FISH and FISHERIES

FISH and FISHERIES, 2014, **15**, 209–230

# Mapping China's freshwater fishes: diversity and biogeography

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*Received 20 Mar 2012*
*Accepted 16 Nov 2012*

## Abstract

Freshwater fishes worldwide face an array of threats from dam construction, river fragmentation, pollution, over-exploitation and interactions with introduced species. Such impacts are especially prevalent in densely populated countries undergoing rapid development, and their effects are felt most strongly where regional fish diversity is high. We reviewed studies of the distribution of freshwater fish species throughout China to map a biogeographical pattern and ascertain the environmental factors contributing to this distribution. We then linked this information to identify geographic areas to be recommended as the focus of conservation efforts.

A total of 920 species in 302 genera, 54 families and 21 orders were recorded. Among the recorded species, 73% were Cypriniformes and 12% were Siluriformes. Cyprinidae was the most dominant family with 473 species, followed by Balitoridae with 157 species. The administrative division of the biogeography of China's freshwater fishes consisted of nine regions, including the Qinghai-Tibetan Plateau Region, Oriental Region, Northwest Region, South Region, Loess Plateau Region, Heilongjiang Region, Upper Yangtze Region, 3H Plain Region and Middle-Lower Yangtze Plain Region. The river system was the primary factor in determining China's freshwater fish biogeography. Under stepwise regression analysis, river discharge was found to be the most influential factor in determining richness, followed by population size and net primary productivity. The higher level of fish endemicity and sensitivity to environmental change led to the identification of Southwest China and the higher areas of Qinghai-Tibetan Plateau as the primary areas to be considered for fish conservation and potential natural reserves.

**Keywords** Cyprinidae, discharge, distribution, geological event, NPP, river system



 DOI: 10.1111/faf.12011 

## Introduction

Presently, the worldwide biota is entering into a sixth mass extinction (Dirzo and Raven 2003; Wake and Vredenburg 2008; Barnosky *et al.* 2011). Moreover, fishes, which comprise the largest group of vertebrates, are now experiencing a marked change at a global scale (Casey and Myers 1998; Pauly *et al.* 2003; Xenopoulos *et al.* 2005). Thus, the geographic map of fishes on this planet needs to be redrawn (Sala *et al.* 2000; Butchart *et al.* 2010; Hugueny *et al.* 2011). To mitigate such changes, fisheries management should aim at robust and functional ecosystems to reach a sustainable use of fisheries resources. Spatial-temporal distribution data, combined with the application of biogeographical principles and theories, need to be clarified and updated. The general and fundamental characteristics of freshwater fish fauna, for example, spatial patterns and distribution–environment relationship at global (Oberdorff *et al.* 1995; Lévêque *et al.* 2008) and continental scales (Oberdorff *et al.* 1999; Reyjol *et al.* 2007; Kang *et al.* 2009) have been clearly delineated.

China's freshwater fish fauna, which is characterized by the dominance of Cyprinidae, includes a part of the Oriental subregion of the Indian Region (south and south-west parts of China) and a part of the Central Asia subregion of the Palearctic Region (north, east and middle parts of China) (Rainboth 1991; Reshetrukov and Shakirova 1993; Jayaram 1999). Several ichthyologists have designated China as the 'centre of dispersal' of the world's freshwater fishes (Darlington 1957; Wu 1964, 1977; Menon 1987; Banarescu 1992).
A 400-million-year-old fossil fish *Psarolepis romeri*, Incertae sedis, considered as the origin of bony fishes, was discovered in Southwest China (Yu 1998; Zhu *et al.* 1999). The current distribution of China's freshwater fish fauna formed in the late Tertiary to early Quaternary during the uplift of the Qinghai-Tibetan Plateau and the global climate cooling. During periods of glaciations, fish species retreated southwards, which favoured frequent land connections between the south-eastern mainland of China and western Pacific islands. In the interglacial periods, species spread back to the north, resulting in the formation of dispersal species and relict species (Zakaria-Ismail 1994; Chang *et al.* 1996; Chang and Chen 2000). Alternate glacial and interglacial changes also enabled fish exchanges among sections of large rivers, and these species differentiated in the upper, middle and lower reaches under the pressure of habitat change.

Since the 1950s, ichthyologists have analysed China's freshwater fish fauna at different levels, mainly by considering the differences in climate and drainage, as well as by empirical appraisal of fish distribution. Zhang (1954) first divided Chinese freshwater fishes into five divisions (Appendix S1). According to palaeogeohistory and ecological distribution information on 767 China's freshwater species and subspecies from 209 genera, 33 families and 13 orders, Li (1981) divided the fish fauna into five divisions and 21 subdivisions (Appendix S2). Pan *et al.* (1985) reanalysed the fish data from the study by Li (1981) at a subregional level using cluster analysis. Although no new division was suggested in the work of Pan *et al.* (1985), the authors doubted the results of Li (1981). Based on the concept of 'Faunistic Complex' (referring to a group of animals which originated and developed in the same geographic zone and a certain time, see Stegmann 1938; Никольский, 1956), Shi (1985) found eight faunistic complexes that explained China's freshwater fish fauna. Although Shi (1985) provided lists of the typical fish species in each complex, he did not identify the geographic distribution patterns in detail; instead, he worked them out in mostly unorganized combinations of plain/mountain and south/north.

In contrast, Liu and Chen (1998) divided China's freshwater fish fauna into six types based on extant Cyprinidae. Their conclusion was primarily based on fish biology and ignored the inclusion of climate and ecological factors. Thus, the divisions that Liu and Chen (1998) formed were vague, with many overlapping areas. With continuous improvements in the data and statistical analysis methods on fish species, a more detailed study on the structure of China's freshwater fish fauna is now possible.

Freshwater fishes disperse in response to climate or topographical changes, as well as to evolutionary history and geological events (Olden *et al.* 2010). A species-discharge hypothesis (Welcomme 1979; Brönmark *et al.* 1984) similar to the species–area curve in terrestrial systems, which implies that fish species richness increases logarithmically with river discharge, is generally used to explain the biogeography of fish spatial distribution. The species–energy hypothesis (Wright 1983), which predicts that species richness is positively correlated with energy availability, also gained attention in biogeographical studies (Guégan *et al.* 1998; Vörösmarty *et al.* 2010). In addition, other factors (e.g. latitudinal zonation, longitudinal process, habitat heterogeneity, contemporary climate, physicochemical variability) have been considered to have marginal importance in shaping the spatial patterns of fish fauna (Hurlbert *et al.* 1972; Oberdorff *et al.* 1997; Leprieur *et al.* 2008; Araújo *et al.* 2009; Pracheil *et al.* 2009). Anthropogenic factors such as overexploitation, pollution, dam construction and river fragmentation have significant effects on the abundance and distribution of fishes (Allan *et al.* 2006; Dudgeon *et al.* 2006). Integration of information about these factors in China and in other parts of the world can provide insights into the catalysts of prime conservation problems and predictions about the fate of key species and ecosystems (Whittaker *et al.* 2005; Olden *et al.* 2010). Official governance on biological resources is generally determined at an administrative level in China, so a biogeographical analysis that establishes appropriate administrative divisions will be helpful in developing effective conservation efforts.

The present work aims to answer the following questions: (i) what is the current freshwater fish biogeographical pattern in China? (ii) how do environmental factors affect fish species distribution and richness? and (iii) what areas are key ecoregions for conservation efforts based on species distribution and biodiversity? To answer these questions, we first collected all the available data on fish species and their distribution and compiled a species presence/absence data matrix at an administrative unit level. We then analysed the matrix to determine a geographical distribution pattern. The relationships between environmental factors and fish species richness were derived using multiple regression analysis. Finally, we reviewed the current threats to Chinese freshwater fishes and recommended critical areas for conservation efforts.

## Materials and methods

### Study area

China is one of the largest countries in the world, spanning about 50° of latitude (between 4°15′ N and 53°31′ N) and 63° of longitude (73°40′ E and 135°50′ E). Approximately 98% of China's land area is located between 20 and 50 north latitude, including plateaus, plains, basins, foothills and mountains. The territory of China extends approximately 5200 km from west to east and 5500 km from north to south. Based on the administrative scale, China is divided into 34 units including 23 provinces, 5 autonomous regions, 4 municipalities and 2 special administrative regions. A total of 28 units (23 provinces and 5 autonomous regions) were analysed in this work (Fig. 1).

### Fish data

Extensive literature surveys were conducted to obtain information on all native and non-native freshwater fish species, as well as their distributions. Literature was gathered from more than 200 bibliographic sources including published papers, books and grey literature databases (main references see Appendix S3). Estuarine species, which have to spend at least a part of their life cycles in oceanic conditions, were excluded. Gathered data were then revised according to www.fishbase.org to avoid invalid species, as well as synonyms and homonyms. Presence/absence data scored the presence of a species in an area as '1' and the absence as '0'.

