



## Land use outweighs other stressors in declining fish biodiversity in lakes of Eastern China during the 1980s-2010s

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### ABSTRACT

Understanding patterns and driving factors of freshwater fish biodiversity in metacommunities is essential for biological conservation but rarely studied in regions experiencing rapid land use changes. We examined changes of both alpha and beta fish diversities in taxonomic, functional, and phylogenetic facets during the 1980 s to 2010 s, and quantified contributions from natural and human drivers in lakes located in China's fastest economic development region. Results showed that almost all indices of alpha and beta diversity decreased through time. For alpha diversity, taxonomic and functional richness declined by 13 to 15%. Rheophilic and piscivorous fish species declined by 50 and 36%, respectively. For beta diversity, the decline of overall functional (-31%) diversity was greater than taxonomic (-17%) and phylogenetic (-19%) diversity. The decline of multiple facets of beta diversity indicated that fish communities in these lakes have homogenized through time. Land use (i.e., increased urban land and aquaculture ponds), hydrology (i.e., increased water level), climate (i.e., increased air temperature), and fishing (i.e., increased lake fishery catch) factors all made significant contributions to both alpha and beta fish diversity decline in multiple facets. The overall contribution from land use to the decline of multidimensional fish diversity was greater than those of other stressors. While attention should be given to both local human disturbance and regional climate factors, in regions experiencing rapid economic development and land use changes, local disturbances should be considered as a priority in biodiversity management plans.

### 1. Introduction

Global climate change and local human disturbances have led to a massive loss of global biodiversity, and the worldwide biota is now in the midst of the sixth mass extinction (Dirzo and Raven, 2003; Wake and Vredenburg, 2008; Cardinale et al., 2012; Su et al., 2021). As the most diverse ecosystems, per unit area, freshwaters occupy only 3% of the earth's surface yet support 9.5% of animal species (Balian et al., 2008). However, they are also among the most vulnerable ecosystems in the world, as the biodiversity decline in freshwater ecosystem is much faster than terrestrial and marine ecosystems (WWF, 2020; Albert et al., 2021). Many environmental stresses, such as fragmentation, land use change, overfishing, invasions, infectious diseases, flow alteration, nutrient enrichment, climate change and other threats, have already led to sharp

declines in freshwater biodiversity (Reid et al., 2019; Chen et al., 2020; Liu et al., 2022a).

Biodiversity can be viewed through multiple facets, including taxonomic, functional and phylogenetic diversities that can be measured locally (alpha) or between localities (beta) (Su et al., 2021). Taxonomic diversity (e.g., species richness, Shannon-Weiner index) is widely used in describing biodiversity in broad-scale studies (Cai et al., 2019; Guo et al., 2020). However, it does not reflect functional traits and evolutionary relatedness among species, which are important in revealing mechanisms of ecosystem function and biodiversity maintenance (Villéger et al., 2008; Pavoine and Bonsall, 2011).

Species responses to environmental changes or interactions with other species depend not only on species identity, but also on the functional characteristics of the species (McGill et al., 2006), while

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phylogenetic diversity reflects the evolutionary history of species assemblages (Mouquet et al., 2012). Therefore, a combination of taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD), could help reveal different patterns of biodiversity and ecological processes underpinning species assembly (Gianuca et al., 2017; Teichert et al., 2018; Xie et al., 2018). In addition to investigating different facets of community diversity within sites (i.e., alpha diversity), it is also necessary to characterize species composition variations across communities (i.e., beta diversity, Anderson et al., 2011; Villéger et al., 2013). Beta diversity includes two separate components: species turnover or replacement and nestedness or species gain/loss (Baselga, 2010). The species turnover pattern is mainly caused by the replacement of species between different communities (Leprieur et al., 2011), while the nestedness pattern is often caused by differences in species richness among communities (Gaston and Blackburn, 2008).

Changes in multiple dimensions of biodiversity could vary considerably in response to the same human disturbance. For instance, the introduction of non-native species caused the overall increase in all three aspects of alpha diversity of fish assemblages in river basins, but it reduced beta diversity between river basins, with larger decreases of functional than that of taxonomic and phylogenetic beta diversity (Jia et al., 2020; Su et al., 2021). Therefore, evaluation of multiple facets of diversity may provide further insights into how local communities react to human-induced environmental changes (Socolar et al., 2016). In rapid developing regions with intensive land use changes, the response of fish biodiversity to stressors could differ among facets, but such multifaceted approaches are still rarely achieved (Chen et al., 2020; Xiong et al., 2021).

Although impacts from individual drivers are fairly well understood, ecological responses to multiple stressors and their relative contributions may differ across regions or river basins (Collen et al., 2014; Guo et al., 2016; Kuczynski et al., 2017; Henriques et al., 2017; Chen et al., 2020). Climate drivers are considered key factors in structuring fish diversity patterns, for example, warmer temperatures may favor the establishment of species with warmer heat preferences, thereby reducing the abundance of many high-value species that depend on cooler waters for survival (Heino et al., 2009; Collen et al., 2014; Guo et al., 2016; Henriques et al., 2017). Assemblage shifts also depend on human related components of global change, such as land use changes (e.g., Laliberté et al., 2010; Budnick et al., 2019) or introductions of non-native species (Chapin et al., 2000). However, in rapid developed regions where usually experienced heavily land use changes and complex human disturbances, it is still unclear how human and natural factors contributed to biodiversity patterns over long-term and large spatial scales (Devictor et al., 2008; Budnick et al., 2019), especially when considering responses of multiple dimensions and facets of biodiversity to these stressors together (Guo et al., 2019; Su et al., 2021).

China has experienced fast economic growth during the past several decades. Since its reform and opening up in the 1980 s, its Gross Domestic Product (GDP) has increased nearly 100 times (National Bureau of Statistics of China, 2021), especially in the Eastern China where Shanghai and other mega-cities are located (Chen et al., 2017). In Eastern China, major human stressors include urban development, aquaculture expansions around lakes, water diversion, overfishing, and others (Chen et al., 2017; Chen et al., 2020; Qu et al., 2020). This region has also experienced climate change effects with temperature changes and increasing frequency of extreme climatic events such as droughts and floods (Guo et al., 2016; Xia et al., 2022). Thus, this region can be viewed as a natural experimental unit for us to detect long-term and large-scale changes of fish biodiversity.

Here, we quantified how local and global environmental descriptors explain taxonomic, functional and phylogenetic diversities, by specifically testing the role of climate and geography, while have been reported as important in the literature (Walther et al., 2002; Schleuter et al., 2012; Zhou et al., 2020; Lento et al., 2020). We also tested the role of human related components of global change, including land use

changes or introductions of non-native species, that are also recognized as drivers of biodiversity changes (e.g., Chapin et al., 2000; Laliberté et al., 2010; Budnick et al., 2019).

Thus, we measured taxonomic, functional, and phylogenetic aspects of fish alpha and beta diversity in five large Eastern China lakes as well as associated human and natural factors over the past 40 years (1980 s–2010 s). We aimed to: 1) quantify temporal trends in alpha and beta fish diversity in multiple facets; and 2) quantify contributions of different environmental drivers (e.g. land use, hydrology, climate and fishing) to these multifaceted components of diversity in lakes experiencing rapid land use changes. We hypothesized that 1) all three facets of alpha and beta diversity declined during the 1980s–2010 s; 2) local human disturbances (e.g. land use, hydrology, and fishing) and climate factors contributed differently to explaining variations in fish diversity. Moreover, local human disturbances might have greater impacts because of intensive anthropogenic disturbance in the study region (Qu et al., 2020; Xia et al., 2022).

