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Tao Xiang

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Tao Xiang. Determinants and consequences of current and future freshwater fish invasions in China. Biodiversity and Ecology. Université Paul Sabatier - Toulouse III, 2023. English. NNT : 2023TOU30186 . tel-04390845

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# THÈSE

En vue de l'obtention du  
**DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE**  
Délivré par l'Université Toulouse 3 - Paul Sabatier

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Présentée et soutenue par  
**Tao XIANG**

Le 25 octobre 2023

**Déterminants et conséquences des invasions actuelles et futures  
d'espèces de poissons d'eau douce en Chine**

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Ecole doctorale : **SEVAB - Sciences Ecologiques, Vétérinaires, Agronomiques et  
Bioingenieries**

Spécialité : **Ecologie, biodiversité et évolution**

Unité de recherche :  
**EDB - Evolution et Diversité Biologique**

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**Determinants and consequences of current and future freshwater fish invasions  
in China**

Ph.D. thesis

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## Acknowledgements

Every time I read the doctoral theses of other scholars that I am particularly interested in, I have a habit of instinctively reading their acknowledgments section first. This time, when it's my turn to start writing this section, I can't help but feel deeply moved. It cannot be said that the journey of doctoral life has been difficult, but it has also not been easy. Time flies like an arrow. In the blink of an eye, four years have passed. Reflecting on these four years of my PhD period, there have been moments of confusion and hesitation when faced with difficulties, as well as moments of satisfaction upon completing a task. Such is life!

I am truly grateful to my doctoral supervisor, Gaël GRENOUILLET. I have always been fortunate to have obtained his permission in the summer of 2018 to get the opportunity to pursue a doctoral degree in Toulouse, France. Without his unwavering support and assistance, I would not have been able to complete this thesis. His patient guidance and earnest teachings enlightened me about the beautiful and rare native fish species in China's freshwater ecosystems, as well as non-natives with potential risks. He also taught me how to conduct large-scale ecological research and encouraged me to engage in intellectual battles with journals' editors and reviewers..... Over these four years, I have truly gained valuable professional knowledge from Gaël. However, due to my limited abilities, I regret not being able to learn more solid knowledge and skills from him.

I am truly grateful to my co-authors (e.g., Xianghong) and many of the laboratory staff and colleagues (e.g., Dominique, Shengli, Lucie, Vanna, Luis, Sebastien, Pablo A.,

Daniel, and Guohuan). Thank you for lending a helping hand when I encountered difficulties, allowing me to feel the enthusiasm even in a foreign land.

I am truly grateful to my jury members (i.e., Thierry, Christine, Marc, and Robert).

Thank you for your invaluable suggestions on my doctoral thesis.

I am truly grateful to many Chinese companions who have studied together with me in France. Even though we are all in France, over 8,000 km away from China, I can still feel the warmth of home from all of you. I so miss the days when we enjoyed French cuisine and homemade Chinese dishes together.

I want to thank my family. Without your support over these four years, it would have been difficult for me to persevere. Whenever I talk to you through video chats, it soothes my anxiety and uneasiness the most.

Lastly, I would like to express my gratitude to the China Scholarship Council (CSC) for the financial support, as well as to the EDB lab for providing me with various research facilities and conveniences.

花开堪折直须折，莫待无花空折枝！

Tao XIANG, Toulouse

## ABSTRACT

Over the past 120 years, the introduction of non-native freshwater fish species and the comparatively fewer extinctions of native species have emerged as major environmental and ecological concerns in China's freshwater ecosystems. However, the availability of information on freshwater fish species at the country scale is limited, which includes fish lists, species traits that facilitate fish introductions, consequences and determinants of human impacts on freshwater fish biodiversity, and how species' ranges respond to global changes. This limitation hinders the development and implementation of effective conservation and management strategies that target specific issues. To address these issues, we first compiled an up-to-date inventory of native and non-native freshwater fish species found in China's water bodies. This inventory of species was developed at the basin (or hydrological unit) level, and was further enriched by creating a comprehensive database containing information about species traits like morphological and life history traits, as well as their phylogeny. Furthermore, we collected species occurrence data on several well-known invasive freshwater fish species in China to assess their range shifts in current and future periods.

First, we found that native species were significantly ( $P < 0.001$ ) different from both exotic and translocated species in terms of their 12 quantitative species traits, while no remarkable differences between exotic and translocated species were detected ( $P = 0.93$ ). Additionally, species with relatively higher vulnerability (intrinsic vulnerability of fishes to fishing), trophic level, and pectoral fin vertical position, but with lower

resilience and lateral body shape (higher hydrodynamism), were deemed as potential candidates for introduction and dispersal in China compared to native species.

Second, we evaluated 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. We further developed a new biodiversity index of multifaceted changes in fish biodiversity to evaluate the consequences of fish introductions and extinctions on freshwater fish biodiversity. Our results showed that fish populations in more than 80% of China's water bodies, which make up over 80% of the country's surface area, were currently experiencing taxonomic, functional, and phylogenetic homogenization. More specifically, fish assemblages in Northwest and Southwest China had undergone extreme temporal and multifaceted changes in fish biodiversity compared to other regions. These changes were mainly driven by environmental factors.

Last, we applied species distribution models to assess the potential distributions of six notorious invasive fish species in current and future periods along with their determinants. Our results showed that the habitat suitability for the six species substantially benefited from temperature conditions. In future periods, species ranges of all six fishes would undergo varying degrees of shifts. During the given time periods, there were also observed transitory fluctuations in the potential ranges of all six species.



All of these results provided new insights into the inventory and distribution of native and non-native freshwater fish species in China, species traits that mediated the invasion of non-native fish species, current status of freshwater fish biodiversity, and responses of invasive fish species' habitat suitability to global changes. These results also offered scientific basis and reference for freshwater fish conservation and fisheries management in China.

**Keywords:** Native and non-native fish; Species traits; Freshwater fish biodiversity; Global changes; Species distribution models

## RESUME

Au cours des 120 dernières années, les introductions d'espèces non-natives de poissons d'eau douce et les rares extinctions d'espèces natives sont devenues une préoccupation majeure sur le plan environnemental et écologique en Chine. Cependant, les informations disponibles à l'échelle du pays restent limitées, concernant notamment les listes d'espèces présentes, les traits des espèces facilitant leurs introductions, les conséquences et les déterminants des impacts humains sur la biodiversité, ainsi que les réponses des aires de répartition des espèces de poissons d'eau douce aux changements globaux. Cette limitation entrave le développement et la mise en œuvre de stratégies efficaces de conservation et de gestion. Pour remédier à ces problèmes, nous avons tout d'abord compilé un inventaire des espèces de poissons d'eau douce natives et non-natives présentes en Chine. Cet inventaire a été réalisé au niveau des bassins (unités hydrologiques), enrichi par la création d'une base de données contenant des informations sur les caractéristiques des espèces (traits morphologiques, cycles de vie), ainsi que leur phylogénie. De plus, nous avons collecté des données sur la présence d'espèces envahissantes bien connues en Chine afin de projeter les modifications potentielles de leurs aires de répartition futures.

Premièrement, nous avons constaté que les espèces natives différaient significativement ( $P < 0,001$ ) des espèces exotiques et transloquées en terme de traits quantitatifs, tandis qu'aucune différence remarquable n'a été détectée entre espèces exotiques et transloquées ( $P = 0,93$ ). Comparées aux espèces natives, les espèces introduites en

Chine présentaient également une vulnérabilité relativement plus élevée (vulnérabilité intrinsèque à la pêche), un niveau trophique et une position verticale des nageoires pectorales plus élevés, mais une résilience plus faible et une forme corporelle latérale moins prononcée (meilleur hydrodynamisme).

Deuxièmement, nous avons évalué, à l'échelle des bassins hydrographiques, les changements temporels sur plus d'un siècle des facettes taxonomique, fonctionnelle et phylogénétique de la diversité (alpha et beta) des poissons d'eau douce. Nous avons développé un nouvel indice multi-facette des changements de biodiversité pour évaluer les conséquences des introductions et des extinctions d'espèces de poissons d'eau douce. Nos résultats ont montré que dans plus de 80 % des bassins en Chine, (plus de 80 % de la surface du pays), les assemblages de poissons connaissaient actuellement une homogénéisation taxonomique, fonctionnelle et phylogénétique. Plus précisément, les assemblages du Nord-Ouest et Sud-Ouest de la Chine avaient subi des changements temporels et multifacettes extrêmes par rapport aux autres régions, principalement causés par des facteurs environnementaux.

Enfin, nous avons appliqué des modèles de distribution d'espèces pour évaluer les distributions potentielles de six espèces de poissons envahissantes notoires entre les périodes actuelle et future, ainsi que leurs déterminants. Nos résultats ont montré que la favorabilité de l'habitat pour les six espèces bénéficiait considérablement des conditions thermiques. Pour le futur, les aires de répartition des six espèces de poissons

pourraient subir des changements variables, avec des fluctuations transitoires observées lors des différentes périodes étudiées.

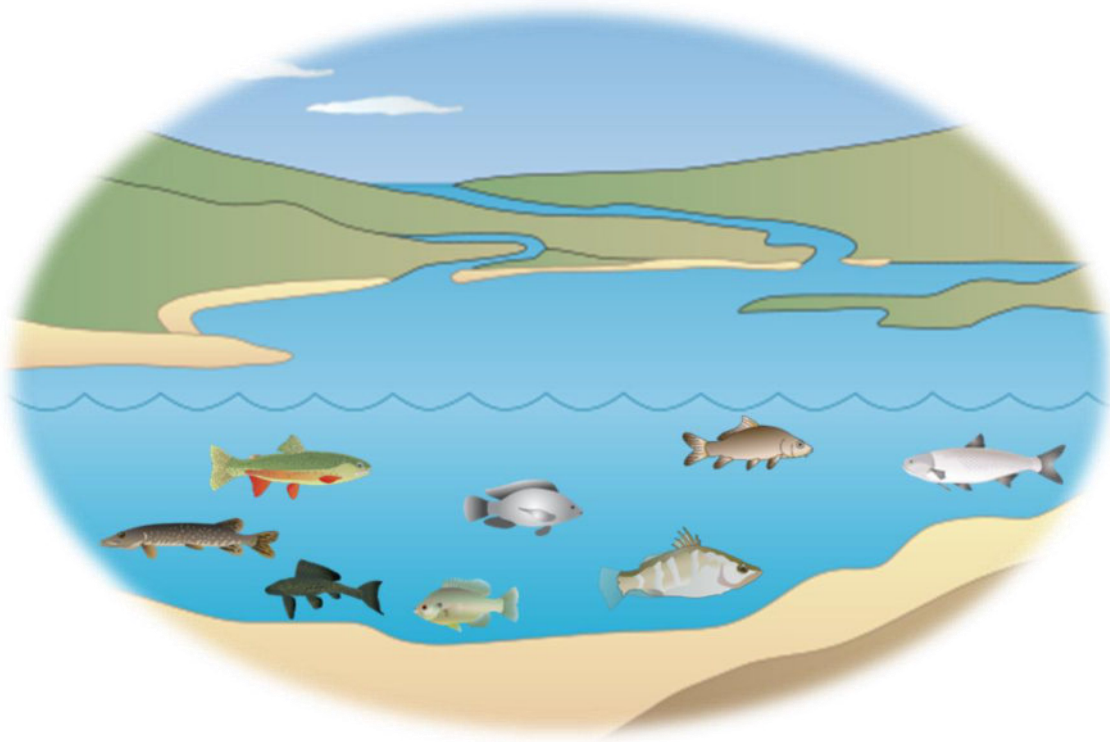
Tous ces résultats apportent de nouvelles connaissances concernant les inventaires et la répartition des espèces de poissons d'eau douce natives et non-natives en Chine, les traits des espèces non-natives qui facilitent leur introduction, l'état actuel de la biodiversité des poissons d'eau douce, et les modifications de l'habitat favorable d'espèces envahissantes en réponse aux changements globaux. Ces résultats peuvent servir de base scientifique et de référence pour la conservation des poissons d'eau douce et la gestion des pêches en Chine.

**Mots-clés:** Poissons natifs et non-natifs ; Traits des espèces ; Biodiversité des poissons d'eau douce ; Changements globaux ; Modèles de distribution d'espèces

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## Chapter 1: General introduction

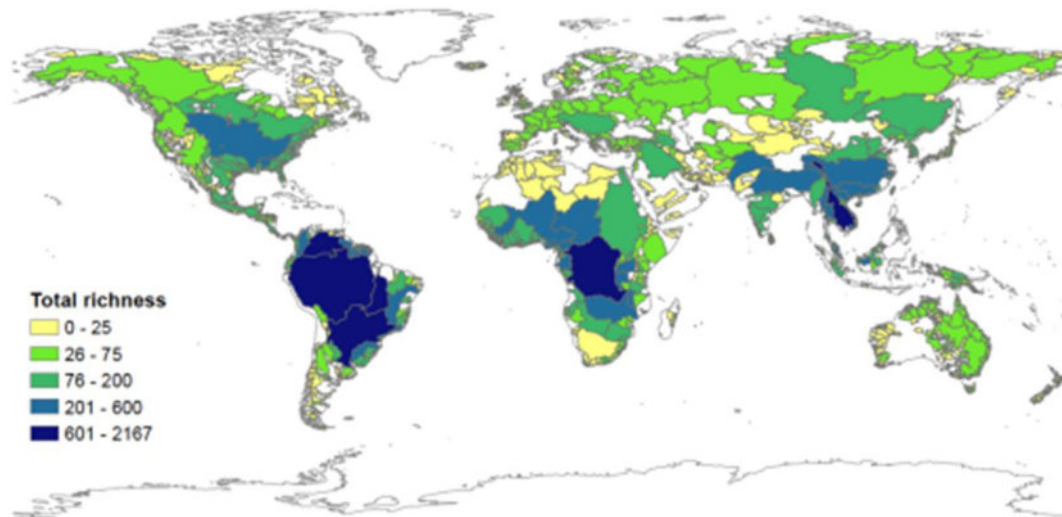


***Acknowledgements:*** The river base cross section and fish species illustrations used in the figure were sourced from Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/media-library](http://ian.umces.edu/media-library)).

## 1.1 The freshwater fish biodiversity crisis

Freshwater habitats, which occupy about 0.8% of the Earth's surface (Dudgeon et al., 2006), are home to around 10% of all known species (Strayer and Dudgeon, 2010). Both nature (e.g., ecosystem functioning) and society (e.g., human livelihoods and well-being) benefit significantly from the constitution of inland waters and freshwater biodiversity (Dudgeon et al., 2006; Albert et al., 2021; Maasri et al., 2022). Regrettably, increasing human activities have resulted in a significant loss in distribution ranges and abundance of freshwater species (Dudgeon et al., 2006; Strayer and Dudgeon, 2010; Comte et al., 2013). For example, since 1970 alone, it is estimated that freshwater species populations have suffered an average decline of 83% (Harrison et al., 2018; WWF, 2018).

Among freshwater species, fishes are the most threatened group of aquatic animals (Duncan and Lockwood, 2001). As occupying different trophic levels within freshwater ecosystems, fish species perform a wide and diverse range of ecological roles in structuring the ecosystems (Darwall and Freyhof, 2016; Guo et al., 2023). In addition, they are also valuable resources for human nutrition, recreation, and scientific research (Mota et al., 2014; Darwall and Freyhof, 2016). Until now, roughly 18,000 freshwater fish species have been found in worldwide freshwaters (van der Laan, 2018; Fricke et al., 2023), with nearly 15,000 of these species described at the river basin scale (Fig. 1) (Tedesco et al., 2017; Oberdorff, 2022). With new fish species being discovered each year currently (Fricke et al., 2023), the final total could far surpass 18,000.



**Fig. 1.** Global freshwater fish species richness in river basins (adapted from [Oberdorff, 2022](#)).

**Source:** Oberdorff, T. (2022). Freshwater ecosystems under threats with global change. [⟨hal-03614358⟩](#)

Nevertheless, due to various widely known threats, including fish invasions, human-induced climate change, and other human activities, perhaps 170 freshwater fish species have been considered extinct or extinct in the wild since the 18<sup>th</sup> century and thousands of fish species are currently regarded as endangered or critically endangered ([Su et al., 2021](#); [IUCN, 2023](#)). Furthermore, a new index, cumulative change in biodiversity facets, indicates that over 50% of the world’s rivers have been experiencing marked human-mediated freshwater fish biodiversity declines ([Su et al., 2021](#)).

### **1.1.1 Non-native freshwater fish species introduction threats**

Non-native freshwater fish species are generally defined as those that have been



introduced to areas outside their native ranges (Xiong et al., 2015). Fish introductions have a long history, dating back thousands of years (Xiong et al., 2015; Bernery et al., 2022). With the growth of human activities, such as global trade, an increasing number of non-native fish species have been introduced worldwide over the last two centuries (e.g., Su et al., 2021; Bernery et al., 2022). Among them, numerous fish species have been introduced without proper registration or record (Xiong et al., 2015), and conservatively, it is estimated that 551 non-native freshwater fish species have established feral populations globally (Bernery et al., 2022). While fish introductions can offer significant societal benefits (Gozlan, 2008), it is widely acknowledged that non-native fish species, once established and becoming invasive, have the potential to cause negative impacts on various aspects, such as the economy, public health, and biodiversity (e.g., Olden et al., 2006; Gozlan et al., 2010; Liu et al., 2021; Su et al., 2021; Haubrock et al., 2022).

In general, the success of colonization and survival of one fish species in recipient areas depends on a multitude of factors that operate on various spatial and temporal scales (Rahel et al., 2007; Grabowska and Przybylski, 2015). Among these factors, abiotic factors, e.g., characteristics of recipient habitats, play crucial roles in determining the success of fish invasions (Grabowska and Przybylski, 2015). For instance, a key determinant of successful fish invasions in California streams and estuaries is the degree of compatibility between the invasive species and hydrologic regime regardless of the biota already present (Moyle and Light, 1996). Nevertheless, fish invasion success is not solely determined by abiotic factors, as biological or ecological

characteristics of non-native species are also evident in playing a role in mediating such invasions in many areas when they reach new environments through human selection or assistance (Marchetti et al., 2004; Azzurro et al., 2014; Grabowska and Przybylski, 2015). Numerous studies have demonstrated that successful invasive species tend to possess certain distinct characteristics that enable them to occupy vacant niche positions in recipient areas (e.g., Olden et al., 2006; Azzurro et al., 2014). In order to identify biological or ecological characteristics that could mediate fish invasions, it is common practice in many previous studies to compare invasive species to native species or non-invasive species (e.g., Van Kleunen et al., 2010; Grabowska and Przybylski, 2015). For example, compared with native fish species, non-natives with shorter longevity, earlier maturation, lower fecundity, larger eggs, and so on are considered potential invaders in the Central European bioregion (Grabowska and Przybylski, 2015). As a consequence, biological or ecological characteristics of fish species are increasingly being adopted to assess and forecast the likelihood of fish invasions (e.g., Olden et al., 2006; Jia et al., 2019). Unfortunately, identifying a universal suite of biological or ecological characteristics that would ensure successful fish invasions in novel areas for all fish species is not feasible (Grabowska and Przybylski, 2015), as it depends on various factors, including distinct native and non-native fish faunas, specific geographical scales being studied, and characteristics of freshwater ecosystems involved (e.g., Vila-Gispert et al., 2005; Grabowska and Przybylski, 2015). As a result of the factors mentioned above, ecological or biological characteristics of successful invaders from different areas can vary, ranging from slight differences to complete opposites (Vila-

Gispert et al., 2005). Beyond biological or ecological characteristics of species, it is also vital to consider taxa of non-natives (Lockwood et al., 2001; Alcaraz et al., 2005). Mounting evidence unequivocally demonstrates that distributions of non-natives among taxa are not random, and these species appear to exhibit similar patterns of establishment within specific taxonomic groups (e.g., Blackburn and Duncan, 2001). In other words, certain taxa may have more non-natives compared to others (Alcaraz et al., 2005). Additionally, invaders also tend to belong to taxa that are not present in native faunas (Lockwood et al., 2001; Alcaraz et al., 2005). A typical example occurred in the Iberian Peninsula, where invasive fishes belong to a wide spectrum of families not native to this recipient area (Alcaraz et al., 2005).

### **1.1.2 Human-induced climate change threats**

The global climate is changing at an unprecedented pace, primarily attributed to anthropogenic activities, such as increases in greenhouse gases (Crowley, 2000; Thuiller, 2007). Since the pre-industrial period (1880–1900), the global average surface temperature has risen by approximately 1.06 °C (Lindsey and Dahlman, 2023). During 2081–2100, the Earth’s climate is further anticipated to warm by up to 4.4 °C on average under the SSP5-8.5 scenario (IPCC, 2023), with corresponding changes in precipitation patterns (Thuiller, 2007). Climate is a major driver that influences global biodiversity, with manifold ecological effects on natural populations, including impacts on their growth, reproduction, and geographical distributions (Parmesan and Yohe, 2003; Thomas et al., 2004; Thuiller, 2007; Hoffmann and Sgrò, 2011). In return, these impacts

can also induce changes in community compositions and species interaction nature (Parmesan and Yohe, 2003; Hoffmann and Sgrò, 2011). Evidence shows that climate change is partly or wholly responsible for the extinction of up to 20 species (Cahill et al., 2013). Furthermore, contractions at the warm edges of species' ranges have been shown to cause species extinctions locally (Cahill et al., 2013). Hence, climate change could remain a primary threat to global biodiversity in the future, with 0–54% of species being at risk of extinction (Urban, 2015).

As one of the most endangered ecosystems on the planet, freshwater ecosystems are particularly vulnerable to the effects of global climate change (Woodward et al., 2010; Yousefi et al., 2020; Barbarossa et al., 2021): on the one hand, air temperature and precipitation patterns play crucial roles in determining both water temperature and availability in freshwaters; on the other hand, organisms dwelling in fragmented freshwater habitats show limited capacity for dispersal with climate change (Woodward et al., 2010). Freshwater fish species are among the most diverse and threatened organisms within freshwater habitats (Yousefi et al., 2020), and they are highly vulnerable to global warming (Barbarossa et al., 2021). As ectotherms, ambient water temperature does directly affect various aspects of freshwater fishes, including physiology (e.g., growth rates, reproduction, and phenology), species range shifts (e.g., migration and adaptation), and extinctions (e.g., mortality crisis) (e.g., Comte and Olden, 2017; Jarić et al., 2019; Barbarossa et al., 2021; Huang et al., 2021; Araújo et al., 2022). Barbarossa et al. (2021) have pointed out that 4–36% of the freshwater fish species are projected to have over half of their present-day geographic range threatened

in a 1.5–3.2 °C warmer world. This potential crisis, along with other factors such as increasing anthropogenic activities, could aggravate risk of fish extinctions (Barbarossa et al., 2021), thereby leading to a loss of freshwater fish biodiversity in aquatic ecosystems (Su et al., 2021; Barry et al., 2023). However, given that species range shifts are among the most immediate effects of climate change on natural populations (Thuiller, 2007), it is thus an undeniable fact that numerous non-native fish species are likely to benefit from climate change by expanding into new habitats (e.g., Liu et al., 2017; Kim et al., 2022). This, in turn, poses a threat to local freshwater ecosystems (Van Zuiden et al., 2016; Liu et al., 2017). For example, by 2050s and 2070s, up to 83 non-native freshwater fish species are projected to increase their suitable habitats in China under global climate change, which increases invasion risk locally due to their habitat expansions (Liu et al., 2017).

### **1.1.3 Other well-known human activity threats**

Apart from non-native freshwater fish introduction and climate change threats, there are also some other well-known main human activities that can pose a serious threat to freshwater fish species, including habitat destruction, degradation, or fragmentation, water pollution, and fisheries overexploitation (Dudgeon et al., 2006; Strayer and Dudgeon, 2010).

#### **1.1.3.1 Habitat destruction, degradation, or fragmentation threats**

Habitat destruction, degradation, or fragmentation results from a variety of interacting

factors, including land-use changes (e.g., urbanization, agricultural expansion, and deforestation), freshwater resource overuse (e.g., industrial and agricultural water consumption), mineral mining and extraction (e.g., excavation of river sand), and hydraulic constructions (e.g., dam and reservoir constructions) (e.g., [Dudgeon et al., 2006](#); [Cheng et al., 2018](#); [Zarfl et al., 2019](#); [Koehnken et al., 2020](#); [Macpherson and Salazar, 2020](#)). Typically, these threats manifest in the form of river bottom clogging, drought, floodplain aggradation, flow regulation, and river network fragmentation ([Dudgeon et al., 2006](#); [Grill et al., 2015](#); [Lennox et al., 2019](#); [Oberdorff, 2022](#)), which limit availability and transfer of energy, matter (e.g., water and food sources), and organisms ([Pringle, 2003](#); [Lațiu et al., 2022](#)). In return, the persistence of freshwater fish species could be at risk in the face of these deplorable habitat conditions (e.g., [Zarfl et al., 2019](#); [Lațiu et al., 2022](#)). For instance, the pelagic-spawning riverine fishes throughout the Great Plains and Southwest United States are susceptible to flow regulation and fragmentation, and as a result, many of them are in decline (e.g., [Dudley and Platania, 2007](#)).

### **1.1.3.2 Water pollution threats**

Water pollution, which refers to the presence of pollutants (e.g., nutrient loadings, heavy metals, microplastics, pesticides, domestic sewage, and industrial wastewater) in waters that can cause aesthetic or detrimental effects on various forms of life ([Goel, 2006](#); [Parker et al., 2021](#)), has become a global concern ([Schwarzenbach et al., 2010](#)).

Among all living organisms, freshwater fish species are the most threatened as they are

chronically exposed to highly stable pollutants present in contaminated waters (Alazemi et al., 1996; Dunier, 1996). Water pollution can have acute and chronic effects on fish species, which could harm their gills, livers, kidneys, epithelial layers, immune systems, and metabolisms (Zeitoun and Mehana, 2014; Malik et al., 2020). What's worse, pollutants can induce accumulations of contaminants in various biological systems, especially in top predators, which increases the incidence and mortality rates of fish diseases (Malik et al., 2020). Hence, decreasing fish populations resulting from water pollution could alter fish community compositions and ultimately threaten freshwater ecosystems (Malik et al., 2020; Oberdorff, 2022).

### **1.1.3.3 Fisheries overexploitation threats**

Freshwater fisheries are crucial for supporting the livelihoods of hundreds of millions of people worldwide, providing affordable protein, recreational opportunities, and economic benefits, especially in areas where other options for nutrition and employment are limited (Bartley et al., 2015; McIntyre et al., 2016). However, the increasing global population along with the growing demand for animal protein in diets, particularly in regions like Asia and Africa, is expected to result in a rise in worldwide inland fishing pressure (McIntyre et al., 2016; Oberdorff, 2022). Despite their economic and social importance, fisheries overexploitation can induce precarious circumstances for fish species, ultimately causing changes in fish population dynamics, community compositions, and food web structures (Allan et al., 2005; Strayer and Dudgeon, 2010; Zhang et al., 2020). Thus, fishery management should be improved and strengthened

for conserving biodiversity in freshwater ecosystems.

## **1.2 Freshwater fish biodiversity facets**

One of the most apparent consequences of anthropogenic activities and environmental changes, such as non-native fish introductions and climate change, on freshwater ecosystems is changes in taxonomic facet of freshwater fish biodiversity (Toussaint et al., 2014; 2016a). However, freshwater fish biodiversity loss is related not only to changes in taxonomic facet but also to functional and phylogenetic facets (Su et al., 2021). These facets are responsible for species' ecological features and evolutionary divergence, respectively, and are strongly influenced by anthropogenic and environmental factors (Marques et al., 2021; Su et al., 2021).

### **1.2.1 Taxonomic facet of freshwater fish biodiversity**

Anthropogenic activities, in conjunction with environmental changes, can lead to native fish species extirpations and non-native species introductions (Su et al., 2021). These two processes can alter the composition and richness (i.e., taxonomic alpha diversity) of local fish assemblages, resulting in subsequent dissimilarity among them, including taxonomic homogenization or differentiation (i.e., taxonomic beta diversity) (Villéger and Brosse, 2012; Villéger et al., 2014; Toussaint et al., 2014; 2016a). Taxonomic homogenization refers to an increase in the similarity of biotas over time, which occurs when successful invaders become widespread and native species become extinct (Rahel, 2002). Taxonomic differentiation refers to a decrease in the similarity of biotas over



time (Campbell and Mandrak, 2020). More specifically, the majority of exotic species typically have a greater effect on taxonomic differentiation, while species translocated within a region or few widespread exotic species tend to promote taxonomic homogenization (Toussaint et al., 2016a). In addition, compared to taxonomic differentiation reported in relatively few water bodies, taxonomic homogenization has emerged as the major current crisis for fish biodiversity in freshwater ecosystems worldwide (e.g., Villéger et al., 2011; 2014; Toussaint et al., 2016a). For example, Su et al. (2021) have pointed out that freshwater fish faunas in up to 58% of global river basins are undergoing taxonomic homogenization. While the taxonomic homogenization process has been shown to increase local freshwater fish biodiversity (Rahel, 2002; Su et al., 2021), it is essential to note that invaders may continue to expand their ranges and pose a threat to the survival of native species, particularly as human activity intensifies and increases over time (McKinney and Lockwood, 1999; Rahel, 2002).

### **1.2.2 Functional facet of freshwater fish biodiversity**

In contrast to taxonomic diversity which ignores ecological or biological differences among species (Jarzyna and Jetz, 2016; Marques et al., 2021), functional diversity, reflecting ecosystem processes, relies on the utilization of functional traits, which are biological attributes that affect how organisms function (Violle et al., 2007; Buisson et al., 2013; Chao et al., 2019; Su et al., 2022). Over the past decades, functional diversity has been widely adopted in freshwater ecosystems, particularly in fish species (e.g.,

Buisson et al., 2013; Toussaint et al., 2016b; Su et al., 2022). Fish species play a vital role in freshwater ecosystems through biological functions, including food acquisition, locomotion, excretion, physiological regulation, reproduction, protection, and behaviour (Villegger, 2008; Villéger et al., 2017; Su, 2020). Among these biological functions, food acquisition and locomotion are commonly used in assessments of functional diversity (e.g., Su et al., 2022), as strategies for the two functions largely determine ecosystem functions performed by fish species (Villegger, 2008). Furthermore, ecomorphology has been the subject of numerous studies regarding these two biological functions (Gatz, 1979; Winemiller, 1991; Villegger, 2008), and many morphological traits have been found to be associated with them (e.g., Villegger, 2008; Toussaint et al., 2018). For instance, maximum body length of a fish is linked to its metabolism, trophic impacts, locomotion ability, and nutrient cycling (Toussaint et al., 2016b), while oral gape position of a fish indicates its feeding position in the water column (Dumay et al., 2004; Lefcheck et al., 2014). Based on a database encompassing ten morphological traits of over 9,000 species, Toussaint et al. (2016b) have revealed the global pattern of functional diversity of freshwater fish species.