Fish data were determined at administrative unit scale instead of watershed scale (generally considered by many studies) to map the biogeographical pattern due to the following three reasons: (i) Governance: current laws and regulations concerning biodiversity conservation in China are constituted and executed under administrative departments, (ii) Data: surveys on fishes are generally conducted by each provincial unit and (iii) History: over the long course of establishment and abolishment of state power, China has to a great extent, established administrative units according to the natural environmental boundaries which have been beneficial in war, culture or governance, either consciously or subconsciously. Thus, current administrative units are assumed to represent the differences in natural environmental conditions, especially for conservation biogeography.

### Environmental factors

Species richness is influenced by the environmental characteristics of habitat geomorphology, climate and species interactions. Eight factors including river discharge, altitude, latitude, longitude, air temperature, precipitation, net primary productivity (NPP) and human population were used here to determine the relationships between environment and fish species richness under regression analysis (as described below).

#### *Geographical data*

Primary geographic information of administrative unit divisions and major river networks was obtained from the Chinese National Fundamental Geographic Information System (National Geomatics Center of China, http://ngcc.sbsm.gov.cn/article/en/or/dp/, 31 October 2012). Altitude, latitude and longitude data were originally obtained from Shuttle Radar Topography Mission Database with a resolution at 30 arc-second grid (http://srtm.usgs.gov/index.php, last accessed 31 October 2012). Such resolution is equivalent to approximately 0.86 $km^2$ at the equator and less elsewhere and commonly referred to '1-km' resolution. The mean altitude data of each unit were calculated by averaging the values of each grid within the unit. River discharge data at administrative unit level were obtained from The Ministry of Water Resources of the People's Republic of China (http://www.mwr.

  

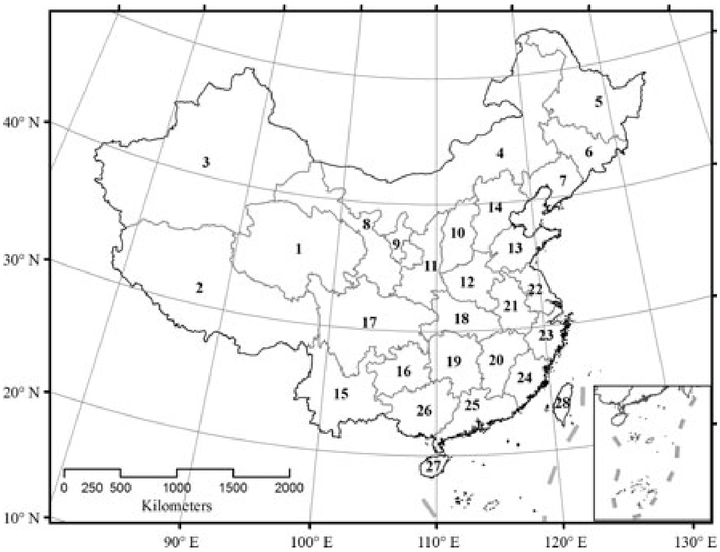


**Figure 1** Sketch map of China at the provincial scale. The map shows 34 units in the whole country, among which 28 units were defined in this work for freshwater fish fauna analysis. 1. Qinghai Province, 2. The Tibet Autonomous Region, 3. The Xinjiang Uygur Autonomous Region, 4. Inner Mongolian Autonomous Region, 5. Heilongjiang Province, 6. Jilin Province, 7. Liaoning Province, 8. Gansu Province, 9. The Ningxia Hui Autonomous Region, 10. Shanxi Province, 11. Shaanxi Province, 12. Henan Province, 13. Shandong Province, 14. Hebei Province, 15. Yunnan Province, 16. Guizhou Province, 17. Sichuan Province, 18. Hubei Province, 19. Hunan Province, 20. Jiangxi Province, 21. Anhui Province, 22. Jiangsu Province, 23. Zhejiang Province, 24. Fujian Province, 25. Guangdong Province, 26. The Guangxi Zhuang Autonomous Region, 27. Hainan Province, 28. Taiwan Province. The remaining six units including four municipalities, namely Beijing, Shanghai, Tianjin, Chongqing, and two special administrative regions, namely Hong Kong and Macau, were excluded mainly because of their small areas. Freshwater fishes in these places were combined into corresponding provinces according to their geological locations.

gov.cn/weiye/fubiao/biao3.html, last accessed 31 October 2012).

*Climatic data*

Primary climate change data were obtained through the WorldClim-Global Climate Data (http://www.worldclim.org/, last accessed 31 October 2012), including monthly total precipitation, monthly mean, minimum and maximum temperature. The data measured at weather stations were compiled monthly for the period 1950–2000, with a 30-arc-second resolution grid equivalent to ‘1-km’ resolution. The mean precipitation and mean temperature values of each unit were calculated by averaging each grid data within a unit, instead of the average of the maximum and the minimum.

*Biological data*

In most places, the NPP (kg year$^{-1}$) in an aquatic ecosystem was not directly available. However, terrestrial NPP data were used in this work because aquatic primary productivity covaried closely with that of the terrestrial ecosystem (Reshetrukov and Shakirova 1993). NPP data were gathered from the Oak Ridge National Laboratory Distributed Active Archive Centre (http://daac.ornl.gov/cgi-bin/dataset_lister.pl?p=13, last accessed 31 October 2012). The human population data used as a surrogate of human influences on aquatic ecosystems were obtained from the National Science and Technology Platform-Data Sharing Infrastructure of Earth System Science (http://www.geodata.cn/Portal/?isCookieChecked=true, last accessed 31 October 2012).

### Statistical analysis

*Richness and endemism*

The presence/absence matrix data were encoded into the software Bio-Dap for computation of species richness and endemism (Thomas 2000). The species richness covered the total number/or the logarithm of the total number of freshwater fish species from each administrative unit in this study. Given the inconsistent use of the term endemism, the endemic status of fishes could depend on the size of the geographical area under consideration

(Anderson 1994). In this study, an 'endemic' species was defined as a species inhabiting only one administrative unit.

*Cluster analysis*

The presence/absence matrix data were also used for the cluster analysis to determine the biogeographical division of the fish fauna. First, we produced similarity matrices based on the Bray–Curtis index to determine the relationships among provincial units according to the fish distribution data. A favourable characteristic of the similarity coefficients is their ability to exclude double-zeros; otherwise, regions with low species richness would be grouped on the basis of shared absences rather than presences (Legendre and Legendre 1983). Based on the similarity matrices, Pearson correlation coefficients among all the similarity coefficients were grouped by the linkage between groups method to classify the fauna into different divisions with significant differences.

*Regression analysis*

We used a multiple linear regression approach to determine the environmental variables that could best explain the multivariate relationship of the fish assemblage. The contribution of different and independent variables to the among-variation in species richness was derived by forward and backward multiple regression procedures. The results that best fitted all the data points were retained. In each iteration, the variable showing the highest partial correlation with the dependent variable was stepwise included into the model with the standard $F = 0.01$ for acceptance. When no other variable could be added to the model, the procedure was terminated. All statistical analyses were performed using SPSS v.18.

## Results

### Diversity

A total of 920 fish species in 302 genera, 54 families and 21 orders were included in this analysis after the species revision. The details of taxonomic categories are listed in Appendix S4. Among the included species, 40.54% belong to unit 15 (Yunnan, see Fig. 1 for unit names) with 373 species, followed by unit 17 with 232 species. Units 18–27 in Southeast and South China contain more than 150 species per unit, whereas units 11–14 in the Middle-Lower Yellow River watershed possess 100–150 species per unit. The least number of species appears in unit 9 with 34 species in 25 genera, 7 families and 3 orders, which is <10% of the numbers in unit 15. At the genus level, unit 15 also ranks first with 155 genera, accounting for 51.32% of the total, followed by unit 25 with 116 genera and unit 26 with 115 genera. The largest differences amount to 138 genera between unit 15 and unit 1. At the family level, units 23 and 26 head the list with 32 families, whereas units 1 and 2 contain only five families each. Units 22 and 26 possess 14 orders per unit, sharing the first place in the order level (Table 1).

Among the included fish species, 73% belong to Cypriniformes with 675 species, which dominate China's freshwater fish fauna. Cyprinidae is the most dominant family with 473 species, followed by Balitoridae with 157, Cobitidae with 41 from the Order Cypriniformes, Sisoridae with 43 and Bagridae with 31 species from the Order Siluriformes. There are 203 species of Cyprinidae in Unit 15, then 137 in unit 17 and 121 in unit 16, which are all in Southwest China. Unit 15 is also the most abundant in Balitoridae with 59 species, followed by 34 in unit 17. Unit 1 possesses the least number of species in the Cyprinidae with 20, and no Balitoridae are found in units 21 and 22. Cyprinidae includes more species than Balitoridae at the unit level, except in unit 1 where both families contain 20 species (Table 1).