## 2. Materials and methods

### 2.1. Study area and lakes

Our study area is located on the Eastern Plain of China, across from Jiangsu to Shandong provinces, one of the most rapidly developing regions in China (Fig. 1, Table S1). During the past 40 years, the gross regional product (GRP) of this region has increased by about 30,056%, and its average industrial production value has increased by about 26,740% (National Bureau of Statistics of China, 2021). As one of the most densely populated areas in China, the average population density has increased from 457 to 569 people/km<sup>2</sup> in 1978 to 637–788 people/km<sup>2</sup> in 2019 (Jiangsu Provincial Bureau of Statistics, 2021; Shandong Provincial Bureau of Statistics, 2021). This urban development was surrounding the lakes and settled in drainages that flow to the lakes. Thus, this region has experienced rapid and intensive human development.

We considered the five largest lakes (i.e., Gaoyou, Hongze, Luoma, Nansi and Dongping Lakes) in northern Yangtze River of the East Plain of China. All five lakes are set in a similar geological and altitudinal context (Fig. 1). These lakes range from 209 to 2,125 km<sup>2</sup> in area, and from 2.0 to 4.0 m in average water depth. The background environmental conditions such as nutrients of these lakes were relatively similar. The Huai River divides them into subtropical monsoon lakes (Gaoyou and Hongze Lakes) in the south and temperate monsoon lakes (Luoma, Nansi, and Dongping Lakes) in the north (Fig. 1; Guo et al., 2020; Qu et al., 2020). These lakes have been disturbed by human activities over the past several decades, and major human stressors include land use changes, fishing, hydrological modifications, and others (Qu et al., 2020; Xia et al., 2022).

### 2.2. Fish data

We collected the available fish occurrence data from the five lakes in two periods: historical (1980 s: 1978–1987) and current (2010 s: 2010–2020). For the historical period, we collected data from journal articles and associated appendices, monographs, scientific and survey reports, books, online materials and grey literature databases during the 1980 s (Guo et al., 2019). For the current period, we obtained data from the above-mentioned literature collections as well as field investigations and commercial fishing surveys during the 2010 s. To form a list of fish as complete as possible, yearly data for each lake were averaged over each of the two considered periods. In field investigations, a total of 70 sampling sites were set up in these lakes using a combination of multi-mesh gillnets and ground trap nets during 2017–2020. More details about the sampling gears and procedures are available in Guo et al. (2020). At the same time, commercial fishing landing catches of different fishing gears from these lakes were collected during the fishing



Fig. 1. Location of studied lakes in the Eastern Plain of China.

seasons. For literature related data in both periods, we have followed a strict data screening and quality control approach, including removals of uncertain species, corrections of fish scientific names by referring to the Catalog of Fishes of the California Academy of Sciences (Fricke et al., 2023), and other quality control measures (Guo et al., 2019). Thus, we generated a list of historical and current fish occurrence (i.e., presence-absence) data, with a total of 113 fish species, for the studied lakes. In the current study, we did not use the fish abundance data because of differences in fish sampling protocols between time periods could affect our results (Guo et al., 2019).

For fish functional diversity calculations, a total of 10 functional traits were selected. They are from five categories of main functions performed by fish species, including food acquisition, mobility, defense against predation, nutrient budget, and reproduction (Villéger et al., 2017; Table S2). Potential intraspecific variations (differences in individual traits of the same species) were not considered as most functional traits were discrete variables, and thus not influenced by intraspecific variations. Life history, age at sexual maturity, adult total length, and food habits were obtained from published monographs and literature, including Fishes of Jiangsu Province (Ni and Wu, 2006) and Fauna Sinica Osteichthyes (Chen, 1998). The remaining traits data were obtained from FishBase (Froese and Pauly, 2021; <https://www.fishbase.org/>). For species without recorded traits (a total of 31 species missing one or more traits data, out of the 113 species considered), we referred to fishes of the same genus with similar morphologies (Liu et al., 2022b).

As no complete fish phylogeny is available for all the fish species considered, we used taxonomic hierarchies based on path lengths in the Linnean taxonomic trees as a proxy (Clarke and Warwick, 1998). This approach has been often used in literature dealing with lack of true phylogeny (Schweiger et al., 2008; Cai et al., 2019; Ji et al., 2020). We thus built a taxonomic evolutionary tree based on the taxonomic composition of studied fishes (Fig. S1). A total of 8 taxonomic levels were used: species, genera, subfamilies, families, suborders, orders, subclasses, and classes (Cai et al., 2019; Liu et al., 2022b).

### 2.3. Environmental drivers

We used land use, fishing, hydrology, and climate factors as major drivers of fish diversity patterns. We matched the available data as closely as possible with fish data for the two periods, the 1980 s and 2010 s, using a multi-year average for each period.

The land use data were provided by the Resource and Environmental Science and Data Center of the Chinese Academy of Sciences (<http://www.resdc.cn/>). The 1-km resolution images in the 1980 and 2018 were used to represent historical and current land use conditions, respectively. ArcGis10.2 software was used to build buffer zones and extract land use around each lake. The land use types were divided into seven categories: urban, agriculture, forest, grass, surface water, aquaculture pond, and bare land. We built four buffer zones (i.e., terrestrial areas around each lake): 1 km, 5 km, 15 km and 30 km, and correlation analysis were carried out between land use and fish diversity indices (Table S3). Those analyses showed that the 15 km buffer zone had overall the best correlation. Thus, we used the 15 km buffer zone data for further analyses.

Annual fishery catch in each lake was used as a proxy of fishing disturbance. The data were extracted from the statistical yearbooks and fishery reports of various regions over the two study periods (City Statistical Bureaus and Lake Fishery Management Commissions). The daily average water level (WL) data of each lake during 1978–2018 were used to represent the hydrological changes. These hydrological data were from the hydrological monitoring network provided by the hydrological monitoring departments over the years and the hydrological yearbooks of the studied lakes (Lake Water Conservancy Authorities).

For climate variables, average precipitation (AP, mm), mean precipitation in the wettest month (MPW, mm), mean precipitation in the driest month (MPD, mm), average maximum air temperature (ATmax, °C), average minimum air temperature (ATmin, °C), average temperature of the warmest month (AWM, °C), and average temperature of the coldest month (ACM, °C) were used. These 7 variables were extracted from the Worldclim database (<https://www.worldclim.org>). The 30 s spatial interpolation data of historical (1978–1987) and current

(2010–2019) climate were used. The average value for each lake was extracted using ArcGIS 10.2.

Pearson correlation analysis was used to test the correlation among the above factors, and those with correlation coefficients  $> 0.7$  were eliminated to avoid high collinearity. The resulting set of independent human and climate factors were included in the final analysis: land use (including urban, agriculture, grass, and aquaculture pond), fishing (fishing), hydrology (water level), and climate (ATmax).

