater fish species, contributing a lot to various human livelihoods, numerous ecosystem services, rich biological diversities, and so on (e.g., Dudgeon et al., 2006; Naylor et al., 2021; Stokes et al., 2021), are capturing more and more concerns from local governments and worldwide conservation groups and researchers (Zhang et al., 2020; IUCN, 2021). Nonetheless, there is growing evidence that many fish species are currently undergoing a mass survival crisis, primarily due to environmental changes and anthropogenic activities, such as climate change, habitat destruction, pollution, overexploitation, and fish introductions (Sax and Gaines, 2003; Dudgeon et al., 2006; Barbarossa

et al., 2021; Su et al., 2021). The most apparent aftermath of this crisis is ongoing changes in compositions and richness of local fish assemblages, i.e., some fish species are being extirpated from their native ranges and/or colonizing novel areas (Villéger et al., 2014; Su et al., 2021), which may cause ecological, evolutionary, and economic impacts to varying degrees (Cucherousset and Olden, 2011; van der Veer and Nentwig, 2015).

China, the world's most populous developing country (National Bureau of Statistics, 2021) and second largest economy (Zhao et al., 2021), as well as the one with a megadiverse native fish fauna (He et al., 2020; Xiang et al., 2021), plays an oversized role in the development of aquaculture, fisheries, aquariums, and relevant trades around the world attributed to a large demand for fish proteins and growing spiritual and cultural needs (Cao et al., 2015; Xiong et al., 2015; Naylor et al., 2021). Meanwhile, China has to face a severe challenge by the imbalance between high-speed economic development (e.g., urbanization, dam constructions, and fish introductions for aquaculture) and inefficient freshwater biodiversity conservation (e.g., spawning grounds degraded or destroyed by dams and functional niche of native species undermined by non-natives) (Xiong et al., 2015; Shuai et al., 2018; Zhang et al., 2019; Mi et al., 2021). Over the past centuries, at least 200 non-native freshwater fish species have been introduced into the wild in China (Xiang et al., 2021) and 4 fishes have been declared to be extinct or extinct in the wild (Liu et al., 2017) mainly owing to human-mediated disturbances. Such widespread fish introductions along with a few fish extinctions in several areas have caused taxonomic homogenization of China's freshwater fish faunas and loss of biological antiquity (Liu et al., 2017). This biodiversity loss, however, is not only related to changes in the taxonomic facet of biodiversity (Marques et al., 2021), since functional and phylogenetic facets of biodiversity, which describe species' functional trait varieties and evolutionary history breadth within the fish assemblage, respectively (Kuczynski et al., 2018), are also strongly affected by both fish introductions and extinctions (Villéger et al., 2014; Kuczynski et al., 2018; Su et al., 2021). For example, phylogenetic diversity provides different and valuable information from taxonomic diversity when evaluating human impacts on fish assemblages in the Lancang River in China (Zhang et al., 2018, 2019). Further, even though there is no obvious change in local fish species richness of the Pearl River in southern China which has been invaded by non-native fish species, changes in some functional facets of biodiversity within the fish assemblage have been detected (Shuai et al., 2018). These multiple facets of biodiversity which could be helpful to better describe and evaluate the underlying processes affecting freshwater fish biodiversity patterns (Jia et al., 2020) are thus increasingly applied for fish conservation worldwide. Regrettably, consequences of fish introductions and/or extinctions on the functional and phylogenetic facets as well as the taxonomic facet of biodiversity in China remain only partially and locally studied, i.e., temporal changes in the three facets at a national scale are incompletely understood (Liu et al., 2017; Su et al., 2021). For instance, so far only in some Chinese rivers or isolated plateau lakes have phylogenetic differentiation or homogenization of the fish faunas been found (e.g., Jiang et al., 2019; Zhang et al., 2018, 2019), and just in some rivers, e.g., the Yellow River, have temporal changes in the alpha and beta components of the three facets of fish biodiversity in response to human disturbances been examined (e.g., Jia et al., 2020). In addition, relevant studies on identifications of relatively sensitive areas along with stressors (i.e., environmental and anthropogenic drivers) influencing freshwater fish biodiversity patterns at the basin level in China, which can be a crucial step forward for fish conservation efforts, are still pending and urgent.

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

2. Materials and methods

2.1. Fish occurrences

Based on previously reported basins or hydrological units for China's freshwater fishes (e.g., Lehner and Grill, 2013; Liu et al., 2017; He et al., 2020) and the best available fish distribution information, a total of 97 hydrological units throughout China were divided (Fig. 1). Afterwards, China's freshwater fish species reported by former works (e.g., Xiang et al., 2021) were assembled in each of these 97 hydrological units in historical (before the 1900s, i.e., before human-mediated species introductions and extinctions) and current (after the 1900s) periods, respectively, according to a comprehensive literature review, including peer-reviewed articles, monographs, fish databases, and official survey reports. Each species in each hydrological unit in the historical and/or current period was paired with a species status, i.e., extant native, non-native, or extinct. Extant native species referred to species which had been being present in a given unit (n = 1,657), while a species present in the wild of a unit in China but not present originally in this unit before the 1900s was deemed as non-native to the matching unit, no matter it originated from outside or within China (n = 191). Besides, species that were documented to be extinct in their native units in China after the 1900s were considered as extinct ones (n = 6) (e.g., Yue and Chen, 1998; IUCN, 2021). Consequently, the fish occurrences of a total of 1,742 species in the 97 hydrological units in historical (i.e., extant native species + extinct species) and current (i.e., extant native species + non-native species) periods were obtained.