A total of 613 species are found endemic within China, defined as a species found in only one unit. Among them, 216 endemic species appear in unit 15, a number that is seven times higher than in units 2, 3 and 17. Approximately 53.02% or 325 species of the total endemic species belong to Cypriniformes. Species from the genera *Anabarilius*, *Schizothorax*, *Yunnanilus*, *Triplophysa* and *Glyptothorax* form the largest number of endemics. No endemic species have been recorded in units 9, 10, 11 and 19 (Table 1).

### Biogeography

Geographic patterns of freshwater fish species in China are divided by cluster analysis into nine regions (Fig. 2). Each region owes its special characteristic to different dominance/or endemism at the genus level (Fig. 3).

*Qinghai-Tibetan Plateau Region*

This region includes units 1 (Qinghai) and 2 (Tibet). A total of 86 species have been recorded in

  

**Table 1** Composition of China's freshwater fishes, with number of species, genera, family and order, as well as the species number of Cyprinidae and the endemicity in each administrative unit.

| Administrative unit | Order | Family | Genus | Species | Cyprinidae | Endemic species |
|---|---|---|---|---|---|---|
| 1 | 3 | 5 | 17 | 46 | 20 | 8 |
| 2 | 3 | 5 | 22 | 63 | 34 | 30 |
| 3 | 11 | 20 | 59 | 84 | 44 | 31 |
| 4 | 10 | 17 | 69 | 100 | 58 | 1 |
| 5 | 13 | 21 | 71 | 98 | 52 | 12 |
| 6 | 9 | 16 | 61 | 81 | 52 | 5 |
| 7 | 11 | 21 | 64 | 87 | 52 | 5 |
| 8 | 6 | 12 | 62 | 90 | 49 | 1 |
| 9 | 3 | 7 | 25 | 34 | 24 | 0 |
| 10 | 5 | 15 | 50 | 65 | 41 | 0 |
| 11 | 7 | 15 | 76 | 135 | 81 | 0 |
| 12 | 9 | 17 | 68 | 110 | 72 | 2 |
| 13 | 9 | 19 | 69 | 109 | 69 | 1 |
| 14 | 13 | 22 | 75 | 104 | 62 | 2 |
| 15 | 8 | 26 | 155 | 373 | 203 | 216 |
| 16 | 7 | 21 | 102 | 197 | 121 | 7 |
| 17 | 8 | 20 | 108 | 232 | 137 | 29 |
| 18 | 12 | 27 | 103 | 167 | 94 | 2 |
| 19 | 10 | 25 | 93 | 154 | 87 | 0 |
| 20 | 12 | 26 | 97 | 190 | 106 | 1 |
| 21 | 11 | 23 | 72 | 108 | 59 | 1 |
| 22 | 14 | 27 | 77 | 120 | 63 | 2 |
| 23 | 13 | 32 | 95 | 158 | 81 | 4 |
| 24 | 12 | 31 | 105 | 161 | 78 | 4 |
| 25 | 13 | 30 | 116 | 186 | 94 | 16 |
| 26 | 14 | 32 | 115 | 191 | 114 | 8 |
| 27 | 9 | 24 | 89 | 116 | 62 | 11 |
| 28 | 9 | 18 | 59 | 68 | 31 | 20 |
| Total | 21 | 54 | 302 | 920 | 473 | 613 |

this region. Highly specialized *Triplophysa* and *Schizothorax* comprise nearly half of the total fish fauna in this region, followed by *Gymnocypris*, *Schizopygopsis* and members of the Sisoridae. A few species such as the torrent stone carp (*Psilorhynchus homaloptera*, Psilorhynchidae), *Oxygymnocypris stewartii*, Cyprinidae; *Herzensteinia microcephalus*, Cyprinidae; and *Nemacheilus subfusca*, Balitoridae, are distributed only in this area in the world. Fishes in this region are mostly cold-water species adapting to rapid current and high altitude.

*Oriental Region*

Unit 15 (Yunnan) is the only unit in this region. Fishes here exhibit an extraordinarily high level of endemism. Approximately 57.90% of the species located in this region are endemic to China, but similar to species in other countries in South-East Asia. Fishes in the Oriental Region show a great range of ecological traits, adapting them to multiple kinds of habitat. Moreover, endemic species from *Barbodes*, *Poropuntius*, *Glyptothorax*, *Anabarilius* and *Schistura;* 10 species of *Yunnanilus;* and 11 species of *Cyprinus* are highly specialized to the plateau streams and lakes and only found in this area in the world.

*North-west Region*

This region also includes only one administrative unit, namely unit 3 (Xinjiang). Two components, which are composed of (i) *Acipenser*, *Phoxinus*, *Hucho* and *Leuciscus* in the Arctic water systems and (ii) *Schizothorax* and *Triplophysa*, dominate the fish fauna in this region. Fishes in this region prefer cold and clear water. The Balkhash perch (*Perca schrenkii*, Percidae), *Gymnocephalus cernua*, Percidae, together with the Danube salmon (*Hucho taimen*, Salmonidae) and the northern pike (*Esox lucius*, Esocidae) show high abundance and are endemic to the country.

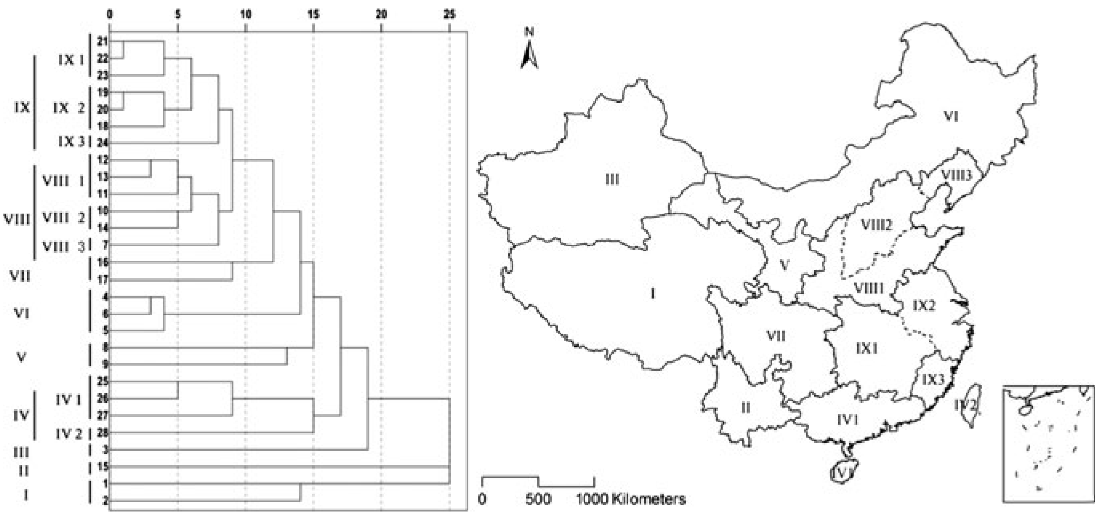


**Figure 2** China's freshwater fish fauna was divided into nine divisions under cluster analysis, as shown on the map of China. Region I, Qinghai–Tibetan Plateau Region. Region II, Oriental Region. Region III, Northwest Region. Region IV, South Region. Region V, Loess Plateau Region. Region VI, Heilongjiang Region. Region VII, Upper Yangtze Region. Region VIII, 3H Plain Region. Region IX, Middle-Lower Yangtze Plain Region.

*South Region*

This region includes units 25 (Guangdong), 26 (Guangxi), 27 (Hainan) and 28 (Taiwan) with 283 species. Although Taiwan and Hainan islands generally exhibit specific fish fauna, such islands are not separately clustered. The characteristic of the fish fauna in this region is abundant in biodiversity, including *Rhodeus*, *Acheilognathus*, *Hemibarbus*, *Acrossocheilus*, *Onychostoma*, Gastromyzonidae, Serranidae, Eleotridae, Gobiidae and others. All species flourish in the warm and eutrophic water.

This region could be further divided into subregions IV1 (units 25 + 26 + 27) and IV2 (unit 28) under cluster analysis. In the first subregion, the whip stingray (*Dasyatis akajei*, Dasyatidae in the Rajiformes) in unit 25 is the only freshwater fish in Chondrichthyes in China. *Neodontobutis hainanensis*, Odontobutidae; *Garra hainanensis*, Cyprinidae; and *Sarcocheilichthys hainanensis*, Cyprinidae, in unit 27 are endemic. In the second subregion, aside from the endemic species such as Moltrecht's minnow (*Pararasbora moltrechti*, Cyprinidae) and white cloud mountain minnow (*Tanichthys albonubes*, Cyprinidae), the Formosan landlocked salmon (*Oncorhynchus masou formosanus*, Salmonidae) is the only cold-water species in the tropical area.