#### 2.4. Taxonomic, functional, and phylogenetic alpha diversity

The alpha taxonomic diversity (TD) of each lake was assessed as species richness, the total number of species collected in each lake during each study period. Functional diversity (FD) was quantified as functional richness, FRic, the amount of functional space occupied by the community (Mason et al., 2003; Villéger et al., 2008). Functional diversity was computed using the package “FD” in R software. A taxonomic difference index based on classification distance was used as a proxy of phylogenetic distance (PD): average taxonomic distinctness (Delta +) and variation in taxonomic distinctness (Lambda +) (Clarke and Warwick, 2001; Heino et al., 2007). Average taxonomic distinctness (Delta +) represents the average path length of any two species in a community, and variation in taxonomic distinctness (Lambda +) was used to characterize the variance of the path length between these species, reflecting the evenness of the phylogenetic tree (Clarke and Warwick, 2001; Heino et al., 2007). Fish species richness of two types of life history (i.e., Rheophilic, Limnophilic) and four types of feeding (i.e., Planktivore, Piscivore, Invertivore, Omnivore) groups were used as a representative of the diversity index of different fish functional groups.

#### 2.5. Taxonomic, functional, and phylogenetic beta diversity

To elucidate underlying patterns in community assembly between time periods, the relative contribution of turnover and nestedness components to dissimilarity was calculated following the methods described by Baselga (2010) and Baselga and Orme (2012). For the taxonomic beta diversity, we used the function “beta.pair” in the R package “betapart” to calculate the taxonomic Sorensen difference matrix between lakes, and used TDSor, TDsim and TDsne to represent the three aspects of taxonomic beta diversity. To calculate functional beta diversity, we used the method proposed by Villéger et al. (2013). We first calculated a trait distance matrix between species based on Gower distance using the function “gowdis” in the R package FD (Laliberté et al., 2015), and then generated Principal Coordinates Analysis (PCoA) trait vectors based on the distance matrix using the function “pcoa” in the R package ape. Mantel analysis was used to test correlations between the functional PCoA vectors and the original trait. The result showed that Euclidean distance matrix based on the first three functional PCoA vectors was highly correlated to the original trait Gower distance matrix ( $R = 0.897$ ,  $P < 0.001$ ); the first three PCoA vectors were used as functional traits for the next calculation. Then, functional Sorensen dissimilarity matrix was calculated based on site-by-species matrix and functional traits (PCoA vectors) using the function “functional.beta.pair” from the R package betapart.

To calculate the phylogenetic diversity matrix, we generated a phylogenetic classification tree based on the classification distance as a proxy of the phylogenetic distance, and then used the function “phylo.beta.pair” in the R package “betapart” to calculate the three phylogenetic Sorensen dissimilarity matrices. The dissimilarity matrices of different functional groups were directly measured by the Euclidean distance of functional groups among lakes.

#### 2.6. Statistical analyses

An analysis of variance (ANOVA) was used to compare the driving factors, fish taxonomic, functional, and phylogenetic alpha and beta

diversity between the 1980 s and 2010 s. Before analysis, the data were tested for normality and homogeneity of variance. The relationship between the three beta diversity indices and their respective two components was calculated using Mantel’s test with 9999 permutations to evaluate their significance (Nekola and White, 1999).

Multiple linear regression (MLR) was performed to analyze relationships between alpha diversity indices and different driving factors. In MLR models, forward selection was used to select the key explanatory variables in each model, and the AIC (Akaike Information Criterion) was used to measure the effect of adding variables. We then used hierarchical partitioning to reveal the effects of driving factors on each alpha diversity index (Chevan and Sutherland, 1991).

To determine the relative importance of each driving factor on beta diversity and its two components of taxonomic, phylogenetic and functional diversity, principal coordinate analysis (PCoA) was used to extract the characteristic vectors of the paired beta diversity and its two components between lakes as response variables. A redundancy analysis (RDA) in combination with variation partitioning (Peres-Neto et al., 2006) was conducted to disentangle the drivers of beta diversity patterns. For the final variation partitioning analysis, we first selected predictor variables in the RDA models of each set of driving factors using forward selection method (Blanchet et al., 2008), then we used variation partitioning to reveal the pure and shared effects of driving factor groups on each beta diversity facet (Peres-Neto et al., 2006). All the above analysis was carried under package “vegan”, “ape”, “hier.part” and “betapart” in R software.

### 3. Results

#### 3.1. Patterns of fish alpha and beta diversity

For alpha diversity, all three facets of fish diversity decreased over time except Delta+, the average taxonomic distinctness (Fig. 2). From the 1980 s to 2010 s, taxonomic richness decreased on average by 15.34%. In the 1980 s, 104 fish species belonging to 10 orders, 18 families, and 66 genera were documented in the studied lakes. In the 2010 s, 81 fish species, 8 orders, 16 families, and 53 genera were documented. Of which, Gaoyou Lake fell from 56 to 53 species (-5.36%), Hongze Lake fell from 78 to 64 species (-17.95%), Luoma Lake fell from 72 to 61 species (-15.28%), Nansi Lake fell from 67 to 51 species (-23.88%), and Dongping Lake fell from 53 to 47 species (-22.12%) (Table S4). Functional diversity indices FRic had change rates of -13.15%. Phylogenetic diversity indices had opposite trends, with 0.91% increase of Delta + but 0.68% decrease of Lambda+, the variation in taxonomic distinctness (Fig. 2). Among the functional groups, rheophilic (-50.00%) and piscivorous (-35.82%) fish species had larger reductions than others (Fig. 3).

For beta diversity, all three facets of fish diversity and their components (SIM and SNE) also decreased over time (Fig. 4). The overall beta diversity declined more for functional (-30.57%) than phylogenetic (-19.09%) and taxonomic (-17.24%) facets. The nestedness component of the functional beta diversity declined by -54.66%. In both periods, turnover was the dominant component in both taxonomic and phylogenetic diversity. Mantel tests showed that the changes of the three facets of beta diversity were significantly correlated with each other (Fig. S2).

#### 3.2. Factors driving fish alpha and beta diversity

During the past 40 years, land use, fishing, hydrology, and climate have experienced great changes in the study region. Aquaculture pond (96.79%), urban (38.44%), and bare land (9.65%) surfaces increased, whereas grass land (-25.60%), agriculture (-8.91%), surface water (-4.22%), and forest (-4.12%) decreased (Table S5). Fishing has increased by 112.60%. Water level (WL) has increased by about 0.65 m or 2.86% on average. Both precipitation and air temperature variables

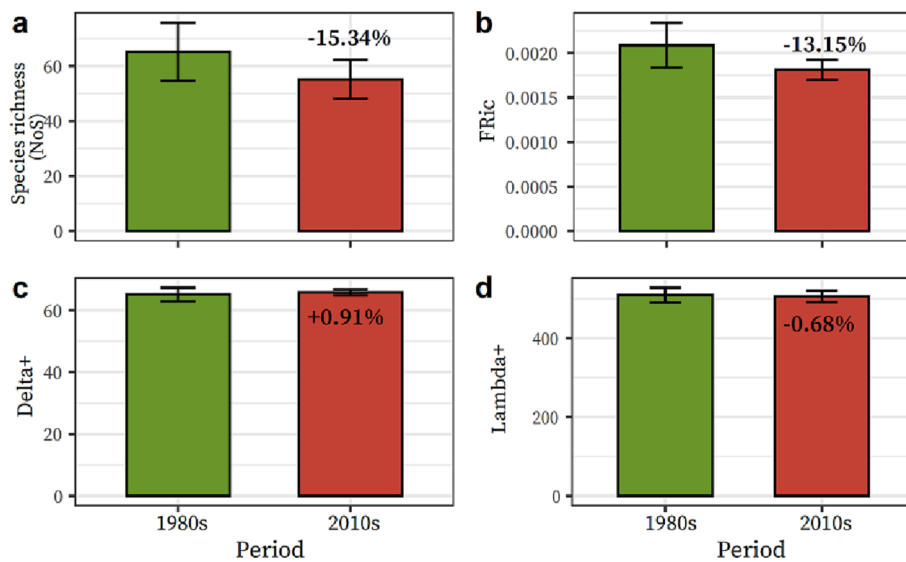


Fig. 2. Comparisons of fish alpha diversity in taxonomic (TD), functional (FD) and phylogenetic (PD) facets between the historical (1980 s) and current (2010 s) periods. “NoS” refers to number of species.