As an important facet of biodiversity, functional diversity can also respond to anthropogenic and environmental changes (Chao et al., 2019), including changes in functional richness (i.e., functional alpha diversity), and functional homogenization (i.e., a reduction in functional beta diversity) or differentiation (i.e., an increase in functional beta diversity) (Campbell and Mandrak, 2020). The widespread introduction of non-native freshwater fish species and relatively few extirpations of native fish

species have profoundly altered the global pattern of functional diversity among fish species (Toussaint et al., 2018; Su et al., 2021). Currently, in addition to an increase in functional richness that has been found in over half of global rivers, freshwater fish assemblages in approximately 85% of global rivers have experienced functional homogenization, whereas functional differentiation has only occurred in about 15% of global rivers (Su et al., 2021).

### **1.2.3 Phylogenetic facet of freshwater fish biodiversity**

Phylogenetic diversity is a fundamental facet of biodiversity, as it encapsulates evolutionary information that reflects evolutionary history of species assemblages (Jarzyna and Jetz, 2016; Rabosky et al., 2018; Nakamura et al., 2021). Like the two facets of biodiversity previously mentioned, phylogenetic diversity is also likely to be impacted by non-native freshwater fish species introductions and native species extirpations, i.e., changes in phylogenetic richness, and phylogenetic homogenization or differentiation (e.g., Zhang et al., 2018; Jiang et al., 2019; Su et al., 2021). Over the past two centuries, an increase in phylogenetic richness of freshwater fish species has been observed in approximately 62% of global rivers, while phylogenetic dissimilarity has increased in as many as 65% of them (Su et al., 2021).

## **1.3 Thesis conduct and structure**

As one of the megadiverse freshwater regions on the planet, China possesses an extensive and diverse array of inland water bodies (e.g., rivers and lakes) and

environments (e.g., geomorphology and climates), providing a broad range of habitats for freshwater fish species (Kang et al., 2014; Xiong et al., 2015; He et al., 2020). However, freshwater fish populations are currently experiencing a biodiversity crisis due to various factors, such as climate change and biological invasions (Liu et al., 2017; Su et al., 2021). Unfortunately, research on evaluating the current crisis faced by freshwater fish species in China is limited to some specific regions, such as certain plateaus, lakes or river basins (e.g., Ding et al., 2017; Zhang et al., 2018; Su et al., 2021), or not comprehensively evaluated, such as lacking assessments of functional and phylogenetic diversity (e.g., Liu et al., 2017). The lack of important datasets, such as a publicly available list of freshwater fish species in China (e.g., native, non-native, or extinct fish species), functional traits, phylogeny, and species distribution information, is a challenge in studying China's fish biodiversity crisis on a national scale. Apart from the current freshwater crisis, freshwater fish biodiversity may also be threatened in the foreseeable future because potential suitable areas for invasive fish species may shift with global changes, such as climate warming, posing a threat to local native fish species (Liu et al., 2019; Perrin et al., 2021). Given this, Liu et al. (2019) have evaluated current and future freshwater fish invasion risks in China based on occurrence records of 51 current invaders and 64 potential invaders. Nevertheless, research into the range shifts of various invasive fish species that are widely acknowledged, such as *Cyprinus carpio* Linnaeus, 1758, which tend to capture more public and policymaker attention, is yet to be completed. What's more, previous studies have also neglected to consider the significance of transitory range dynamics (i.e., habitats that provide a suitable

environment for a species, but only for a brief period of time) of invasive fish species in China with regards to global changes (e.g., [Liu et al., 2019](#)), which can reveal the availability and accessibility of habitats ([Huang et al., 2020](#); [Shiple et al., 2022](#)).

Consequently, the primary purpose of our study was to evaluate consequences and determinants of current and future freshwater fish invasions in China from multiple perspectives, such as species trait differences, diversity approaches, and habitat suitability. To accomplish this, we began by compiling an up-to-date inventory of freshwater fish species found in the wild habitats of China, including both native and non-native species. This inventory was created at the basin (hydrological unit) level, and was complemented by the creation of an extensive and comprehensive database of phylogeny and species traits (e.g., morphological and life history traits) through a thorough review of various sources. Additionally, we collected species occurrence data on several well-known invasive freshwater fish species in China. This goal was to assess their range shifts in both current and future periods, as well as identify areas where the fish species would experience transitory fluctuations within specific time periods. Specifically, we aimed to investigate the effects of global changes on distributions of these fish populations, and provide a reference for the assessment of potential distributions of other invasive fish species.

Overall, my doctoral thesis has three main aspects, as follows:

**(A) Profiling freshwater fish species, including native and non-native species (i.e., translocated and exotic species), in the wild in China at the basin level.**

(a) Compiling an up-to-date inventory of native and non-native freshwater fish species in China's wild habitats along with the most comprehensive species trait database for these fishes.

(b) Examining whether there are significant differences in distributions of native and non-native species across taxonomic groups.

(c) Testing whether native and non-native species differ in their ecological or biological traits.

**(B) Consequences of freshwater fish introductions and extinctions on fish biodiversity patterns.**

(a) Evaluating 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.

(b) Analysing multifaceted changes in these facets of biodiversity to identify relatively sensitive hydrological units as priority conservation zones.

(c) Disentangling the relative importance of environmental and anthropogenic drivers to temporal and multifaceted changes in the facets of biodiversity.

**(C) Modeling current and future distributions of several well-known invasive freshwater fish species in China.**

(a) Exploring the spatial patterns of current and future habitat ranges of six notorious invasive fishes (i.e., *Coptodon zillii*, *Cyprinus carpio*, *Gambusia affinis*, *Hemiculter*

*leucisculus*, *Oreochromis mossambicus*, and *Oreochromis niloticus*) in China.

(b) Disentangling the relative importance of environmental and anthropogenic variables driving the habitat suitability of these fishes.

(c) Identifying areas of transitory fluctuations of the fishes to determine the availability and accessibility of habitats.

**Chapter 2: Databases and methodology**





## 2.1 The list of freshwater fish species in China

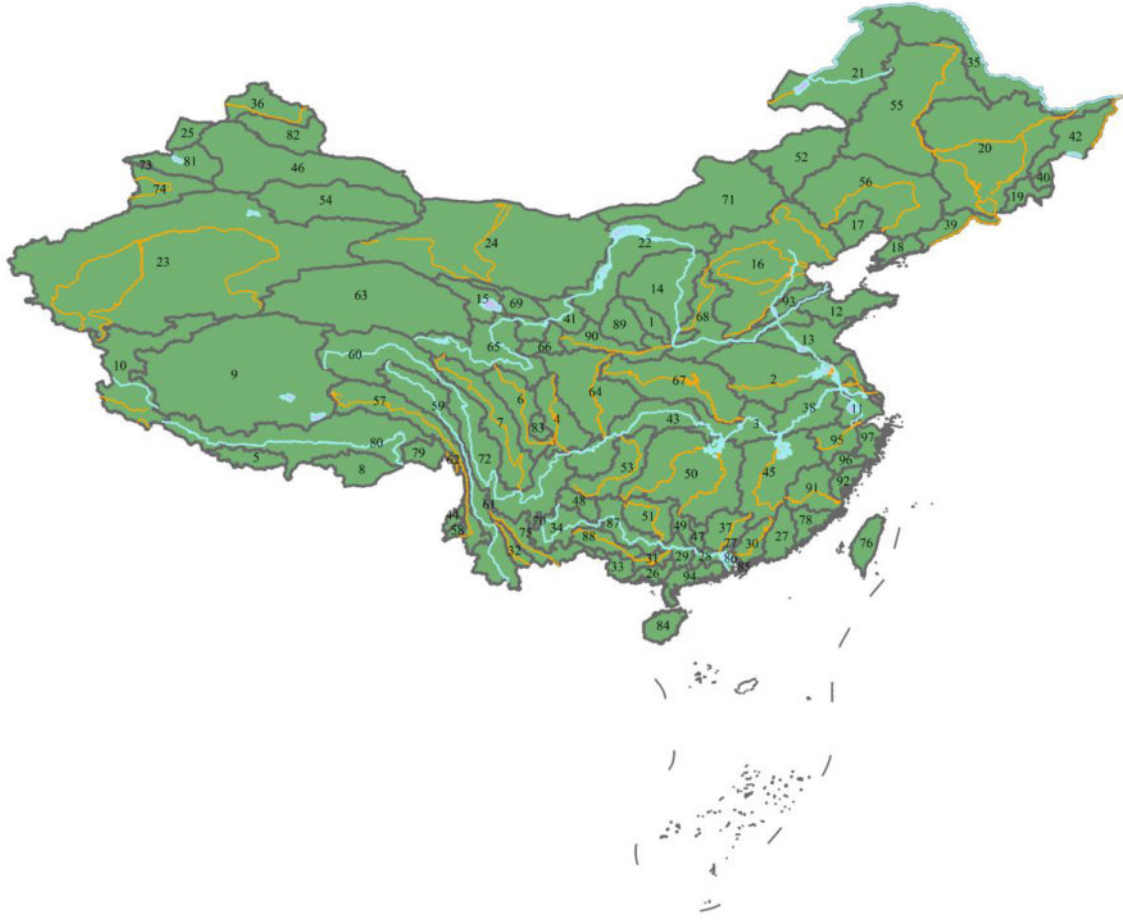
Our study only included fish species that either live their entire lives in freshwaters or spend a portion of their life cycles, such as spawning and feeding, in freshwaters. We excluded species with controversial status, such as mrigal carp (*Cirrhinus cirrhosus*, Cyprinidae) and *Acheilognathus tabira*, Cyprinidae, as well as those that only occasionally occur in freshwaters. We here defined native fish species as those that were native to China and had not been introduced to any other basins in this country. Non-native fish species were defined as those that had been introduced to areas beyond their native ranges (Kolar and Lodge, 2001; Xiong et al., 2015). Additionally, considering the potential for different negative effects associated with non-native freshwater fish species of diverse origins (e.g., Villéger et al., 2014), we further defined two statuses for non-natives in China's wild habitats: (a) exotic species are species introduced from other country or countries but not present originally in any basins in China and (b) translocated species are species native in one or more basins in China (e.g., common carp (*Cyprinus carpio*, Cyprinidae) and goldfish (*Carassius auratus*, Cyprinidae)) which had been introduced to other basin or basins in this country where they were not present originally. It should be pointed out that given China's long history of fish translocations (Xiong et al., 2015), our definition of translocated species was limited to events occurring after the 1900s.

For the above three statuses of fish species, we conducted a comprehensive literature review to obtain information on native, exotic, and translocated freshwater fishes in China. This review included peer-reviewed articles, monographs, various fish databases

(e.g., FishBase (<https://www.fishbase.org/search.php>) (Froese and Pauly, 2019) and The Fish Database of Taiwan (<http://fishdb.sinica.edu.tw/>) (Shao, 2020)), official survey reports, and other sources. Most importantly, each species validity had been cross-checked and verified using FishBase (Froese and Pauly, 2019) and Eschmeyer's Catalog of Fishes (Fricke et al., 2020). This fish list was applied to the analyses in **Chapter 3**.

## **2.2 Fish occurrences in hydrological units (river basins) in China**

A total of 97 hydrological units spanning China have been delineated (Fig. 1), drawing on previously reported basins or hydrological units for China's freshwater fish species (e.g., Lehner and Grill, 2013; Liu et al., 2017; He et al., 2020), as well as considering the best available fish distribution information (e.g., we merged small rivers or areas that have not been thoroughly investigated) (e.g., He et al., 2020). Subsequently, a comprehensive literature review was conducted, which included peer-reviewed articles, monographs, fish databases, and official survey reports. Based on previous works, such as the fish list in **Chapter 3**, China's freshwater fish species were then assembled in each of the 97 hydrological units. This was done separately for historical (before the 1900s, i.e., before human-mediated species introductions and extinctions) and current (after the 1900s) periods. 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.



**Fig. 1.** Sketch map of China at the basin (hydrological unit) 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.

Extant native species referred to those species that were known to have been present in a given unit ( $n = 1,657$ ). Conversely, any species present in the wild in a given unit in China but not originally present in that unit before the 1900s was considered non-native to the matching unit, regardless of its origin within or outside of China ( $n = 191$ ). In addition, any species that were documented to be extinct in their native units in China

after the 1900s were considered extinct ( $n = 6$ ) (e.g., Yue and Chen, 1998; IUCN, 2021).

As a result, the fish occurrences of a total of 1,742 species in the 97 hydrological units during historical (i.e., extant native species + extinct species) and current (i.e., extant native species + non-native species) periods were determined.

Meanwhile, we further divided non-native fish species into two categories: exotic species originating from outside China ( $n = 81$ ) and translocated species originating from within China ( $n = 110$ ). This distinction allowed us to investigate the introduction effects on beta diversity. For the exotic species introduction pattern, we assumed that only exotic species had been introduced (i.e., extant native species + exotic species) to determine the current fish assemblages. Similarly, for the translocated species introduction pattern, we assumed that only translocated species had been introduced (i.e., extant native species + translocated species) to determine the current fish assemblages.

This dataset was applied to the analyses in **Chapter 4**.

### **2.3 Invasive freshwater fish species occurrences**

Six notorious invasive freshwater fish species were selected for **Chapter 5**: Redbelly tilapia *Coptodon zillii* (Gervais, 1848), Common carp *Cyprinus carpio* Linnaeus, 1758, Mosquitofish *Gambusia affinis* (Baird & Girard, 1853), Sharpbelly *Hemiculter leucisculus* (Basilewsky, 1855), Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852), and Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758). To obtain their occurrences, a thorough literature review was conducted, which encompassed peer-

reviewed articles, monographs, and databases (i.e., FishBase (<https://www.fishbase.se/search.php>; retrieved in February 2022) (Froese and Pauly, 2022), the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>; retrieved in February 2022), and the Fish Database of Taiwan (<http://fishdb.sinica.edu.tw/>; retrieved in February 2022) (Shao, 2022)). The search included the most recent presence records up to 2022, and any duplicates or unreliable occurrences, such as incomplete or terrestrial records, were eliminated from the dataset.

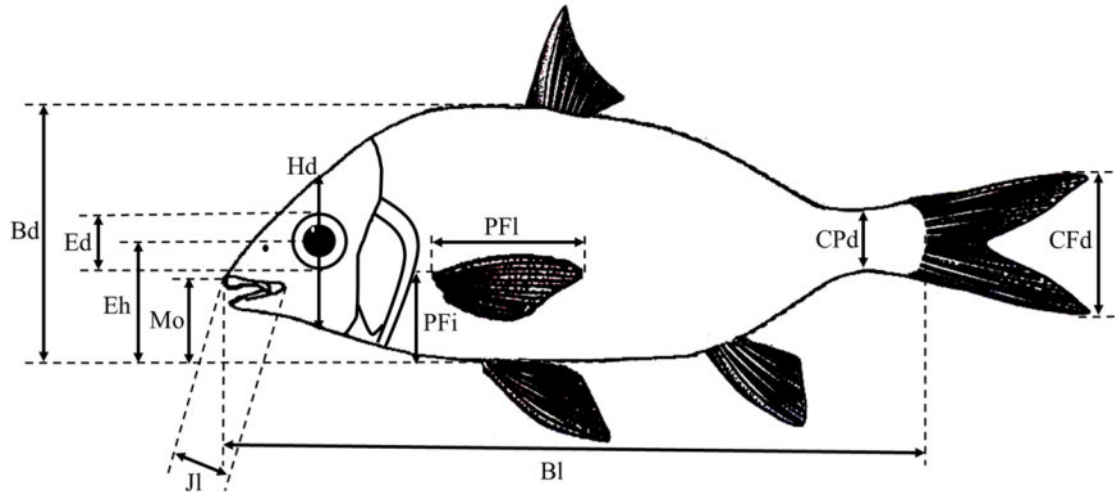
#### **2.4 Life history and morphological traits**

We collected three life history traits, i.e., resilience, trophic level, and vulnerability, from FishBase for freshwater fish species in China (Froese and Pauly, 2019). These traits encompass various ecological and life-history strategies, such as growth, longevity, reproduction, diet, and mortality. For example, species with large lengths, high ages at first maturity, low natural mortality, restricted geographic ranges, low fecundities, or high spatial behavior strength generally exhibit high vulnerability (Cheung et al., 2005). The life history trait database was applied to analyses in **Chapter**

### **3.**

For morphological trait difference tests in **Chapter 3** and functional diversity assessments in **Chapter 4**, 11 morphological measurements for each species (i.e., body length (*Bl*), body depth (*Bd*), head depth (*Hd*), caudal peduncle depth (*CPd*), caudal fin depth (*CFd*), eye diameter (*Ed*), eye position (*Eh*), oral gape position (*Mo*), maxillary jaw length (*Jl*), pectoral fin length (*PFl*), and pectoral fin position (*PFi*), Fig. 2) were

measured on at least one scientific side-view drawing or good-quality picture of an entire adult animal collected from FishBase (Froese and Pauly, 2019), The Fish Database of Taiwan (Shao, 2020), Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>; retrieved in December 2020), and related literature using ImageJ software (<https://imagej.nih.gov/ij/>). For species with particular morphologies, several rules detailed in Toussaint et al. (2016b) and Su et al. (2019) have been adopted: (a) For the species with no visible caudal fin (e.g., anguillid species), caudal peduncle throating (CFd/CPd) was set to zero; (b) For the species with the mouth positioned under the body (e.g., balitorid species), oral gape position (Mo/Bd) was set to zero; (c) For the species having a specialized sucker mouth for grazing algae (e.g., loricariid species), relative maxillary length (Jl/Hd) was set to zero; (d) For flatfishes (e.g., cynoglossid species), body depth (Bd) was the body width. These 11 morphological measurements were adopted to compute 9 unitless morphological traits associated with food acquisition and locomotion (Table 1). In addition, maximum body lengths describing fish size were also considered for the morphological traits used in the analyses. These maximum body lengths were obtained from FishBase (Froese and Pauly, 2019), and any unreasonable data, such as the maximum body length of one species provided by FishBase being much shorter than its maximum total length, were removed or replaced with appropriate records referring to the related literature.



**Fig. 2.** The morphological measurements measured on each fish species. *Bl* body length, *Bd* maximum body depth, *Hd* head depth at the vertical of eye, *CPd* minimum depth of the caudal peduncle, *CFd* maximum depth of the caudal fin, *Ed* vertical diameter of the eye, *Eh* vertical distance between the centre of the eye to the bottom of the body, *Mo* vertical distance from the top of the mouth to the bottom of the body, *Jl* length from snout to the corner of the mouth, *PFl* length of the longest ray of the pectoral fin, *PFi* vertical distance between the upper insertion of the pectoral fin to the bottom of the body.

**Table 1.** List of 10 morphological traits associated with food acquisition and locomotion (cited from [Toussaint et al., 2016b](#) and [Su et al., 2019](#) without modification).

Morphological traits	Formula	Potential link with fish functions	References
Maximum body length	$BL_{max}$	Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling	e.g., <a href="#">Toussaint et al., 2016b</a> ; <a href="#">Froese and Pauly, 2019</a>
Body elongation	$\frac{Bl}{Bd}$	Hydrodynamism	<a href="#">Reecht et al., 2013</a>

Eye vertical position	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column	Winemiller, 1991
Relative eye size	$\frac{Ed}{Hd}$	Visual acuity	Boyle and Horn, 2006
Oral gape position	$\frac{Mo}{Bd}$	Feeding position in the water column	Dumay et al., 2004; Lefcheck et al., 2014
Relative maxillary length	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw	Toussaint et al., 2016b
Body lateral shape	$\frac{Hd}{Bd}$	Hydrodynamism and head size	Toussaint et al., 2016b
Pectoral fin vertical position	$\frac{Pfi}{Bd}$	Pectoral fin use for swimming	Dumay et al., 2004
Pectoral fin size	$\frac{Pfl}{Bl}$	Pectoral fin use for swimming	Fulton et al., 2001
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag	Webb, 1984

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## 2.5 Phylogenetic data

The R package ‘FishPhyloMaker’ was utilized to create phylogenies describing the phylogenetic diversity of China’s freshwater fish species (Nakamura et al., 2021). This package can automatically insert and prune fish species from the most comprehensive phylogenetic tree (Rabosky et al., 2018) based on their taxonomic hierarchy. This dataset was applied to the analyses in **Chapter 4**.

## 2.6 Environmental and anthropogenic drivers used for modeling

In **Chapter 4**, we selected 10 representative drivers that encompass various geomorphological, hydrological, climatic, social, and economic features based on various data sources: (a) unit area, (b) elevation, (c) average annual temperature, (d) average



annual precipitation, (e) net primary productivity, (f) river fragmentation, (g) human footprint, (h) consumptive water loss, (i) aquaculture pressure, and (j) fishing pressure. These drivers are widely adopted in research on fish invasion ecology and conservation management (e.g., [Kuczynski et al., 2018](#); [Lin et al., 2021](#); [Su et al., 2021](#)), and we utilized them to describe China's hydrological units. Subsequently, we used random forest models to identify the potential drivers affecting the temporal and multifaceted changes in freshwater fish biodiversity facets.

In **Chapter 5**, we selected nine bioclimatic and non-bioclimatic variables based on various data sources, which are biologically and ecologically significant in determining the spatial distributions of the six species: (a) annual mean temperature, (b) maximum temperature of warmest month, (c) minimum temperature of coldest month, (d) annual precipitation, (e) precipitation of wettest month, (f) precipitation of driest month, (j) elevation, (h) dam area, and (i) human population density. We used these variables as predictors in the species distribution models (the MaxEnt algorithm).

### Chapter 3: Ecological and biological traits of non-native freshwater fish species

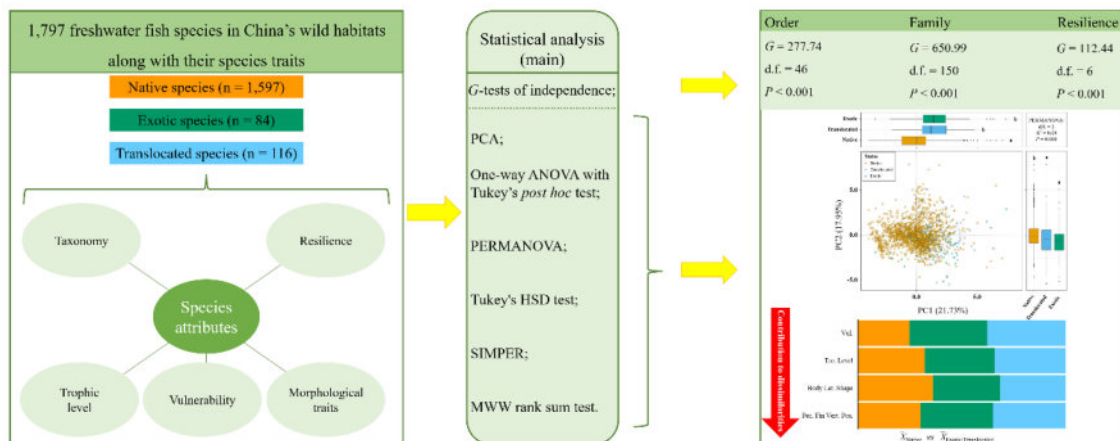
differentiate them from native species in China

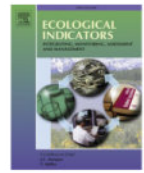
*Ecological Indicators*, **131**, 108218

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## Ecological and biological traits of non-native freshwater fish species differentiate them from native species in China

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### ARTICLE INFO

#### Keywords:

Exotic species  
Translocated species  
Freshwater ecosystems  
Ecological traits  
Biological traits  
Taxonomic category

### ABSTRACT

China's freshwater ecosystems are gradually invaded by an increasing number of non-native fish species. However, to date, some controversy about the number of native and non-native freshwater fish species in wild habitats and very limited information on ecological or biological traits mediating fish introduction success at a national scale have prevented the proposal and implementation of targeted conservation and management strategies. To address these urgent issues, first we compiled an up-to-date inventory of 1,797 fish species (1,597, 84, and 116 native, exotic (originating from outside China), and translocated (originating from within China) species, respectively) along with 13 traits encompassing various ecological and life-history strategies for each species, which is the most comprehensive freshwater fish database in China as we know. Here, we found that non-native species mainly belonged to three orders (Perciformes, Siluriformes, and Cypriniformes) and three families (Cichlidae, Cyprinidae, and Salmonidae). Native species were significantly ( $P < 0.001$ ) different from both exotic and translocated species according to their quantitative traits, while no remarkable differences between exotic and translocated species were detected ( $P = 0.93$ ). Specifically,  $G$ -tests of independence, Similarity Percentage Analysis (SIMPER), and Mann-Whitney-Wilcoxon rank sum tests showed that compared to native species, species with relatively higher vulnerability (intrinsic vulnerability of fishes to fishing), trophic level, and pectoral fin vertical position, but less resilience and lateral body shape were deemed as potential candidates for introduction and dispersal in China.

### 1. Introduction

Over the past two hundred years, a considerable number of fish species have been intentionally or unintentionally introduced into novel regions across the globe, many of which established feral populations that inevitably exert effects on both aquatic ecosystems and economy in their recipient areas (Strauss et al., 2006; Gozlan, 2008; Cucherousset and Olden, 2011; Seebens et al., 2017). For instance, the most apparent effect of fish introductions to novel regions is changes in the composition of fish assemblages, which can cause taxonomic homogenization or differentiation (Toussaint et al., 2016a). Specifically, foreign exotic species tend to promote taxonomic differentiation (i.e., decrease in community similarity), while domestic translocated species normally exert a greater effect on taxonomic homogenization (i.e., increase in community similarity) (Leprieur et al., 2008; Toussaint et al., 2016a; Liu

et al., 2017a).

With the increasing number of fish species introductions, fish invasions is becoming a more tricky environmental issue (Vitule et al., 2009; Gozlan et al., 2010) which poses a series of critical matters and challenges for fish conservation and management (Britton et al., 2011a; Britton et al., 2011b; Winfield et al., 2011). To develop and take effective conservation and management strategies aiming at minimizing dispersal and negative impacts of non-native species, mounting researches have been carried out to (a) identify species traits of successful invaders to monitor and reduce introductions of species with these traits or environmental characteristics (e.g., hydrology) of invaded habitats (e.g., Alcaraz et al., 2005; Vila-Gispert et al., 2005; Ribeiro et al., 2008; Su et al., 2020), (b) assess which species are more likely to become potential invaders affecting biodiversity (e.g., Moyle and Marchetti, 2006; Belmaker et al., 2013), and (c) predict potential invasive areas (e.g.,

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<https://doi.org/10.1016/j.ecolind.2021.108218>

Received 18 June 2021; Received in revised form 14 September 2021; Accepted 15 September 2021

Available online 24 September 2021

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Fletcher et al., 2016). Among these studies, identifying species traits associated with fish introductions is receiving growing concern and paramount to help understand the ability of introduced species to spread and integrate themselves successfully into non-native regions (Marchetti et al., 2004; García-Berthou, 2007; Ribeiro et al., 2008; Belmaker et al., 2013). Many previous studies have evidenced that ecological or biological traits related to growth, reproduction, diet, food acquisition, or locomotion (Vila-Gispert et al., 2005; Toussaint et al., 2016b) could mediate non-native fish species establishment success (García-Berthou, 2007; Azzurro et al., 2014; Grabowska and Przybylski, 2015; Su et al., 2020). Nevertheless, ecological or biological traits involved in the success or failure of fish invasions from different regions are varied or even completely opposite due to various factors, such as distinct native fish faunas, invaders, studied geographical scales, ecosystem types, and socioeconomic activities (Vila-Gispert et al., 2005; Grabowska and Przybylski, 2015; Toussaint et al., 2018; Comte et al., 2021). Targeted researches on species traits of non-native species in particular regions are thus warranted.

Benefitting from diverse aquatic habitats and environments, China is one of the megadiverse countries containing high freshwater fish species richness (Xiong et al., 2015; Xing et al., 2016; He et al., 2020), but also providing suitable habitats for non-native fish species (Xiong et al., 2015). According to historical records, at least 439 non-native fish species were introduced in China (Xiong et al., 2015), representing the highest number of documented non-native fishes around the world, likely to put some of China's native fish species at high risk of extinction (Shuai et al., 2018; Zhang et al., 2018). For example, Liu et al. (2017a) demonstrated freshwater fish faunas homogenization across China resulted from species introductions and extirpations. With the increasing focus on the consequences of fish invasions in China, numerous related studies have been promoted in the past few years, such as testifying significant differences in functional attributes between native and non-native fish species in the Pearl River (Shuai et al., 2018) and evaluating current and future invasion risk of non-native freshwater fish species in China (Liu et al., 2019). Besides, several inventories of native and/or non-native freshwater fish species in China were also compiled (Kang et al., 2014; Xiong et al., 2015; Xing et al., 2016; Liu et al., 2017a; He et al., 2020). However, there is still some controversy about the number of native and non-native freshwater fish species in China's wild habitats, and our understanding of species traits involved in successful fish introductions at a national scale remains limited.

Here, our main objectives were to (a) compile an up-to-date inventory of native and non-native freshwater fish species in China's wild habitats along with the most comprehensive species trait database for these fishes through an extensive review of various sources, (b) explore whether the taxonomic distributions of native and non-native species differed significantly, and (c) test whether native and non-native species differed in their ecological or biological traits. We believe our compiled database could serve as a basis for further works and be useful for fishery scientists and resource managers to develop proactive strategies aiming at preventing more introductions of non-native species with traits related to fish introductions and ensuing fish invasions across China as well as in other countries.

## 2. Methods

### 2.1. Fish list

According to Kolar and Lodge (2001) and Xiong et al. (2015), a species introduced to areas beyond its native range is deemed as non-native species. Hence, we here defined two statuses for non-native freshwater fish species in China's wild habitats based on their definite distributional information provided by various resources: (a) exotic species are species introduced from other country or countries but not present originally in any basins in China and (b) translocated species are species native in one or more basins in China (e.g., common carp

(*Cyprinus carpio*, Cyprinidae) and goldfish (*Carassius auratus*, Cyprinidae)) which had been introduced to other basin or basins in this country where they were not present originally. Moreover, native species are defined as species native in China which were not introduced to any other basins in this country according to related literature. Here, a comprehensive literature review, including about 800 peer-reviewed articles, monographs, various fish databases (e.g., FishBase and The Fish Database of Taiwan), official survey reports, and other sources, was conducted to obtain information on native, exotic, and translocated freshwater fishes in China. Species which spend a part of their life cycles (e.g., spawn and feed) in freshwaters were also included, but species with controversial status (e.g., mirgial carp (*Cirrhinus cirrhosus*, Cyprinidae) and *Acheilognathus tabira*, Cyprinidae) or occasionally occurring in freshwaters were excluded in our study. Most importantly, each species validity has been cross-checked and verified using FishBase (Froese and Pauly, 2019) and Eschmeyer's Catalog of Fishes (Fricke et al., 2020).