*Loess Plateau Region*

This region contains two provincial units, namely units 8 (Gansu) and 9 (Ningxia), which are located in the Upper Yellow and Hexi Corridor, the transition zone from eastern China to the northwestern regions. This region is mainly formed under the uplift of the Qilian Mountains in the Cenozoic, and the main action of the wind and dry denudation has lead to a widely distributed desert, apart from a small area of oasis. A total of 113 species appear in this region. No genus dominates the fauna, although Cyprinidae occupy a relatively large portion. Few endemic species are found in this region, except for *Triplophysa wuweiensis*, Balitoridae. Fishes in this region have strong ecological adaptability with omnivorous feeding habits and physiological tolerance to low oxygen concentrations.

*Heilongjiang Region*

Units 4 (Inner Mongolian), 5 (Heilongjiang) and 6 (Jilin) are included in this region with 144 species. Salmoniformes, especially Salmonidae, are the primary component in this region, while no Salangidae have been recorded. Moreover, the fauna in this region contains a large number of species in the genera *Rhynchocypris*, *Gobio*, *Rhinogobio*, *Cobitis* and *Cottus* all in the Cyprinidae; however, no Gastromyzonidae have been found. Most of the endemic species are cold-water species, such as the Amur sturgeon (*Acipenser schrenckii*, Acipenseridae), kaluga (*Huso dauricus*, Acipenseridae), Amur pike(*Esox reichertii*, Esocidae) and the chum salmon (*Oncorhynchus keta*, Salmonidae).

  

*Upper Yangtze Region*

Units 16 (Guizhou) and 17 (Sichuan) constitute this region, which includes 303 species. Aside from species in the genera *Xenocypris*, *Leptobotia*, *Pseudobagrus*, *Rhinogobio*, *Onychostoma*, *Siniperca* and *Xenocypris*, 15 species from *Schizothorax* and 18 from *Triplophysa* also occur in high mountain streams. A large number of species are located only in this region in the world, such as *Sinocrossocheilus guizhouensis*, Cyprinidae; *Anabarilius qionghaiensis*, Cyprinidae; *Homatula wujiangensis*, Balitoridae; *Beaufortia szechuanensis*, Balitoridae; and *Ctenogobius chengtuensis*, Gobiidae.

*The 3H Plain Region*

The name of the region derives from the three rivers it contains, all with names beginning with H, namely the Huang (which is another name for the Yellow River), the Huai and the Hai. This region contains six provincial units, including units 7 (Liaoning), 10 (Shanxi), 11 (Shaanxi), 12 (Henan), 13 (Shandong) and 14 (Hebei). A total of 217 species are found in this region. Compared with other regions, this one shows a more diverse composition. Fishes from Petromyzoniformes, Salangidae, Cyprinae, Gobioninae and Bagridae are the primary or special components in this region.

This region can be further divided into three subregions using cluster analysis: VIII1 (units 11 + 12 + 13), VIII2 (units 10 + 14) and VIII3 (unit 7). Unit 7 is located in the Liaohe watershed with endemic Petromyzontidae and *Abbottina liaoningensis*, Cyprinidae. Although 117 species can be found in subregion VIII2, only *Triplophysa cuneicephala*, Balitoridae and *Leptobotia flavolineata*, Cobitidae are endemic. The genera *Pseudobagrus*, *Gobiobotia* and *Saurogobio* dominate subregion VIII3, along with a large number of endemic species, such as *Squalidus intermedius*, Cyprinidae; *Gnathopogan polytaenia*, Cyprinidae; and *Stolephorus shantungensis*, Engraulidae.

*Middle-Lower Yangtze Plain Region*

This region contains seven units as 18 (Hubei), 19 (Hunan), 20 (Jiangxi), 21 (Anhui), 22 (Jiangsu), 23 (Zhejiang) and 24 (Fujian) with a total of 309 species. Fishes in this region are characterized by the speciation of Cyprinidae. The genera *Tenualosa*, *Coilia*, *Siniperca* and the species Chinese sturgeon (*Acipenser sinensis*, Acipenseridae), Chinese paddlefish (*Psephurus gladius*, Polyodontidae) and Chinese sucker (*Myxocyprinus asiaticus*, Catostomidae) are endemic, economic or endangered, thus showing an importance for biodiversity.

Three subregions are grouped from this division: IX1 (units 18 + 19 + 20), in which the four popular farmed species, black carp (*Mylopharyngodon piceus*, Cyprinidae), silver carp (*Hypophthalmichthys molitrix*, Cyprinidae), bighead (*Aristichthys nobilis*, Cyprinidae) and grass carp (*Ctenopharyngodon idella*, Cyprinidae) comprise the most popular fisheries; IX2 (units 21 + 22 + 23), with roughskin sculpin (*Trachidermus fasciatus*, Cottidae) and representative species from *Salana*, *Mugilidae*, *Takifugu*; and IX3 (unit 24), where *Sarcocheilichthys sinensis fukiensis*, Cyprinidae, and a number of special species from *Formosania* can be found.

### Relationship between richness and environmental factors

All factors in the multiple regression analysis were considered, and eight models were finally retained. Considering the balance between the highest standard regression value and the least number of factors, as well as covariations among all the factors, the best model is

$$Y = 0.179X_1 + 0.322X_2 + 0.281X_3 - 0.025X_4 + 2.161(r^2 = 0.840),$$

where $Y$ as richness, $X_1$ as Ln(river discharge), $X_2$ as Ln(NPP), $X_3$ as Ln(population) and $X_4$ as Longitude. River discharge ($X$) was the single factor used to explain the fish richness ($Y$) variation as $Y = 0.284X + 2.913$ ($r^2 = 0.411$) (Table 2).

## Discussion

### Diversity

Globally there are more than 10 000 extant freshwater fish species, excluding migratory and euryhaline species (Eschmeyer 1998, 2012; Nelson 2006). China is one of the countries with the most abundant freshwater fish richness with 920 species, which is higher than that in the U.S.A. (800 species), Europe (233), Canada (218), Japan (211 species), Russia (206) and Australia (167) (Scott and Crossman 1998; Yuma *et al.* 1998; Unmack 2003; Lévêque *et al.* 2008). However, freshwater fish richness in China is significantly lower than that in Brazil (3200 species) and the Neotropical Region (6000 species) (Reis *et al.* 2003; Agostinho *et al.* 2005). Cyprinidae, with half of the total