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

2.2. Phylogeny

'FishPhyloMaker' package, which can automatically insert in and prune fish species from the most comprehensive phylogenetic tree (Rabosky et al., 2018) for the provided species following their taxonomic hierarchy, was used to generate phylogenies for describing phylogenetic diversity of China's freshwater fish species (Nakamura et al., 2021).

2.3. Functional traits

Ten morphological traits associated with food acquisition and locomotion which are widely considered in functional diversity of freshwater fish species (e.g., Toussaint et al., 2016; Su et al., 2021) were adopted to describe China's freshwater fish species (Fig. S1; Table S1). Except for maximum body lengths describing fish size taken from FishBase (Froese and Pauly, 2019) and related literature, the remaining 9 morphological traits are ratios of 11 morphological measurements
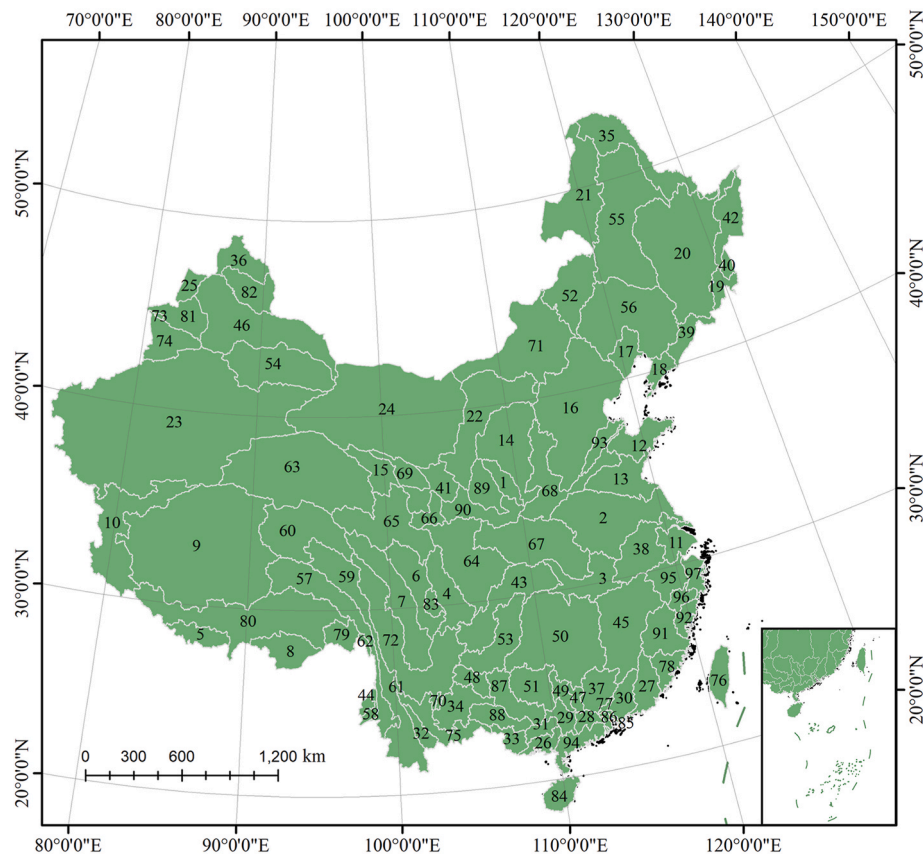
Fig. 1. Sketch map of China at the basin level. The map showed 97 hydrological units within the whole country, among which 95 units were defined for the subsequent analysis. Unit 8 (Xibaxiaqu River basin) and 73 (Sayram Lake basin) were excluded from the following functional diversity calculation due to fewer than five fish species in each unit.

measured on at least one scientific side-view drawing or good-quality picture of an entire adult animal (Fig. S1) collected from various fish databases (e.g., FishBase and Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; retrieved in December 2020)) and literature using ImageJ software (https://imagej.nih.gov/ij/). All measurement rules of the 11 morphological measurements were detailed in Toussaint et al. (2016) and Xiang et al. (2021), and the morphological trait data were available for the 1,742 species with 16,077 traits (92.29%) in this study. For the missing morphological traits (7.71%), the 'Rphylopars' package, which can be used for phylogenetic imputation of missing data and estimation of trait covariance across species and within species, was applied (Bruggeman et al., 2009; Goolsby et al., 2017). Furthermore, it's worth mentioning that the 10 traits turned out to be hardly correlated to each other (the absolute values of Spearman's rho for all the 45 pairwise comparisons ranged from 0.005 to 0.648 with an average of 0.211) after filling the missing values. Then, a principal coordinates analysis (PCoA) using the morphological trait-based distances was carried out to generate a multidimensional space (Mouillot et al., 2013). Considering a trade-off between the quality of PCoA-based multidimensional space and time cost (Maire et al., 2015), we selected the first four PCoA axes (the mean absolute deviation was equal to 0.013) to compute functional diversity indices.