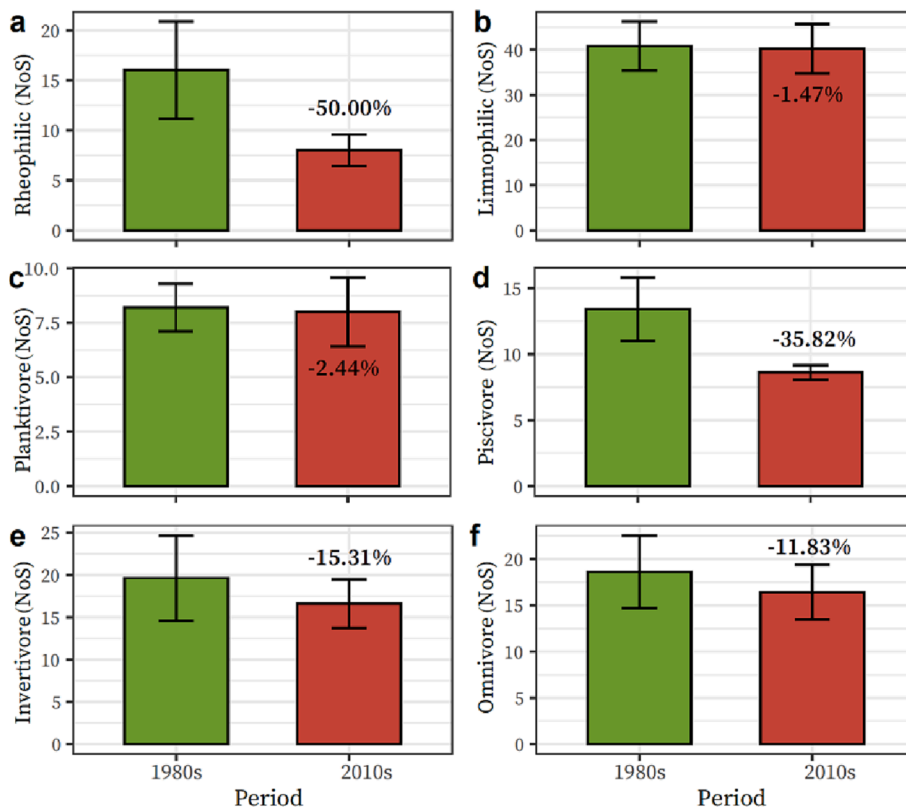


Fig. 3. Comparisons of fish functional groups between the historical (1980 s) and current (2010 s) periods. “NoS” refers to number of species.

increased between the 1980 s and 2010 s, with change rates from 3.36 % to 11.66% (Table S5).

For alpha diversity, the MLR and partitioning analyses showed that land use and hydrology drivers together explained 73.6% of the variance in species richness (Fig. 5, Table S6), which included 54.3% of variance from pure land use and 19.3% of variance from pure hydrology. The driving factors had no significant relationship with alpha FD and PD. Land use and hydrology together explained 60.8% of the variance of limnophilic fishes, which included 34.4% of variance from pure land use and 26.4% of variance from pure hydrology (Fig. 5, Table S6).

Hydrology, climate, and land use together explained 78.1% of the variance of planktivorous fishes, which included 56.1% of variance from pure hydrology, 14.9% of variance from pure climate, and 7.1% of variance from pure land use. Land use, hydrology, and fishing together explained 85.5% of the variance of piscivorous fishes, which included 72.6% of variance from pure land use, 7.6% of variance from pure hydrology, and 5.3% from pure fishing. Land use, hydrology, and fishing together explained 66.5% of the variance of omnivorous fishes, which included 52.0% of variance from pure land use, followed by pure hydrology (8.8%) and pure fishing (5.7%; Fig. 5, Table S6).

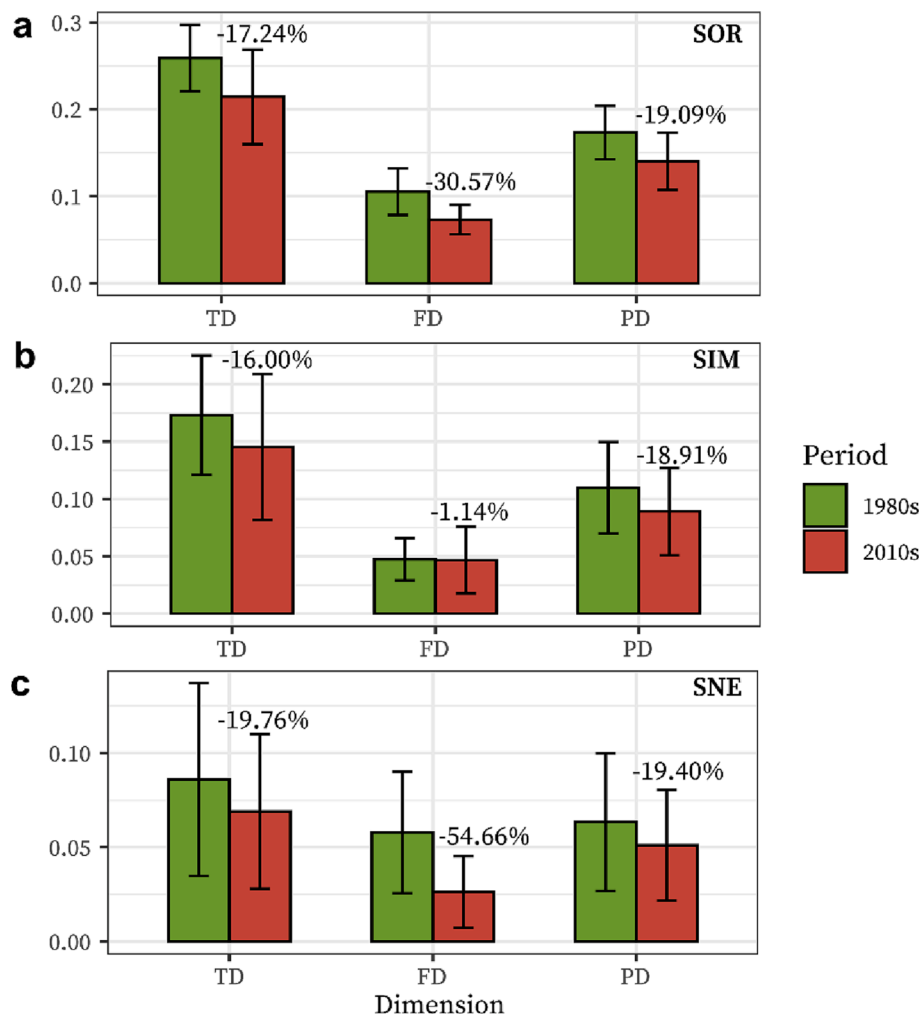


Fig. 4. Comparisons of fish a) overall (SOR) beta diversity of taxonomic (TD), functional (FD) and phylogenetic (PD) dissimilarities, b) turnover (SIM) and c) nestedness (SNE) components, between the historical (1980 s) and current (2010 s) periods.