### 2.2. Species traits

Based on previous studies (e.g., Vila-Gispert et al., 2005; Ribeiro et al., 2008; Grabowska and Przybylski, 2015) and our expert' opinions, we collected 3 traits (i.e., resilience, trophic level, and vulnerability) that encompass various ecological and life-history strategies, such as growth, longevity, reproduction, diet, and mortality. What's more, morphological traits, determining fish roles in aquatic ecosystems (Toussaint et al., 2016b; Villéger et al., 2017) and evidenced to be related to fish introductions (Ribeiro et al., 2008; Su et al., 2020), were also selected.

One qualitative trait was taken into account: resilience (high, medium, low, and very low). Resilience obtained from FishBase means the minimum population doubling time of species estimated based on the rate ( $\text{year}^{-1}$ ) at which the asymptotic length is approached (i.e., the von Bertalanffy Growth Function (VBGF) parameter  $K$ ), fecundity, age at first maturity ( $t_m$ ), or approximate maximum age of the population ( $t_{max}$ ) (Froese et al., 2000; Froese et al., 2017; Froese and Pauly, 2019).

Twelve quantitative traits were taken into consideration as follows: trophic level, vulnerability, and 10 morphological traits mainly

**Table 1**  
List of 10 morphological traits associated with food acquisition and locomotion (cited from Toussaint et al. (2016b) and Su et al. (2019) without modification).

Morphological traits	Formula	Potential link with fish functions	Reference
Maximum body length	$BL_{max}$	Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling	e.g., Toussaint et al., 2016b; Froese and Pauly, 2019
Body elongation	$\frac{Bl}{Bd}$	Hydrodynamism	Reecht et al., 2013
Eye vertical position	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column	Winemiller, 1991
Relative eye size	$\frac{Ed}{Hd}$	Visual acuity	Boyle and Horn, 2006
Oral gape position	$\frac{Mo}{Bd}$	Feeding position in the water column	Dumay et al., 2004; Lefcheck et al., 2014
Relative maxillary length	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw	Toussaint et al., 2016b
Body lateral shape	$\frac{Hd}{Bd}$	Hydrodynamism and head size	Toussaint et al., 2016b
Pectoral fin vertical position	$\frac{PFI}{Bd}$	Pectoral fin use for swimming	Dumay et al., 2004
Pectoral fin size	$\frac{PFI}{Bl}$	Pectoral fin use for swimming	Fulton et al., 2001
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag	Webb, 1984

associated with food acquisition and locomotion of fishes (Table 1). Trophic level and vulnerability both taken from FishBase describe the rank of a species in a food web estimated based on diet information, food items or an ecosystem model, and intrinsic vulnerability of fishes to fishing estimated based on maximum length,  $t_{\text{m}}$ , VBGF parameter  $K$ , natural mortality rate,  $t_{\text{max}}$ , geographic range, fecundity or spatial behaviour strength, respectively (Froese et al., 2000; Cheung et al., 2005; Froese and Pauly, 2019). For maximum body lengths describing fish size taken from FishBase (Froese and Pauly, 2019), the unreasonable data (e.g., the maximum body length of one species provided by FishBase was found to be much shorter than its maximum total length) were removed or replaced by other appropriate records referring to the related literature. For the remaining morphological traits which are ratios of morphological measurements, 11 morphological measurements for each species (i.e., body length ( $Bl$ ), body depth ( $Bd$ ), head depth ( $Hd$ ), caudal peduncle depth ( $CPd$ ), caudal fin depth ( $CFd$ ), eye diameter ( $Ed$ ), eye position ( $Eh$ ), oral gape position ( $Mo$ ), maxillary jaw length ( $Jl$ ), pectoral fin length ( $PFl$ ), and pectoral fin position ( $PFi$ ), Fig. 1) were measured on at least one scientific side-view drawing or good-quality picture of an entire adult animal collected from FishBase (Froese and Pauly, 2019), The Fish Database of Taiwan (Shao, 2020), Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>; retrieved in December 2020), and related literature using ImageJ software (<https://imagej.nih.gov/ij/>). For species with particular morphologies, several rules detailed in Toussaint et al. (2016b) and Su et al. (2019) have been adopted. For example, we only considered male morphology for species with sexual dimorphism due to the scarcity of female pictures for most species (e.g., Perciform and Cyprinodontiform species).

### 2.3. Statistical analysis

For possible missing traits in this study, an iterative imputation method, 'missForest', was adopted to fill the missing values among these traits (Stekhoven and Bühlmann, 2012; Penone et al., 2014). To test the efficiency of the random forest algorithm used to fill the missing values, the ratio of the number of possible missing values to the total number of actual and possible missing values was calculated and species along with complete values were extracted accordingly. Furthermore, actual values of the extracted values were randomly set as missing values according to the aforementioned ratio. A 'missForest' procedure was carried out to replace these missing values with simulated values and then these simulated values were compared to the actual values based on Spearman and/or Pearson correlation test.

For the qualitative variables (i.e., taxonomic order, family, and resilience),  $G$ -tests of independence ( $G$ -statistic) were applied to assess the association between the three species statuses and those aforementioned qualitative variables.

For the quantitative traits, a normalized principal component analysis (PCA) was applied (Abdi and Williams, 2010). The differences in PCA scores for native, exotic, and translocated species along the first two principal component (PC) axes were tested using one-way Analysis of Variance (ANOVA) with Tukey's *post hoc* tests. A Permutational Multivariate Analysis of Variance (PERMANOVA; 999 permutations) was also conducted, followed by multiple comparisons (Tukey's honestly significant difference test) to investigate the sources of variation in the quantitative traits among species status. When differences were detected, a Similarity Percentage Analysis (SIMPER) was applied to determine the individual contribution of each trait to the dissimilarity among species status after scaling the values for these quantitative traits by Min-Max normalization, with normalized values ranging from 0 to 1 (Clarke, 1993; Patro and Sahu, 2015). Finally, the nonparametric Mann-Whitney-Wilcoxon rank sum test was also chosen to test for each trait difference among species status (Wilcoxon, 1945; Mann and Whitney, 1947).

Likewise, the aforementioned analysis methods were also conducted for the subset of species without missing data (see Appendix B).

All statistical analyses were performed with R software version 3.5.2 (R Core Team, 2018) using the packages RVAideMemoire, missForest, factoextra, FactoMineR, pspearman, multcomp, and vegan.

## 3. Results

### 3.1. Taxonomic distributions

A total of 1,797 freshwater fish species belonging to 415 genera, 76 families, and 24 orders were recorded in China. The largest order was Cypriniformes (69.84%), followed by Perciformes (11.69%) and Siluriformes (10.91%). Moreover, the Cyprinidae (42.52%), Nemachelilidae (16.25%), and Gobiidae (5.73%) were the three most dominant families. Of the 1,797 fish species, 1,597 species, 61 families and 20 orders were native in China, 84 species, 23 families and 11 orders were exotic in at least one basin in China, and 116 species, 27 families and 12 orders were translocated in at least one basin in China, respectively. Among these species, taxonomic order and family frequencies significantly differed among species status (order:  $G = 277.74$ , d.f. = 46,  $P < 0.001$ ; family:  $G = 650.99$ , d.f. = 150,  $P < 0.001$ ). At the order level, the dominant orders of native, exotic, and translocated species were Cypriniformes (73.51%), Siluriformes (11.08%) and Perciformes (9.77%), Perciformes (42.86%), Siluriformes (14.29%) and Cypriniformes (10.71%), and Cypriniformes (62.07%), Perciformes (15.52%), Siluriformes (6.03%) and Osmeriformes (6.03%), respectively (Fig. 2). In addition, 3 and 1 of the 24 orders were only represented by exotic species (i.e., 3 lepisosteiform species, 4 characiform species, and 6 cyprinodontiform species) and translocated species (i.e., 1 gadiform species), respectively. At the family level, the dominant families of native, exotic, and translocated species

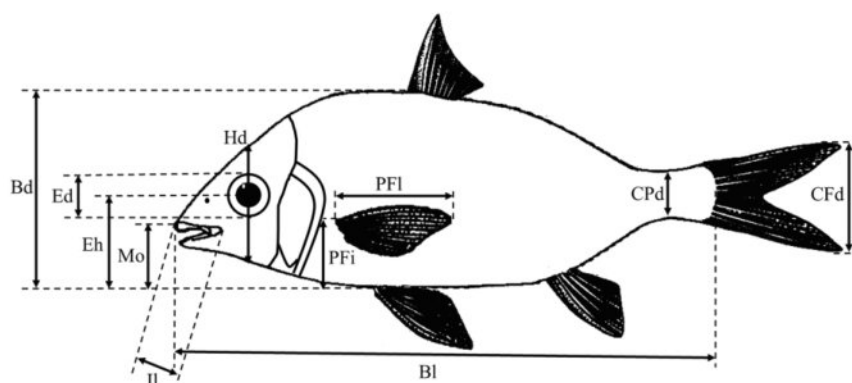
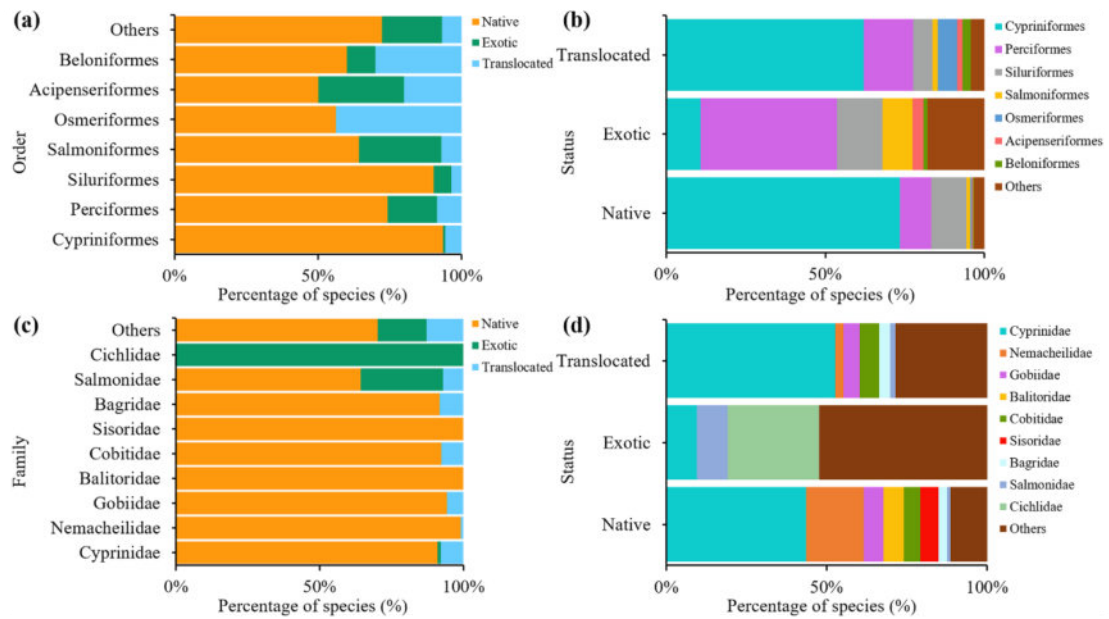


Fig. 1. The morphological measurements measured on each fish species.  $Bl$  body length,  $Bd$  maximum body depth,  $Hd$  head depth at the vertical of eye,  $CPd$  minimum depth of the caudal peduncle,  $CFd$  maximum depth of the caudal fin,  $Ed$  vertical diameter of the eye,  $Eh$  vertical distance between the centre of the eye to the bottom of the body,  $Mo$  vertical distance from the top of the mouth to the bottom of the body,  $Jl$  length from snout to the corner of the mouth,  $PFl$  length of the longest ray of the pectoral fin,  $PFi$  vertical distance between the upper insertion of the pectoral fin to the bottom of the body.



**Fig. 2.** (a) Percentages of the three species statuses in orders (only those with at least 10 species); (b) percentages of species in orders of each species status; (c) percentages of the three species statuses in families (only those with at least 20 species); (d) percentages of species in families of each species status.

were Cyprinidae (43.52%), Nemacheilidae (18.10%) and Balitoridae (6.32%), Cichlidae (28.57%), Cyprinidae (9.52%) and Salmonidae (9.52%), and Cyprinidae (52.59%), Cobitidae (6.03%) and Gobiidae (5.17%), respectively (Fig. 2). Besides, 10 and 4 of the 76 families were only represented by exotic species (i.e., 1 prochilodontid species, 1 osteoglossid species, 2 ambassid species, 3 serrasalmid species, 3 leptoosteid species, 3 ictalurid species, 5 loricariid species, 6 poeciliid species, 7 centrarchid species, and 24 cichlid species) and translocated species (i.e., 1 lateolabracid species, 1 latid species, 1 lotid species, and 1 plecoglossid species), respectively (see Appendix A: Table A.1).

3.2. Species traits

In total, 21,456 (91.85%) traits for 1,797 freshwater fish species including resilience, trophic level, vulnerability, and morphological traits were obtained in this study (Table 2). For the efficiency of the random forest algorithm used to fill the missing values, the Spearman's rho for the qualitative trait, resilience, was 0.88 and Pearson's r for the 12 quantitative traits ranged from 0.52 to 0.91 (Table 2), with an average of 0.75, indicating an overall good performance of the algorithm.

3.3. Analyses for the qualitative trait

Resilience frequencies significantly differed among the three species statuses ( $G = 112.44$ , d.f. = 6,  $P < 0.001$ ). The majority (59.11%) of native species were found to have high resilience in contrast to 26.19% of exotic species and 21.55% of translocated species (Fig. 3). In addition, there were 7.58% of native species with low or very low resilience.

3.4. Analyses for the quantitative traits

The PERMANOVA test (see Appendix A: Table A.2) revealed significant traits differentiation among the three species statuses (PERMANOVA,  $F = 80.17$ ,  $P = 0.001$ ). Further multiple-comparisons (Tukey's HSD tests) showed that native species were significantly different from exotic species ( $P < 0.001$ ) and translocated species ( $P < 0.001$ ) for the

**Table 2**  
Summary of data availability and efficiency of the random forest algorithm used to fill the missing values for the 13 traits (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).

Species trait (Trait code)	Native (%)	Exotic (%)	Translocated (%)	Algorithm efficiency
Resilience (Res.)	86.91	95.24	100	0.88***
Trophic level (Tro. Level)	94.24	100	100	0.52***
Vulnerability (Vul.)	94.30	100	100	0.91***
Maximum body length (Max. Body Length)	93.55	98.81	100	0.80***
Relative eye size (Rel. Eye Size)	93.49	100	100	0.60***
Oral gape position (Oral Gape Pos.)	92.36	100	100	0.82***
Relative maxillary length (Rel. Maxil. Length)	73.07	97.62	92.24	0.72***
Eye vertical position (Eye Vert. Pos.)	91.67	100	100	0.82***
Body elongation (Body Elong.)	93.36	100	100	0.89***
Body lateral shape (Body Lat. Shape)	91.73	100	100	0.78***
Pectoral fin vertical position (Pec. Fin Vert. Pos.)	92.11	100	99.14	0.80***
Pectoral fin size (Pec. Fin Size)	92.36	98.81	100	0.62***
Caudal peduncle throating (Cau. Ped. Throt.)	92.67	100	100	0.68***

12 quantitative traits, while no significant differences between exotic and translocated species were detected ( $P = 0.93$ ). Consistent with the results from the PERMANOVA test, PCA scores of native species were significantly different from exotic and translocated species on both PC1 and PC2 axis, while no significant differences were observed between exotic and translocated species (Fig. 4). In addition, the first two PC axes

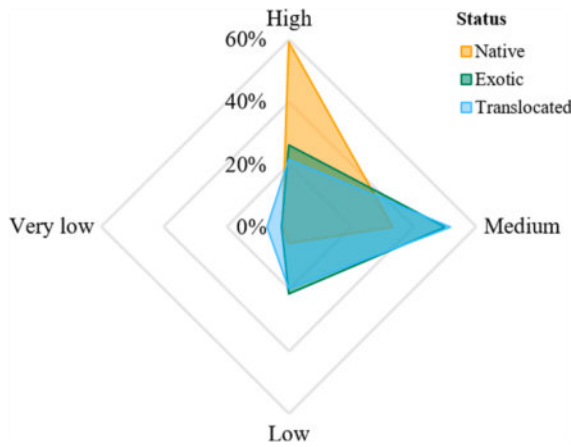


Fig. 3. Percentages of each resilience capacity (high, medium, low, and very low) within the different species statuses.

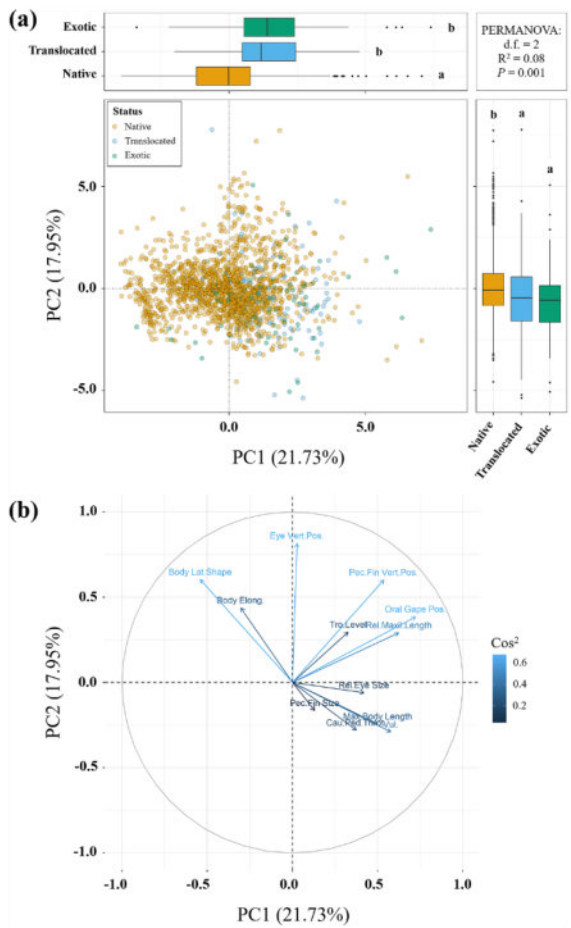


Fig. 4. Principal component analysis of the 12 quantitative traits for native, exotic, and translocated species in China: (a) species scores on the first two PC axes (different letters indicated significant differences); (b) correlation circle with squared cosine of the traits. Trait codes as in Table 2.

explained 39.68% of the total variance among the China's fish traits (see Appendix A: Table A.3). The PC1 axis mainly integrated oral gape position, relative maxillary length, and vulnerability (squared cosine of each trait  $\geq 0.3$ ). Species with higher positive values on PC1 were typically characterized as ferocious carnivorous species, e.g., some lepisosteid and silurid species while those with lower negative values were characterized as phytophagous or omnivorous species, e.g., some nemacheilid and balitorid species. The PC2 axis mainly integrated eye vertical position, body lateral shape, and pectoral fin vertical position (squared cosine of each trait  $\geq 0.3$ ). Species with higher positive values on PC2 were typically characterized as species with poor swimming ability inhabiting slow-flowing habitats, e.g., some gobiid species while those with lower negative values on PC2 were characterized as species with sustained or robust swimming ability inhabiting demersal habitats, e.g., some migratory species, acipenserid species.

The results of the Mann-Whitney-Wilcoxon rank sum tests of the 12 quantitative traits exhibited that native and exotic species as well as native and translocated species showed significant differences for 9 traits except relative eye size, eye vertical position, and relative maxillary length and for 11 traits except pectoral fin size, respectively (Table 3). The results of the SIMPER analyses demonstrated that the 12 quantitative traits differed in their contribution to the dissimilarity of native versus exotic species and native versus translocated species, respectively (Table 3). For these two groups, the cumulative contribution of the most shared discriminating species traits, vulnerability, trophic level, body lateral shape, and pectoral fin vertical position accounted for approximately 50% to the overall dissimilarities.

#### 4. Discussion

In this study, 1,797 freshwater fish species in China were recorded accounting for over 10% of the total number of freshwater fish species across the world (Froese and Pauly, 2019), which is considerably greater than the numbers in any previous studies (e.g., 1,323 species in Xing et al., 2016 and 1,651 species in He et al., 2020) even though we adopted the same definition of freshwater fishes. Both the most comprehensive literature for collecting species and incorporating new species is speculated to be the key factors contributing to the highest species richness in the present study.

The increase of human activities, e.g., global trades and fishery activities, are generally accompanied by fish introductions (Xiong et al., 2015; Su et al., 2021). In China, the majority of exotic species were intentionally introduced for the purposes of trading, aquaculture, aquarium, and biocontrol (Xiong et al., 2015; Froese and Pauly, 2019). In contrast, except some translocated species with commercial or ecological importance intentionally introduced for human use, a significant proportion of them were inadvertently introduced. For instance, the introduction of *Rhinogobius cliffordpopei*, Gobiidae and *Rhinogobius giurinus*, Gobiidae, two small-bodied goby species with highly abundant populations in many lakes of China outside their natural ranges competing with native species for food resources (e.g., Guo et al., 2013), resulted from releasing other commercial fishes mingled with these two species (Du and Li, 2001). To date, a total of 200 non-native freshwater fish species (84 exotic species and 116 translocated species) were introduced and documented in wild habitats, which was the highest record of non-native fish species compared to previous studies and can represent the current situation of fish introductions in China's wilds to some extent (Xiong et al., 2015; Liu et al., 2017a). Our results suggested that the number of native, exotic, and translocated species by taxonomic order and family depended on their status. Exotic (23 families and 11 orders) and translocated (27 families and 12 orders) species belonged to relatively narrow spectrums of orders and families compared to native species (61 families and 20 orders), whereas translocated species belonged to a wider spectrum of orders and families than exotic species. Notably, like approximately 80% and 40% of non-native species in the other countries across the world just belonging to five orders

**Table 3**

The results of each quantitative trait difference between native and exotic species and native and translocated species tested by the Mann-Whitney-Wilcoxon rank sum tests and SIMPER summary of each trait contributing to the Bray-Curtis dissimilarity between these two groups (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).

Trait	Native (average)	Exotic (average)	Translocated (average)	Native vs Exotic (% contribution)	Native vs Translocated (% contribution)
Vulnerability	28.43	42.39***	42.66***	14.29	15.75
Trophic level	3.01	3.13*	3.17***	14.07	12.35
Body lateral shape	0.58	0.52***	0.50***	10.20	11.43
Pectoral fin vertical position	0.27	0.31***	0.31**	10.01	10.57
Oral gape position	0.33	0.43***	0.44***	8.85	8.72
Relative eye size	0.32	0.33	0.39***	8.11	9.88
Pectoral fin size	0.17	0.20***	0.16	7.93	6.01
Caudal peduncle throating	2.22	2.63***	2.52***	6.74	6.79
Body elongation	5.15	3.68***	4.76***	6.74	6.27
Eye vertical position	0.56	0.54	0.54*	5.34	6.03
Relative maxillary length	0.41	0.49	0.50***	4.23	3.41
Maximum body length	18.28	57.29***	43.87***	3.49	2.79

(Cypriniformes, Perciformes, Cyprinodontiformes, Siluriformes, and Salmoniformes) and three families (Cyprinidae, Cichlidae, and Salmonidae), respectively (Tedesco et al., 2017), Perciformes, Siluriformes, and Cypriniformes and Cichlidae, Cyprinidae, and Salmonidae were also dominant for China's non-native species. It seems that non-native species have tendencies to come from these orders or families. Besides, as pointed out by Moyle and Marchetti (2006), local familiarity with a taxon can contribute to spread of non-native species. In this study, even though 1 of the 24 orders and 4 of the 76 families were only represented by translocated species, all of them were historically already present in the ecosystem as native species, which may favour their spread. As for exotic species, 8 of the 20 native orders and 12 of the 61 native families contained both native and exotic species, conducive to their spread, but we found that there were 3 of the 24 orders and 10 of the 76 families only represented by exotic species. Hence, except for the most dominant taxa from exotic and translocated species, it's imperative to monitor the new record taxa in China as invaders were more likely to come from taxa that hadn't been already present in the native areas (Lockwood et al., 2001).

Generally, non-native species of interest for humans with various morphological traits mainly resulted from human selection or assistance (Su et al., 2020). Exotic species in China mostly selected by humans tended to have higher pectoral fin vertical position (swimming), but less lateral body shape (hydrodynamism) than native species, which indicated that considerable differences existed in their locomotion and habitat types. Intriguingly, although the purposes or ways of fish introductions between the majority of exotic and translocated species were distinct, we found that translocated species also possessed higher pectoral fin vertical position and less lateral body shape than native species, but were not considerably different from exotic species according to their morphology. Hence, not only purposes or ways of introduction dependent, the environmental filtering or biotic interactions should also be the probable explanations for the phenomenon (Kraft et al., 2015). Notably, corroborating the findings from many previous studies (e.g., Vila-Gispert et al., 2005; Toussaint et al., 2018; Su et al., 2020), exotic and translocated species in China were also found to have larger body size and less elongated body than native species but the fact was that maximum body length and body elongation only drove very few dissimilarities among the three species statuses (i.e., native vs exotic and native vs translocated). Namely, there's a more obvious trend for non-native species with higher pectoral fin vertical position and less lateral body shape to spread within China.

Trophic level was also a key trait distinguishing native and non-native species. Non-native species with different trophic levels, once introduced, might prey on or compete with native species for food resources, thereby inducing trophic niche shift in recipient areas (Britton et al., 2010; Correa et al., 2012). For example, some native species in Bosten Lake, China had been extinct due to the heavy predation effects of a translocated species, european perch (*Perca fluviatilis*, Percidae) (Xie

and Chen, 1999). Besides, the composition of the fish fauna of Dianchi Lake, China obviously changed partly from feeding competition of massive populations of small-bodied non-native species, e.g., stone moroko (*Pseudorasbora parva*, Cyprinidae) and *Acheilognathus macropterus*, Cyprinidae (He and Liu, 1985). Beyond that, overfishing is another critical challenge to native species, as well as non-native species because almost all main water bodies in China were under heavy capture pressure (Zhao et al., 2015; Chen et al., 2020). Surprisingly, compared with exotic and translocated species, native species showed lower vulnerability (i.e., higher resilience), reflecting tendencies to have relatively smaller body size, lower age at first maturity, faster growth rate, higher natural mortality rate and fecundity, shorter potential longevity, or lower spatial behaviour strength (Froese et al., 2000; Cheung et al., 2005). Nonetheless, species with low vulnerability and/or high resilience would still face extinction risk considering threats from non-native species. As an example, the population of *Cyprinus chilia*, Cyprinidae, a native species with low vulnerability and high resilience used in the capture fishery, was on a declining trend in Dianchi Lake, China owing to their eggs fed on by non-native fish species during the spawning season (He and Liu, 1985). Additionally, it should also be noted that the minimum population doubling time for 7.58% of native species with low or very low resilience in China is as far as 4.5 years or more (Froese and Pauly, 2019), which may place them at the risk of extinction if they are confronted with long-term threats, such as the loss of spawning grounds and negative biotic interactions with non-native species (He and Liu, 1985; Du and Li, 2001; Guo et al., 2013; IUCN, 2021). Indeed, not each non-native species is likely to lead to adverse ecological effects, but could threaten native biodiversity if becoming invasive (Gozlan, 2008; Britton et al., 2011b). Thus, more seriously for native species is that some low vulnerable and/or high resilient exotic and translocated species with minor or no commercial importance exposed to less fishing pressure were found with high abundance in many lakes outside their natural ranges, e.g., *R. giurinus* and *Toxabramis swinhonis*, Cyprinidae (e.g., He and Liu, 1985; Ye et al., 2015), which seemed to confer competitive advantages to them in China's water bodies.

## 5. Conclusions

In conclusion, based on the largest number of freshwater fish species reported in China, this study evidenced that China's native species were significantly different from exotic and translocated species in their life-history traits and ecological species features which may provide abilities for non-native species to spread and establish populations or even replace native species in recipient areas (Liu et al., 2017b; Shuai et al., 2018). Since both exotic and translocated species differed from native species in their traits, further works are clearly needed to address how fish communities are affected by both introductions and translocations. Disentangling the effects of exotic and translocated species on



community diversity (e.g., functional or phylogenetic) could be helpful to better understand how recipient communities have changed.

#### CRediT authorship contribution statement

**Tao Xiang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Visualization, Writing - original draft, Writing - review & editing. **Xianghong Dong:** Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing - review & editing. **Gaël Grenouillet:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, 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.

#### Acknowledgements

This study was funded by the China Scholarship Council (CSC). The EDB laboratory was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). We are very grateful to Sébastien BROSSE for providing us with plenty of good-quality pictures and scientific drawings of freshwater fish species, good morphological data, and valuable suggestions on morphological measurements.

#### Data availability statement

The data (e.g., the fish list and morphological data) that support the findings of this study are available from the corresponding author upon reasonable request.

#### Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108218>.