2.4. Environmental and anthropogenic drivers

A total of 10 representative drivers encompassing various geomorphological, hydrological, climatic, social, and economic features, which are widely adopted in fish invasion ecology and conservation management research (e.g., Kuczynski et al., 2018; Lin et al., 2021; Su et al., 2021), were selected to describe China's hydrological units: (a)

unit area (UAR), (b) elevation (ELE), (c) average annual temperature (AAT), (d) average annual precipitation (AAP), (e) net primary productivity (NPP), (f) river fragmentation (RFR), (g) human footprint (HFP), (h) consumptive water loss (CWL), (i) aquaculture pressure (APR), and (j) fishing pressure (FPR) (Table S2). We then calculated the mean value of the cells within each hydrological unit for all drivers so as to apportion the attribute values of each stressor to corresponding units.

2.5. Diversity indices

Here, we adopted six diversity indices, including three alpha diversity indices (i.e., taxonomic richness (TRic), functional richness (FRic), and phylogenetic richness (PRic)) and three beta diversity indices (i.e., Jaccard-index for taxonomic dissimilarity (TDis), beta-FRic for functional dissimilarity (FDis), and UniFrac for phylogenetic dissimilarity (PDis)), to measure for fish assemblages in China's hydrological units in the historical and current periods, respectively. These indices are the most often applied in assessing multiple facets of freshwater fish biodiversity (e.g., Villéger et al., 2014; Kuczynski et al., 2018; Su et al., 2021). Notably, the two units (Xibaxiaqu River basin and Sayram Lake basin) with fewer than five fish species were excluded from the functional diversity calculation as four functional dimensions were kept. Among the three alpha diversity indices, TRic referred to the total number of species in one hydrological unit, FRic was estimated as the volume of the minimum convex hull shaping all the species from one hydrological unit in the 4-dimensional functional space (Cornwell et al., 2006; Villéger et al., 2008), and PRic was measured as the sum of the branch lengths connecting all species present in one hydrological unit within the phylogenetic tree (Faith, 1992). For the three beta diversity indices, TDis was measured using the percentage of dissimilarity in

species composition between each pair of fish assemblages present in hydrological units (Jaccard, 1912; Baselga, 2012; Villéger et al., 2013), FDis was measured as the non-shared fraction of total functional space volume between each pair of fish assemblages (Villéger et al., 2011a, 2013), and PDis was measured as the unique fraction of total phylogenetic diversity between each pair of fish assemblages (Lozupone and Knight, 2005; Lozupone et al., 2006). Considering China's topography, e.g., the sizeable east-west and north-south span, we therefore adopted the inverse of geographical distance between focal units as weights (Villéger et al., 2013). Each beta diversity index for every hydrological unit was then calculated using the weighted average value of the pairwise comparisons between the fish assemblage in the target unit and all the other assemblages in corresponding units.

2.6. Statistical analyses

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

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

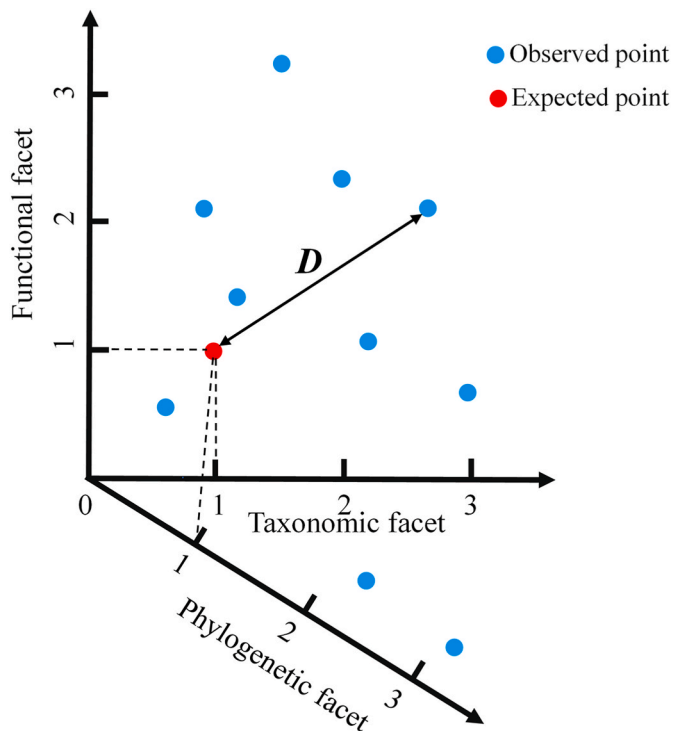where, r_i is the above-mentioned ratio for each unit. Further, we used the

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

quartile method to divide the 95 temporal changes for each diversity index as well as the multifaceted changes into different groups, and then we defined outlier changes (if existed) as extreme ones.