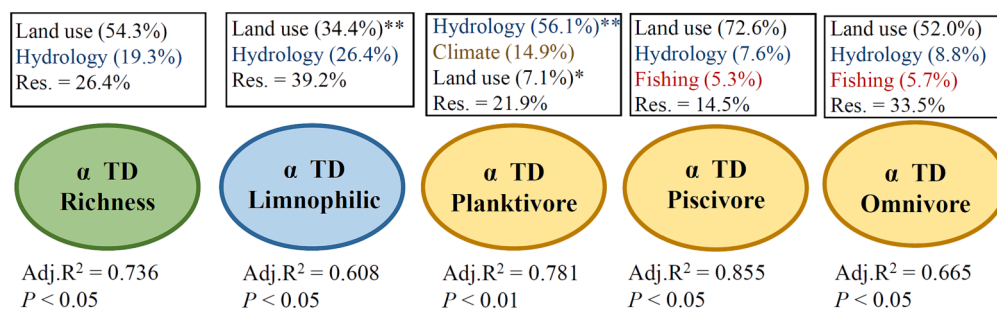


Fig. 5. Relationships between driving factors (land use, hydrology, climate, and fishing) and fish alpha taxonomic diversity (TD) and functional groups. Partitioning results: pure contributions of different kinds of drivers in rank and residuals were shown in the boxes above. In each box, the black, dark blue, yellow, and red text indicated land use, hydrology, climate, and fishing drivers, respectively. The Adj R<sup>2</sup> and P values are provided below the response variables. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of

this article.)

For beta diversity, RDA and partitioning analyses indicated that environmental factors significantly drove temporal changes of five components of fish beta diversity, including TDsor, TDsim, FDsim, PDsor, and PDsim (Fig. 6, Table S7), accounting for 29.3%, 22.9%, 15.9%, 40.5% and 36.4% of the total variation, respectively. Land use was the leading driving factor in explaining the observed variations (8.6% – 29.8%) for the five beta diversity components (Fig. 6, Table S7). Hydrology played an important role in explaining TDsor (6.6%), TDsim (1.9%), and PDsor (10.7%). Climate slightly contributed to variations of

TDsor (0.0%), TDsim (3.2%), and PDsim (3.9%) (Fig. 6, Table S7). Land use and hydrology together explained 21.5% of the variance of limnophilic fishes, which included 14.5% of variance from pure land use and 4.5% of variance from pure hydrology (Fig. 7, Table S7). Land use and climate together explained 16.6% of the variance of invertivorous fishes, which included 10.1% of variance from pure land use and 1.7% of variance from climate (Fig. 7, Table S7).

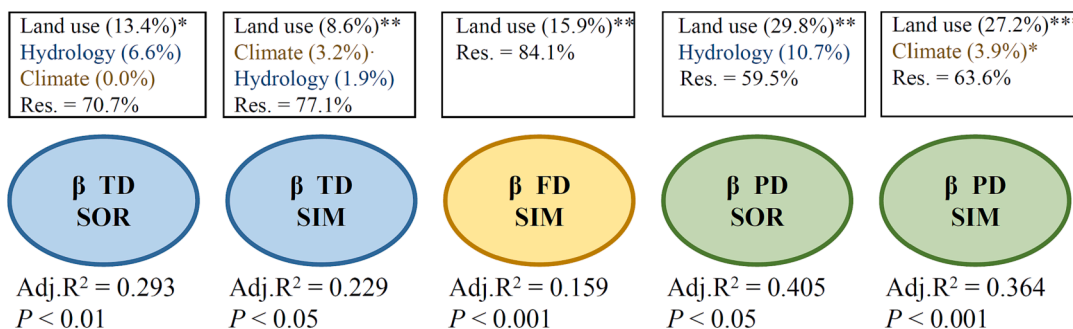


Fig. 6. Relationships between driving factors (land use, hydrology, climate, and fishing) and fish beta diversity (the overall diversity SOR and the turnover component SIM) in taxonomic (TD), functional (FD) and phylogenetic (PD) facets. Partitioning results: pure contributions of different kinds of drivers in rank and residuals were shown in the boxes above. In each box, the black, dark blue, and yellow, text indicated land use, hydrology, and climate drivers, respectively. The Adj R<sup>2</sup> and P values are provided below the response variables. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

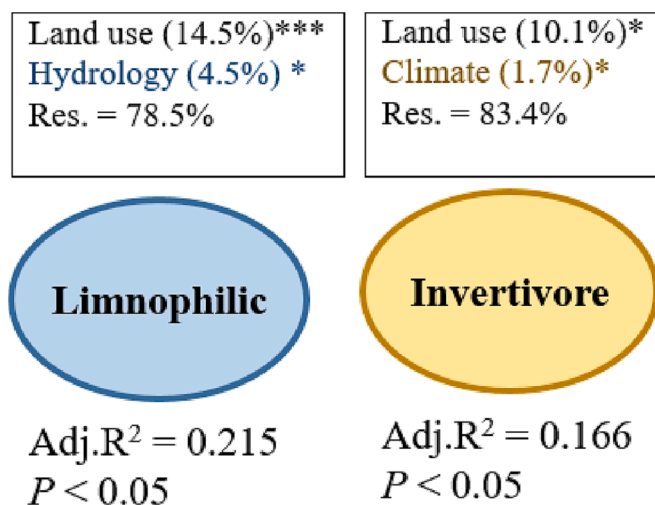


Fig. 7. Relationships between driving factors (land use, hydrology, climate, and fishing) and the difference matrix of functional groups. Partition results: pure contributions of different kinds of drivers in rank and residuals were shown in the boxes above. In each box, the black, dark blue, and yellow text indicated land use, hydrology, and climate drivers, respectively. The Adj R<sup>2</sup> and P values are provided below the response variables. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 4. Discussion

##### 4.1. Patterns of fish alpha and beta diversity

Our results showed that both alpha and beta diversity in taxonomic, functional, and phylogenetic facets have decreased over the past 40 years in the studied lakes, which supported our hypothesis one. Those biodiversity changes paired with rapid land use changes, supporting therefore the hypothesis that rapid land use changes deeply eroded biodiversity. This result markedly differs from the global trend toward an increase of local taxonomic, functional, and phylogenetic richness due to the accumulation of non-native species in most rivers of the globe (Toussaint et al., 2018; Su et al., 2021).

In the five studied lakes, alpha diversity indices, species richness (richness) and FRic declined over the past 40 years, while phylogenetic diversity (Delta + and Lambda +) changed slightly. This is explained by the replacement of the native fauna by functionally similar and closely related species (Purschke et al., 2013). The extinction of closely related species and introduction of distantly related species could lead to dramatic changes in overall phylogenetic diversity (Winter et al., 2013). In

the current study, however, the 32 species that were extirpated from their native lakes in the past 40 years belong to 6 orders and 7 families, while introduced species belong to 3 orders and 4 families. This led to the increase of Cypriniform dominance in the lakes, the representation of which increased from 68.75% to 77.78% of the species. In the current study, we used the taxonomic evolutionary tree as a proxy for the phylogenetic tree. It should be recognized that taxonomic distances are not true phylogenetic distances, and they could magnify or reduce the phylogenetic distances between some species to some extent, and equalize the distances between species in the tree, which might amplify the impact of the loss of some closely related species on the phylogenetic diversity (Schweiger et al., 2008). Species richness changed along with marked functional declines, which may put the fish functions at risk due to a loss of functional redundancy (Díaz and Cabido, 2001). For instance, non-native species were mainly the same limnophilic species established in the lakes after intentional introduction (e.g., silver carp *Hypophthalmichthys molitrix*, bighead carp *Hypophthalmichthys nobilis*, and common carp *Cyprinus carpio*) or unintentional spread through water diversions (e.g. *Tridentiger bifasciatus*, *Taenioides cirratus*, Qin et al., 2019), which therefore reduced dispersal limitation processes that historically occurred among these lakes.