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## Appendix A

**Table A.1.** Number of native, exotic, and translocated freshwater fish species in China by taxonomic categories.

Order	Family	Genus	Native species	Exotic species	Translocated species	Order	Family	Genus	Native species	Exotic species	Translocated species
Acipenseriformes	Acipenseridae	2	4	2	2	Perciformes	Ambassidae	1	0	2	0
	Polyodontidae	2	1	1	0		Anabantidae	1	1	0	0
Anguilliformes	Anguillidae	1	3	1	1		Badidae	1	2	0	0
	Muraenidae	1	1	0	0		Blenniidae	1	1	0	0
	Ophichthidae	1	2	0	0		Callionymidae	1	1	0	0
Beloniformes	Adrianichthyidae	1	3	0	2		Centrarchidae	3	0	7	0
	Belonidae	1	1	0	0		Channidae	1	10	1	2
	Hemiramphidae	1	1	0	1		Cichlidae	14	0	24	0
	Zenarchopteridae	2	1	1	0		Eleotridae	6	10	1	0
Characiformes	Prochilodontidae	1	0	1	0		Gobiidae	25	97	0	6
	Serrasalminidae	3	0	3	0		Kuhliidae	1	2	0	0
Clupeiformes	Clupeidae	1	2	0	0		Lateolabracidae	1	0	0	1
	Engraulidae	2	3	0	0		Latidae	1	0	0	1
Cypriniformes	Acheilognathidae	2	2	0	0		Odontobutidae	5	11	0	2
	Balitoridae	16	101	0	0	Osphronemidae	2	1	0	3	
	Botiidae	1	2	0	0	Percichthyidae	2	13	0	1	
	Catostomidae	2	0	1	1	Percidae	3	1	1	2	
	Cobitidae	16	83	0	7	Polynemidae	1	1	0	0	
	Cyprinidae	166	695	8	61	Pomacentridae	1	1	0	0	
	Gyrinocheilidae	1	1	0	0	Rhyacichthyidae	1	1	0	0	

	Nemacheilidae	25	289	0	3		Scatophagidae	1	1	0	0
	Psilorhynchidae	1	1	0	0		Terapontidae	2	2	0	0
Cyprinodontiformes	Poeciliidae	3	0	6	0	Petromyzontiformes	Petromyzontidae	2	4	0	0
Esociformes	Esocidae	1	1	0	1	Pleuronectiformes	Cynoglossidae	1	2	0	0
Gadiformes	Lotidae	1	0	0	1	Scorpaeniformes	Cottidae	5	8	0	0
Gasterosteiformes	Gasterosteidae	2	4	0	0	Siluriformes	Akysidae	2	2	0	0
Lepisosteiformes	Lepisosteidae	2	0	3	0		Amblycipitidae	3	13	0	0
Mugiliformes	Mugilidae	1	2	0	0		Bagridae	8	44	0	4
Myliobatiformes	Dasyatidae	1	1	0	0		Clariidae	1	1	2	1
Osmeriformes	Osmeridae	2	1	0	2		Cranoglanididae	1	3	0	0
	Plecoglossidae	1	0	0	1		Heteropneustidae	1	1	0	0
	Salangidae	5	8	0	4		Ictaluridae	2	0	3	0
Osteoglossiformes	Notopteridae	2	1	0	1		Loricariidae	2	0	5	0
	Osteoglossidae	1	0	1	0		Pangasiidae	3	5	1	0
Synbranchiformes	Mastacembelidae	3	7	0	0		Schilbeidae	1	4	0	0
	Synbranchidae	1	1	0	1		Siluridae	6	15	1	2
Syngnathiformes	Syngnathidae	3	5	0	0		Sisoridae	14	89	0	0
Salmoniformes	Salmonidae	8	18	8	2	Tetraodontiformes	Tetraodontidae	2	5	0	0
Total 24	76	415	1,597	84	116						

**Table A.2.** Results of the PERMANOVA test on the 12 quantitative traits among the three species statuses.

Source	d.f.	SS	MS	<i>F</i>	<i>R</i> <sup>2</sup>	<i>P</i>
Status	2	8.65	4.32	80.17	0.08	0.001
Residual	1,794	96.76	0.05		0.92	
Total	1,796	105.41			1	

**Table A.3.** Results of the Principal Components Analysis on the 12 quantitative traits.

(a) Eigenvalues and percentages of variance explained by the first two PC axes. (b)

Squared cosine of each quantitative trait to the first two PC axes.

(a)

	PC1	PC2
Eigenvalues	2.61	2.15
Proportion of Variance	21.73	17.95
Cumulative Proportion	21.73	39.68

(b)

	PC1	PC2
Trophic level	0.11	0.09
Vulnerability	0.33	0.08
Relative eye size	0.18	< 0.01
Oral gape position	0.52	0.15
Relative maxillary length	0.39	0.08
Eye vertical position	< 0.01	0.67
Body elongation	0.09	0.19
Body lateral shape	0.29	0.36
Pectoral fin vertical position	0.29	0.36
Pectoral fin size	0.02	0.03
Caudal peduncle throttling	0.14	0.08
Maximum body length	0.25	0.06

## Appendix B

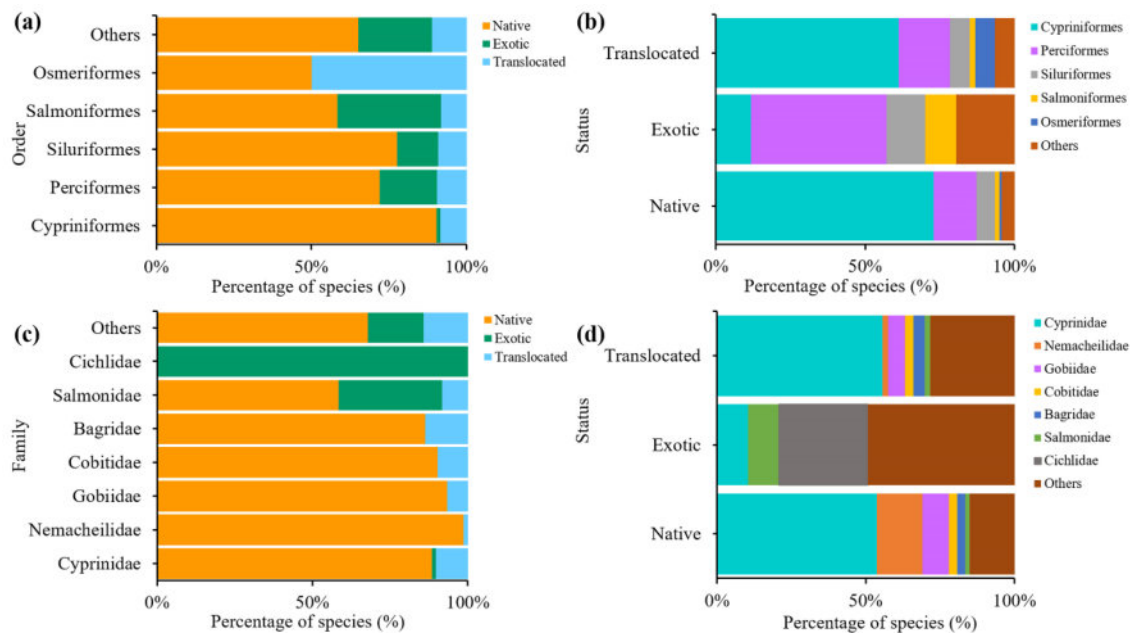
### The analysis results for the subset of species without missing data

#### Results

##### *Taxonomic distributions*

A total of 1,132 freshwater fish species without missing species traits belonging to 326 genera, 62 families, and 21 orders were recorded in this study. The largest order was Cypriniformes (67.67%), followed by Perciformes (16.70%) and Siluriformes (6.71%). Moreover, the Cyprinidae (50.97%), Nemacheilidae (12.99%), and Gobiidae (7.95%) were the three most dominant families. Of the 1,132 fish species, 949 species, 45 families and 17 orders were native in China, 77 species, 20 families and 9 orders were exotic in at least one basin in China, and 106 species, 25 families and 10 orders were translocated in at least one basin in China, respectively. Among these species, taxonomic order and family frequencies significantly differed among species status (order:  $G = 224.12$ , d.f. = 40,  $P < 0.001$ ; family:  $G = 519.70$ , d.f. = 122,  $P < 0.001$ ). At the order level, the dominant orders of native, exotic, and translocated species were Cypriniformes (72.92%), Perciformes (14.33%) and Siluriformes (6.22%) and, Perciformes (45.45%), Siluriformes (12.99%) and Cypriniformes (11.69%), and Cypriniformes (61.32%), Perciformes (16.98%), Siluriformes (6.60%) and Osmeriformes (6.60%), respectively (Fig. B.1). In addition, 3 and 1 of the 21 orders were only represented by exotic species (i.e., 3 lepisosteiform species, 4 characiform species, and 6 cyprinodontiform species) and translocated species (i.e., 1 gadiform species), respectively. At the family level, the dominant families of native, exotic, and

translocated species were Cyprinidae (53.74%), Nemacheilidae (15.28%) and Gobiidae (8.85%), Cichlidae (29.87%), Cyprinidae (10.39%) and Salmonidae (10.39%), and Cyprinidae (55.66%), Gobiidae (5.66%), Bagridae (3.77%) and Salangidae (3.77%), respectively (Fig. B.1). Besides, 10 and 4 of the 62 families were only represented by exotic species (i.e., 1 prochilodontid species, 1 pangasiid species, 2 ambassid species, 3 serrasalmid species, 3 lepisosteid species, 3 ictalurid species, 3 loricariid species, 6 poeciliid species, 7 centrarchid species, and 23 cichlid species) and translocated species (i.e., 1 lateolabracid species, 1 latid species, 1 lotid species, and 1 plecoglossid species), respectively.



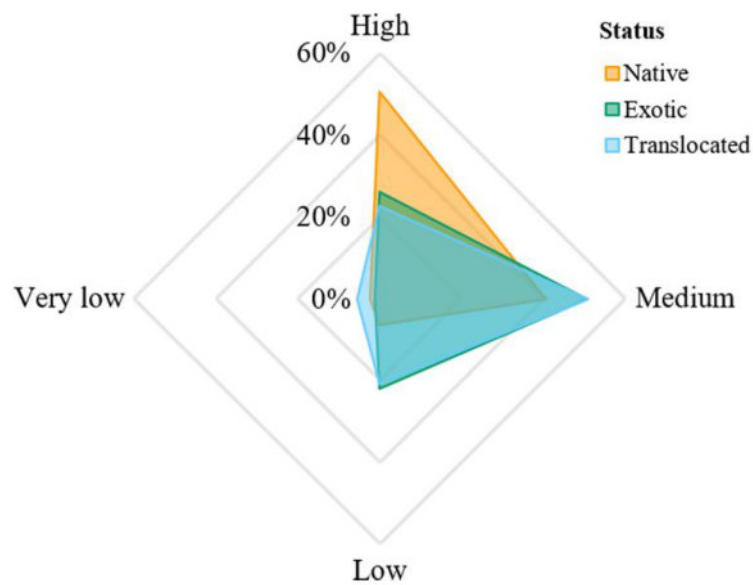
**Fig. B.1.** (a) Percentages of the three species statuses in orders (only those with at least 10 species); (b) percentages of species in orders of each species status; (c) percentages of the three species statuses in families (only those with at least 20 species); (d) percentages of species in families of each species status.

### *Species traits*

In total, 14,716 traits for 1,132 freshwater fish species including resilience, trophic level, vulnerability, and morphological traits were obtained in this study.

### *Analyses for the qualitative trait*

Resilience frequencies significantly differed among the three species statuses ( $G = 65.14$ , d.f. = 6,  $P < 0.001$ ). The majority (50.68%) of native species were found to have high resilience in contrast to 25.97% of exotic species and 22.64% of translocated species (Fig. B.2). In addition, there were 8.75% of native species with low or very low resilience.



**Fig. B.2.** Percentages of each resilience capacity (high, medium, low, and very low) within the different species statuses.



### *Analyses for the quantitative traits*

The PERMANOVA test (Table B.1) revealed significant traits differentiation among the three species statuses (PERMANOVA,  $F = 49.70$ ,  $P = 0.001$ ). Further multiple-comparisons (Tukey's HSD tests) showed that native species were significantly different from exotic species ( $P = 0.002$ ) and translocated species ( $P < 0.001$ ) for the 12 quantitative traits, while no significant differences between exotic and translocated species were detected ( $P = 0.66$ ). Consistent with the results from the PERMANOVA test, PCA scores of native species were significantly different from exotic and translocated species on both PC1 and PC2 axis, while no significant differences were observed between exotic and translocated species (Fig. B.3). In addition, the first two PC axes explained 40.17% of the total variance among the China's fish traits (Table B.2). The PC1 axis mainly integrated eye vertical position, pectoral fin vertical position, and body lateral shape (squared cosine of each trait  $\geq 0.3$ ). The PC2 axis mainly integrated maximum body length, relative maxillary length, vulnerability, and pectoral fin size (squared cosine of each trait  $\geq 0.3$ ).

**Table B.1.** Results of the PERMANOVA test on the 12 quantitative traits among the three species statuses.

<b>Source</b>	<b>d.f.</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>R<sup>2</sup></b>	<b>P</b>
Status	2	5.39	2.69	49.70	0.08	0.001
Residual	1,129	61.21	0.05		0.92	
Total	1,131	66.60			1	

**Table B.2.** Results of the Principal Components Analysis on the 12 quantitative traits.

(a) Eigenvalues and percentages of variance explained by the first two PC axes. (b)

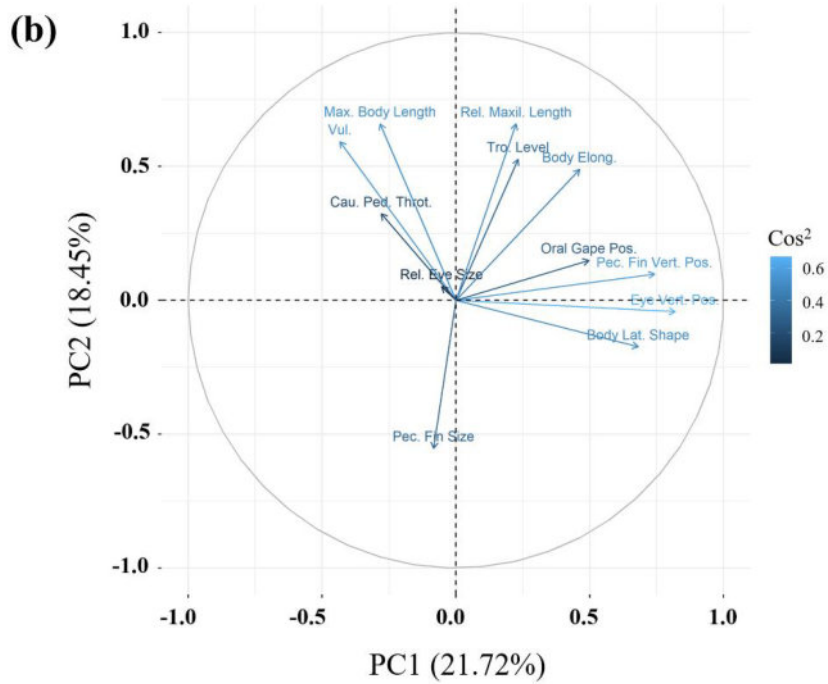
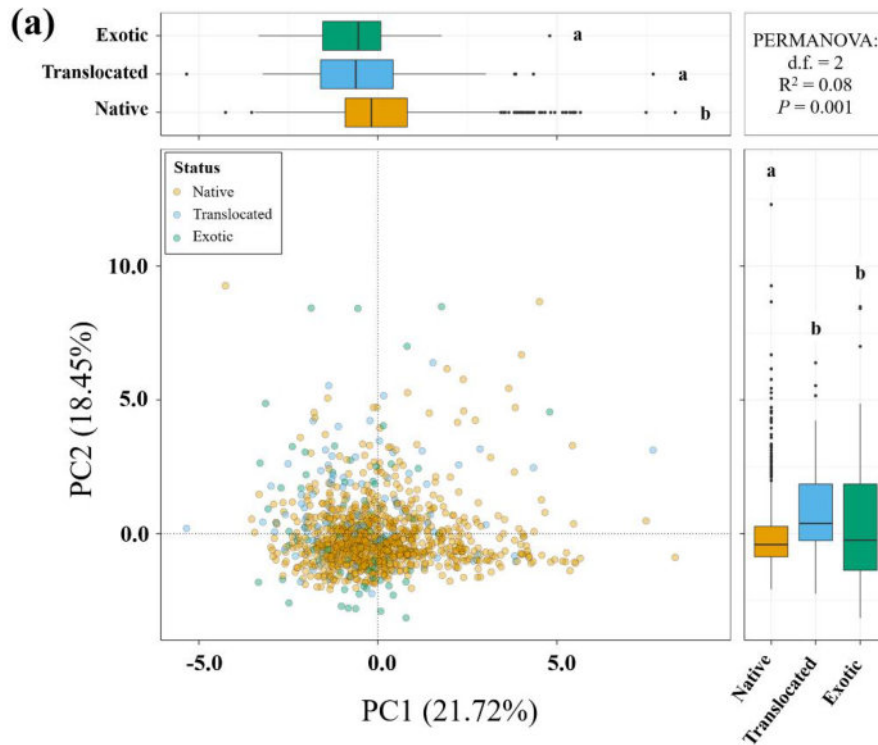
Squared cosine of each quantitative trait to the first two PC axes.

(a)

	PC1	PC2
Eigenvalues	2.61	2.21
Proportion of Variance	21.72	18.45
Cumulative Proportion	21.72	40.17

(b)

	PC1	PC2
Trophic level	0.05	0.28
Vulnerability	0.19	0.35
Relative eye size	< 0.01	< 0.01
Oral gape position	0.25	0.02
Relative maxillary length	0.05	0.43
Eye vertical position	0.67	< 0.01
Body elongation	0.21	0.24
Body lateral shape	0.46	0.03
Pectoral fin vertical position	0.55	0.01
Pectoral fin size	0.01	0.31
Caudal peduncle throttling	0.08	0.10
Maximum body length	0.08	0.43



**Fig. B.3.** Principal component analysis of the 12 quantitative traits for native, exotic, and translocated species in China: (a) species scores on the first two PC axes (different letters indicated significant differences); (b) correlation circle with squared cosine of the traits.

The results of the Mann-Whitney-Wilcoxon rank sum tests of the 12 quantitative traits exhibited that native and exotic species as well as native and translocated species showed significant differences for 10 traits except relative eye size and eye vertical position and for 9 traits except pectoral fin vertical position, pectoral fin size, and relative maxillary length, respectively (Table B.3). The results of the SIMPER analyses demonstrated that the 12 quantitative traits differed in their contribution to the dissimilarity of native versus exotic species and native versus translocated species, respectively (Table B.3). For these two groups, the cumulative contribution of the most shared discriminating species traits, vulnerability, trophic level, and body lateral shape accounted for approximately 40% to the overall dissimilarities.

**Table B.3.** The results of each quantitative trait difference between native and exotic species and native and translocated species tested by the Mann-Whitney-Wilcoxon rank sum tests and SIMPER summary of each trait contributing to the Bray-Curtis dissimilarity between these two groups (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).

Trait	Native (average)	Exotic (average)	Translocated (average)	Native vs Exotic (% contribution)	Native vs Translocated (% contribution)
Vulnerability	30.57	42.38***	42.08***	14.05	15.55
Trophic level	3.04	3.16*	3.17**	14.73	13.26
Body lateral shape	0.56	0.51***	0.49***	10.25	11.35
Relative eye size	0.35	0.34	0.40***	9.21	10.72
Pectoral fin vertical position	0.32	0.33***	0.33	8.82	10.08
Pectoral fin size	0.17	0.20**	0.17	10.04	7.29
Oral gape position	0.40	0.44**	0.46***	6.96	6.91
Eye vertical position	0.56	0.54	0.54**	5.78	6.86

Caudal peduncle throttling	2.34	2.60***	2.54**	6.31	6.25
Body elongation	4.76	3.49***	4.51**	6.14	5.59
Relative maxillary length	0.46	0.49*	0.51	4.36	3.47
Maximum body length	20.18	55.02***	41.76***	3.35	2.67

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**Chapter 4:** Anthropogenic activities and environmental filtering have reshaped freshwater fish biodiversity patterns in China over the past 120 years

*Journal of Environmental Management*, **344**, 118374

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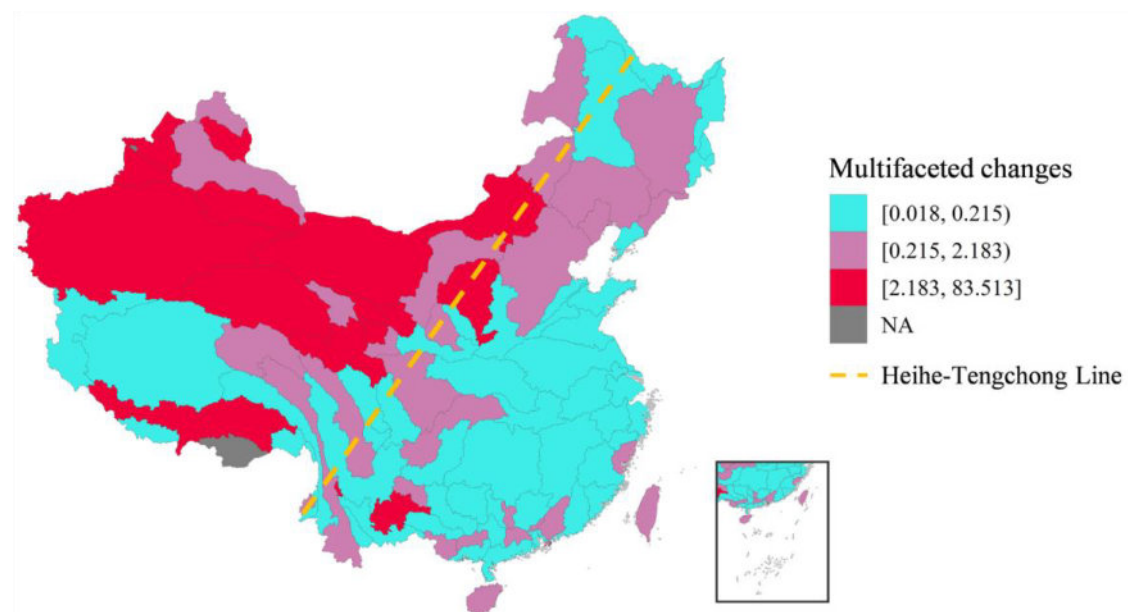
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## Research article

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

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## ARTICLE INFO

Handling Editor: Jason Michael Evans

## Keywords:

Fish extinctions  
Fish introductions  
Global changes  
Biotic homogenization  
Multifaceted changes in fish biodiversity

## 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

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<https://doi.org/10.1016/j.jenvman.2023.118374>

Received 29 March 2023; Received in revised form 6 June 2023; Accepted 9 June 2023

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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 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).

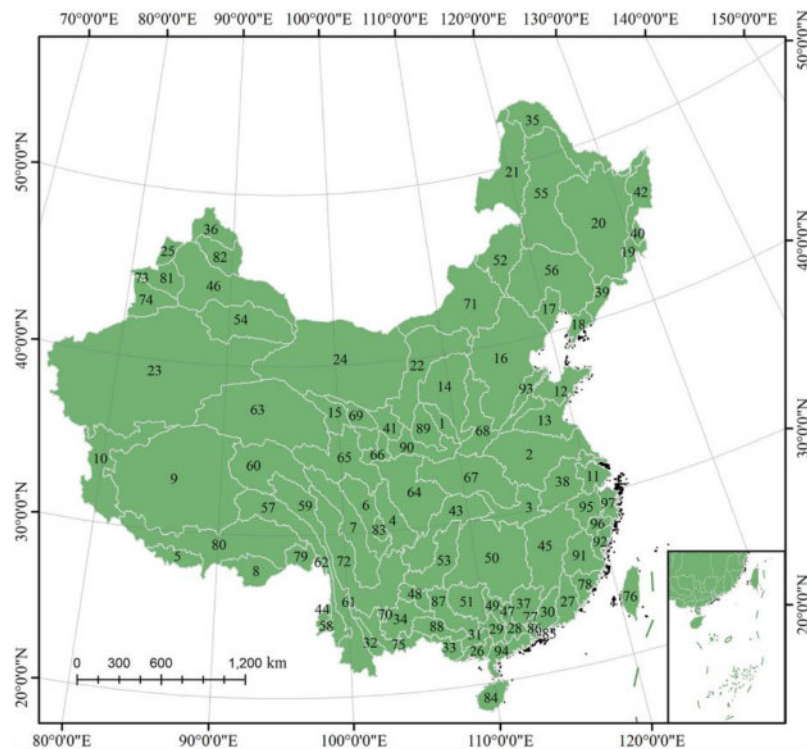
### 2.2. Phylogeny

'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 ‘Rphylopar’ 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

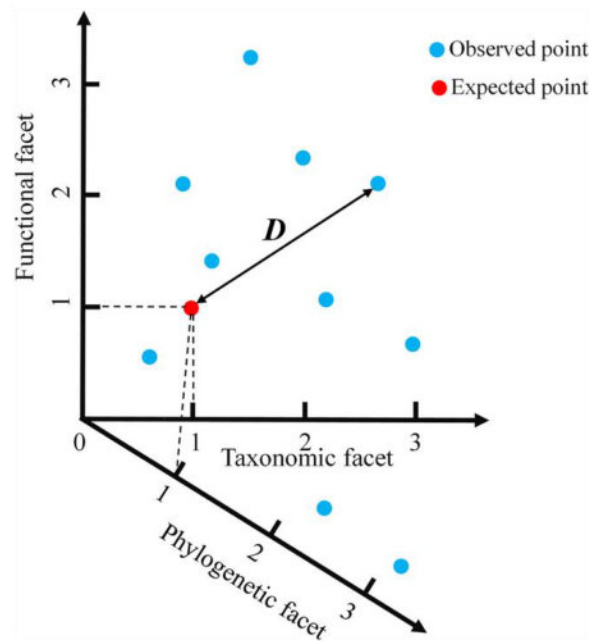


Fig. 2. Sketch of the three(six)-dimensional Cartesian coordinate system.  $D$  referred to the Euclidean distance between an observed point and the expected point.

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, Rphylopar, 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

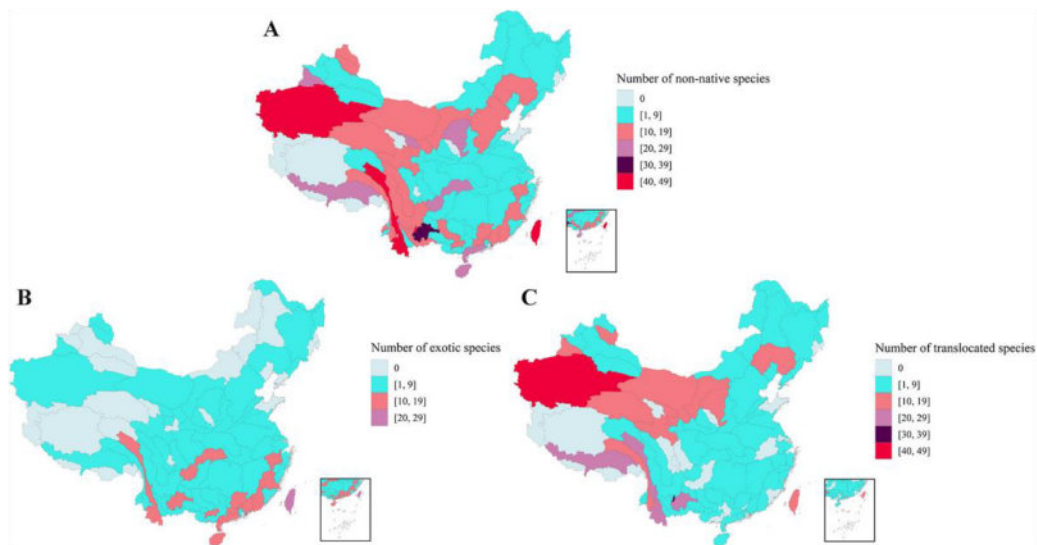


Fig. 3. Number of (A) non-native (i.e., exotic + translocated), (B) exotic, and (C) translocated species in China's hydrological units.

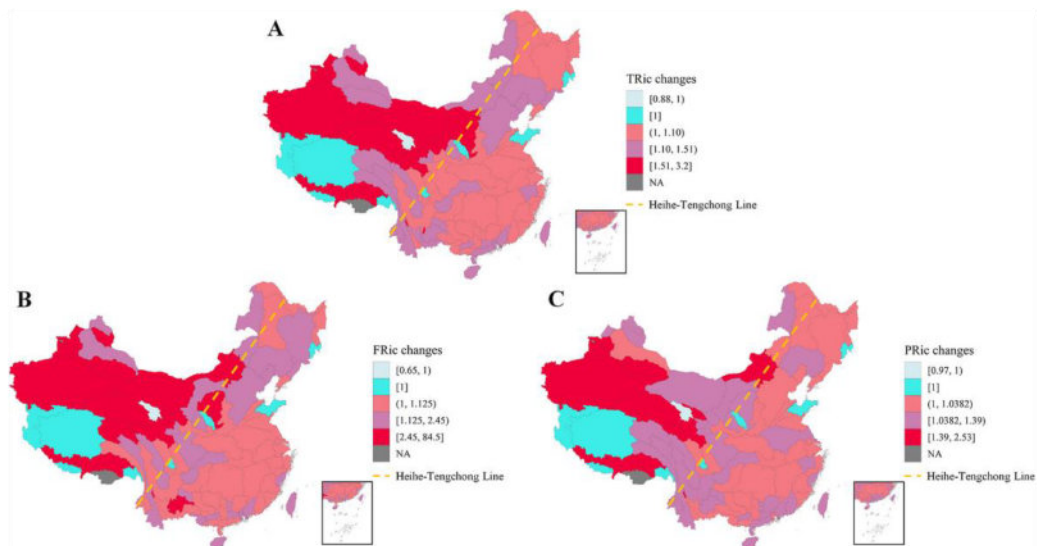


Fig. 4. Temporal changes in (A) TRic, (B) FRic, and (C) PRic of freshwater fish assemblages in China's hydrological units. TRic: taxonomic richness; FRic: functional richness; PRic: phylogenetic richness. The Heihe-Tengchong Line is an important geographical dividing line related to populations, environments,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

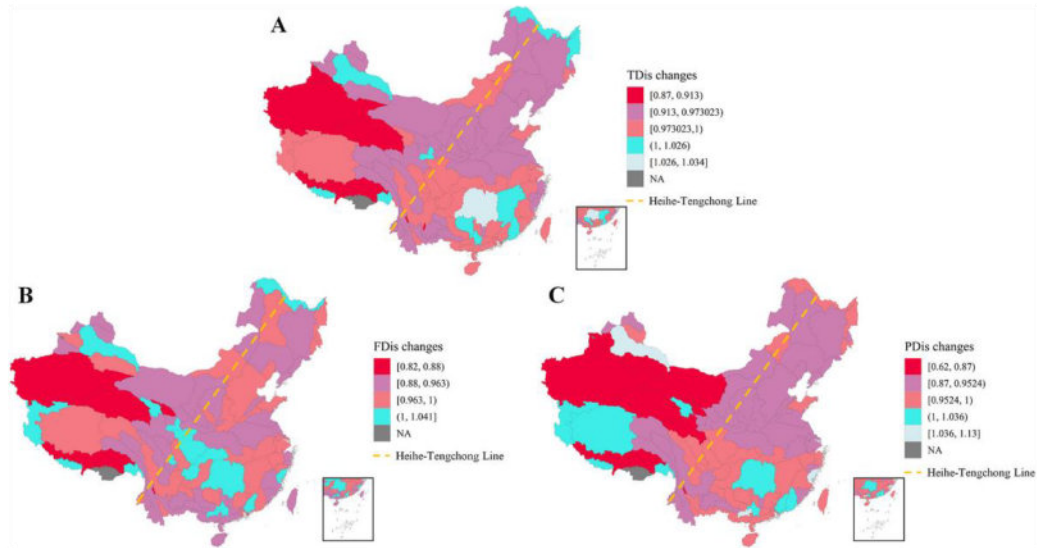


Fig. 5. Temporal changes in (A) TDis, (B) FDis, and (C) PDis of freshwater fish assemblages in China's hydrological units. TDis: taxonomic dissimilarity; FDis: functional dissimilarity; PDis: phylogenetic dissimilarity.