Afterwards, in order to identify the potential drivers affecting the temporal and multifaceted changes in biodiversity facets, random forest models which show less sensitivity to the issues of multicollinearity and spatial autocorrelation and play a good performance in analysing a very large number of independent variables without screening (Breiman, 2001a, 2001b) were applied. In the random forest models, the 10 drivers and temporal and multifaceted changes ($log_{10}(X)$-transformed if the distributions were not Gaussian) were considered as the explanatory and response variables, respectively. We employed 5,000 decision trees in the random forest models, and the percentage increase in mean squared error (%IncMSE) and total decrease in node impurities from splitting on the variable, averaged over all trees (IncNodePurity), were used to measure the importance of the drivers. Finally, partial dependence plots were adopted to visualize the relationships between relatively important drivers identified by the random forest models and the temporal and multifaceted changes (Friedman, 2001).

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

3. Results

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

3.1. Temporal changes in alpha diversity

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

3.2. Temporal changes in beta diversity

Overall, fish assemblages in the 95 hydrological units showed a trend towards biotic homogenization, i.e., the three facets of beta diversity decreased by 3.20% (TDis), 4.00% (FDis) and 5.76% (PDis) on average, respectively, and the trends of the temporal changes predominantly showed negative longitudinal gradients from southeast to northwest (Fig. 5). More specifically, fish assemblages in 86.60% (88.52% of China's surface), 81.44% (85.86%) and 83.51% (84.03%) of the units showed a trend towards taxonomic, functional, and phylogenetic homogenization, respectively, and extreme decreases mostly occurred in Northwest and Southwest China (Fig. 5; Fig. S3).

The exotic species introduction pattern resulted in slight trends towards taxonomic (0.21%), functional (0.06%), and phylogenetic (0.49%) differentiation. More specifically, exotic introductions induced
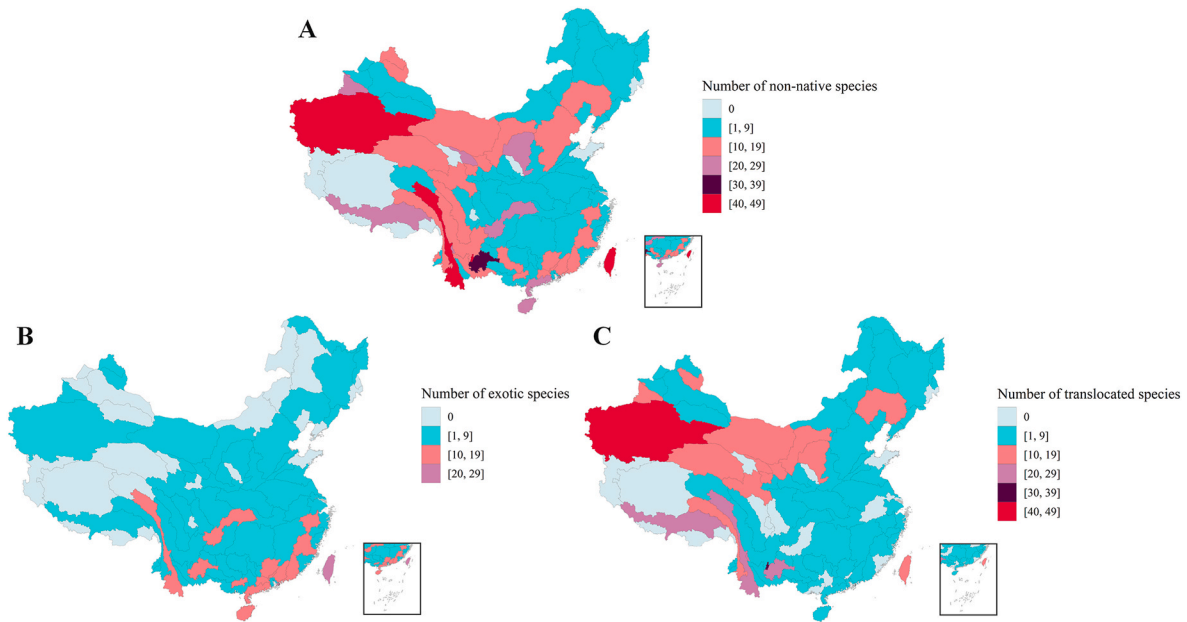
Fig. 3. Number of (A) non-native (i.e., exotic + translocated), (B) exotic, and (C) translocated species in China's hydrological units.
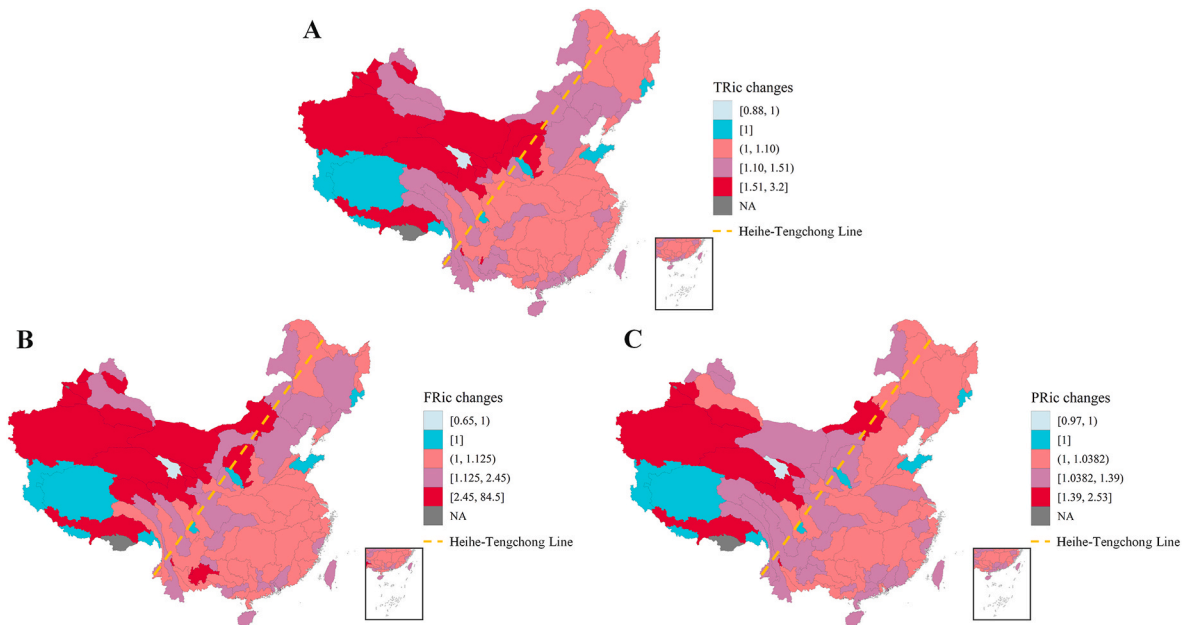