The decline of native species, combined with introduction of the same non-native species, led to a steep decline of fish taxonomic, functional and phylogenetic beta diversity. For instance, *Luciobrama microcephalus*, a large-sized predator belonging to Cyprinidae has been extirpated from Lake Luoma, whereas Lakes Nansi and Dongping, experienced the extirpation of *Gobiobotia filifer* and *Saurogobio gymnocheilus*, two small-sized invertivore belonging to Cyprinidae (Fu et al., 2003; Chen et al., 2020). Such extirpation thus triggers taxonomic, functional and phylogenetic homogenization across the region, explaining why homogenization trends largely exceeded those reported across the world river fish faunas (Su et al., 2021). Empirical investigations conducted by previous studies found that introductions rather than extinctions contribute more to homogenization (Olden and Poff, 2004; Spear and Chown, 2008; Toussaint et al., 2018). In our study, the number of extirpated species exceeded the number of non-native species, thus leading to a net loss of biodiversity at both local (alpha diversity) and regional (beta diversity) scales, and for all the considered facets of biodiversity.

##### 4.2. Determinants of fish alpha and beta diversity

Our study showed that land use and hydrological factors strongly drove multifaceted components of fish alpha and beta diversity in regions with rapid land use changes. This supports the hypothesis that local human disturbances might have greater impacts because of the intensive anthropogenic disturbance in the study region. Land use was

the main driving factor, confirming that in rapid developing regions the harsh local disturbances experienced by ecosystems overwhelmed natural environmental determinants. Therefore, factors such as climate changes driving fish species richness, composition and functional structure at continental and global scales (Schleuter et al., 2012; Brucet et al., 2013; Guo et al., 2019; Su et al., 2022) are no longer considered as the major drivers of the considered lakes, where local human disturbance (e.g. land use) mainly drove biodiversity. Moreover, among anthropic driving forces, local disturbances, such as land use changes and hydrological alteration had a higher influence on fish biodiversity than climate change, one of the leading global determinants of the current extinction crisis (Urban, 2015).

Land use was the leading factor in driving fish biodiversity change in five considered lakes. Changes of land use types were closely related to aquatic habitats and water quality (Heitke et al., 2006; Xiong et al., 2022), which in turn drive the structure of aquatic communities (Xiong et al., 2021). Among land use changes, urbanization contributed significantly to the decline of fish diversity, as urban areas generate diverse pervasive effects on ecosystems, ranging from the habitat loss to fish uptake for protein supply, and to the release of pollutants (Chen et al., 2017; Chen and Olden, 2020), it is therefore not surprising it constitutes a significant component of the land use effects on fish faunas.

In summary, we have detected decreasing patterns of all the facets of fish diversity in lakes of the Chinese Eastern Plain that experiencing rapid land use changes over the past 40 years. Our study revealed that land use played a more important role than other stressors in driving the fish diversity. Limitations still exist in the current study. For instance, we speculate that the decline of rheophilic species may be related to the disconnection of lakes from rivers, which was confirmed in many lakes of the middle and lower reaches of the Yangtze River (Liu and Wang, 2010; Jiang et al., 2020), but data limitations in this study (i.e., we did not have the data before and after the construction of controlled locks and gates between lakes and rivers) make it difficult to test this. In addition, due to the lack of complete historical data in the 1990 s and 2000 s in the studied lakes, it prevented us from providing a comprehensive and continuous pattern of fish diversity changes over time.

In a global conservation perspective, attention should be given to both local human disturbance and climate changes, but in the regions experiencing rapid economic development and land use changes, local disturbances such as urban development, reclamation of lake shores to aquaculture ponds, hydrological modification, and fishing in the current study should be considered as a priority in biodiversity management plans to change the step biodiversity decline that are currently experiencing.

#### CRediT authorship contribution statement

**Yushun Chen:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110390>.

#### References

- Albert, J.S., Destouni, G., Duke-Sylvester, S.M., Magurran, A.E., Oberdorff, T., Reis, R.E., Winemiller, K.O., Ripple, W.J., 2021. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50, 85–94. <https://doi.org/10.1007/s13280-020-01318-8>.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14 (1), 19–28.
- Balian, E.V., Segers, H., Martens, K., Lévêque, C., 2008. The freshwater animal diversity assessment: an overview of the results. In: Balian, E.V., Lévêque, C., Segers, H., Martens, K. (Eds.), *Developments in Hydrobiology/Freshwater Animal Diversity Assessment*. Springer Netherlands, Dordrecht, pp. 627–637.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. <https://doi.org/10.2307/40405792>.
- Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>.
- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecology* 89, 2623–2632. <https://doi.org/10.1890/07-0986.1>.
- Brucet, S., Pedron, S., Mehner, T., Lauridsen, T.L., Argillier, C., Winfield, I.J., Volta, P., Emmrich, M., Hesthagen, T., Holmgren, K., Benejam, L., Kelly, F., Krause, T., Palm, A., Rask, M., Jeppesen, E., 2013. Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. *Freshw. Biol.* 58, 1779–1793. <https://doi.org/10.1111/fwb.12167>.
- Budnick, W.R., Lebourcher, T., Belliard, J., Soinenen, J., Lavoie, I., Pound, K., Jamoneau, A., Tison-Rosebery, J., Tales, E., Pajunen, V., Campeau, S., Passy, S.I., Bahn, V., 2019. Local and regional drivers of taxonomic homogenization in stream communities along a land use gradient. *Glob. Ecol. Biogeogr.* 28 (11), 1597–1609.
- Cai, Y., Xu, J., Zhang, M., Wang, J., Heino, J., 2019. Different roles for geography, energy and environment in determining three facets of freshwater molluscan beta diversity at broad spatial scales. *Sci. Total Environ.* 659, 451–462. <https://doi.org/10.1016/j.scitotenv.2018.12.373>.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11448>.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242. <https://doi.org/10.1038/35012241>.
- Chen, Y., 1998. *Fauna Sinica. China, Science Press, Beijing.*
- Chen, K., Olden, J.D., 2020. Threshold responses of riverine fish communities to land use conversion across regions of the world. *Global Change Biol.* 26 (9), 4952–4965. <https://doi.org/10.1111/gcb.15251>.
- Chen, Y., Zhang, S., Huang, D., Li, B., Liu, J., Liu, W., Ma, J., Wang, F., Wang, Y., Wu, S., Wu, Y., Yan, J., Guo, C., Xin, W., Wang, H., 2017. The development of China's Yangtze River Economic Belt: how to make it in a green way? *Sci. Bull.* 62, 648–651. <https://doi.org/10.1016/j.scib.2017.04.009>.
- Chen, Y., Qu, X., Xiong, F., Lu, Y., Wang, L., Hughes, R.M., 2020. Challenges to saving China's freshwater biodiversity: fishery exploitation and landscape pressures. *Ambio* 49, 926–938. <https://doi.org/10.1007/s13280-019-01246-2>.
- Chevan, A., Sutherland, M., 1991. Hierarchical Partitioning. *Am Stat.* 45, 90–96. <https://doi.org/10.1109/ICCAD.1996.569862>.
- Clarke, K., Warwick, R., 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531. <https://doi.org/10.1046/j.1365-2664.1998.3540523.x>.
- Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol.-Prog. Ser.* 216, 265–278. <https://doi.org/10.3354/meps216265>.
- Collen, B., Whitton, F., Dyer, E.E., Baillie, J.E.M., Cumberlidge, N., Darwall, W.R.T., Pollock, C., Richman, N.I., Soulsby, A.-M., Böhm, M., 2014. Global patterns of freshwater species diversity, threat and endemism. *Glob. Ecol. Biogeogr.* 23, 40–51. <https://doi.org/10.1111/gcb.12096>.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Glob. Ecol. Biogeogr.* 17, 252–261. <https://doi.org/10.1111/j.1466-8238.2007.00364.x>.



- Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2).
- Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.* 28, 137–167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>.
- Fricke, R., Eschmeyer, W. N. & Van der Laan, R. (eds) 2023. Eschmeyer's catalog of fishes: genera, species, references. (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>). Electronic version accessed 10 Apr 2023.
- Froese, R., Pauly, D., Editors., 2021. FishBase. World Wide Web electronic publication. [www.fishbase.org](http://www.fishbase.org), version (06/2021).
- Fu, C., Wu, J., Chen, J., Wu, Q., Lei, G., 2003. Freshwater fish biodiversity in the Yangtze River basin of China: Patterns, threats and conservation. *Biodivers. Conserv.* 12, 1649–1685. <https://doi.org/10.1023/A:1023697714517>.
- Gaston, K., Blackburn, T., 2008. *Pattern and Process in Macroecology*. Wiley, New York.
- Gianuca, A.T., Declerck, S.A.J., Cadotte, M.W., Souffreau, C., De Bie, T., De Meester, L., 2017. Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography* 40, 742–752. <https://doi.org/10.1111/ecog.02263>.
- Guo, C., Chen, Y., Lek, S., Li, Z., 2016. Large scale patterns in the diversity of lake fish assemblages in China and the effect of environmental factors. *Fundam. Appl. Limnol.* 188 (2), 129–145.
- Guo, C., Chen, Y., Gozlan, R.E., Li, Z., Mehner, T., Lek, S., Paukert, C.P., 2019. Biogeographic freshwater fish pattern legacy revealed despite rapid socio-economic changes in China. *Fish. Fish.* 20, 857–869. <https://doi.org/10.1111/faf.12380>.
- Guo, C., Chen, Y., Gozlan, R.E., Liu, H., Lu, Y., Qu, X., Xia, W.T., Xiong, F.Y., Xie, S.G., Wang, L.Z., 2020. Patterns of fish communities and water quality in impounded lakes of China's south-to-north water diversion project. *Sci. Total Environ.* 713, 136515 <https://doi.org/10.1016/j.scitotenv.2020.136515>.
- Heino, J., Mykrä, H., Kotanen, J., Muotka, T., 2007. Ecological filters and variability in stream macroinvertebrate communities: do taxonomic and functional structure follow the same path? *Ecography* 30, 217–230. <https://doi.org/10.1111/j.0906-7590.2007.04894.x>.
- Heino, J., Virkkala, R., Toivonen, H., 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol. Rev. Camb. Philos. Soc.* 84, 39–54. <https://doi.org/10.1111/j.1469-185X.2008.00060.x>.
- Heitke, J.D., Pierce, C.L., Gelwicks, G.T., Simmons, G.A., Siegwirth, G.L., 2006. Habitat, land use, and fish assemblage relationships in Iowa streams: preliminary assessment in an agricultural landscape. *Am. Fish. Soc. Symp.* 48, 287–303.
- Henriques, S., Guilhaumon, F., Villéger, S., Amoroso, S., França, S., Pasquaudo, S., Cabral, H.N., Vasconcelos, R.P., 2017. Biogeographical region and environmental conditions drive functional traits of estuarine fish assemblages worldwide. *Fish. Fish.* 18, 752–771. <https://doi.org/10.1111/faf.12203>.
- Ji, L., Jiang, X., Liu, C., Xu, Z., Wang, J., Qian, S., Zhou, H., 2020. Response of traditional and taxonomic distinctness diversity indices of benthic macroinvertebrates to environmental degradation gradient in a large Chinese shallow lake. *Environ. Sci. Pollut. Res.* 27, 21804–21815. <https://doi.org/10.1007/s11356-020-08610-w>.
- Jia, Y., Kennard, M.J., Liu, Y., Sui, X., Li, K., Wang, G., Chen, Y., 2020. Human disturbance and long-term changes in fish taxonomic, functional and phylogenetic diversity in the Yellow River, China. *Hydrobiologia* 847, 3711–3725. <https://doi.org/10.1007/s10750-020-04244-8>.
- Jiang, X., Pan, B., Sun, Z., Cao, L., Lu, Y., 2020. Application of taxonomic distinctness indices of fish assemblages for assessing effects of river-lake disconnection and eutrophication in floodplain lakes. *Ecol. Indic.* 110, 105955 <https://doi.org/10.1016/j.ecolind.2019.105955>.
- Jiangsu Provincial Bureau of Statistics., 2021. Jiangsu Statistical Yearbook. Retrieved from <http://stats.jiangsu.gov.cn/col/col4009/index.html>.
- Kuczynski, L., Legendre, P., Grenouillet, G., 2017. Concomitant impacts of climate change, fragmentation and non-native species have led to reorganization of fish communities since the 1980s. *Glob. Ecol. Biogeogr.* 27, 213–222. <https://doi.org/10.1111/geb.12690>.
- Laliberté, E., Legendre, P., Shipley, B., 2015. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Package 1.0-12. <https://CRAN.R-project.org/package=FD>.
- Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.* 13, 76–86. <https://doi.org/10.1111/j.1461-0248.2009.01403.x>.
- Lento, J., Laske, S.M., Lavoie, I., Bogan, D., Brua, R.B., Campeau, S., Chin, K., Culp, J.M., Levenstein, B., Power, M., Saulnier-Talbot, E., Shaftel, R., Swanson, H., Whitman, M., Zimmerman, C.E., 2020. Diversity of diatoms, benthic macroinvertebrates, and fish varies in response to different environmental correlates in Arctic rivers across North America. *Freshw. Biol.* 67 (1), 95–115. <https://doi.org/10.1111/fwb.13600>.
- Leprieux, F., Tedesco, P.A., Hugué, B., Beauchard, O., Dürr, H.H., Brosse, S., Oberdorff, T., 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecol. Lett.* 14, 325–334. <https://doi.org/10.1111/j.1461-0248.2011.01589.x>.
- Liu, H., Chen, Y., Gozlan, R.E., Qu, X., Xia, W., Cheng, F., Wang, L., Paukert, C.P., Olden, J.D., Xie, S., 2022a. Fish diversity reduction and assemblage structure homogenization in lakes: A case study on unselective fishing in China. *Wat. Bio. Sec.* 1 (3), 100055.
- Liu, H., Qu, X., Xia, W., Chen, Y., 2022b. Taxonomic, functional, and phylogenetic diversity patterns reveal different processes shaping river fish assemblages in the Eastern Huai River Basin. *China. Wat. Bio. Sec.* 100078 <https://doi.org/10.1016/j.watbs.2022.100055>.
- Liu, X., Wang, H., 2010. Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain. *Divers. Distrib.* 16, 932–940. <https://doi.org/10.1111/j.1472-4642.2010.00706.x>.
- Mason, N.W.H., MacGillivray, K., Steel, J.B., Wilson, J.B., 2003. An index of functional diversity. *J. Veg. Sci.* 14, 571–578. <https://doi.org/10.1111/j.1654-1103.2003.tb02184.x>.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>.
- Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O.J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münckmüller, T., Pavoine, S., Prinzing, A., Rodrigues, A.S.L., Rohr, R.P., Thébaud, E., Thuiller, W., 2012. Ecophylogenetics: advances and perspectives. *Biol. Rev.* 87 (4), 769–785.
- National Bureau of Statistics of China., 2021. National Data. Retrieved from [www.stats.gov.cn/](http://www.stats.gov.cn/).
- Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26, 867–878. <https://doi.org/10.1111/j.0906-7590.2007.04817.x>.
- Ni, Y., Wu, H.L., 2006. *Fishes of Jiangsu Province*. China Agriculture Press, Beijing, China.
- Olden, J.D., Poff, N.L., 2004. Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology* 85, 1867–1875. <https://doi.org/10.1890/03-3131>.
- Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.* 86, 792–812. <https://doi.org/10.1111/j.1469-185X.2010.00171.x>.
- Peres-Neto, P., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. [https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2).
- Purschke, O., Schmid, B.C., Sykes, M.T., Poschod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M., Prentice, H.C., Fridley, J., 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *J. Ecol.* 101, 857–866. <https://doi.org/10.1111/1365-2745.12098>.
- Qin, J., Cheng, F., Zhang, L., Schmidt, B.V., Liu, J., Xie, S.G., 2019. Invasions of two estuarine gobiid species interactively induced from water diversion and saltwater intrusion. *Manag. Biol. Invasion* 10, 139–150. <https://doi.org/10.3391/mbi.2019.10.1.09>.
- Qu, X., Chen, Y., Liu, H., Xia, W., Lu, Y., Gang, D.-D., Lin, L.S., 2020. A holistic assessment of water quality condition and spatiotemporal patterns in impounded lakes along the Eastern Route of China's South-to-North Water Diversion Project. *Water Res.* 185, 116275 <https://doi.org/10.1016/j.watres.2020.116275>.
- Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. <https://doi.org/10.1111/brv.12480>.
- Schleuter, D., Daufresne, M., Veslot, J., Mason, N.W.H., Lanoiselée, C., Brosse, S., Beauchard, O., Argillier, C., 2012. Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins. *Glob. Ecol. Biogeogr.* 21, 1083–1095. <https://doi.org/10.1111/j.1466-8238.2012.00763.x>.
- Schweiger, O., Klotz, S., Durka, W., Kühn, I., 2008. A comparative test of phylogenetic diversity indices. *Oecologia* 157, 485–495. <https://doi.org/10.1007/s00442-008-1082-2>.
- Shandong Provincial Bureau of Statistics., 2021. Public Data. <http://tj.shandong.gov.cn/>.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How Should Beta-Diversity Inform Biodiversity Conservation? *Trends Ecol. Evol.* 31, 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>.
- Spear, D., Chown, S.L., 2008. Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *J. Biogeogr.* 35, 1962–1975. <https://doi.org/10.1111/j.1365-2699.2008.01926.x>.
- Su, G., Logez, M., Xu, J., Tao, S., Villegier, S., Brosse, S., 2021. Human impacts on global freshwater fish biodiversity. *Science* 371, 835–838. <https://doi.org/10.1126/science.abd3369>.
- Su, G., Tedesco, P.A., Toussaint, A., Villéger, S., Brosse, S., Leprieux, F., 2022. Contemporary environment and historical legacy explain functional diversity of freshwater fishes in the world rivers. *Glob. Ecol. Biogeogr.* 31 (4), 700–713.
- Teichert, N., Lepage, M., Lobry, J., 2018. Beyond classic ecological assessment: the use of functional indices to indicate fish assemblages sensitivity to human disturbance in estuaries. *Sci. Total Environ.* 639, 465–475. <https://doi.org/10.1016/j.scitotenv.2018.05.179>.
- Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P.A., Brosse, S., Villéger, S., Vila, M., 2018. Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecol. Lett.* 21 (11), 1649–1659.
- Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348, 571–573. <https://doi.org/10.1126/science.aaa4984>.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301. <https://doi.org/10.1890/07-1206.1>.

- Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional beta-diversity reveals that low functional beta-diversity is driven by low functional turnover in European fish assemblages. *Glob. Ecol. Biogeogr.* 22, 671–681. <https://doi.org/10.1111/geb.12021>.
- Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., Vanni, M.J., 2017. Functional ecology of fish: current approaches and future challenges. *Aquat. Sci.* 79, 783–801. <https://doi.org/10.1007/s00027-017-0546-z>.
- Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11466–11473. <https://doi.org/10.1073/pnas.0801921105>.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395. <https://doi.org/10.1038/416389a>.
- Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: where are we? *Trends Ecol. Evol.* 28, 199–204. <https://doi.org/10.1016/j.tree.2012.10.015>.
- WWF., 2020. Living Planet Report 2020: bending the curve of biodiversity loss. Almond, R.E.A., Grooten M., and Petersen, T. (Eds). WWF, Gland, Switzerland.
- Xia, W., Zhu, B., Zhang, S., Liu, H., Qu, X., Liu, Y., Rudstam, L.G., Anderson, J.T., Ni, L., Chen, Y., 2022. Climate, hydrology, and human disturbance drive long-term (1988–2018) macrophyte patterns in water diversion lakes. *J. Environ. Manage.* 319, 115726 <https://doi.org/10.1016/j.jenvman.2022.115726>.
- Xie, G., Lundholm, J.T., Maclvor, J.S., 2018. Phylogenetic diversity and plant trait composition predict multiple ecosystem functions in green roofs. *Sci. Total Environ.* 628, 1017–1026. <https://doi.org/10.1016/j.scitotenv.2018.02.093>.
- Xiong, F., Olden, J.D., Lu, Y., Liu, H., Qu, X., Xia, W., Guo, C., Wu, X., Infante, D.M., Wang, L., Chen, Y., 2021. Riparian land use and in-channel stressors drive fish community structure in the Yangtze River. *Landsc. Ecol.* 36, 3079–3095. <https://doi.org/10.1007/s10980-021-01278-8>.
- Xiong, F., Chen, Y., Zhang, S., Xu, Y., Lu, Y., Qu, X., Gao, W., Wu, X., Xin, W., Gang, D.D., Lin, L.-S., 2022. Land use, hydrology, and climate influence water quality of China's largest river. *J. Environ. Manage.* 318, 115581 <https://doi.org/10.1016/j.jenvman.2022.115581>.
- Zhou, S., Wu, N., Zhang, M., Peng, W., He, F., Guo, K., Yan, S., Zou, Y., Qu, X., 2020. Local environmental, geo-climatic and spatial factors interact to drive community distributions and diversity patterns of stream benthic algae, macroinvertebrates and fishes in a large basin. Northeast China. *Ecol. Indic.* 117, 106673 <https://doi.org/10.1016/j.ecolind.2020.106673>.