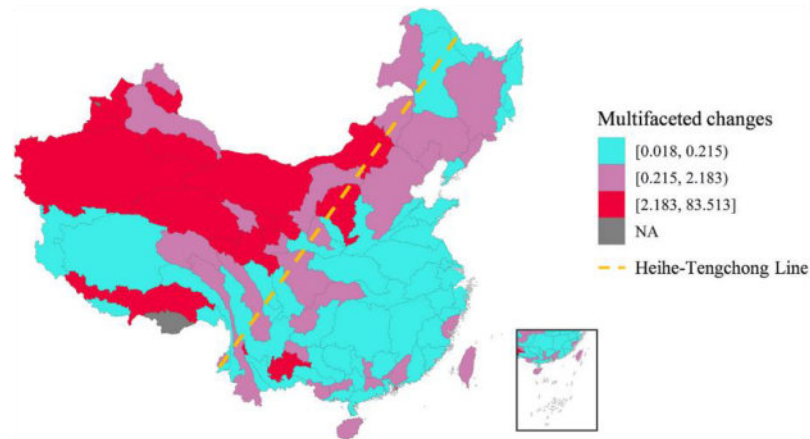


Fig. 6. Multifaceted changes in biodiversity of freshwater fish assemblages in China's hydrological units.

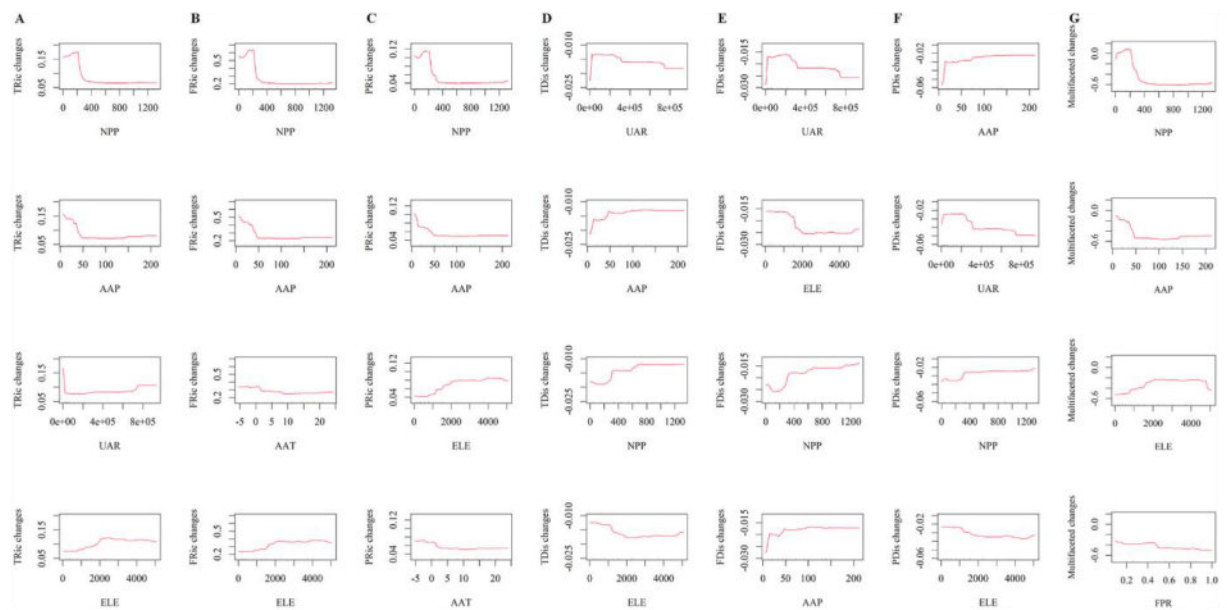
multifaceted changes explained 36.60% (TRic changes), 21.61% (FRic changes), 19.92% (PRic changes), 20.86% (TDis changes), 2.89% (FDis changes), 8.22% (PDis changes), and 28.51% (Multifaceted changes) of the total variances, respectively. Environmental factors (e.g., NPP, ELE, UAR, AAT, and AAP) were 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., Bruce 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).

#### 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

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.

#### Acknowledgements

T.X. was funded by the China Scholarship Council (CSC). X.H.D. was funded by the Guizhou University High-Level Personnel Research Project ([2021]65). The EDB laboratory was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). We are very grateful to Shengli TAO from Peking University and Xiaofeng CAO from Tsinghua University for their kind assistance in some basin data.

#### 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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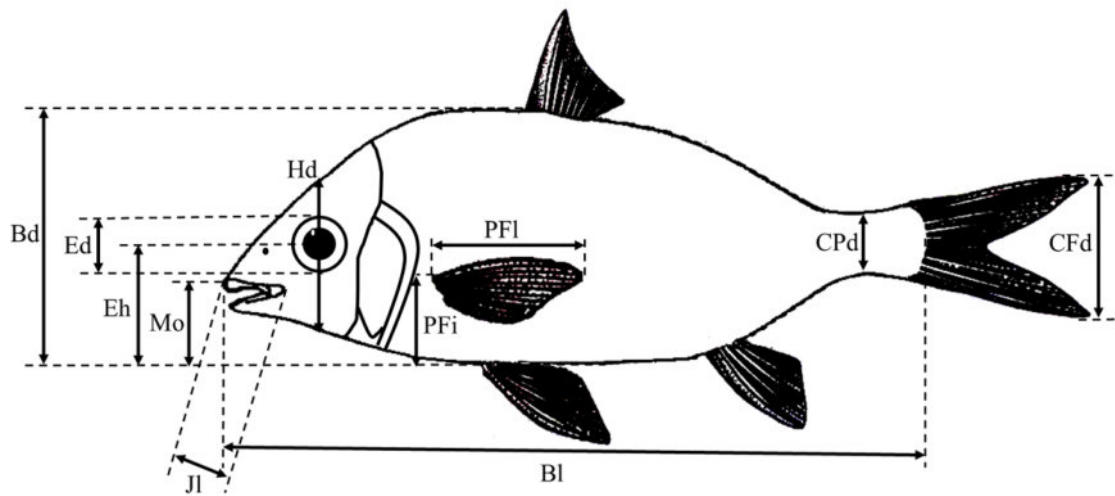
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**Supplementary material:**



**Fig. S1** The morphological measurements measured on each fish species. *Bl* body length, *Bd* maximum body depth, *Hd* head depth at the vertical of eye, *CPd* minimum depth of the caudal peduncle, *CFd* maximum depth of the caudal fin, *Ed* vertical diameter of the eye, *Eh* vertical distance between the centre of the eye to the bottom of the body, *Mo* vertical distance from the top of the mouth to the bottom of the body, *Jl* length from snout to the corner of the mouth, *PFl* length of the longest ray of the pectoral fin, *PFi* vertical distance between the upper insertion of the pectoral fin to the bottom of the body

**Table S1** List of 10 morphological traits associated with food acquisition and locomotion (cited from [Toussaint et al., 2016](#) and [Su et al., 2019](#) without modification)

Morphological traits	Formula	Potential link with fish functions	References
Maximum body length	$BL_{max}$	Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling	e.g., <a href="#">Toussaint et al., 2016</a> ; <a href="#">Froese &amp; Pauly, 2019</a>
Body elongation	$\frac{Bl}{Bd}$	Hydrodynamism	<a href="#">Reecht et al., 2013</a>
Eye vertical position	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column	<a href="#">Winemiller, 1991</a>
Relative eye size	$\frac{Ed}{Hd}$	Visual acuity	<a href="#">Boyle &amp; Horn, 2006</a>
Oral gape position	$\frac{Mo}{Bd}$	Feeding position in the water column	<a href="#">Dumay et al., 2004</a> ; <a href="#">Lefcheck et al., 2014</a>
Relative maxillary length	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw	<a href="#">Toussaint et al., 2016</a>
Body lateral shape	$\frac{Hd}{Bd}$	Hydrodynamism and head size	<a href="#">Toussaint et al., 2016</a>
Pectoral fin vertical position	$\frac{Pfi}{Bd}$	Pectoral fin use for swimming	<a href="#">Dumay et al., 2004</a>
Pectoral fin size	$\frac{Pfl}{Bl}$	Pectoral fin use for swimming	<a href="#">Fulton et al., 2001</a>
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag	<a href="#">Webb, 1984</a>

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**Table S2** List of 10 environmental and anthropogenic drivers associated with various geo-morphological, hydrological, climatic, social, and economic features

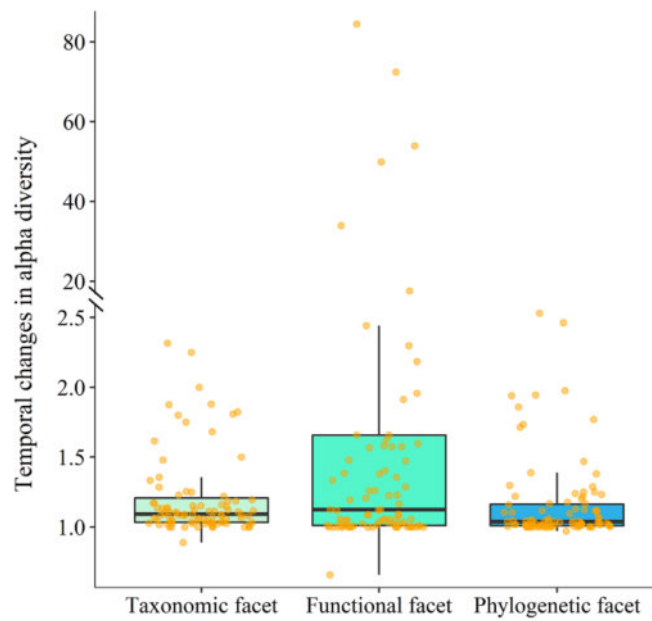
Driver	Code	Additional information	References or Sources
Unit area	UAR	Species-area hypothesis	<a href="#">Oberdorff et al., 1995</a> ; This study
Elevation	ELE	Habitat heterogeneity	<a href="#">Guégan et al., 1998</a> ; <a href="https://www.worldclim.org/data/worldclim21.html">https://www.worldclim.org/data/worldclim21.html</a>
Average annual temperature	AAT	Energy availability	<a href="#">Oberdorff et al., 1995</a> ; <a href="#">Fick &amp; Hijmans, 2017</a>
Average annual precipitation	AAP	Water availability	<a href="#">Fick &amp; Hijmans, 2017</a>
Net primary productivity	NPP	Energy availability	<a href="#">Oberdorff et al., 1995</a> ; <a href="#">Resource and Environment Science and Data Center, Chinese Academy of Sciences, 2010</a>
River fragmentation	RFR	It can reduce population sizes and gene flow of aquatic species and restrict animal migrations	<a href="#">Vörösmarty et al., 2010</a>
Human footprint	HFP	It was measured using built-up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways	<a href="#">Venter et al., 2016</a> ; <a href="#">2018</a>
Consumptive water loss	CWL	It's related to contaminant dilution potential, habitat area, and flow patterns	<a href="#">Vörösmarty et al., 2010</a>
Aquaculture pressure	APR	A proxy for the impact of aquaculture on freshwater biodiversity	<a href="#">Vörösmarty et al., 2010</a>
Fishing pressure	FPR	A proxy for the local impact of fishing on	<a href="#">Uusi-Heikkilä et al., 2008</a> ;

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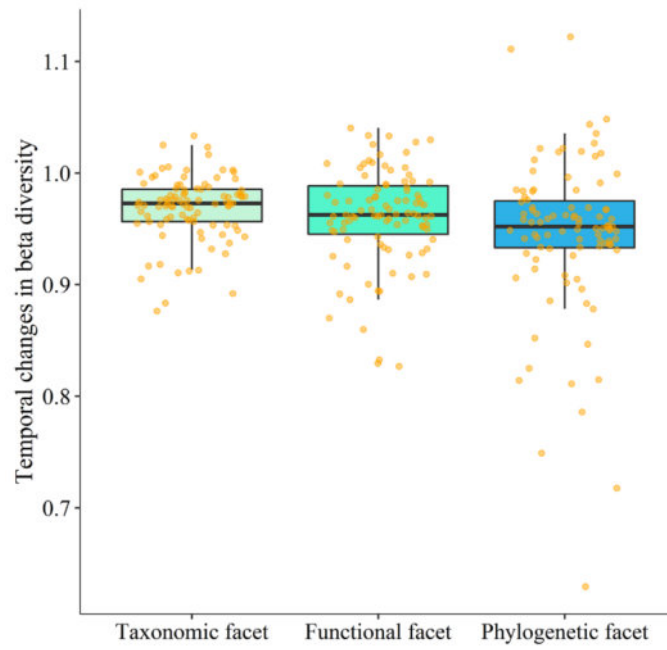
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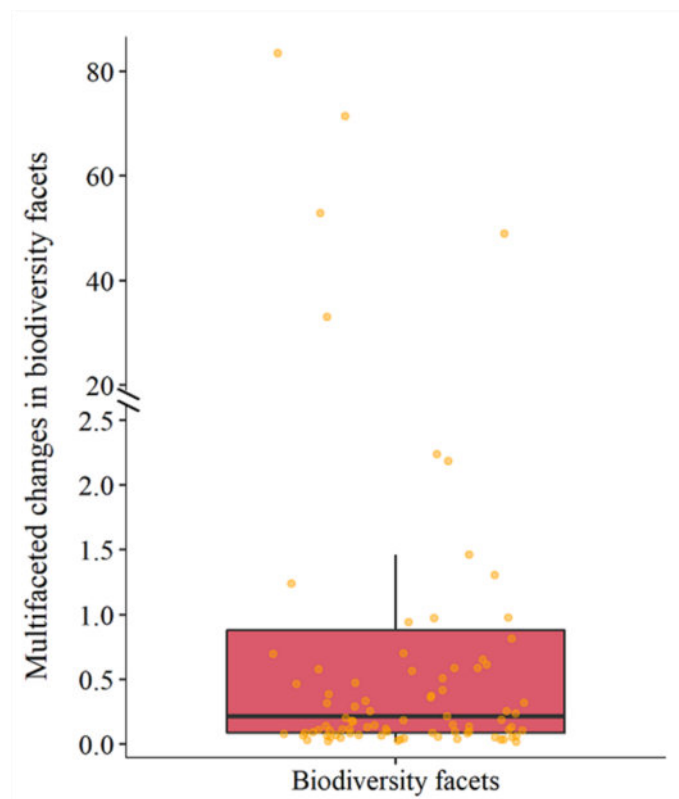
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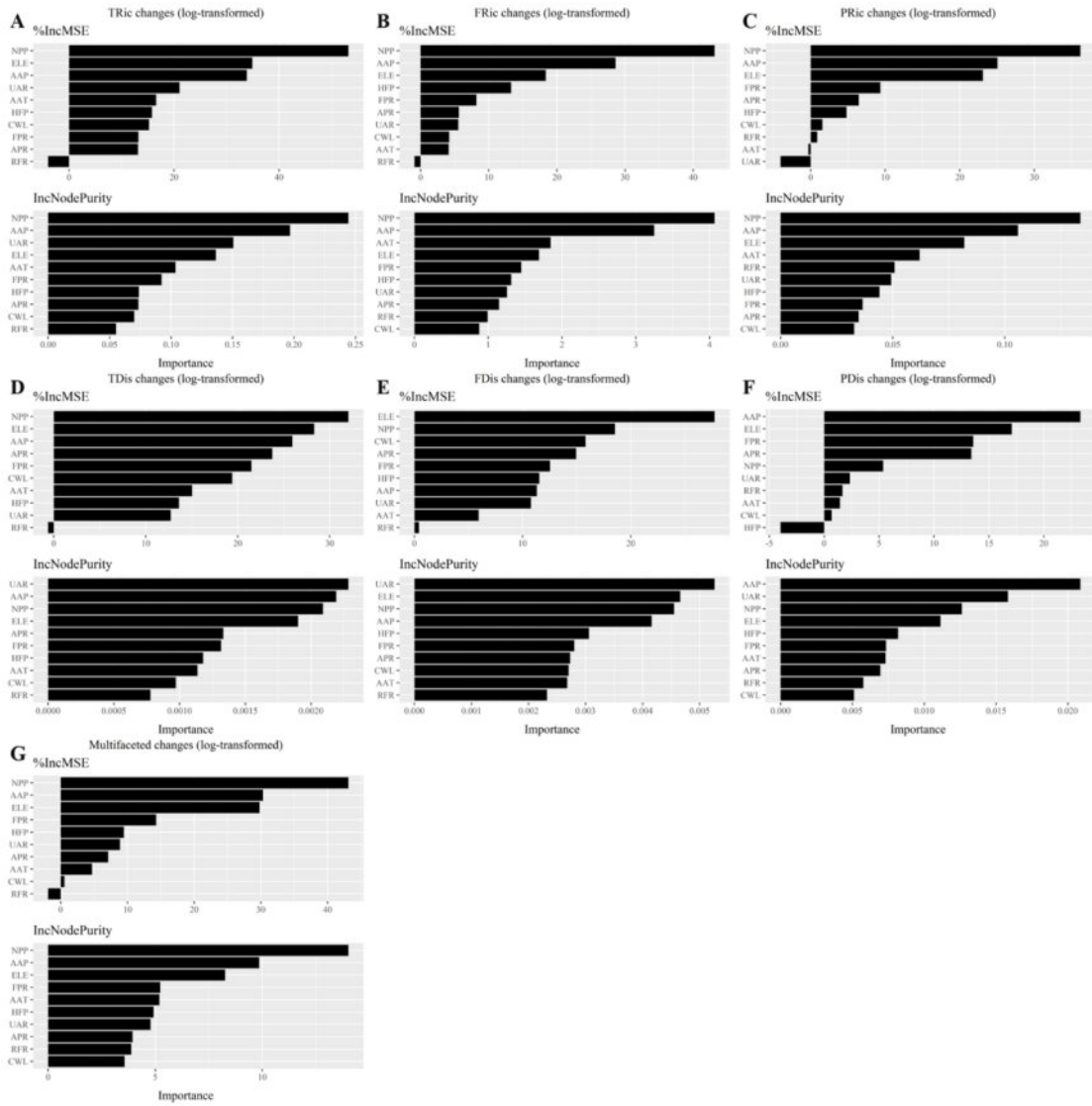
**Fig. S2** Boxplots of temporal changes in alpha diversity (i.e., TRic, FRic, and PRic changes)



**Fig. S3** Boxplots of temporal changes in beta diversity (i.e., TDis, FDis, and PDis changes)

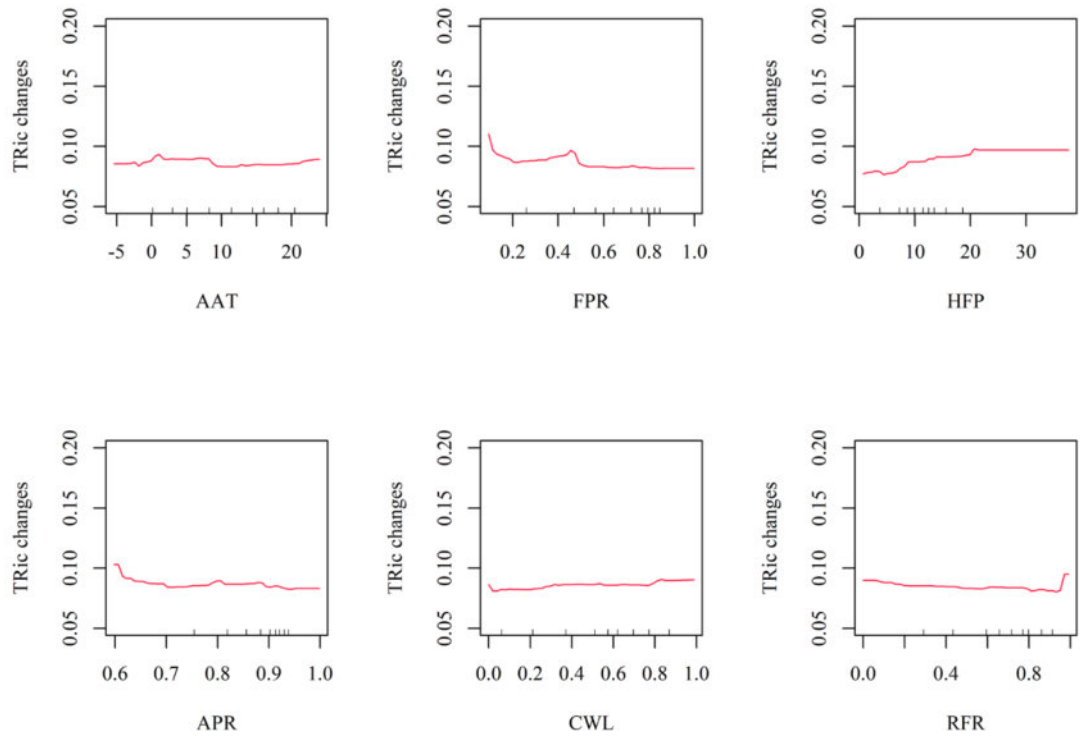
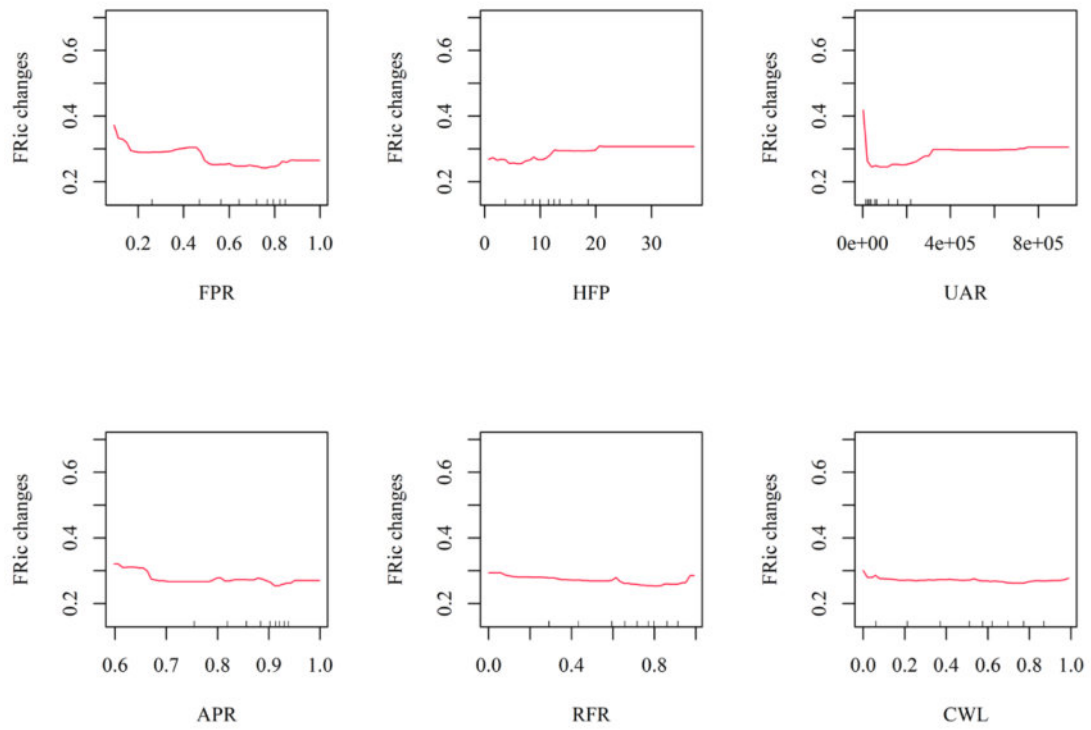


**Fig. S4** Boxplot of multifaceted changes in biodiversity facets

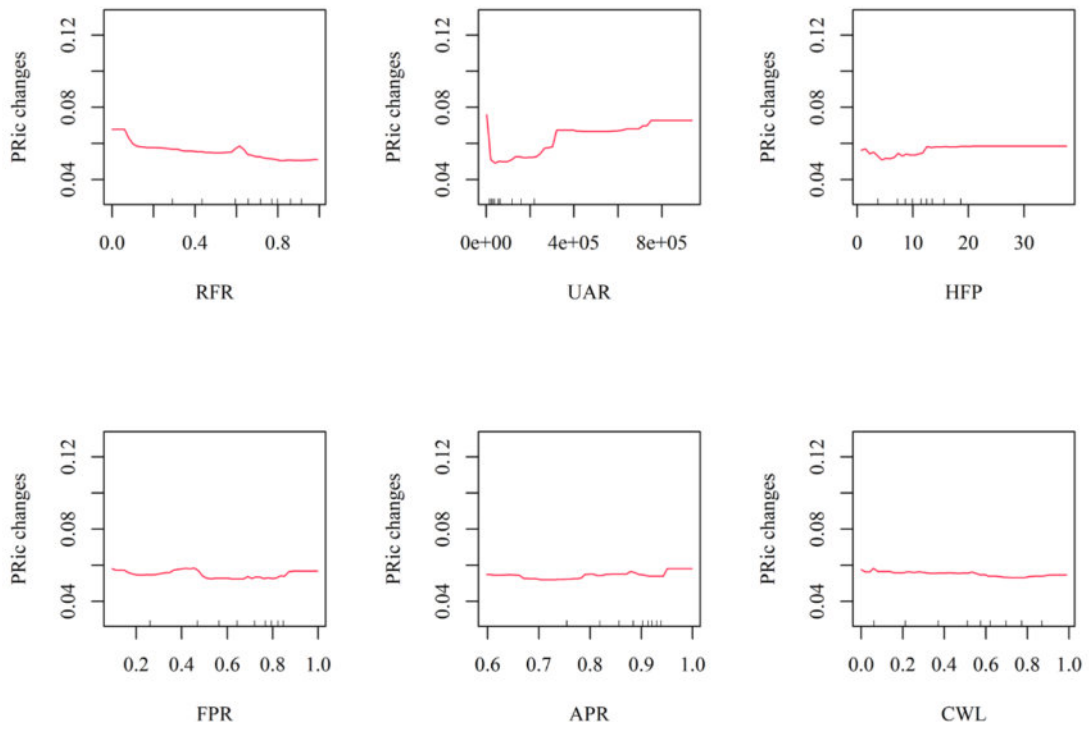


**Fig. S5** Driver importance for the seven response variables in terms of %IncMSE and IncNodePurity. The seven response variables were: (A) TRic changes, (B) FRic changes, (C) PRic changes, (D) TDis changes, (E) FDis changes, (F) PDis changes, and (G) multifaceted changes. UAR: unit area; ELE: elevation; AAT: average annual temperature; AAP: average annual precipitation; NPP: net primary productivity; RFR: river fragmentation; HFP: human footprint; CWL: consumptive water loss; APR: aquaculture pressure; FPR: fishing pressure

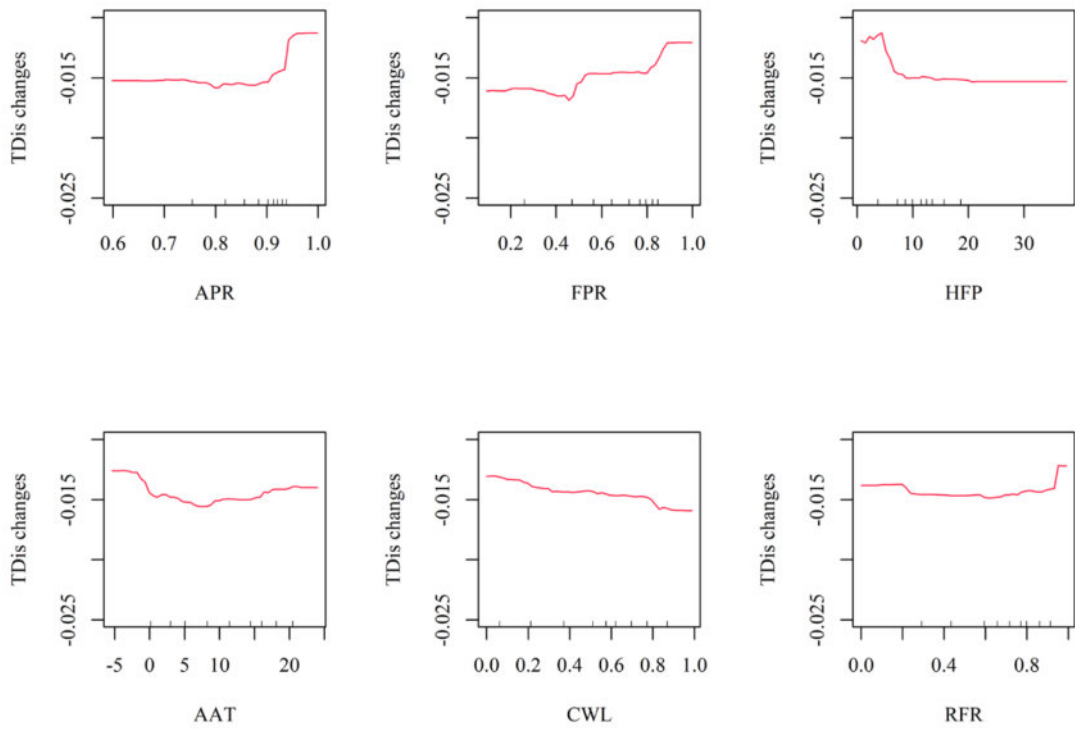


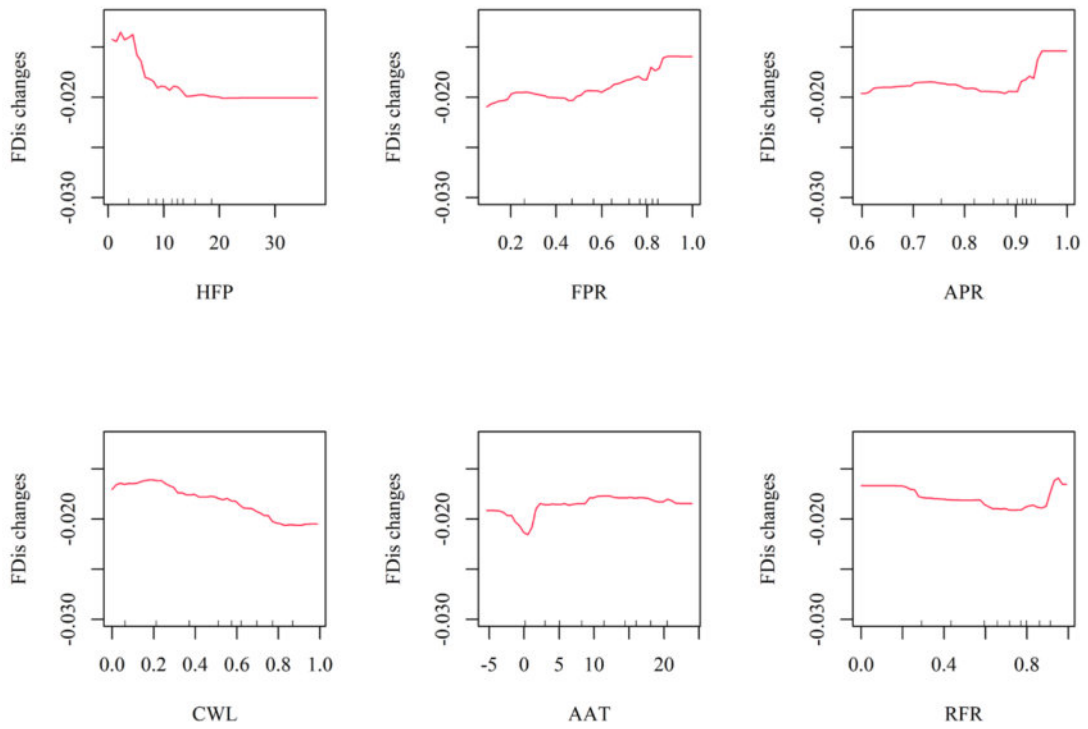
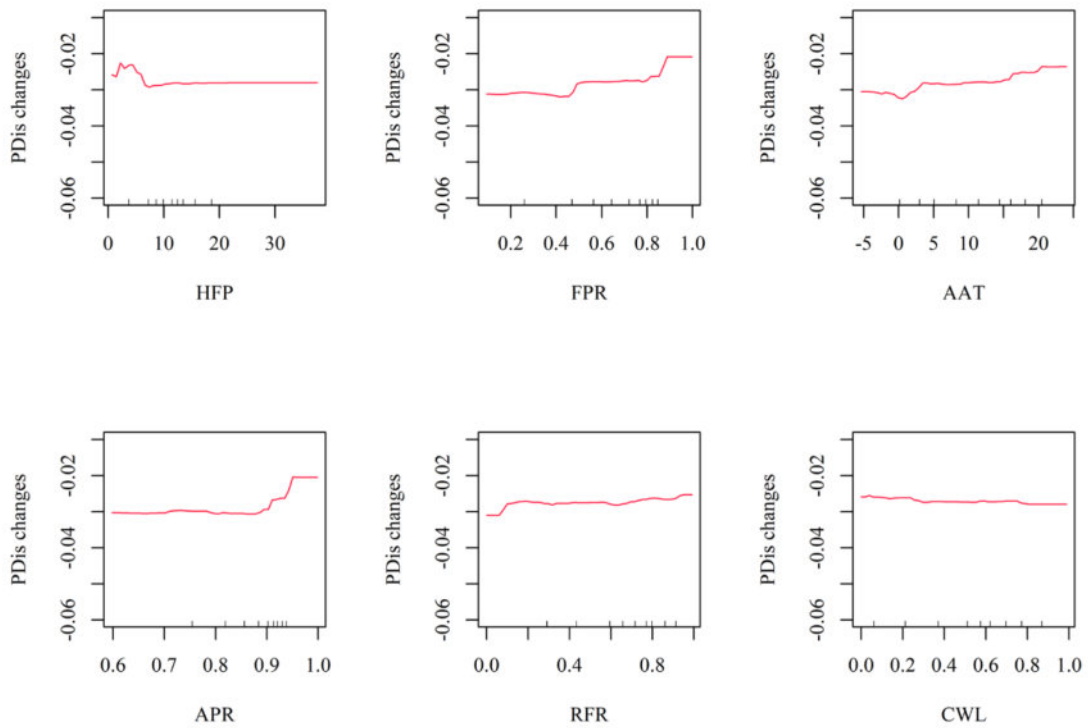
**A****B**