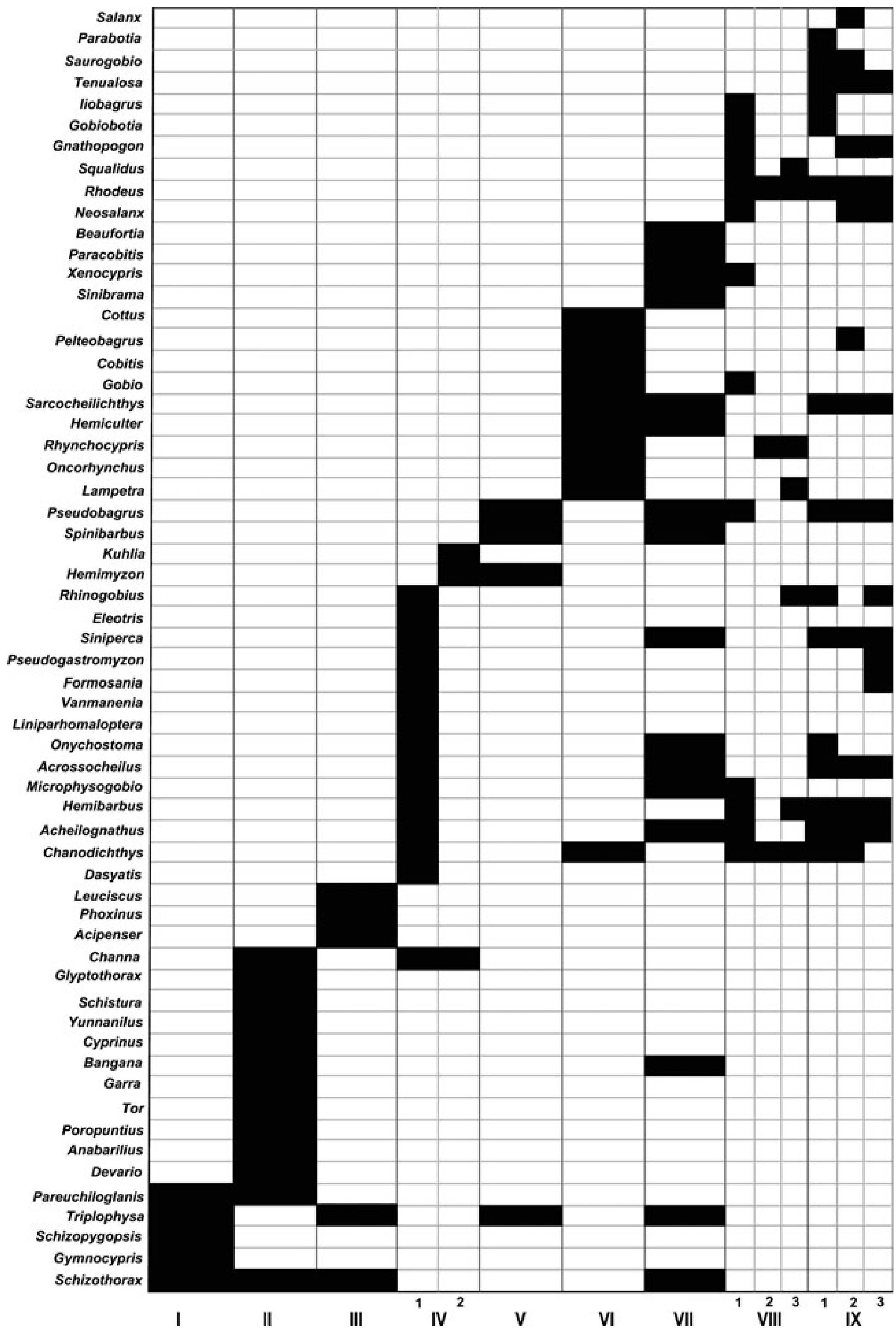
Salanx
Parabotia
Saurogobio
Tenualosa
liobagrus
Gobiobotia
Gnathopogon
Squalidus
Rhodeus
Neosalanx
Beaufortia
Paracobitis
Xenocypris
Sinibrama
Cottus
Pelteobagrus
Cobitis
Gobio
Sarcocheilichthys
Hemiculter
Rhynchocypris
Oncorhynchus
Lampetra
Pseudobagrus
Spinibarbus
Kuhlia
Hemimyzon
Rhinogobius
Eleotris
Siniperca
Pseudogastromyzon
Formosania
Vanmanenia
Liniparhomaloptera
Onychostoma
Acrossocheilus
Microphysogobio
Hemibarbus
Acheilognathus
Chanodichthys
Dasyatis
Leuciscus
Phoxinus
Acipenser
Channa
Glyptothorax
Schistura
Yunnanilus
Cyprinus
Bangana
Garra
Tor
Poropuntius
Anabarilius
Devario
Pareuchiloglanis
Triplophysa
Schizopygopsis
Gymnocypris
Schizothorax
I
II
III
1 2
IV
V
VI
VII
1 2 3
VIII
1 2 3
IX

**Table 2** Multiple linear regression models of the relationships between fish richness and environmental conditions derived from forward and backward stepwise procedures.

| Model | $R^2$ | SE | | Coefficients | SE | t | Significance |
|---|---|---|---|---|---|---|---|
| 1 | 0.840 | 0.2219 | (Constant) | 2.161 | 0.618 | 3.499 | 0.002 |
| | | | Ln(Discharge) | 0.179 | 0.041 | 4.337 | 0.000 |
| | | | Longitude | −0.025 | 0.007 | −3.706 | 0.001 |
| | | | Ln(net primary productivity) | 0.322 | 0.069 | 4.656 | 0.000 |
| | | | Ln(Population) | 0.281 | 0.061 | 4.609 | 0.000 |
| 2 | 0.411 | 0.4005 | (Constant) | 2.913 | 0.435 | 6.690 | 0.000 |
| | | | Ln(Discharge) | 0.284 | 0.067 | 4.262 | 0.000 |

species, is the most dominant family in the world's freshwater fish fauna, followed by Siluroidae. In this study, a total of 473 species of Cyprinidae accounted for 51.52% of the total freshwater fishes in China, which was supported by Zhang (1954). Balitoridae, Cobitidae and Sisoridae accounted for 25.11%, which was equal to the sum of Cobitiidae and Siluridae (Zhang 1954). The difference could be explained by the change in classification standard, mostly the establishment/abolishment of species, genus or even family (e.g. the abolition of Homalopteridae and the establishment of Balitoridae).

In Europe, Cyprinidae contain half of the total fish fauna, followed by Cobitidae, Gobiidae and Salmonidae, with approximately 4.3% each (Reyjol *et al.* 2007). In Japan, Cyrinidae also constitute the most dominant family with only 28.9% of the total species, followed by Gobiidae (20.9%) and Salmonidae (10.9%) (Yuma *et al.* 1998). In Australia, a continent with no dispersal of Cyprinidae because of the continent's isolation, Eleotridae is the most dominant family with 17.37% of the total species, followed by Terapontidae (14.37%) and Percichthyidae (10.18%) (Unmack 2003).

China also exhibits a high percentage of endemics, especially highly specialized *Schizothorax* and *Cyprinus* in the Qinghai-Tibetan Plateau and its adjacent regions. This endemism can be attributed to the unique stream and lake habitats created by the uplift of the Qinghai-Tibetan Plateau (He and Chen 2006; Li *et al.* 2009). The differentiation of endemic species in Erhai Lake in unit 15 is also remarkable, with nine species from *Cyprinus* (e.g. *C. barbatus*, *C. chilia*, *C. megalophthalmus*, *C. longipectoralis* and *C. daliensis*, all Cyprinidae) found only in this location in the world (Chen *et al.* 1998; Kang *et al.* 2009). Unit 15 contains the most endemic species, and fauna in this unit are mostly similar to that of South-East Asia instead of other units in China. The wide appearance of extant primary Barbinae and Danioninae, together with fossil records, supports that Southwest China

**Figure 3** The dominant or endemic fish genera of China's freshwater fishes at the biogeography scale. Region I was dominated by higher specialized *Schizothoracinae* and *Triplophysa*, which evolved under the uplift of the Qinghai-Tibetan Plateau. Region II was characterized by original Cyprinidae, for example Barbinae. The fishes in this area were mostly diverse under multiple kinds of microhabitats caused by variations of topography and climate. The fishes in Region III were similar to those of Central Asia or farther north, although the less specialized *Schizothorax* and *Triplophysa* also accounted for a part. Region IV was located in South China, and the abundant rainfall and higher temperature supported the rich species of Cypriniformes, Siluriformes, and Perciformes. The special species in this area were Labeoninae and Balitorinae. Region V was the least abundant among the divisions. The species in this area were mostly barbus and loaches with nearly no endemicity. In Region VI, the cold species from Salmoniformes and Leuciscinae of Cypriniformes were dominant and formed a large fishery. In Region VII, which is the transition zone connecting the first step and the second step of China's topography, the fishes also covered a large range of taxonomic categories. Region VIII was dominated by Gobioninae, Rhodeinae, Xenocyprininae and Bagridae. These fishes were dispersed species that seemed to enjoy high sediments in the area. Region IX contained mostly Cyprinidae, together with many other families. The temperate climate, abundant water and diverse habitats brought most species in this division, including dispersed Cultrinae, Gobioninae, Siluridae and some endemic or endangered species, for example Chinese paddlefish (*Psephurus gladius*, Polyodontidae) Chinese sturgeon (*Acipenser sinensis*, Acipenseridae) and roughskin sculpin (*Trachidermus fasciatus*, Cottidae).

(in South-East Asia) is the origin of Cyprinidae and reflects geological processes.

## Richness and environment

The species–area relationship forms the basis of analyses to explain species richness. In aquatic ecosystems, 'river discharge', which determines the actual habitat space for aquatic species, should be a better measure than area (Xenopoulos *et al.* 2005; Xenopoulos and Lodge 2006). Even so, most studies still use 'area' instead of 'river discharge' because the area data are more convenient to obtain. In this work, we used river discharge to explain fish taxon richness, and a rough positive relationship was found. This relationship could be even more significant when Region I is removed. Although the Qinghai-Tibetan Plateau has plenty of water, the low primary production, partially high salinity and low temperature limit the dispersal of fishes (Wu and Wu 1992). NPP can be chosen as an effective factor to explain the richness variation because it reflects the multiple influences of rainfall and temperature on the earth's surface (Guégan *et al.* 1998; Waide *et al.* 1999; Hawkins *et al.* 2003). At a local scale, species richness responded with a unimodal curve to increasing primary production, whereas at a regional or a global scale, species richness linearly increased with energy (Wright 1983; Rosenzweig and Abramsky 1993). In this work conducted at a regional scale, the logarithm species richness was positively linearly related to NPP after deleting extreme values of Regions II and III. The human population has an important effect on ecosystem function (Vitousek *et al.* 1997; Vörösmarty *et al.* 2000). In this work, fish richness shows an interesting correlation with population size. Generally, biota prefer to gather in the most suitable habitats, so different species including human beings in an ecosystem would probably show similar distribution patterns. Another explanation we should emphasize is that the greater the human population in a unit, the more intensive the fish sampling activities will be, thereby resulting in the discovery of more species.