Fig. 4. Temporal changes in (A) TRic, (B) FRic, and (C) PRic of freshwater fish assemblages in China's hydrological units. TRic: taxonomic richness; FRic: functional richness; PRic: phylogenetic richness. The Heihe-Tengchong Line is an important geographical dividing line related to populations, environments,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

taxonomic, functional, and phylogenetic differentiation of fish assemblages in 58.76% (56.54% of China's surface), 42.27% (34.34%), and 64.95% (57.48%) of the units, respectively. The translocated species introduction pattern resulted in more pronounced trends towards taxonomic (3.53%), functional (4.44%), and phylogenetic (7.46%) homogenization. More specifically, translocations induced taxonomic, functional, and phylogenetic homogenization of fish assemblages in 87.63% (89.16% of China's surface), 86.60% (87.98%), and 88.66% (85.34%) of the units, respectively.

3.3. Multifaceted changes in biodiversity facets

Multifaceted changes experienced by fish assemblages showed a

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

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

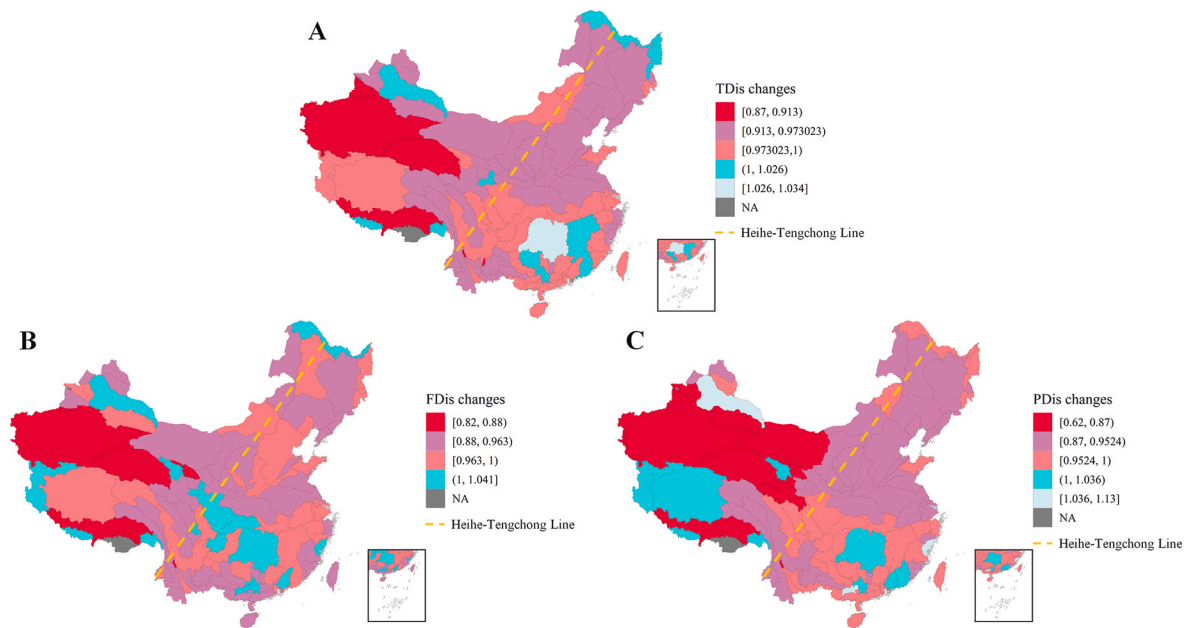The random forest models with all 10 drivers for temporal and