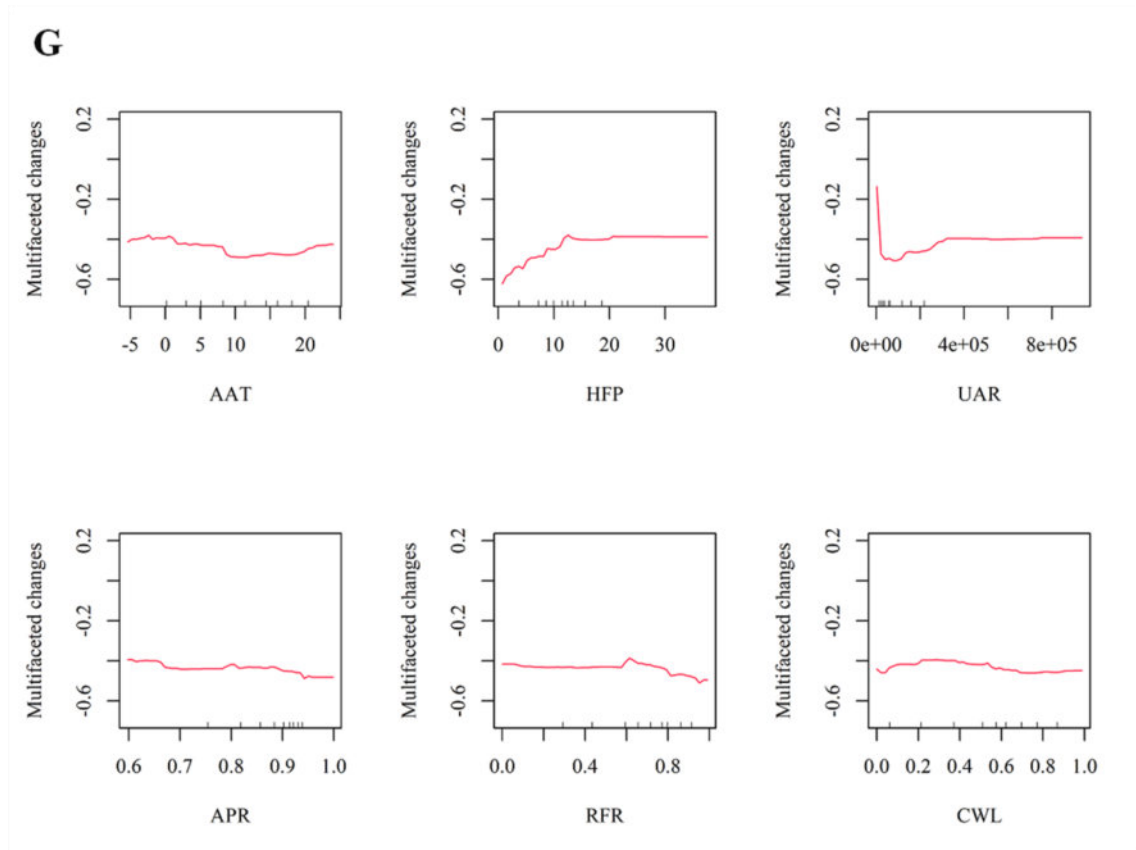
**C**



**D**



**E****F**



**Fig. S6** Partial dependence plots for the remaining drivers for temporal and multifaceted changes (log-transformed) in biodiversity facets through the random forest models. 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. UAR: unit area; AAT: average annual temperature; RFR: river fragmentation; HFP: human footprint; CWL: consumptive water loss; APR: aquaculture pressure; FPR: fishing pressure

**Chapter 5: Species range shifts of notorious invasive fish species in China under global changes: Insights and implications for management**

*Journal of Environmental Management, 347, 119197*

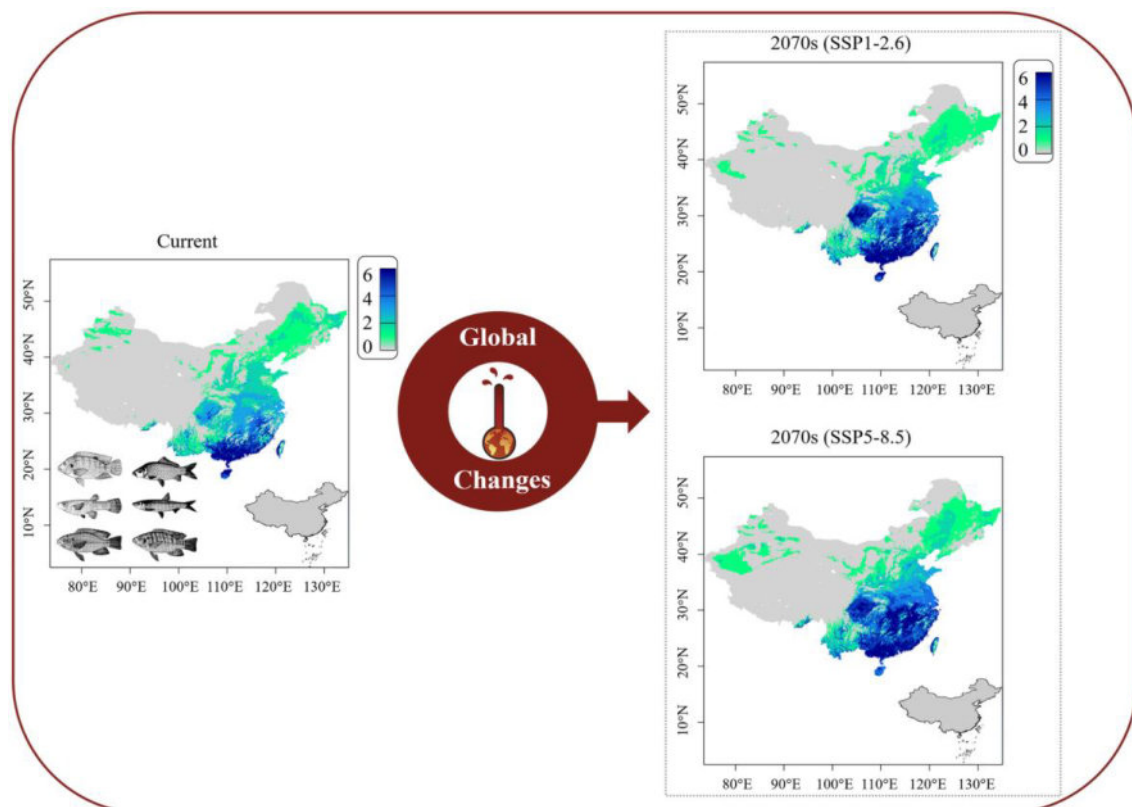
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Research article

## Species range shifts of notorious invasive fish species in China under global changes: Insights and implications for management

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## ARTICLE INFO

Handling Editor: Jason Michael Evans

## Keywords:

Invasive fish species  
Climate change  
Human activities  
Species distribution models  
Habitat suitability  
Transitory range dynamics

## ABSTRACT

Due to global changes, e.g., climate change and trade globalization, China is facing an increasingly severe threat from invasive freshwater fish species, which have the potential to cause negative impacts across various aspects and pose significant challenges for their eradication once established. Therefore, prioritizing the understanding of invasive species' potential ranges and their determinants is vital for developing more targeted management strategies. Moreover, it is equally essential to consider the transitory range dynamics of invasive species that reflect changes in habitat availability and accessibility. Here, we used species distribution models (the maximum entropy algorithm) to assess the potential distributions of six notorious invasive fish species (i.e., *Coptodon zillii*, *Cyprinus carpio*, *Gambusia affinis*, *Hemiculter leucisculus*, *Oreochromis mossambicus*, and *Oreochromis niloticus*) in current and future (i.e., the 2030s, 2050s, and 2070s) periods along with their determinants, under two Shared Socio-economic Pathways scenarios (SSP1-2.6 and SSP5-8.5; global climate model: MRI-ESM2-0). Our results showed that the habitat suitability for the six species substantially benefited from temperature conditions (i.e., annual mean temperature or maximum temperature of warmest month). Throughout the given time periods, dramatic range expansions would occur for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, ranging from 38.61% to 291.90%. In contrast, the range of *C. carpio* would change slightly and irregularly, while *H. leucisculus* would contract marginally, with losses ranging from 1.06% to 12.60%. By the 2070s, species richness of these species would be relatively high in South, Central, and East China and parts of Southwest China. Furthermore, transitory fluctuations in the species ranges for all six species were observed throughout the entire time period (the 2030s–2070s). Given the range shifts for each species during different time periods, as well as time costs and budgets, adaptation strategies should be developed and implemented in the areas where they are most needed in each time period.

## 1. Introduction

Global freshwater fish introductions are a major environmental and ecological threat, with hundreds of non-native freshwater fish species having been found worldwide (Su et al., 2021; Xiang et al., 2021; Bernery et al., 2022). These widespread fish introductions have caused negative impacts on biodiversity, economy, and public health (e.g., transmission of parasites and pathogens) in their recipient areas (Gozlan et al., 2010; Su et al., 2021; Haubrock et al., 2022). With increasing human activities, such as fishery activities and trade globalization, new

fish introductions are likely to be facilitated, which could further exacerbate the adverse impacts of fish invasions (e.g., Bae et al., 2018; Dong et al., 2020). More concerning is the fact that climate change, a key driver of fish species responses, can also promote the establishment of non-native species, increasing the uncertainty and likelihood of fish invasions (Early et al., 2016; Kuczynski et al., 2018; Liu et al., 2019; Essl et al., 2020). One of the most direct effects of climate change on fish species is their range shift (e.g., species range expansions or contractions), which is considered a major threat to biodiversity in recipient areas (Comte and Grenouillet, 2015; Schickele et al., 2021). Generally,

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<https://doi.org/10.1016/j.jenvman.2023.119197>

Received 11 April 2023; Received in revised form 20 June 2023; Accepted 30 September 2023

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the potential for successful fish invasions depends on the availability of habitats with climates similar to those in their current ranges (Bae et al., 2018). Since the pre-industrial era (1880–1900), the global climate, e.g., temperature and precipitation patterns, has demonstrably changed, and this trend is expected to continue or even worsen at both global and regional scales as greenhouse gases continue to be emitted (IPCC, 2022; Lindsey and Dahlman, 2023). In the foreseeable future, non-native freshwater fish species are likely to find other more climatically suitable habitats, either through human selection or assistance, which would increase the number of fish invasions in new areas and lead to subsequent negative impacts (Murphy et al., 2015; Bae et al., 2018; Comte et al., 2021).

Although legislation and policies on non-natives have already been promulgated in many countries (e.g., Li et al., 2020), unfortunately, most countries, especially developing economies with high biodiversity, lack the capacity to effectively manage increasing species invasions (Early et al., 2016; Vythalingam et al., 2022). In addition to the previously mentioned effects of global changes and budget limitations, a lack of timely and comprehensive data on invasive species' occurrences and their potential distributions in large territories remains a significant barrier to managing biological invasions (Aschim and Brook, 2019). As the largest developing country and one with vast inland waters and diverse environments (Xiong et al., 2015), China faces higher and increasing stress from invasive species (Xiong et al., 2015; Liu et al., 2019). Until now, at least 200 non-native freshwater fishes have been identified in various water bodies throughout China (Xiang et al., 2021), causing significant losses to various aspects of biodiversity and the economy (Liu et al., 2017, 2021a; Xiang et al., 2023). Given the difficulty in eradicating invasive fish species (Britton et al., 2011), preventing their introduction, establishment, and spread is considered the most effective and promising approach (Liu et al., 2019; Vythalingam et al., 2022). It is therefore essential to understand how the ranges of invasive fish species would respond to future global changes to improve prevention and management of fish invasions in China.

Species distribution models (SDMs) are recognized as efficient methods for early monitoring and prevention of biological invasions, as they examine species' potential habitats along with the stressors influencing their distributions through the associations between species distribution data and underlying environmental or spatial conditions (Bae et al., 2018; Liu et al., 2019; Dong et al., 2020; Shipley et al., 2022). Over the past decades, SDMs have been widely used to estimate current and future potential distributions of many non-native freshwater fish species in China (e.g., Liu et al., 2019; Dong et al., 2020). However, studies on species range shifts of several universally recognized invasive fish species (e.g., *Cyprinus carpio* Linnaeus, 1758 and *Oreochromis niloticus* (Linnaeus, 1758)), which are better at eliciting attention from the public and decision-makers, are still pending. Furthermore, the importance of transitory range dynamics of invasive species in China under global changes, which can reflect habitat availability and accessibility (Huang et al., 2020; Shipley et al., 2022), has been overlooked by previous studies (e.g., Liu et al., 2019). Exploring real-time and accurate spatial expansions or contractions during different time periods is fundamental for adopting corresponding cost-effective and labor-saving strategies (Shrestha and Shrestha, 2019; Huang et al., 2020). Therefore, research on applying SDMs over multiple time steps to evaluate the transitory habitat stability of China's notorious invasive fishes, along with the spatial and temporal patterns and trends of their species richness, is required and urgent.

In the present study, six common non-native fish species were selected as they are universally recognized as invasive globally and known to have ecological, healthy, and economic impacts if they continue to spread (e.g., Lowe et al., 2000; Luque et al., 2014; Dong et al., 2020). Our main objectives, addressed using the maximum entropy model (MaxEnt), one of the most popular and effective algorithms, were to: (a) explore the spatial patterns of current and future habitat ranges of the six notorious invasive fishes in China, (b) disentangle the

relative importance of environmental and anthropogenic variables driving the habitat suitability of these fishes, and (c) identify areas of transitory fluctuations of the fishes to determine the availability and accessibility of habitats. To our knowledge, this is the first study evaluating transitory range dynamics of invasive fish species under global changes in China, which has the potential to not only prevent and manage fish invasions with reasonable costs and efforts, but also provide early warnings and lessons for fish invasion management in China, as well as in other geographical areas.

## 2. Materials and methods

### 2.1. Selection of invasive freshwater fishes

Six invasive freshwater fish species were selected for this study: Redbelly tilapia *Coptodon zillii* (Gervais, 1848), Common carp *Cyprinus carpio* Linnaeus, 1758, Mosquitofish *Gambusia affinis* (Baird & Girard, 1853), Sharpbelly *Hemiculter leucisculus* (Basilevsky, 1855), Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852), and Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758). These six species are widely distributed in the wild in China and have been demonstrated to possess relatively high invasive potentials (e.g., Li et al., 2017; Gu et al., 2019; Dong et al., 2020; Xiang et al., 2023). They can cause significant negative impacts in the recipient areas within China, including declines in fishery income, biotic homogenization, local extinctions of native species, and instances of eutrophication and habitat alteration (e.g., Gu et al., 2019; Xiang et al., 2023). Notably, among these species, *C. carpio*, *O. mossambicus*, and *G. affinis* are listed among the 100 worst invasive species in the world (Lowe et al., 2000).

### 2.2. Species occurrences

Species occurrences were obtained through a comprehensive literature review, including peer-reviewed articles, monographs, and databases (i.e., FishBase (<https://www.fishbase.se/search.php>; retrieved in February 2022), the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>; retrieved in February 2022), and the Fish Database of Taiwan (<http://fishdb.sinica.edu.tw/>; retrieved in February 2022)). The latest presence records from 2022 were included, and duplicates and dubious occurrences (e.g., incomplete and terrestrial records) were removed. Based on the best available fish distribution information, we here adopted the 2.5 arc-minutes spatial resolution, ca. 4.5 km<sup>2</sup> at the equator. Only one occurrence in one environmental grid cell was kept for mitigating the effect of spatial auto-correlation originating from spatial clustering of presence records (Dong et al., 2020). Additionally, an environmental-subsampling technique described in Varela et al. (2014) and Castellanos et al. (2019) was used to diminish sampling bias and enhance model performance (Shipley et al., 2022), where each variable was divided into 25 bins and only one point from every individual combination of the bins was chosen for modeling. In total, 65 (*C. zillii*), 660 (*C. carpio*), 163 (*G. affinis*), 344 (*H. leucisculus*), 94 (*O. mossambicus*), and 178 (*O. niloticus*) occurrence records were retained for the six species, respectively.

### 2.3. Variables for modeling

Due to the L1-regularization feature of the MaxEnt algorithm, expert pre-selection of variables for modeling that requires less removal of correlated variables or preprocessing of covariates is generally reasonable and acceptable (Elith et al., 2011). Hence, according to our expert opinions and related studies (e.g., Fourcade, 2016; Bae et al., 2018; Dong et al., 2020), we selected nine bioclimatic and non-bioclimatic variables that are biologically and ecologically significant in determining the spatial distributions of the six species as predictors in our study: Annual Mean Temperature (AMTem, °C), Maximum Temperature of Warmest Month (MaxTemWM, °C), Minimum Temperature of Coldest

Month (MinTemCM, °C), Annual Precipitation (APre, mm), Precipitation of Wettest Month (PreWM, mm), Precipitation of Driest Month (PreDM, mm), Elevation (Elev, m), Dam Area (DamA, km<sup>2</sup>), and Human Population Density (HPD, ind/km<sup>2</sup>).

The six bioclimatic variables (AMTem, MaxTemWM, MinTemCM, APre, PreWM, and PreDM) were obtained from the WorldClim database (<https://www.worldclim.org/>) and used to describe current (1970–2000) and future climatic conditions for the early- (2021–2040; hereafter 2030s), mid- (2041–2060; 2050s), and late-century (2061–2080; 2070s) periods. Since the aim of the current study was not to account for the uncertainty of future climate models, we only selected the best-performing global climate model (GCM), MRI-ESM2-0, over China (Lu et al., 2022) for future predictions. Concerning the future climate scenarios, we here adopted two relatively extreme Shared Socio-economic Pathways (SSPs) for comparison purposes: (a) SSP1: Sustainability—Taking the green road and (b) SSP5: Fossil-fueled development—Taking the highway (O'Neill et al., 2017).

The HPD variable (Gao, 2017, 2020) was used to describe current and future population density. The Elev (Farr et al., 2007; Fick and Hijmans, 2017) and DamA (Lehner et al., 2011a, 2011b) variables were used to describe current conditions. However, it is worth noting that no future datasets were available for elevation and dam areas in China, so we kept these two variables constant in future predictions.

#### 2.4. Modeling approach

To develop SDMs of the six species, we used the 'megaSDM' package (Shipley et al., 2022) in R (R Core Team, 2021). This package integrates subsampling methods, the MaxEnt algorithm, and other statistical tools to generate time-step maps of range change dynamics (e.g., expansions or contractions of species ranges) for the provided species across all considered time periods (Shipley et al., 2022).

For each species, a total of 10,000 background points were yielded due to no absence data. Out of these background points, 50% were randomly set within the buffer around occurrence points with twice the 95% quantile of the minimum distance between each point as the buffer radius, and the remaining 50% were randomly assigned in the whole area (Shipley et al., 2022). Additionally, 80% of the fish occurrence data were randomly selected for modeling each species and the remaining 20% were used for validation. To minimize data-split bias, we generated 10 replicate model runs (Bae et al., 2018), resulting in 10 basal models for each species. The area under the curve (AUC) of receiver operating characteristic (ROC) was then used to evaluate model performance (Hanley and McNeil, 1982). We conducted an ensemble modeling approach using basal models with AUC values no less than 0.7 and computed for each grid cell the median habitat suitability. Habitat suitability was hereafter transformed into binary (presence/absence) projections by applying the corresponding thresholds of maximum test sensitivity and specificity (Shipley et al., 2022). Finally, the six binary species distribution maps were stacked to create species richness maps to illustrate the spatial and temporal patterns and trends of notorious fish species richness.

Likewise, future predictions were also carried out using two other well-performing GCMs (i.e., MPI-ESM1-2-HR and EC-Earth3-Veg) over China (Lu et al., 2022) for reference purposes (see Supplementary data).

All statistical analyses were performed using R software version 4.0.5 (R Core Team, 2021).

### 3. Results

#### 3.1. Model performance

AUC values (mean ± SD) of 0.90 ± 0.02 (*C. zillii*), 0.78 ± 0.02 (*C. carpio*), 0.85 ± 0.02 (*G. affinis*), 0.82 ± 0.02 (*H. leucisculus*), 0.87 ± 0.03 (*O. mossambicus*), and 0.90 ± 0.01 (*O. niloticus*) were obtained for the six notorious fish species, respectively, indicating that the MaxEnt

models provided reliable predictions of the current species distributions.

#### 3.2. Variable importance and species response curves

For the six species, the shapes of most of the response curves depicting the species' habitat suitability to each variable were similar (Fig. 1), while temperature variables (i.e., AMTem or MaxTemWM) contributed more (over 30%) than other variables, such as DamA and precipitation variables, to the models (Table 1). In addition, the habitat suitability of most of the six species showed unimodal responses to the two relatively important temperature variables (i.e., AMTem and MaxTemWM), with the optimal temperature for their presence being around 23 °C and 33 °C, respectively. Notably, Elev was the most important factor in predicting the distribution of *C. carpio*, and the species' habitat suitability was relatively high in low altitude areas of approximately 120 m, followed by a sharp decrease with increasing elevation.

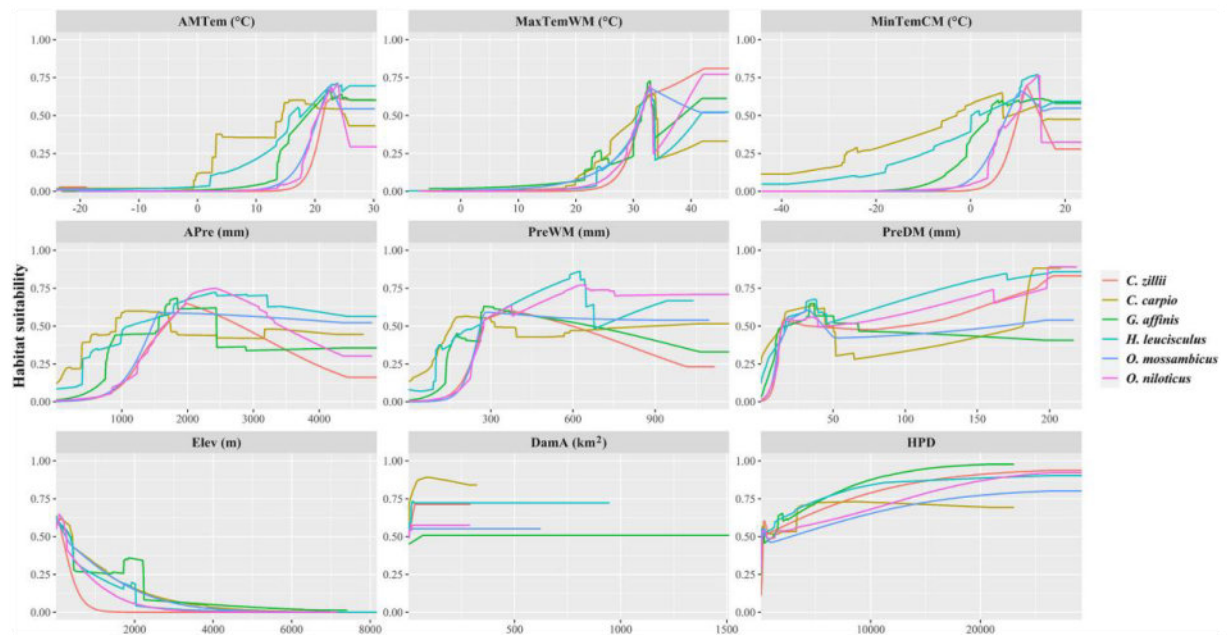
#### 3.3. Species distribution shifts

The models predicted that the ranges of all six species would shift to varying degrees across different time periods under both SSP1-2.6 and SSP5-8.5 scenarios, with range expansions for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus* more severe with increasing SSP severity, while irregular changes in species ranges were observed for *C. carpio* and *H. leucisculus* (Fig. 2; Supplementary Table S1). Overall, under SSP1-2.6 and SSP5-8.5 scenarios, dramatic range expansions would occur for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, ranging from 38.61% to 291.90% throughout the given time periods. Most of their habitat gains would occur in parts of East, Central, Southwest (mainly in Sichuan Basin), and Northwest (mainly in Tarim basin) China, which were far away from their current ranges. Additionally, the range of *C. carpio* would change slightly and irregularly, while that of *H. leucisculus* would contract marginally, with losses ranging from 1.06% to 12.60%. Furthermore, except a southward shift in distribution centroid observed for *H. leucisculus*, there would be apparent northward shifts in distribution centroids for the other five species from current to the 2070s (Supplementary Table S1).

Specifically, concerning *C. zillii*, *O. mossambicus*, and *O. niloticus*, their constantly suitable habitats throughout the entire time period were mostly located in South China. Interestingly, all three species would show a common trend of changes in their ranges, with considerably increased suitable habitats observed in parts of Central, Southwest, and East China across different time periods. However, unlike *C. zillii* and *O. niloticus*, the habitat gains of *O. mossambicus* were predicted to increase by the 2070s with increasing SSP severity, mainly in East China. Additionally, more significant habitat losses for *O. niloticus* were observed across the given time periods, mainly in South China (e.g., Hainan Island). Notably, only sporadic and scattered areas of transitory fluctuations (mainly expansions followed by contractions) were found in parts of Southwest, Central, and East China for the three species, especially under SSP1-2.6 scenario.

Regarding *C. carpio* and *H. leucisculus*, their constantly suitable habitats throughout the entire time period were mostly located in South, East, Central, and Northeast China as well as parts of Southwest and Northwest China. Unlike *C. carpio*, which would mainly expand its suitable habitat along the external boundaries of its current range, *H. leucisculus* would expand its range toward the north (mainly in north-eastern regions) by the 2070s with increasing SSP severity. Meanwhile, under both SSP1-2.6 and SSP5-8.5 scenarios, considerable habitat losses were predicted to occur in parts of Northeast, East, Central, and Southwest China for *H. leucisculus* across the different time periods, while *C. carpio* was found to experience relatively small losses scattered along the external and internal boundaries of its range. Moreover, considerable areas of transitory fluctuations were observed for *H. leucisculus*, particularly contractions followed by expansions and expansions followed by contractions, in parts of Northeast, East, North,





**Fig. 1.** Response curves of the six species' habitat suitability to the variables used for modeling. AMTem: Annual Mean Temperature (°C); MaxTemWM: Maximum Temperature of Warmest Month (°C); MinTemCM: Minimum Temperature of Coldest Month (°C); APre: Annual Precipitation (mm); PreWM: Precipitation of Wettest Month (mm); PreDM: Precipitation of Driest Month (mm); Elev: Elevation (m); DamA: Dam Area (km<sup>2</sup>); HPD: Human Population Density (ind/km<sup>2</sup>).

**Table 1**  
Relative contributions of the variables to the MaxEnt models for the six fish species.

Variables	Contribution (%)					
	<i>C. zillii</i>	<i>C. carpio</i>	<i>G. affinis</i>	<i>H. leucisculus</i>	<i>O. mossambicus</i>	<i>O. niloticus</i>
AMTem	54	7.1	38.7	24.1	57.7	64.1
MaxTemWM	2.5	32.7	22.5	35.4	3.5	2.3
MinTemCM	12.6	6.1	22.1	5.5	12.9	19.3
APre	2.1	1.8	4.3	1.8	12.5	2.2
PreWM	0.6	3.2	3.3	5.9	7.1	3.8
PreDM	1.7	2.8	0.4	1	0.4	1.9
Elev	8.6	34.9	3.2	22.6	2.5	4.1
DamA	0	1.6	0.4	0.2	0	0
HPD	17.9	9.9	5.1	3.7	3.5	2.2

and Southwest China, while relatively few such areas were identified for *C. carpio*, mainly scattered in parts of Northwest, North, and Northeast China.