Several studies have documented the effects of altitude on fish spatial distribution and diversity (Schall and Pianka 1978; Zhao *et al.* 2006). Fish richness usually decreases with increasing altitude. However, no obvious relationship could be drawn at the national scale in our study. Similar results were found in the relationship with latitude. Although the latitudinal gradient of decreasing richness from tropical to temperate areas is one of the oldest geographical patterns recognized by ecology, notable exceptions to the general pattern also exist, with significant variations of the fundamental pattern (e.g. positive linear, negative linear, modal or nonsignificant) (Willig *et al.* 2003; Hawkins and Diniz-Filho 2004). A number of studies concentrated on the effects of longitude (Hughes and Gammon 1987; Araújo *et al.* 2009). China's freshwater fish richness showed an increasing tendency with decreasing longitude from west to east. In east China with low longitude, the coastal climate created a favourable environment for more species. This negative tendency was also reinforced by the fact that the lower river reaches can support more fish species than the headwaters (Vannote *et al.* 1980; Araújo *et al.* 2009), and a large number of rivers in China wind from west to east.

## Factors affecting Chinese freshwater fish biogeography

Four kinds of barriers, which established the characteristics and timescales of influence on biogeographical divisions, were deduced from the Chinese freshwater fish fauna: geological event, river system, climate and habitat. Our study identified the following biogeographical divisions of Chinese freshwater fishes.

### *Qinghai-Tibetan Plateau Region*

This division was first divided by a major geological event, namely the uplift of the Qinghai-Tibetan Plateau. Until 40 million years ago, the collision of the northward drifting Indian Plate with the Eurasian Plate caused the rapid uplift of the region to more than 5000 m, which formed the 'Third Pole'. This process showed four stages, including the raising to an altitude of 2000 m in the Eopleistocene, 3000 m in the Mediopleistocene, 4000 m in the Epipleistocene and continuous speeding up in the Holocene epoch (Zhong and Ding 1996; Chung *et al.* 1998; Tapponnier *et al.* 2001; Wang *et al.* 2010). Correspondingly, the environment gradually changed from a warm and humid climate with numerous rivers and lakes to a cold and dry environment with the disappearance of lakes and the appearance of saline water. This change was also evidenced by the distribution of a specialized genus *Schizothorax* adapting to the corresponding environments (Chen *et al.* 1994; He and Chen 2006; Li *et al.* 2009). When moving to the north and north-west, the plateau becomes progressively higher, colder with temperatures mostly between 0 and −40 °C and drier conditions with annual precipitation ranging from 100 to 300 mm. The region includes mountain ranges and large brackish lakes. Many large rivers in Asia originate in this area, such as Yangtze, Yellow, Ganges, Brahmaputra, Salween and Mekong.

*Oriental Region*

The biogeographical separation of this region, which only consisted of one unit (15, Yunnan), was probably mainly due to the specific habitat conditions in this area. The rugged topography, specific climate, and abundant river systems flowing in various directions give this region extraordinarily diverse habitats and biogeographical peculiarities that support a high number of species (Yang *et al.* 2004; Kang and He 2007; Kang *et al.* 2009). The topography shows a consistent ladder-like multilayered landscape with altitudes from 6740 m at the maximum to 70 m as minimum travelling from the north to the south. These landscapes were caused by a long-term erosion and uplift in the Tertiary. In the upper and middle parts of this region, which belongs to the upper regions of the Yangtze, Red, Mekong, and Salween rivers, numerous dry-hot and dry-warm valleys exist. In the lower part of this region, diverse hot and humid valleys are found. About 2200 billion cubic meters of annual runoff are produced locally and flow through more than 600 rivers and 40 freshwater lakes in the region. The Mekong River, which flows through six countries, possesses the second richest fish biodiversity and the fourth largest inland fisheries in the world (Rainboth 1996). The monsoons arriving from the Pacific and Indian oceans provide high temperature and adequate rainfall supporting a high NPP, thus providing a home to a large variety of flora and fauna. In Zhang (1954), the western unit 15, southern unit 2, and unit 17 of the present paper constituted the Nujiang (Upper Salween)-Lancang (Upper Mekong) Region. In reality, the fish fauna in this area was far beyond the control of the Nujiang and Lancang rivers because of the non-negligible contribution of the Upper Yangtze and Irrawady. In Li's (1981) opinion, the middle-south part of unit 15 was defined as a subregion of the South China Region, together with units 16, 23, 24, 25, 26, 27, and 28. Except for the similarities between the eastern part of unit 15 and units 25–28, the rest of unit 15 retains an endemic fish fauna large enough to produce low similarities <0.146 with the nearby units (Appendix S5). Therefore, unit 15 was separated at the regional scale.

*North-west Region*

This isolated area comprising unit 3 occupies one-sixth of the China mainland area and is characterized by specificities concerning the river system, geographic situation and climate. In the late Tertiary, the gradually receding seawater and seabed uplift under the crustal movement shaped this region a 'two basins clipped in three mountains' topography. This geological process was also supported by palaeontological evidence (Chang *et al.* 2008). The rivers in this area are all isolated from the water networks in other provincial units in China. The Tarim River is the longest inland river in China with a total length of 2000 km and a drainage area of $19.8 \times 10^4$ square kilometres. The Ili River, which is the largest river in this region with an annual runoff volume of 12.3 billion cubic meters, flows into the Balkhash Lake. The Irtysh River, which is the only river in China flowing into the Arctic Ocean, covers an area of 57 000 square kilometres of watershed and an annual runoff up to 11.9 billion cubic meters. Unit 3 was grouped with the Qinghai-Tibetan Plateau or Hexi Corridor in previous works (Zhang 1954; Li 1981). Although this unit shared some genera, such as *Schizothorax* and *Triplophysa* with other areas, species in these genera are different in their specialized morphological characteristics. Furthermore, most species occurring in this area belonged to either the Arctic or inland water systems. The similarities between unit 3 and the other units did not exceed 0.265.

The climate in this area can be classified as either continental dry or temperate. The climate ranges from being cool-temperate in the north to temperate and warm temperate in the south and dramatically arid in the west to subhumid in the east, with an average temperature of 10 °C and an annual rainfall of 155 mm. This area includes some of the hottest and driest places on Earth.

*South Region*

This division was based on the river system boundaries and climate. Geological processes further divided this region into two subregions. This area exhibits a subtropical monsoon climate with an annual average temperature over 20 °C and a rainfall of 1500 mm or more. The vegetation in this area is tropical rain forest, monsoon forest and evergreen broad-leaf forest, and the real tropical vegetation is shrub, subtropical meadow slopes and small pieces of tropical secondary forest (Wu 1980).

Units 25 and 26 are dominated by the middle and lower reach of the Pearl River. The geomorphology includes three basic types, including mountainous, hilly and plains. The mountains in this area mostly reach l000–1500 m towards the north-east. The hills are between 200 and 400 m high in this area and are mainly located in the south-east section. Alluvial plains dominate the estuarine area. Unit 27 (Hainan Island) was still connected to the mainland before the Quaternary, but was separated from unit 26 until the middle Pleistocene by a fault depression due to volcanic activity (Zeng and Zeng 1989; Yan 2006). After several separations–connections occurring before the end of Quaternary glacial period, a dramatic sea level rise shaped the current geography. Corresponding to these changes, the northern biome moved southward during the glacial epoch and the southern biome migrated northward in the interglacial epoch, which favoured the migration, extinction and speciation of fish species in the various rivers in units 25, 26 and 27.

Unit 28 is situated on the edges of the Eurasian and Philippine Sea plates and has both geosynclines and island arc features. In the early Mesozoic era, unit 28 was connected to the mainland as part of unit 24, but began to separate during the Cretaceous and the Palaeocene periods. This connection and separation process repeated several times later in the Eocene and Quaternary ice age, and the receding glaciers of the last ice age resulted in the final separation of unit 28 from the mainland (John *et al.* 1990; Chen and He 2001; Wang *et al.* 2002). Although exchange of species with unit 24 was possible, unit 28 was grouped into this region instead of with unit 24 mainly because of the influence of a changing environment. Unit 28 exhibits a tropical marine climate, where warm or hot weather is experienced throughout the whole year, but with greater frequency of tropical storms and typhoons. The tropical zone, especially in the southern part of unit 28, supported the differentiation of fishes, which enlarged the gap in the fish fauna found across units 28 and 24 as well as the similarity between units 28 and 27. Moreover, a special torrent habitat, with great characteristic differences between dry and rainy seasons, had caused the origin of some endemic species in unit 28, such as the Tawain ku fish, *Onychostoma alticorpus*, Cyprinidae; *Sinogastromyzon puliensis*, Balitoridae; and *Hemimyzon taitungensis*, Balitoridae.