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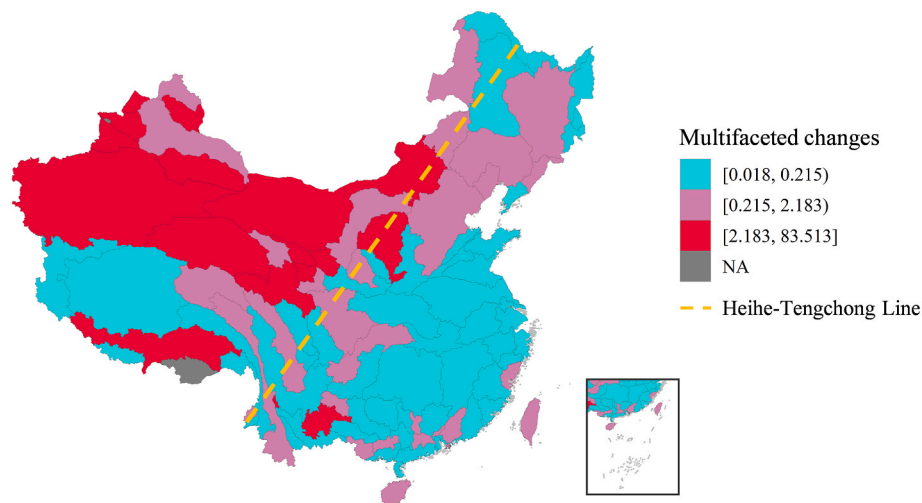

Fig. 6. Multifaceted changes in biodiversity of freshwater fish assemblages in China's hydrological units.

multifaceted changes explained 36.60% (TRic changes), 21.61% (FRic changes), 19.92% (PRic changes), 20.86% (TDis changes), 2.89% (FDis changes), 8.22% (PDis changes), and 28.51% (Multifaceted changes) of the total variances, respectively. Environmental factors (e.g., NPP, ELE, UAR, AAT, and AAP) were the main drivers explaining the temporal changes of the six diversity indices and multifaceted changes (Fig. S5). Partial dependence plots showed negative responses of the temporal changes of alpha diversity and multifaceted changes to NPP and AAP, and positive responses to ELE. On the contrary, the temporal changes of beta diversity showed positive responses to NPP and AAP, and negative responses to UAR and ELE (Fig. 7).

4. Discussion

Fish introductions to various inland water bodies across China inevitably caused overall increases in TRic, FRic, and PRic even though fish extinctions happened in several areas. Additionally, fish assemblages in most of China's water bodies had experienced homogenization

in the three biodiversity facets, which are consistent with previous studies documenting the current biodiversity crisis across the world (Villéger et al., 2011b, 2014; Su et al., 2021).