Lastly, concerning *G. affinis*, constantly suitable habitats throughout the entire time period were mostly found in parts of South, East, Central, and Southwest China. Species range expansions would be aggravated with increasing SSP severity, with habitats expanding towards the northwest. Nevertheless, sparse areas of species range contractions and transitory fluctuations (particularly expansions followed by contractions and contractions followed by expansions) were observed in parts of Southwest and East China across several time periods under both SSP1-2.6 and SSP5-8.5.

### 3.4. Current and future species richness of the six fish species

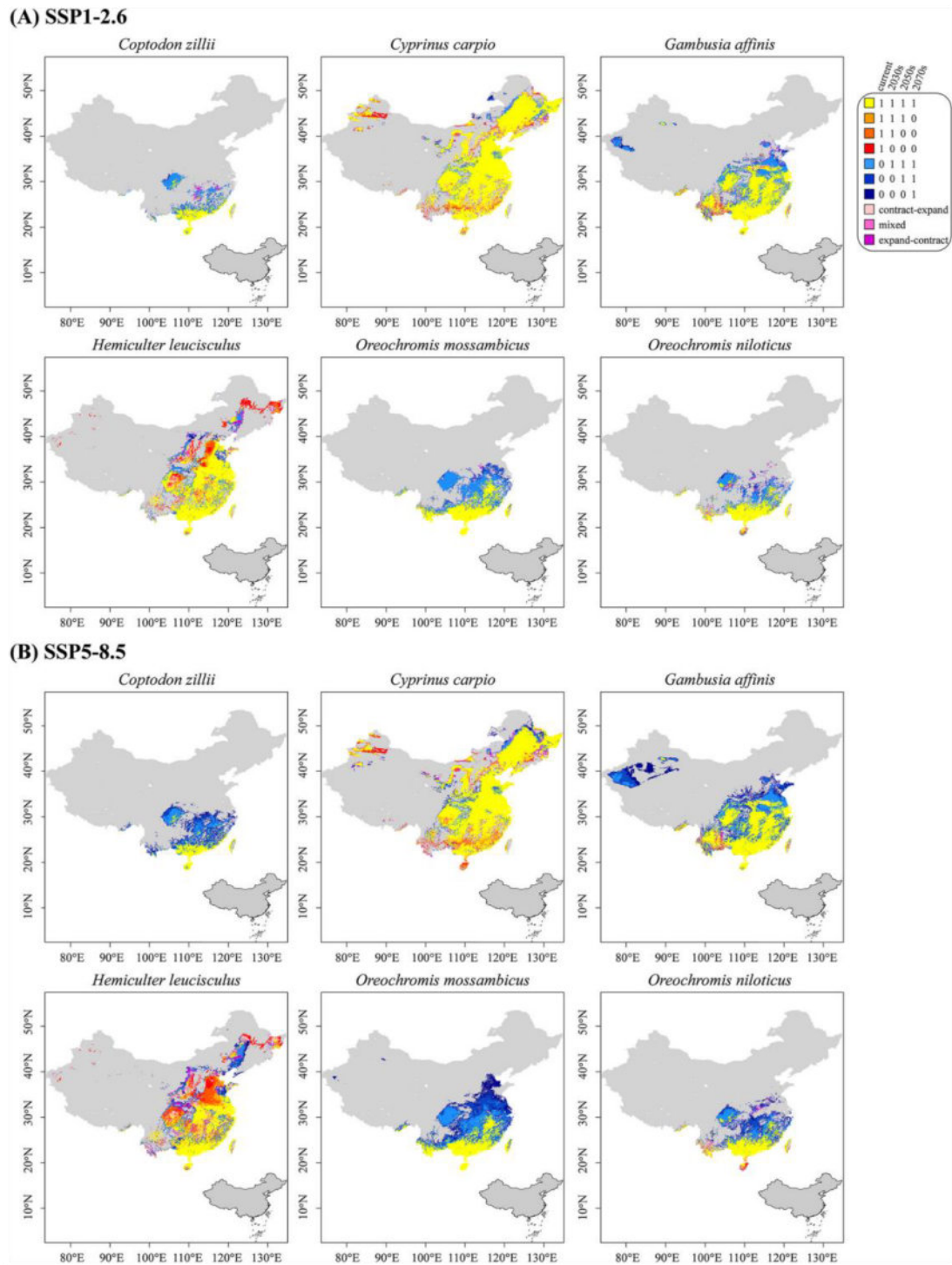
A significant increase in species richness of the six species would predominantly occur in parts of East, Central, and Southwest China across the given time periods under both SSP1-2.6 and SSP5-8.5 scenarios (Fig. 3). By the 2070s, species richness would be relatively high in South, Central, and East China and parts of Southwest China (e.g., Sichuan Basin) under these two scenarios.

## 4. Discussion

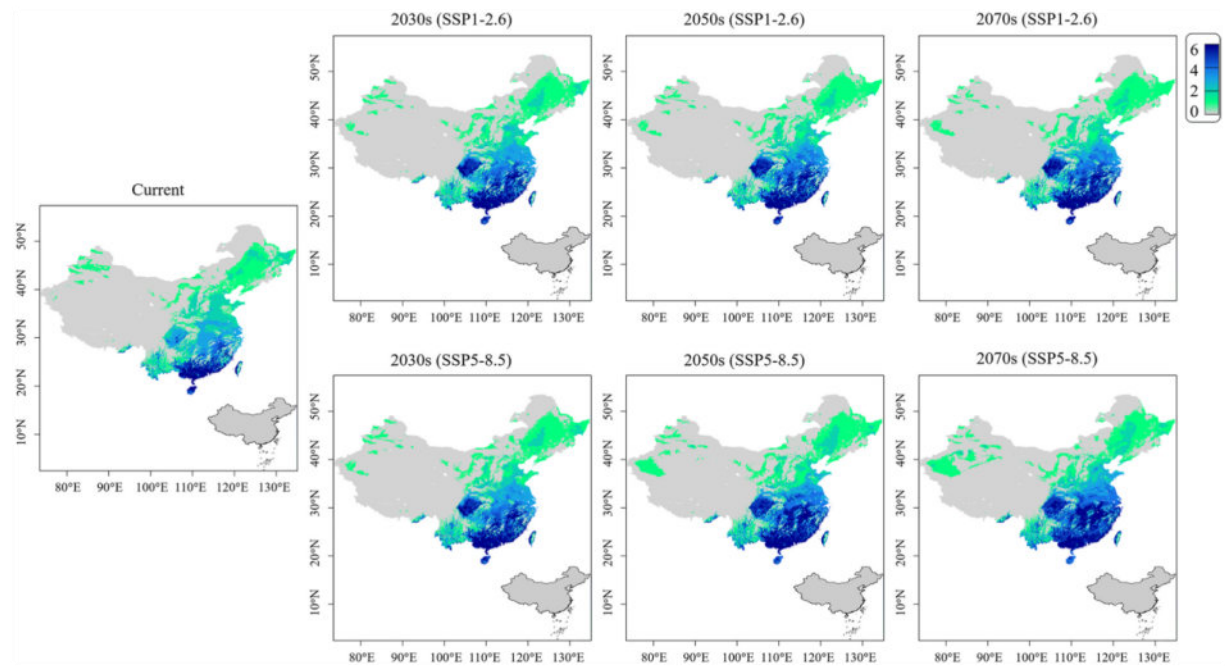
Our study revealed that all six notorious invasive freshwater fish species in China were likely to shift their ranges to varying extents under future global changes (e.g., climate change and human activities), even under a low-emission scenario. Furthermore, areas of transitory fluctuations, which reflect habitat availability and accessibility, were observed for all six species across the time periods studied. This suggests that corresponding strategies and plans should be established in different areas and time periods given time costs and budgets.

### 4.1. Factors influencing species distributions

Air temperature and precipitation patterns are crucial factors in determining geographical distributions of freshwater fish species, by affecting water temperature and the structure and dynamics of freshwater habitats (Knouft and Ficklin, 2017; Barbarossa et al., 2021). However, contrary to many previous findings (e.g., Ruiz-Navarro et al., 2016; Dong et al., 2020), precipitation-related variables were less important for the models in our study. Temperature-related factors (i.e., AMTem or MaxTemWM) contributed the most to the model



**Fig. 2.** Time-step maps detailing range shifts for the six species under two different Shared Socio-economic Pathways scenarios ((A): SSP1-2.6; (B): SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s). “1” and “0” in the legend indicate presence and absence of one species, respectively. The “contract-expand” group in the legend indicates “1001”, “1011”, and “1101”. The “mixed” group in the legend indicates “0101” and “1010”. The “expand-contract” group in the legend indicates “0100”, “0010”, and “0110”.



**Fig. 3.** Species richness maps cumulating the six species distributions forecasted under two different Shared Socio-economic Pathways scenarios (SSP1-2.6 and SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s).

performance for the six species. As ectotherms, various aspects of freshwater fishes, such as physiology, are directly affected by ambient temperature (Angilletta et al., 2004; Pletterbauer et al., 2015; Comte and Olden, 2017; Barbarossa et al., 2021). Among the temperature-related variables, AMTem was the most important factor in predicting the distributions of *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, consistently with many related studies conducted for freshwater fish species (e.g., Ruiz-Navarro et al., 2016). Interestingly, despite variations in temperature tolerances among these four species (Froese and Pauly, 2023), their responses to AMTem were similar, as reflected by the species response curves, revealing that areas with warm annual mean temperature (around 23 °C) were predicted as climatically suitable for them. Under SSP1-2.6 and SSP5-8.5 scenarios, which could result in a mean warming of 2.0 °C–5.0 °C (Hausfather, 2019), these species were projected to shift towards northern areas where they were currently absent. Additionally, MaxTemWM played a vital role in predicting the potential distributions of two other species, *C. carpio* and *H. leucisculus*, indicating that areas with warm summer temperature (around 33 °C) were more conducive to them. However, the habitat suitability of these two species significantly decreased when the maximum temperature of the warmest month exceeded 33 °C. With the increase in maximum temperature records of summer in the future (Suarez-Gutierrez et al., 2020), habitat losses of these two species could worsen locally. Nevertheless, the two species could still benefit from global warming in small amounts of areas along the external boundaries of their current ranges.

Generally, human activities associated with human population density, hydroelectric projects, and so on could facilitate species invasions (Gallardo and Aldridge, 2013; Su et al., 2021; Xiang et al., 2021). Surprisingly, although our study also confirmed this point, these two variables (i.e., HPD and DamA) contributed very little to our models. This suggests that the six species may have a certain tolerance to anthropogenic factors. Similarly, Elev (elevation) also did not contribute significantly to our models, while it is known to be fundamental in explaining habitat suitability for many fish species (e.g., Kim et al.,

2022). In our study, Elev only played a crucial role in determining habitat suitability for *C. carpio*. In the future, habitat losses for this species were expected to occur in several high-elevation areas, such as parts of the Yunnan-Guizhou Plateau, Southeast Hilly region, and Wuyi Mountain.

#### 4.2. Current and future species ranges

Overall, our study identified South China as a hotspot of suitable habitats for all six species along with suitable habitats for several of the six species in other areas. Shared suitable habitats were expected to occur mainly in South, Central, East China and Sichuan Basin as well as range expansions for a few of these species in Northeast China by the late-century. Notably, most areas in Southwest and Northwest China appeared unsuitable for the six species, both currently and in the future. In terms of geographical distribution, almost all current and future suitable habitats for the six species were differentiated along the Heihe-Tengchong Line, an important geographical dividing line related to various factors (e.g., climates and human populations) (e.g., Wang et al., 2014; Wang and Chen, 2016; Zheng et al., 2021). This could be explained by environmental and anthropogenic differences between the west and east sides of the Heihe-Tengchong Line, where the combination of lower elevation, higher precipitation, higher human density, and warmer temperature in the east side make it more suitable for the six invasive fish species (Wang et al., 2014; Wang and Chen, 2016; Liu et al., 2021b; Zheng et al., 2021), thus emphasizing the need to pay more attention to the eastern side of this dividing line.

Due to differences in species-specific sensitivity to global changes (Ruiz-Navarro et al., 2016), the directions and magnitudes of species range expansions or contractions varied among the six species. Specifically, future global changes were expected to drive large species range expansions for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, but relatively little range expansions or contractions for *C. carpio*. However, all these five species were expected to shift northward. These findings are consistent with other studies showing that invasive species tend to

expand their potential distributions northward with global change (e.g., Ruiz-Navarro et al., 2016). On the contrary, previous studies pointed out that global changes could decrease areas of suitable habitats for invasive species or drive them to southern regions (e.g., Kim et al., 2022; Maimela et al., 2022). Here we found that the range of *H. leucisculus* was expected to decrease as a whole in each future period, indicating that suitable niche space for the species was expected to reduce in areas where the species was currently present in response to future global changes.

Suitable or unsuitable habitats for species in some areas may not be constant during each future time period due to the erratic variability of global changes (e.g., non-linear changes in climates) (Early and Sax, 2011; Shipley et al., 2022). Areas of transitory range dynamics for the six species were primarily sporadic and sparse, mainly scattered along the external or internal boundaries of their current ranges. Nonetheless, it is important not to ignore inconspicuous areas of transitory fluctuations unsuitable for species at some point (e.g., areas of contract-expand), as species ranges can expand when ambient conditions improve (Jackson et al., 2009; Early and Sax, 2011). Timely identifying potential areas for invasive species in the corresponding time period is therefore crucial to adjust and adopt targeted and cost-effective management strategies (Dong et al., 2020; Vythalingam et al., 2022).

## 5. Conclusions

This study revealed that global changes (predominantly future thermal conditions) were likely to favour the spread of all six invasive fish species in China, considering the dramatic expansions in species ranges and their transitory range dynamics during future periods. Targeted and timely management strategies for these species and controlling global warming are urgently needed to prevent successful invasions. More specifically, several strategies can be adopted: (a) formulate and reinforce appropriate laws and policies, including strict regulations on fish stocking activities, crackdowns on illegal aquatic trades, and enhancement of border inspections for aquatic organisms; (b) provide scientific training and education for relevant practitioners to enhance their understanding and management capacity regarding fish invasions; (c) strengthen supervision in sensitive areas, such as conducting regular patrols, monitoring, and removal activities in suitable habitats for these six fish species to restrict their further spread; and (d) mitigate the effects of global warming, such as through afforestation, utilizing renewable clean energy, and strengthening communication and cooperation with relevant international organizations.

## CRedit authorship contribution statement

**Tao Xiang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Visualization, Writing – original draft, Writing – review & editing. **Xianghong Dong:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Software, Visualization, Writing – review & editing. **Lei Shi:** Writing – review & editing. **Gaël Grenouillet:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, 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.

## Acknowledgements

T.X. was funded by the China Scholarship Council (CSC). X.H.D. was funded by the Guizhou University High-Level Personnel Research Project ([2021]65). The EDB laboratory was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). The pictures of the six fish species used in the graphical abstract were sourced from FishBase and the book *The Freshwater Fishes of Guangdong Province*. The Earth illustration used in the graphical abstract was sourced from Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/media-library).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2023.119197>.

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**Supplementary table:**

**Table S1.** Changes in distribution centroids and suitable grid numbers of the six species across different scenarios and time periods compared with those in the current period. Current distribution centroids (longitude, latitude): *C. zillii* (111.76, 23.18); *C. carpio* (114.26, 34.88); *G. affinis* (110.83, 26.98); *H. leucisculus* (113.76, 31.00); *O. mossambicus* (110.88, 24.30); *O. niloticus* (110.44, 24.01).

Species	Scenarios	Time periods	Distribution centroid		Change in suitable grid number (%)
			Longitude	Latitude	
<i>C. zillii</i>	SSP1-2.6	2030s	111.16	25.29	112.19
		2050s	111.13	25.38	122.16
		2070s	111.03	25.31	129.29
	SSP5-8.5	2030s	111.33	25.34	117.92
		2050s	111.38	26.03	207.06
		2070s	111.45	26.37	291.90
<i>C. carpio</i>	SSP1-2.6	2030s	114.75	35.13	2.43
		2050s	114.80	35.22	-0.20
		2070s	115.09	35.15	-0.17
	SSP5-8.5	2030s	114.62	35.03	4.03
		2050s	114.82	35.24	3.53
		2070s	115.17	35.66	-1.05
<i>G. affinis</i>	SSP1-2.6	2030s	110.55	28.30	38.61
		2050s	110.46	28.49	40.97
		2070s	110.15	28.70	47.52
	SSP5-8.5	2030s	110.33	28.30	41.49
		2050s	108.98	29.13	63.60
		2070s	107.72	30.12	91.79
<i>H. leucisculus</i>	SSP1-2.6	2030s	113.56	30.46	-2.10
		2050s	113.19	30.07	-5.24
		2070s	113.12	30.13	-2.85
	SSP5-8.5	2030s	113.26	30.30	-1.06
		2050s	113.66	30.57	-6.82
		2070s	113.84	30.71	-12.60
<i>O. mossambicus</i>	SSP1-2.6	2030s	110.89	26.17	88.54
		2050s	111.18	26.69	116.69
		2070s	111.25	26.72	117.46

<i>O. niloticus</i>	SSP5-8.5	2030s	110.96	26.21	90.60
		2050s	111.48	27.36	161.60
		2070s	111.70	28.36	225.44
	SSP1-2.6	2030s	110.67	25.63	63.44
		2050s	110.71	25.80	76.04
		2070s	110.92	25.87	80.49
	SSP5-8.5	2030s	110.51	25.57	60.57
		2050s	110.88	26.28	104.28
		2070s	111.27	26.74	135.38

### Supplementary data:

#### *MPI-ESM1-2-HR:*

#### Main results

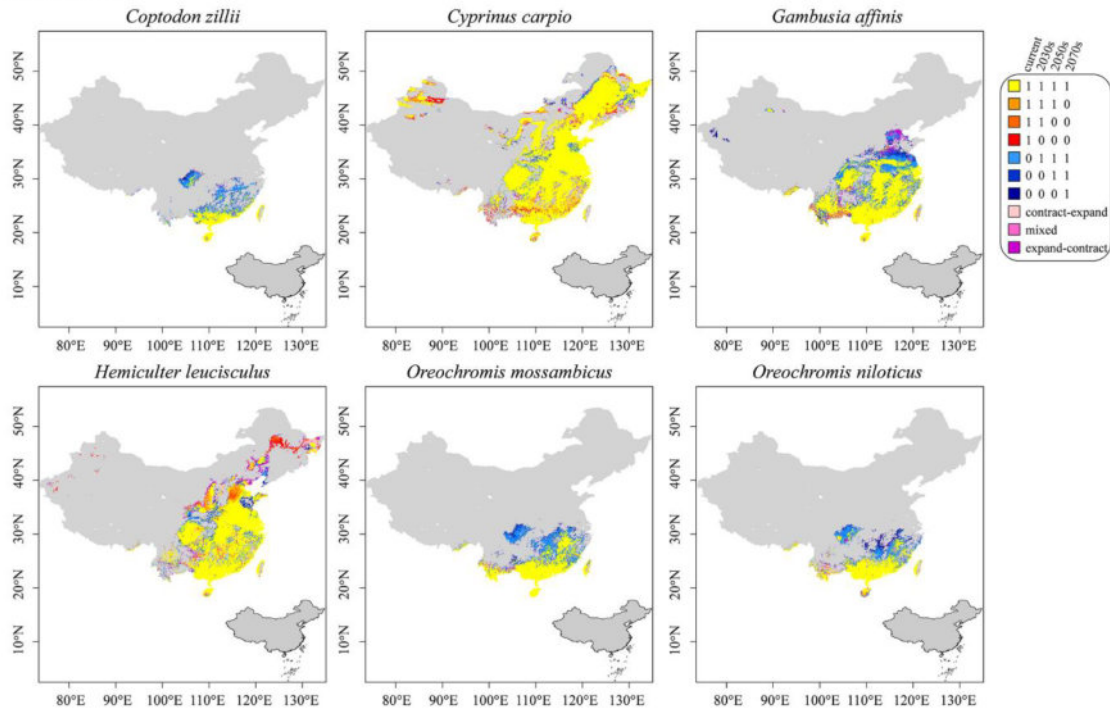
#### Species distribution shifts

The models predicted that the ranges of all six species would shift to varying degrees across different time periods under both SSP1-2.6 and SSP5-8.5 scenarios, with range expansions for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus* more severe with increasing SSP severity, while relatively slight changes in species ranges were observed for *C. carpio* and *H. leucisculus* (Fig. 1; Table 1). Overall, under SSP1-2.6 and SSP5-8.5 scenarios, dramatic range expansions would occur for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, ranging from 33.69% to 299.38% throughout the given time periods. Most of their habitat gains would occur in parts of East, Central, Southwest (mainly in Sichuan Basin), and Northwest (mainly in Tarim basin) China, which were far away from their current ranges. Additionally, the range of *C. carpio* would change slightly and irregularly, while that of *H. leucisculus* would expand marginally, with gains ranging from 1.86% to 8.74%. Furthermore, except a southward

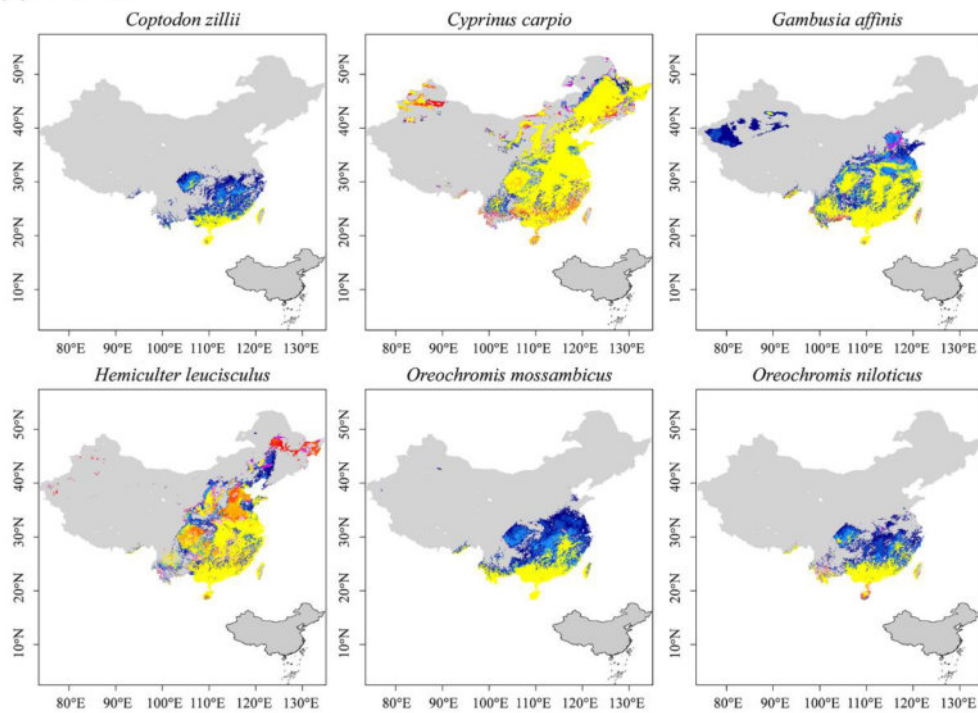
shift in distribution centroid observed for *H. leucisculus*, there would be apparent northward shifts in distribution centroids for the other five species from current to the 2070s (Table 1). Notably, transitory fluctuations in the species ranges for all six species were observed throughout the entire time period (Fig. 1).



**(A) SSP1-2.6**



**(B) SSP5-8.5**



**Fig. 1.** Time-step maps detailing range shifts for the six species under two different Shared Socio-economic Pathways scenarios ((**A**): SSP1-2.6; (**B**): SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s). “1” and “0” in the legend indicate presence and absence of one species, respectively. The “contract-expand”

group in the legend indicates “1001”, “1011”, and “1101”. The “mixed” group in the legend indicates “0101” and “1010”. The “expand-contract” group in the legend indicates “0100”, “0010”, and “0110”.

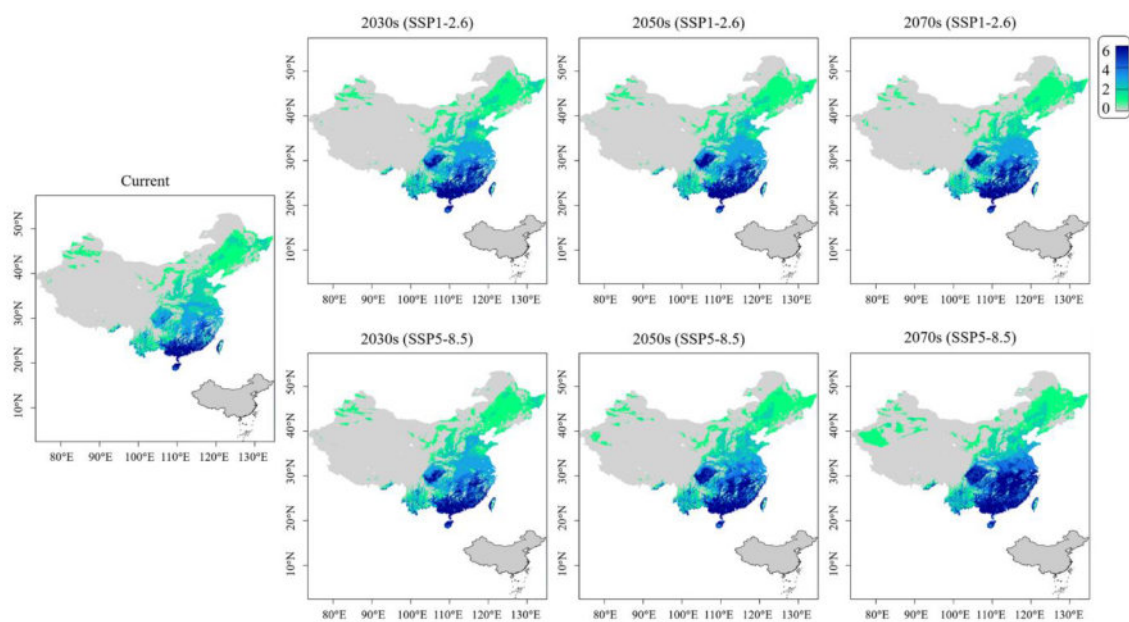
**Table 1.** Changes in distribution centroids and suitable grid numbers of the six species across different scenarios and time periods compared with those in the current period. Current distribution centroids (longitude, latitude): *C. zillii* (111.76, 23.18); *C. carpio* (114.26, 34.88); *G. affinis* (110.83, 26.98); *H. leucisculus* (113.76, 31.00); *O. mossambicus* (110.88, 24.30); *O. niloticus* (110.44, 24.01).

Species	Scenarios	Time periods	Distribution centroid		Change in suitable grid number (%)
			Longitude	Latitude	
<i>C. zillii</i>	SSP1-2.6	2030s	111.65	24.74	89.02
		2050s	111.57	25.04	108.39
		2070s	111.50	25.09	110.70
	SSP5-8.5	2030s	111.71	24.75	73.45
		2050s	111.62	25.55	170.66
		2070s	111.85	26.39	299.38
<i>C. carpio</i>	SSP1-2.6	2030s	114.40	34.91	3.40
		2050s	114.59	34.94	3.51
		2070s	114.86	34.92	-1.05
	SSP5-8.5	2030s	114.47	34.84	4.50
		2050s	114.48	35.10	5.17
		2070s	114.83	35.02	5.75
<i>G. affinis</i>	SSP1-2.6	2030s	111.14	28.02	33.69
		2050s	111.31	28.29	40.18
		2070s	111.10	28.35	42.28
	SSP5-8.5	2030s	111.28	28.26	37.03
		2050s	110.42	28.74	55.71
		2070s	108.00	29.93	92.95
<i>H. leucisculus</i>	SSP1-2.6	2030s	113.41	30.89	8.74
		2050s	113.05	30.43	6.52
		2070s	113.38	30.26	1.86
	SSP5-8.5	2030s	113.18	30.58	6.93
		2050s	112.88	30.47	6.16

<i>O. mossambicus</i>	SSP1-2.6	2070s	113.20	30.66	4.41
		2030s	111.04	25.39	53.02
		2050s	110.94	25.68	64.10
	SSP5-8.5	2070s	111.07	25.80	65.56
		2030s	111.34	25.47	50.20
		2050s	111.36	26.65	114.59
<i>O. niloticus</i>	SSP1-2.6	2070s	111.70	27.62	187.47
		2030s	110.48	25.10	46.90
		2050s	110.69	25.28	53.72
	SSP5-8.5	2070s	111.03	25.55	64.41
		2030s	110.61	25.02	38.62
		2050s	110.88	25.89	84.36
		2070s	111.48	26.82	147.05

### Current and future species richness of the six fish species

A significant increase in species richness of the six species would predominantly occur in parts of East, Central, and Southwest China across the given time periods under both SSP1-2.6 and SSP5-8.5 scenarios (Fig. 2). By the 2070s, species richness would be relatively high in South, Central, and East China and parts of Southwest China (e.g., Sichuan Basin) under these two scenarios.



**Fig. 2.** Species richness maps cumulating the six species distributions forecasted under

two different Shared Socio-economic Pathways scenarios (SSP1-2.6 and SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s).