*Loess Plateau Region*

The isolation of the river systems in the Hexi Corridor and Loess Plateau environments was the main variable used to establish Region V, followed by climate. Originating from the Qinghai-Tibetan Plateau, the Yellow River passes through unit 9, forming more than 20 canyons alternating with broad valleys, cliffs, narrow river beds and large river gradient and rapids. The river accepts many tributaries when it enters unit 8, where river discharge greatly increases. Next, the river flows mostly through deserts and steppes, then the shallow river beds with slow water flow, which forms two large alluvial plains known as the Yinchuan Plain and the Loop Plain.

The climate in this region is influenced by the blocking of the northward movement of the Indian Ocean warm air mass, the strengthening of East Asian monsoons and the mixing of the winter monsoon and westerly jet. Beginning in the Pleistocene, the Loess Plateau came into an alternate warm–humid and cool–dry climate fluctuation under the new tectonic movement. The river systems were developed mostly during this period. In early Late Pleistocene, the climate became dry, which continued in the Holocene until the occurrence of an obvious drought with a northward desertification (Mei and Dregne 2001; Issar 2003). The annual average temperature in this area is about 0 °C, and the rainfall is <300 mm, which limited the dispersal of most fishes. This division was considered as the poorest region in fishes.

*Heilongjiang Region*

The decisive factor for the demarcation of this region is the river system, followed by climate. Except for the western part of unit 4 in the Yellow River watershed, the rest of this division is supported by the Heilongjiang River (Amur River), which has a total length of 3474 km and a watershed area of 887 000 square kilometres in China. The Heilongjiang River contains one of the world's most abundant fishery resources. Every summer chum salmon and kaluga move upstream from the sea for spawning (Ren 1981). Previous studies grouped units 5, 6 and east of unit 4 into one region (Li 1981). Although a gap existed in the fish fauna between the eastern and the western part of unit 4, this unit could not be divided mainly because the analysis by Li (1981) was based on administrative levels. As fishes in the upper Yellow river (western part of unit 4) were scarce, the importance of the fishes in the eastern part induced the formation of units 4, 5 and 6 into one region, instead of putting unit 4 into Region V.

Most of this region has a temperate humid/semi-humid monsoon climate, with an annual mean temperature of about −4 to 6 °C (slightly higher than that of Tibet) and an annual precipitation of between 350 and 700 mm. The vegetation in this area is dominated by temperate grasslands, temperate coniferous-deciduous broad-leaf forest and cold temperate coniferous forest.

*Upper Yangtze Region*

The Upper Yangtze Region was defined in terms of the characteristics of the river system and climate. The Jinsha River (upper reach of Yangtze) had once been connected to the Red River and then was captured by the Yangtze during the uplift of the Yun-Gui Plateau, which doubled the length of the river. In unit 17, the Yangtze receives a number of big tributaries such as Yalongjiang, Minjiang, Tuojiang, Wujiang and Jialingjiang rivers. The Wujiang watershed, occupying 40% of unit 16 with an area of 66 830 square kilometres, is the largest river in unit 16, although the Upper Pearl also flows through this province.

Units 16 and 17 were grouped, respectively, into the Oriental Region and Nujiang-Lancang Region (Zhang 1954) or into the Southwest Region and South Region (Li 1981). In the present work, the two units are grouped together and form an independent region. Although a small part of unit 16 shares fishes with units 25 and 26 in the Pearl River watershed, habitats and water temperature limit the free migration of fishes between the upper Pearl River and the lower Pearl River belonging to Region IV. Moreover, the sharing of abundant *Schizothorax* and *Triplophysa* and some Cyprinidae in the upper Yangtze forces the division of these units. The special topography of both units forms a transition plateau from the first step (Qinghai–Tibetan Plateau) to the second step (Yangtze Plain), as well as a similar humid subtropical climate with an annual average temperature of 15 °C and rainfall of 1100–1300 mm. The north-western part of this division is covered by evergreen broad-leaf forest, the south-western part by dry evergreen broad-leaf forest and the central and eastern parts by humid evergreen broad-leaf forest. The fishes in this area are characterized by the cold-water species adapted to the plateau environment (Zheng 1989).

*3H Plain Region (see earlier for the derivation of this label)*

This region is primarily determined by the characteristics of the river system, followed by geological events and climate. Four larger rivers, namely the Yellow, the Huaihe, the Haihe and the Liaohe, dominate this region. Since the time of the Song Dynasty (420–422 A.D.), the Yellow River has changed its outlets from the Bohai Sea to the East China Sea by capturing the Huaihe River. This situation lasted for a 700-year period until the 1850s when it separated from the Huaihe River back to the Bohai Sea. Historically, complicated river rearrangement events occurred among the four rivers, thus providing opportunities for communication between fish populations. These hydrological processes resulted in the formation of the 3H Plains. In subregion VIII3, the Liaohe River is the dominant river, in addition to some areas belonging to the Haihe River drainage. The Yellow River (62.2% of the total area) and the Huaihe River (37.8%) watersheds compose unit 10, and the Huaihe River and the Haihe River dominate unit 14, both units constituting subregion VIII2. The subregion VIII1 is mostly located in the lower Yellow watershed, together with the north Huaihe drainage.

The limited variation in fish diversity still supported the combination of all the six units into one region, although the altitude decreases from west to east. The climate changes from temperate, warm temperate and subtropical from north to south, with an annual average temperature of 12–15 °C and an annual rainfall of 500–1500 mm.

*Middle-Lower Yangtze Plain Region*

This division was clearly based on the river system, along with additional geological and climate characteristics.

Yangtze, the longest river of Asia, crosses all three terrain levels and can be divided into headwaters and upper, middle and lower reaches. After the Three Gorges, Yangtze flows into the third-step terrain, including Jianghan Plain in unit 18, Dongting Lake Plain in unit 19 and Poyang Lake

Plain in unit 20. The hydrological conditions in this region vary greatly in different seasons, which create large plains for irrigation, shipping, fishing and water supply (Cui and Li 2005). Various landforms, alternating with mountains, hills, mounds and plains, support diverse microhabitats for rich fish resources in richness and abundance. This region has a continental subtropical monsoon climate with an annual average temperature of 18 °C and an annual rainfall of 1500 mm. Units 21 and 22 are dominated by the southern part of the Huaihe drainage and the Yangtze delta, which has the lowest latitude in the country. This area has temperate zone to subtropical zone climate with an annual average temperature of 15 °C and an annual rainfall of 1200 mm. Unit 23 was also included in this subregion mainly because it has the same climate as unit 22 and the river channel connection by the Grand Canal. Subregion IX3 only covered unit 24. The south-eastern part of unit 24 was formed under the collision between the Pacific and Eurasia plates, and the middle part was formed under the collision belt between the Yangtze Plate and Cathaysia on the margins of Pangea. This subregion belongs to the Min River watershed, which is almost isolated from other units. This area has a subtropical monsoon climate with an annual average temperature of 18 °C and an annual rainfall of 1600 mm (Zhao *et al.* 1984).

An interesting case is the home of unit 23 and unit 24. Units 23 and 24 are separated into the River Plain Region and the Oriental Region, respectively (Zhang 1954), and then merge into a subregion of the South China Region (Li 1981). Many studies document that the fishes of unit 24 are similar to those of unit 28 as the two units were connected in history (Chen and He 2001), but this similarity seems to have been lost corresponding to the adaptive differentiation of species under the pressure of environmental changes. In the present study, unit 24 is grouped into the same region as unit 23, but isolated as a subregion. The similarity between units 24 and 28 is 0.285, which is significantly lower than those between units 24 and 18, 19, 20, 21, 22 and 23 (Appendix S5). This finding suggests that environmental factors, such as climate and habitat, together with human activities, have had more influence on extant fish distribution than historical geological events in these areas. Moreover, the remaining effects of the latest glacier movement may still contribute to its retention as a subregion apart from the other units in the same region.

Previous works were used to combine two parts as Regions VIII and IX in the present work into a single River Plain Region (Zhang 1954) or East Region (Li 1981). Although both regions shared many Cyprinidae at subfamily, genus and species levels with a similarity of 0.451, many differences in composition, especially in Gobioninae, Labeoninae, Balitoridae and some species of Percoidei, separate them at the regional scale. The fish composition of Region VIII also shows partial similarity to Region VI as 0.424, which means that Region VIII is a transition zone of fishes between the northern part and the southern part of the country.