A high increase in species richness is generally accompanied by relatively high increases in FRic and PRic but at different rates (Toussaint et al., 2018; Zhang et al., 2018). Among the three facets, the functional facet increased by 16.71% on average and appeared to be the most sensitive facet for detecting changes in alpha diversity, followed by taxonomic (11.99%) and phylogenetic (9.43%) facets. FRic is greatly affected by TRic (Su et al., 2022), however, tremendous alterations might happen in FRic even though little changes in TRic (Toussaint et al., 2018). The typical example occurred in Qaidam basin possessing low species richness but highly distinctive 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
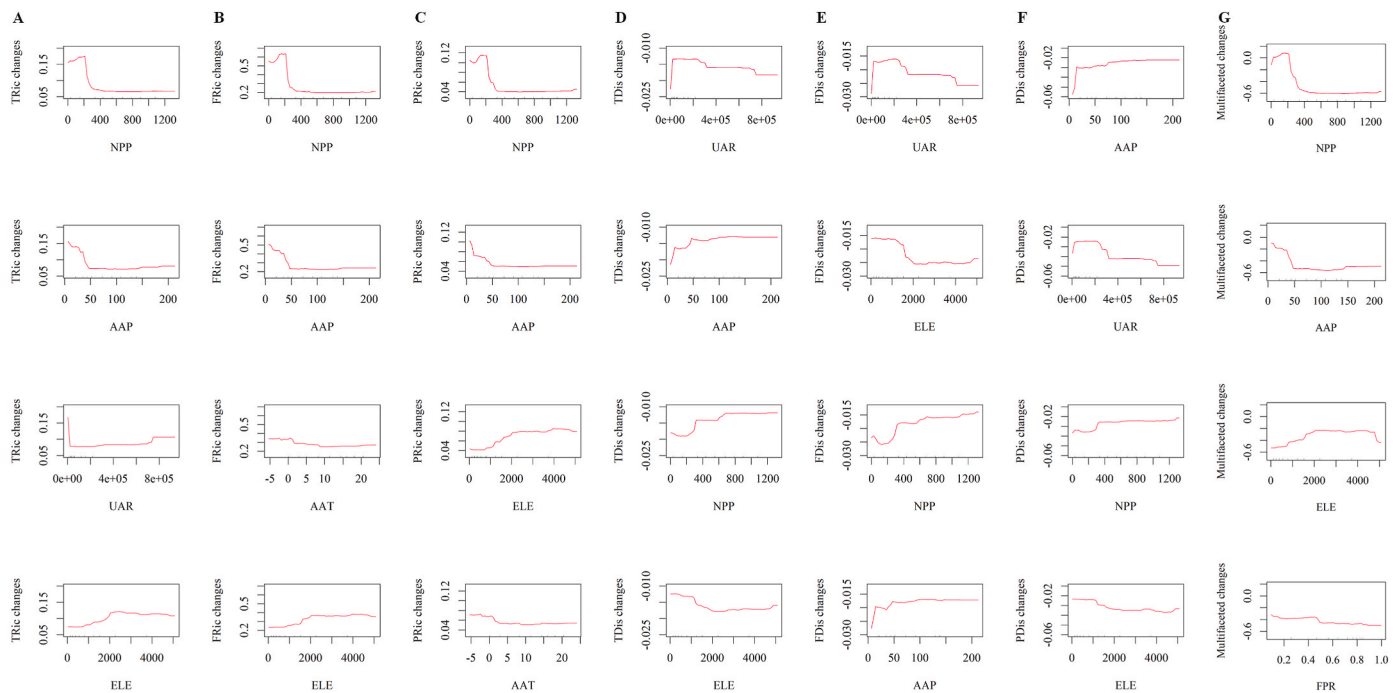
Fig. 7. Partial dependence plots for the four most important drivers (based on IncNodePurity) for temporal and multifaceted changes (log-transformed) in biodiversity facets through the random forest models (for the remaining drivers, see Fig. S6). The *y*-axis in each plot referred to log-transformed changes in biodiversity facets: (A) TRic changes, (B) FRic changes, (C) PRic changes, (D) TDis changes, (E) FDis changes, (F) PDis changes, and (G) multifaceted changes. NPP: net primary productivity; AAP: average annual precipitation; UAR: unit area; ELE: elevation; AAT: average annual temperature; FPR: fishing pressure.

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 introductions than extinctions, biotic homogenization in China's water bodies was largely owing to fish introductions. To be more specific, translocated species are functionally and phylogenetically more similar to other native species than exotic species considering they were historically already present in similar ecosystems as natives (Villéger et al., 2014; Su et al., 2021), which tend to result in biotic homogenization. Our results also confirmed this point as translocated species introductions led to a far larger degree of homogenization in the three biodiversity facets than exotic species introductions which mostly induced mild biotic differentiation. Additionally, compared with exotic species, translocated species were more often introduced in China's hydrological units. Less frequent introductions of functionally and phylogenetically distinct exotic species thus cannot compensate for the

effects of more frequent introductions of functionally and phylogenetically more similar translocated species resulting in the homogenization of recipient units (Su et al., 2021). Massive losses of taxonomic, functional, and phylogenetic distinctiveness predominantly caused by translocated species may weaken the resilience or resistance for these homogenized communities in China to external disturbances (Olden et al., 2004; Villéger et al., 2011b; Jiang et al., 2019; Jia et al., 2020). Translocated species introductions should thus be treated more prudently, especially in Northwest China where highest biotic homogenization mostly occurred.