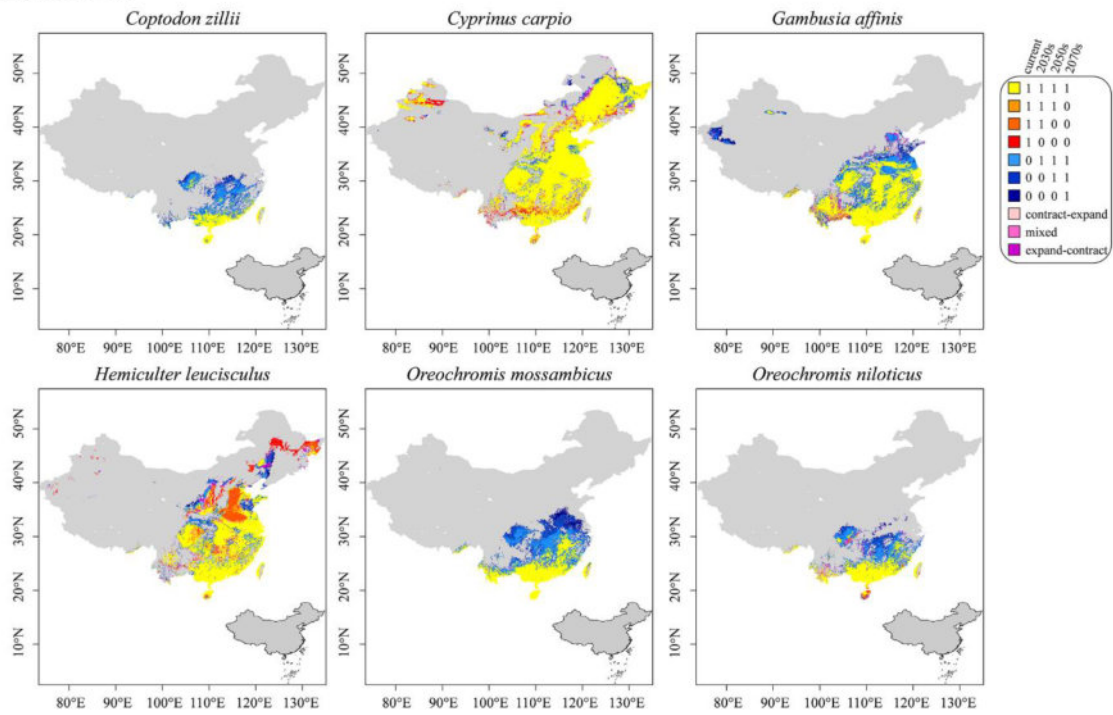
### ***EC-Earth3-Veg:***

#### **Main results**

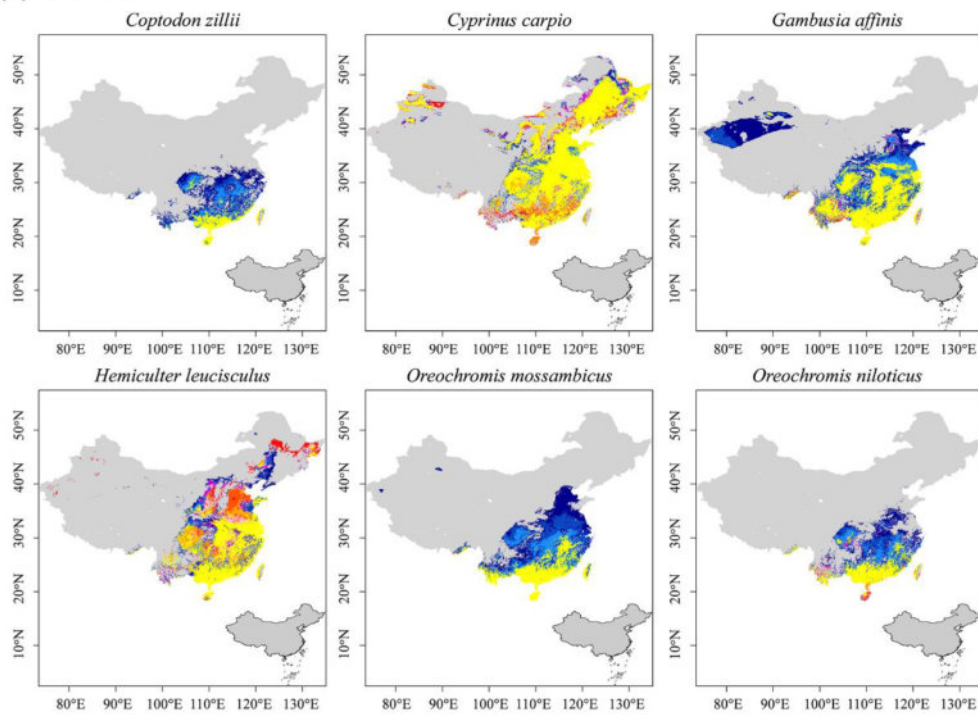
##### **Species distribution shifts**

The models predicted that the ranges of all six species would shift to varying degrees across different time periods under both SSP1-2.6 and SSP5-8.5 scenarios, with range expansions for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus* more severe with increasing SSP severity, while irregular changes in species ranges were observed for *C. carpio* and *H. leucisculus* (Fig. 3; Table 2). Overall, under SSP1-2.6 and SSP5-8.5 scenarios, dramatic range expansions would occur for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, ranging from 35.80% to 378.84% throughout the given time periods. Most of their habitat gains would occur in parts of East, Central, Southwest (mainly in Sichuan Basin), and Northwest (mainly in Tarim basin) China, which were far away from their current ranges. Additionally, the range of *C. carpio* and *H. leucisculus* would change slightly and irregularly. Furthermore, except a southward shift in distribution centroid observed for *H. leucisculus*, there would be apparent northward shifts in distribution centroids for the other five species from current to the 2070s (Table 2). Notably, transitory fluctuations in the species ranges for all six species were observed throughout the entire time period (Fig. 3).

**(A) SSP1-2.6**



**(B) SSP5-8.5**



**Fig. 3.** Time-step maps detailing range shifts for the six species under two different Shared Socio-economic Pathways scenarios ((A): SSP1-2.6; (B): SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s). “1” and “0” in the legend

indicate presence and absence of one species, respectively. The “contract-expand” group in the legend indicates “1001”, “1011”, and “1101”. The “mixed” group in the legend indicates “0101” and “1010”. The “expand-contract” group in the legend indicates “0100”, “0010”, and “0110”.

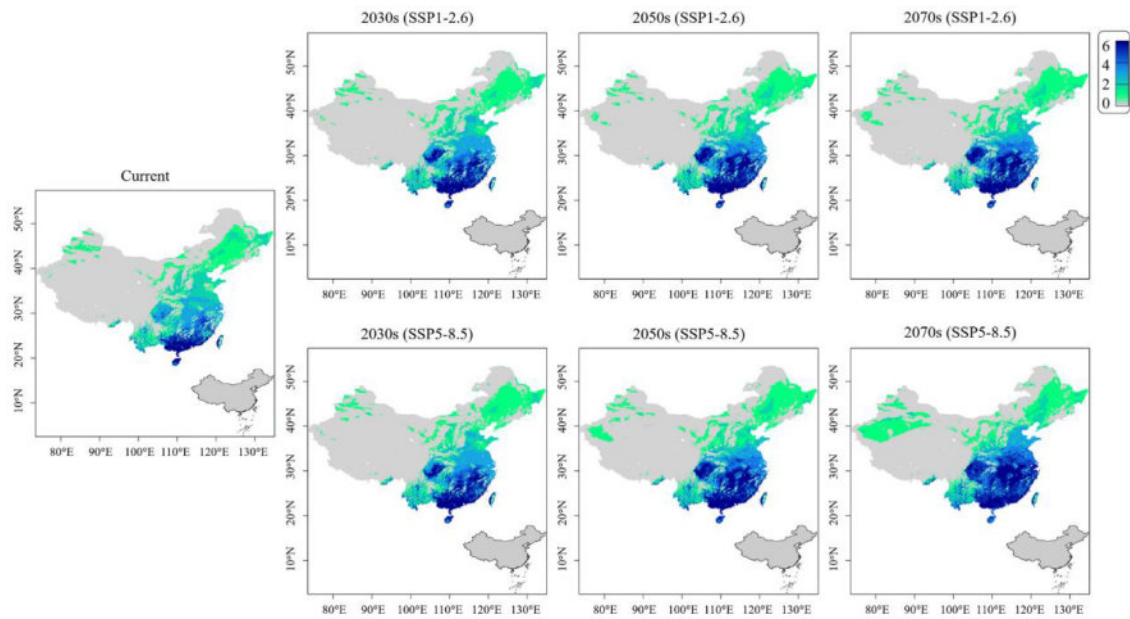
**Table 2.** Changes in distribution centroids and suitable grid numbers of the six species across different scenarios and time periods compared with those in the current period. Current distribution centroids (longitude, latitude): *C. zillii* (111.76, 23.18); *C. carpio* (114.26, 34.88); *G. affinis* (110.83, 26.98); *H. leucisculus* (113.76, 31.00); *O. mossambicus* (110.88, 24.30); *O. niloticus* (110.44, 24.01).

Species	Scenarios	Time periods	Distribution centroid		Change in suitable grid number (%)
			Longitude	Latitude	
<i>C. zillii</i>	SSP1-2.6	2030s	111.63	25.07	114.61
		2050s	111.82	25.77	182.56
		2070s	111.69	25.88	197.91
	SSP5-8.5	2030s	111.81	25.06	114.87
		2050s	111.62	25.87	201.12
		2070s	111.77	26.85	378.84
<i>C. carpio</i>	SSP1-2.6	2030s	114.58	35.03	3.38
		2050s	114.76	35.10	2.58
		2070s	115.09	35.16	0.21
	SSP5-8.5	2030s	114.50	34.95	3.38
		2050s	114.65	35.18	4.37
		2070s	114.89	35.78	-1.70
<i>G. affinis</i>	SSP1-2.6	2030s	111.06	28.14	35.80
		2050s	110.77	28.49	47.71
		2070s	110.35	28.85	54.64
	SSP5-8.5	2030s	111.15	28.09	36.40
		2050s	109.44	29.05	63.40
		2070s	106.31	31.11	118.73
<i>H. leucisculus</i>	SSP1-2.6	2030s	113.24	30.46	3.13
		2050s	113.07	30.11	-3.67
		2070s	113.10	30.11	-5.11
	SSP5-8.5	2030s	113.06	30.05	-0.30

		2050s	112.89	30.07	-1.28
		2070s	113.34	30.52	-4.30
<i>O. mossambicus</i>	SSP1-2.6	2030s	111.02	25.69	70.36
		2050s	111.25	26.68	119.95
		2070s	111.53	27.16	141.89
	SSP5-8.5	2030s	111.12	25.77	73.06
		2050s	111.46	27.11	147.95
		2070s	111.69	28.55	246.32
<i>O. niloticus</i>	SSP1-2.6	2030s	110.76	25.41	59.49
		2050s	110.94	25.87	85.65
		2070s	111.10	26.11	94.22
	SSP5-8.5	2030s	110.82	25.43	59.74
		2050s	110.97	26.30	107.60
		2070s	111.75	27.42	170.07

### Current and future species richness of the six fish species

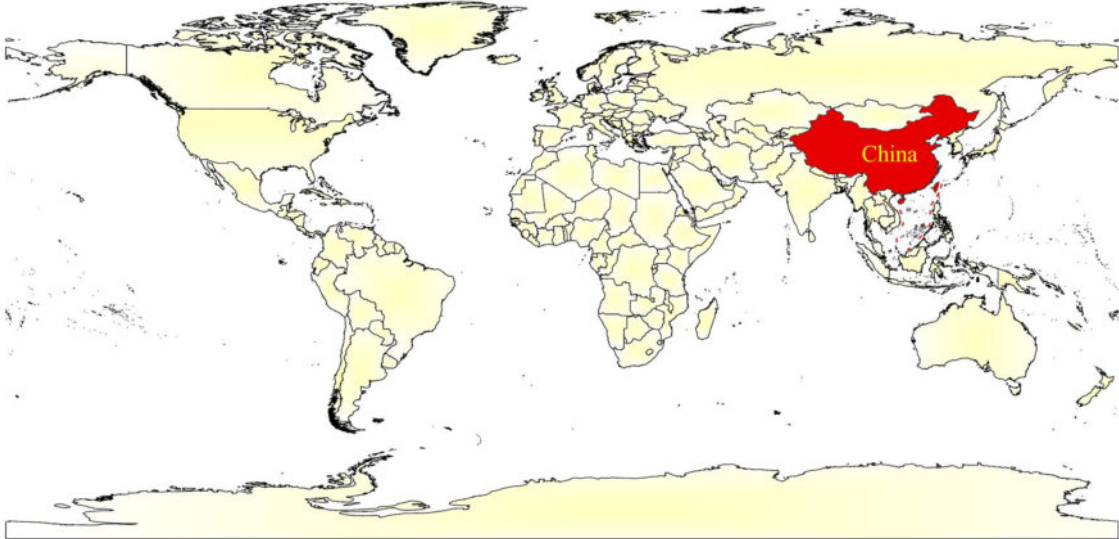
A significant increase in species richness of the six species would predominantly occur in parts of East, Central, and Southwest China across the given time periods under both SSP1-2.6 and SSP5-8.5 scenarios (Fig. 4). By the 2070s, species richness would be relatively high in South, Central, and East China and parts of Southwest China (e.g., Sichuan Basin) under these two scenarios.



**Fig. 4.** Species richness maps cumulating the six species distributions forecasted under two different Shared Socio-economic Pathways scenarios (SSP1-2.6 and SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s).



## Chapter 6: Conclusions and Perspectives



## **6.1 Conclusions**

### **(A) Non-native species differed ecologically or biologically from natives**

In this study, we recorded 1,797 wild freshwater fish species in China, the highest number compared to any previous studies. The largest number of non-native freshwater fish species (84 exotic species and 116 translocated species) in China's wild habitats was also identified. We then analysed data on the largest number of freshwater fish species in China (1,597 native, 84 exotic, and 116 translocated) and species traits related to their ecology and life history. Our findings showed that native species significantly differed from both exotic and translocated species in terms of their quantitative species traits, while no significant differences were found between exotic and translocated species. Additionally, fish species that had higher vulnerability to fishing due to their intrinsic characteristics, trophic level, and pectoral fin vertical position, but lower resilience and lateral body shape, were considered as potential candidates for introduction and dispersal in China, compared to native species (More details can be found in [Fig. 4](#) in **Chapter 3**).

### **(B) Freshwater fish biodiversity patterns in China underwent changes at the basin level**

Over the past 120 years, China's freshwater ecosystems have seen numerous non-native fish introductions as well as a few fish extinctions, which pose a threat to the country's native freshwater fish biodiversity across various facets including taxonomic, functional, and phylogenetic diversity. More specifically, taxonomic, functional, and

phylogenetic richness 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. Moreover, in 86.60% (88.52% of China's land area), 81.44% (85.86%) and 83.51% (84.03%) of the studied units, fish assemblages showed a trend towards taxonomic, functional, and phylogenetic homogenization, respectively. The most significant decreases in biological dissimilarities were observed in Northwest and Southwest China. To better describe and understand synthetic effects of non-native fish introductions and native fish extinctions on biodiversity facets, we developed a new biodiversity index. This index combined taxonomic, functional, and phylogenetic information, using both alpha and beta diversity approaches. We named it 'multifaceted changes in fish biodiversity'. This index indicated that the greatest multifaceted change took place in Ili River basin, followed by 16 other relatively extreme situations, mainly occurring in Northwest, Southwest, and North China. What's more, environmental factors, such as net primary productivity, average annual precipitation, and unit area, were found to largely drive these changes in biodiversity. Thus, taking into account both environmental and anthropogenic factors, it is recommended that targeted conservation and management strategies be proposed and implemented in areas with relatively high levels of change in freshwater fish biodiversity.

### **(C) Invasive fish in China would face range shifts due to global changes**

Once established, invasive fish populations are difficult, if not impossible, to be completely eradicated. The most efficient and hopeful approach is regarded as

preventing the introduction, establishment, and spread of invasive species. It is therefore essential to understand how the ranges of invasive fish species would respond to future global changes along with their determinants. We here utilized species distribution models (the maximum entropy algorithm) to evaluate the potential distributions of six notorious invasive fish species in current and future periods along with their determinants, under two Shared Socio-economic Pathways scenarios. We found that the habitat suitability for the six species substantially benefited from temperature conditions. Furthermore, the potential ranges of all six species were expected to undergo varying degrees of shifts. Transitory fluctuations were also observed in the potential ranges of all six species throughout the entire study period. Overall, our projections indicated that by the 2070s, the species richness of these invasive fish species was expected to be considerably high in South, Central, and East China, as well as in certain areas of Southwest China. Considering this, customized approaches must be created and put into practice in the specific regions that require them the most in each given timeframe.

## **6.2 Perspectives**

### **(A) Assessing the economic losses caused by non-native freshwater fish species**

The widespread introduction of non-native freshwater fish species, combined with relatively few native fish extinctions, has been shown to have caused serious harm to freshwater fish biodiversity in China. However, such crises not only cause losses to freshwater fish biodiversity, but also pose threats to the economy and human society

(Xiong et al., 2015; Liu et al., 2021; Haubrock et al., 2022). Since the 1960s, non-native fish species are believed to have incurred a global cost of over \$37.08 billion (Haubrock et al., 2022). Due to incomplete information on non-native fish species and the fact that the losses caused by non-natives are mainly attributed to fishery management costs and damages to fishery resources (Haubrock et al., 2022), the economic losses caused by non-natives in China may be underestimated. As a result, in future research, we will further improve the basic information of non-native fish species in China, and evaluate the economic losses caused by non-natives from various perspectives, such as commercial and recreational fishery losses, fishery management costs, human health losses, and food security.

### **(B) Exploring mechanisms shaping functional and phylogenetic diversity patterns of native freshwater fish assemblages in China**

Understanding the distribution of biodiversity and its determinants is of significant importance to humanity, which can help humans comprehend the role biodiversity plays in ecosystem processes, potential impacts of global changes (e.g., anthropogenic and environmental factors) on biodiversity maintenance, and so on (Gaston, 2000; Su et al., 2022). Freshwater fish species richness and endemism in China and adjacent areas are strongly driven by ‘Historical’ factors based on 12 variables related to the historical climate stability and isolation degree (He et al., 2020). However, until now, the mechanisms that have shaped the functional and phylogenetic diversity of native fish species assemblages in China are still unclear. Therefore, in future studies, we will

focus on addressing the issues.

### **(C) Predicting potential distributions for invasive fish species in China**

China is the country in the world that suffers the most from invasive freshwater fish species, with over 200 non-native fish species identified in the wild (Xiong et al., 2015; Xiang et al., 2021). In view of the difficulty or impossibility of eradicating invasive freshwater fish once they have established populations (Dong et al., 2020), we have predicted potential areas where invasive fish may thrive. Notably, so far, we have only used a single algorithm to study the current and potential distributions of the six most notorious invasive fish species to respond to global changes. Therefore, in the future, we will further update the inventory and location information of invasive fish species in China. We will also develop an ensemble species distribution model, along with its basal models (using different machine learning algorithms), to study potential distributions of invasive fish species with sufficient occurrence data. However, species distribution models are only adopted to analyse the correlation between species distribution data and environmental or spatial conditions without taking into account likely biotic interactions (Pollock et al., 2014; Dong et al., 2020). In addition to considering ensemble species distribution models, we will also evaluate and predict potential distributions of invasive fish species using joint species distribution models, as such models are expected to enable more accurate predictions by considering interactions between multiple species (Wilkinson et al., 2021).

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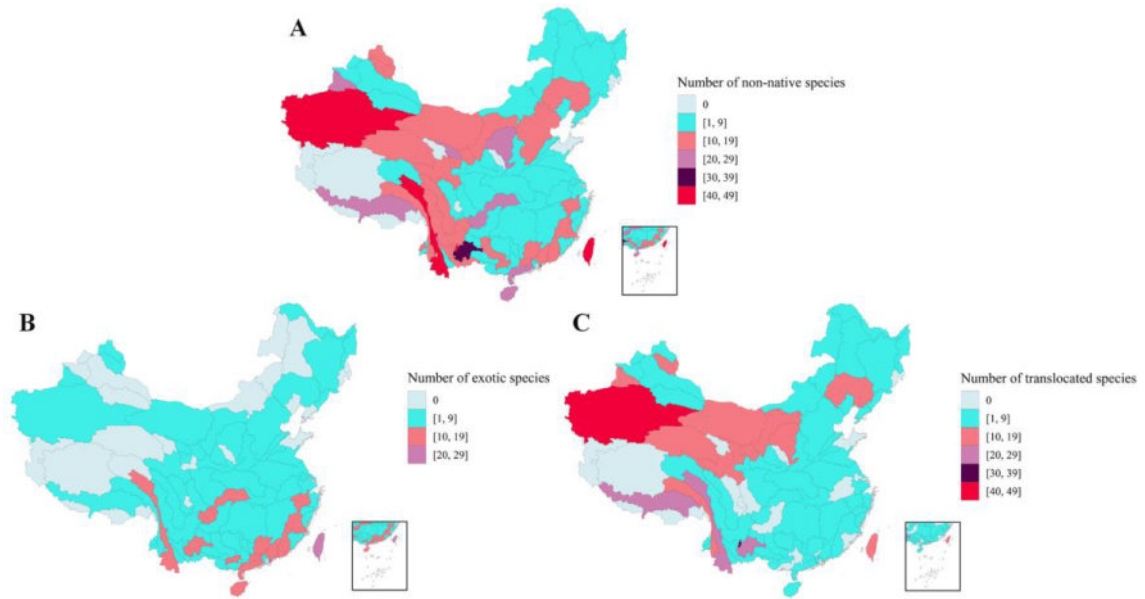
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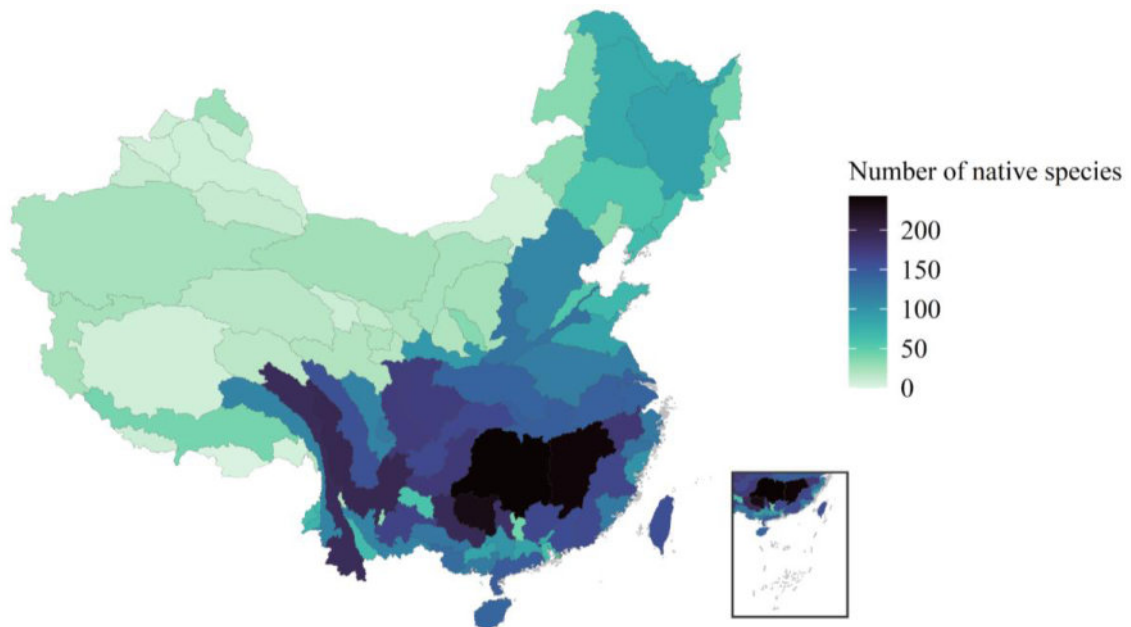
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Appendix I: Species richness maps for hydrological units



**Fig. 1.** Number of (A) non-native (i.e., exotic + translocated), (B) exotic, and (C) translocated species in China's hydrological units.



**Fig. 2.** Number of native species in China's hydrological units.

**Appendix II: Save China's gaurs**

*Science*, **381**(6659), 741

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## Save China's gaurs

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*Science*, **381** (6659), .  
DOI: 10.1126/science.adj4691

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built on farmland, threatening food security (2, 3). Given the ambitious climate pledges of signatory countries to the Paris Agreement, the area of land required to deploy global solar photovoltaics in the coming decades is expected to rise (4). Governments must act now to mitigate the fierce competition for land between solar energy and crops.

Solar energy projects have encroached on farmland across the Northern Hemisphere (3). In 2017 alone, China deployed photovoltaic panels on about 100 km<sup>2</sup> of farmlands in the North China Plain (3), one of China's most important agricultural regions. Solar photovoltaic panels have also been deployed over deserts, abandoned mines (5), artificial canals (6), reservoirs (7), and rooftops (8), but these options are less attractive to developers because they are more scarce, more unstable, or more expensive than farmlands.

To ensure national food security, some countries have released strict farmland protection regulations [e.g., China's Basic Farmland Protection Regulations in 1994, Germany's Federal Regional Planning Act in 1997, and South Korea's Farmland Act in 1994 (9)]. However, solar energy investors and developers continue to occupy farmland illegally (10). Local authorities provide inadequate enforcement, allowing development to proceed at the expense of agriculture.

Mitigating solar energy's land competition will require technological innovation and more sustainable deployment strategies. For example, agrivoltaic systems have been proposed that would allow crops to grow under solar panels (11). However, the solar panels hinder mechanized farming and harvesting, and the solar photovoltaics need to be deployed at a position much higher than crops, making the project more expensive. Scientists have also developed foldable solar cells that can be integrated into buildings (12).

Until these technologies are cost-effective and scalable, governments should preferentially use unproductive lands for large-scale photovoltaic deployment, prevent installations on finite arable land, and provide stricter enforcement of farmland protection policies. Satellite remote sensing technologies should be used to closely monitor solar photovoltaic panels' illegal farmland encroachment and quantify their impacts on food production. Illegally deployed solar photovoltaics should be demolished so that farmland can be restored. Governments, corporations, and nonprofit organizations should also provide funding to scientists to research and develop cost-effective, eco-friendly, energy-efficient solar cells, including agrivoltaic technology. Scientists should

also work to better understand the adverse and unintended consequences of large-scale solar photovoltaic deployment to ensure that the technology provides net benefits in the future.

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10.1126/science.adj1614

## Save China's gaurs

The gaur (*Bos gaurus*), the largest living bovine species, primarily inhabits tropical and subtropical broadleaf forests, bamboo forests, and sparsely tree-covered grasslands (1). In China, the species is mainly found in Xishuangbanna Prefecture in Yunnan Province (1, 2). Anthropogenic changes have brought this population to the brink of extinction. China must take action to save this vulnerable megafauna.

Since the 1950s, crop cultivation has expanded in Yunnan, resulting in the replacement of natural forests (3, 4). In some cases, these cultivated lands have even encroached into natural reserves (3, 5). As a result, the gaur has lost a large area of habitat, likely forcing the population to relocate to steeper natural forest areas (4, 6).

In addition to habitat loss and fragmentation, indiscriminate hunting and illegal trade have contributed to the substantial decline of the gaur population (1). Between 1979 and 1985, a staggering total of 83 individuals were killed by hunters in Xishuangbanna (1). The total gaur population in Xishuangbanna has declined from between 605 and 712 individuals in 1984 to an estimated 152 and 167 individuals in recent decades (1, 6). In Menglun, Xishuangbanna, gaurs are functionally extinct (7).

The gaur is included on the National Class I key protected wildlife list (2) and classified as Critically Endangered on the Red List of China's Vertebrates (8). To protect the remaining gaurs, China has designated the species as a conservation priority in multiple natural reserves (9) and used

technologies such as infrared cameras to monitor them in real time and assess their population dynamics and behaviors (10). However, these efforts are insufficient.

The fragmented habitats within natural reserves should be restored immediately to natural forests. In areas outside natural reserves where the gaur frequently roams (11), poaching should be prevented by means of increased penalties and enforcement. The Chinese government should offer subsidies and tree-planting training programs to incentivize farmers to engage in converting farmland to forests, with rewards based on their farmland area and the number of trees planted. Establishing an ecological compensation mechanism could enable farmers to participate in animal conservation efforts and receive corresponding allowances. Lastly, given that the gaur has a wide range of activity and migratory habits that allow individuals and populations to move based on the weather conditions and the availability of food and water (4, 11, 12), assisted migration may be feasible. When gaurs are trapped in unsuitable locations, unable to migrate due to barriers like villages and highways, translocating some individuals to sparsely populated and environmentally suitable areas could be successful. Without substantial additional conservation strategies, the gaur could soon go extinct in China.

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10.1126/science.adj4691

**Appendix III: Heishan Gorge project: learn from past oversights**

*Nature*, **621** (7977), 42

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## Urbanization is reshaping food production in China

Millions of jobs in food production are disappearing around the world, mostly on smallholder farms, because of increased migration from rural areas to cities (E. S. Brondizio *et al. Nature* **620**, 33–36; 2023). In China, this shift is benefiting other aspects of the economy.

Rural populations are ageing as many members of younger generations depart to seek training in non-farm sectors. This is reshaping China's agricultural employment by boosting a transition from small-scale to large-scale farms run by fewer, but better trained, young agricultural managers (see S. Wang *et al. Nature Food* **2**, 183–191 (2021); C. Ren *et al. Nature* **616**, 96–103; 2023).

Meanwhile, rural migrants gain access to better education and health care. This potentially boosts earnings and career trajectories, as well as promoting economic expansion and job creation. Encouraging more of these new professionals to return to rural areas to work in non-agricultural sectors will raise living standards there and narrow the rural–urban socio-economic divide. Government incentives (for examples, see Y. Li and G. Mo *J. Agriculture* <https://doi.org/krr2>; 2022) and the installation of remote-working infrastructure will help.

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## Measures to ensure clinical trials are trustworthy

I disagree that medicine is plagued by untrustworthy clinical trials, and particularly object to the view that you quote: “If you search for all randomized trials on a topic, about a third of the trials will be fabricated” (*Nature* **619**, 454–458; 2023). That opinion is not backed by independently verified data, so I find this reporting sensationalistic and potentially offensive to medical authors.

Errors in trials can have many causes apart from negligence or fraud. All such cases should be investigated meticulously, and the responsible author(s) formally punished in cases of proven wrongdoing. Articles, their reported data and the authors should not be considered as untrustworthy from the outset.

Clinical trials aimed at regulatory submission must comply with guidelines from the International Council for Harmonisation of Technical Requirements for Pharmaceuticals for Human Use (ICH; see [go.nature.com/3vkms](https://go.nature.com/3vkms)), in particular sections E6 (on good clinical practices) and E8 (on general considerations for clinical-trial design). Those trials should meet strict ethical and scientific standards. They should incorporate quality control and quality assurance based on monitored data and audited processes. This generates a verifiable trail of information. Publishers should require authors to declare that ICH guidelines have been followed and should request more information in cases of doubt.

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## Heishan Gorge project: learn from past oversights

Freshwater biodiversity in China's upper Yellow River is once again under threat, this time from the planned Heishan Gorge hydraulic engineering project. This follows the construction of multiple reservoirs along the Yellow River basin since the 1950s. Local governments should learn from the past and assess the project's potential ecological impacts before going ahead.

Previous projects destroyed the spawning grounds, migratory channels and feeding habitats of local aquatic organisms. The species affected included those that were once economically important, such as the northern bronze-gudgeon (*Coreius septentrionalis*) and Japanese eel (*Anguilla japonica*), which have mostly disappeared from the river's reaches. The Heishan Gorge is the last viable location for high dam and reservoir construction on the upper Yellow River.

Approval of the Heishan Gorge project is being expedited after about 70 years of discussion. The reach of the river that would be affected has a drop of more than 100 metres and contributes about two-thirds of the basin's total annual runoff. It is one of the few remaining natural habitats suitable for aquatic organisms in the basin. I urge local governments to seek ecofriendly alternatives – such as the promotion of renewable-energy technologies and water-efficient irrigation techniques – that would also benefit local residents.

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