### Conclusions from biogeographical region delineation

Except for the geological event grouping the Qinghai-Tibetan Plateau as a special biological region, the river system pattern is confirmed as the primary factor that determines China's freshwater fish biogeography (Appendixes S6 and S7). River capture is a geomorphological process through which stream sections are transferred from one catchment to another (Bishop 1995; Bharatdwaj 2006). This geomorphological process may represent a dominant facilitator of interdrainage transfer and cladogenesis in freshwater-limited taxa. In the same watershed, climate change in various parts further explains the fish spatial distribution patterns. The climate gradient obviously sets an obstacle for the exchange of biota between the north and the south (Roessig *et al.* 2004; Pörtner and Farrell 2008; Cheung *et al.* 2009). However, climatic differences between each pair of these adjacent regions should not be overestimated as many species could survive a wide range of temperature. China's climate shows dramatic features such as (i) a significant continental monsoon and (ii) a complex and varied climate. Additionally, the complex and diverse terrain further shapes the climate diversity (Zhao *et al.* 1984) (Appendixes S8 and S9). Habitat characteristics are also important to explain biogeographical patterns (Hanski 1998; Schoener 2011) if we suppose that species with similar distributional patterns have similar histories and that species as now defined represent monophyletic units. The ecological needs of a species are an important factor in determining the distribution of most endemic fishes. Species with narrow tolerances are restricted to more stable habitats. Especially in one river or the same climate zone, the diversion of habitats can also control the fish biogeography (Fig. 4).

## The possible future tendency of fish biogeography

Fishes have found it difficult to adapt to the pressure of a combination of global climate change, river system redesign through obstructions, fragmentation, new connections between river channels and competition from introduced species (Magurran 2009). By 2050, the total consumption of primary energy in China is expected to reach 3.9–4.9 Giga tons of coal equivalent, according to China's national mid- to long-term development plans, which is very close to the Intergovernmental Panel on Climate Change – Special Report on Emissions Scenarios (IPCC SRES) B2 scenario (mid-low emissions scenario) (Lin 2007; Wu *et al.* 2010). This rate would cause a warming tendency in China. Moreover, hydroprojects are planned for quick development (Qiu 2011) to satisfy the growing needs of the population and energy consumption, for example, large-scale cascade dams in the Upper Yangtze, Salween and Tibet (Qian and Yan 2010). These regional large-scale cascade dams definitely pose a new challenge to the protection of natural ecosystems, as their impacts could be far beyond the influences exerted by small, middle, large or cascade dams.

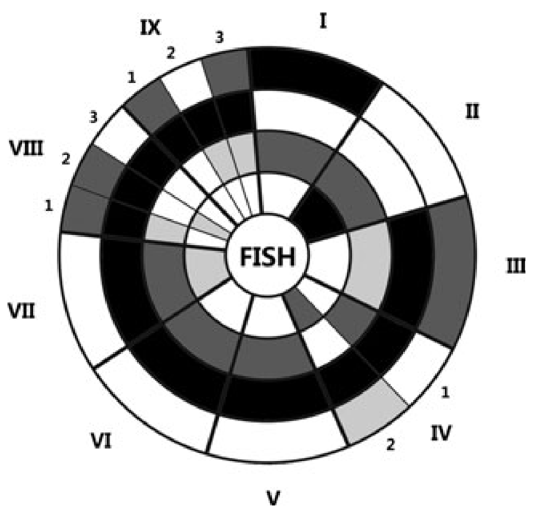


**Figure 4** Factors explaining the biogeography of China's extant freshwater fishes. From the outermost ring to the innermost ring, the geological event, river system, climate and habitat conditions were listed. The black cells indicated the primary factors that determined this division, followed by heavy grey and light grey, based on importance.

In addition to fragmentation, rivers have also been modified by the connection of river channels and other projects for navigation, irrigation and so on. In addition to the Great Canal with a history of more than 2500 years, China is now developing another huge engineering project: the South-to-North Water Diversion. This master plan contains three parts, namely the East, Middle and West Water Diversion Lines, thus connecting Yangtze, Yellow, Huaihe and Hai, forming a 'three vertical and four horizontal' design for the rational allocation of China's water resources (http://www.nsbd.gov.cn/, 31 October 2012). Such projects, together with climate warming, would result in possible biogeographical changes as follows:

1. The linkage of the outer areas of Regions I, II and unit 17, and the isolation of the central part of Region I. As the climate will change towards warming and the discharge will be temporarily increased by the melting glacier in Region I (Chen *et al.* 2011), fishes would move northward into Region I from Region II and unit 17 of Region VII. The local endemic species in Region I would shrink their distribution into smaller and higher-altitude areas, such as the North Qinghai-Tibetan Plateau and Hoh Xil, which will stay as cold as it has so far been on the Qinghai-Tibetan Plateau.
2. The maintenance of Regions III and VI. Although fishes in these regions have changed their distributing patterns, the isolated river systems in these regions give no chance for fish movement, thus maintaining their isolations.
3. The enlargement of Region IV to include unit 16. Fish abundance in unit 17 is expected to decrease corresponding to the change in NPP, whereas in unit 16, fish abundance is expected to increase with increasing NPP. Moreover, the warming tendency would give a chance for fish migration between the upper Pearl and lower Pearl.
4. The connection of Regions VIII and IX. Hydraulic engineering will smooth the barriers through the connection of the main rivers, and the averaging tendency of the temperature would facilitate the exchange of fish species between these regions.

5. Warm species moving northward to higher-altitude areas increase the regional abundance, but also threaten the local higher specialized species. This phenomenon is expected to result in a total decrease in richness at the national scale. Unlike diversity, fish abundance would increase because higher NPP can support more energy in an ecosystem (Guégan *et al.* 1998; Brander 2007; Ficke *et al.* 2007).

## Conclusion

Our results document 920 fish species in 302 genera, 54 families and 21 orders, among which 613 are endemic to China. China's freshwater fish fauna is dominated by Cypriniformes, forming 73% of the total fauna and coinciding with the worldwide trend. Cyprinidae is the largest family in the whole fauna with 473 species, showing diverse characteristics and indicating an important role in the evolution of the Cyprinidae and current distribution patterns worldwide. About 53% of the total endemic species belong to Cypriniformes, mostly belonging to the genera *Anabarilius*, *Schizothorax*, *Yunnanilus*, *Triplophysa* and *Glyptothorax*.

Nine biogeographical divisions have been determined to map China's freshwater fish spatial pattern. The Qinghai-Tibetan Plateau Region is a special division, even considered from a global perspective, and is characterized by highly specialized species in the genera *Schizothoracinae* and *Triplophysa*. The Oriental Region is characterized by original Cyprinidae and has the highest endemism in the country. The Middle-Lower Yangtze Plain Region contains mostly Cyprinidae, together with many other families under the temperate climate, abundant river discharge and diverse habitats. The river system is confirmed as the primary factor that determines China's freshwater fish biogeography. Geological event, climate and habitat could further provide detailed explanations.

Among all the environmental factors, river discharge is the most influential in explaining the variation of fish species richness, followed by human population size and NPP. Considering the fish response to variation under impacts by dam constructions and climate change, the focal areas for fish conservation efforts and potential natural reserves should be redrawn. Regions including Southwest China and the higher part of the Qinghai-Tibetan Plateau, with high fish endemism and sensitivity to environmental changes, should receive high conservation priority.

## Acknowledgements

This work has been supported by the State Key Program of National Natural Science of China (Grant No. U0936602). David Dudgeon, Thierry Oberdorff and Paul J B Hart are deeply acknowledged for their constructive suggestions. Gordon McGregor Reid and Martin Pusch are also acknowledged for their attentive revisions. We also give sincere thanks to Chunguang Zhang, Xiaoyu Kong, Zhongming Wang, Hongdu Lin, Weide Deng, Wei Su, Xiaorong Li, Jinxin Zhong and Qian Zhang for fish data supporting, Shaohong Wu for NPP data supporting, Xingwu Duan, Yungang Li and Xiaoxia Huang for handling GIS data.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Biogeography of China's freshwater fishes by Zhang (1954).

**Appendix S2.** Biogeography of China's freshwater fishes by Li (1981).

**Appendix S3.** Literature used to derive data on China freshwater fish species and their distribution within China.

**Appendix S4.** List of China's freshwater fishes and their distributions.

**Appendix S5.** Two-pair similarities of fishes among all the administrative units.

**Appendix S6.** Map of China topography, including altitude and mountain information.

**Appendix S7.** Map of China watershed.

**Appendix S8.** The long-time average annual value of rainfall of China in 1950–2000.

**Appendix S9.** The long-time average annual value of temperature of China in 1950–2000.

  