Without doubt, human activities (e.g., aquaculture, capture fisheries, and hydraulic constructions) can bring about fish introductions and extinctions which would alter local fish compositions (Villéger et al., 2011b; Xiong et al., 2015; Su et al., 2021). Nevertheless, mounting evidence shows that it is not anthropogenic pressures but environmental factors that play predominant roles in structuring fish assemblage patterns (e.g., Brucet et al., 2013; Kuczynski et al., 2018). For example, environmental variables (e.g., temperature anomaly since the last glacial maximum and river basin area) contribute a lot to the multifaceted changes in biodiversity of fish assemblages from the Neotropical and Australian realms (Su et al., 2021). Consistent with this phenomenon, our study also demonstrated that environmental, not anthropogenic factors, e.g., net primary productivity, elevation, and precipitation strongly drove temporal and multifaceted changes in China's three biodiversity facets. In general, species tend to distribute in the most suitable habitats (Kang et al., 2014). Therefore, whether non-native species introduced to various water bodies for human purposes can establish and spread well at initial entry points partially depends on various environmental conditions, e.g., temperature, precipitation, and duration of drought season (Lin et al., 2015, 2021; Trochine et al., 2018). For instance, several species (e.g., *Hypophthalmichthys nobilis* (Richardson, 1845)) released into Luhunshui Reservoir, lower Yellow River basin cannot survive well because of local insufficient plankton net primary productivity resulting from low precipitation since 1998 (Guo, 2004). As for extinct species, the extinction of both *Anabarilius*

macrolepis Yih & Wu, 1964 and *Cyprinus yilongensis* Yang et al., 1977 in Yilonghu Lake, Nanpanjiang River basin is directly due to the complete drought in 1981 (Darwall and Freyhof, 2016), which heightened the environmental filtering hypothesis (Kraft et al., 2015; Lin et al., 2021). Except positive relationships between the changes in biodiversity facets (i.e., the multifaceted changes, temporal changes of alpha diversity, and extent of biotic homogenization) and elevation, negative relationships were detected between the aforementioned changes and net primary productivity and average annual precipitation. Multifaceted changes, temporal changes in alpha diversity, and extent of biotic homogenization across China were almost differentiated along the Heihe-Tengchong Line with relatively high altitude and low vegetation cover and precipitation in its west side compared with its east side (Wang et al., 2014; Liu et al., 2021; Zheng et al., 2021). Coincidentally, since the 1900s, a large number of non-native fish species including translocated species (e.g., Chinese carps) originating from China's eastern basins and exotic species (e.g., *Oncorhynchus* and *Piaractus* spp.) originating from outside China have been introduced to western basins in this country, many of which now contribute significantly to the production of local fisheries enhancement and aquaculture (e.g., Walker and Yang, 1999), and have established populations in various water bodies of recipient areas. Compared with fish faunas in the east side, those in the west side of the Heihe-Tengchong Line (e.g., Tarim basin, Qaidam basin, Hexi Corridor basin, and Middle Inner Mongolia basin) were more distinct and specialized (e.g., *Triplophysa*, *Schizothorax*, *Hedinichthys*, and *Gymnocypris* spp.) but poorer, which were chiefly attributed to the local environmental conditions including unique river systems, geographic situations, and/or climate (Yan, 2003; Kang et al., 2014). Such sizable regions only holding relatively low richness of native species with periodic life history strategies provided abounding divergent water bodies and vacant niche opportunities for non-native species with opportunistic strategies (e.g., a great range of ecological traits and tremendous variation in morphology and genetics) (Kang et al., 2014; Xing et al., 2016; Liu et al., 2017), where they can find suitable habitats that may be inhospitable to natives (Wei et al., 2021). Compared with other units in the west side of the Heihe-Tengchong Line, striking exceptions mostly occurred in Unit 9 (Changtang basin) and 10 (Shiquan River basin), where fish assemblages experienced very mild multifaceted changes in biodiversity along with minor changes in dissimilarity but no changes in alpha diversity. Such a situation primarily resulted from local traditions and harsh environments of the areas which prevented many anthropogenic activities including aquaculture and fisheries (Zhang and Xing, 1996; Zhang et al., 2020), which caused relatively little chance for non-native species to spread and establish.

In conclusion, China's freshwater fish faunas were currently undergoing taxonomic, functional, and phylogenetic homogenization which is now considered one of the most prominent components of the biodiversity crisis worldwide. Predictably, fish assemblages in China's water bodies would continue to experience biotic homogenization in light of the rapid development of hydro projects, aquaculture, and aquarium trades (Jia, 2016; Liu et al., 2017; Gu et al., 2022), as well as challenges in the eradication of non-native species (Britton et al., 2011). Targeted conservation and management strategies should be urgent, especially for hydrological units with relatively high multifaceted changes in biodiversity, because almost all fish introductions and extinctions were accelerated by human activities, including facilitating biotic exchange among areas and altering habitats. More specifically, certain focused strategies can be implemented: (a) formulate stricter legislation and policies to conserve fish resources; (b) strengthen regulatory efforts for artificial fish propagation and release to prevent non-native fish species from entering novel areas; (c) establish detection and monitoring systems for non-native fish species; (d) provide scientific training for relevant practitioners to enhance their knowledge and awareness of fish invasions and conservation; and (e) reduce anthropogenic disturbances and establish aquatic reserves in vulnerable areas (i.e., areas with relatively high multifaceted changes in biodiversity demonstrated by this study).

Data availability

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118374.

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