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Biogeographic freshwater fish pattern legacy revealed despite rapid socio-economic changes in China

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Abstract

Understanding drivers of freshwater fish assemblages is critically important for biodiversity conservation strategies, especially in rapidly developing countries, which often have environmental protections lagging behind economic development. The influences of natural and human factors in structuring fish assemblages and their relative contributions are likely to change given the increasing magnitude of human activities. To discriminate natural and human drivers of fish diversity and assemblage patterns in developing countries with rapid socio-economic development, a dataset of 908 freshwater fish species and 13 metrics including three categories of both natural (i.e., biogeographic) and human drivers (i.e., economic growth, inland fisheries) in China were analysed with machine learning algorithms (i.e., self-organizing map, random forest). Here, we found that biogeographic drivers explained 21.8% of the observed fish assemblage patterns in China and remained stronger predictors when compared to human drivers (i.e., 15.6%, respectively). Freshwater fish species richness was positively correlated to rainfall, air temperature, surface water area and inland fisheries production but negatively correlated with urbanization. In addition, the strong structuring effects of climatic variables on Chinese fish richness patterns suggested that the fish assemblages could be particularly vulnerable to climate change. Our results showed that natural biogeographic factors still dominate in driving freshwater fish assemblage patterns despite increased human disturbances on aquatic ecosystems in a rapidly developing country. These findings consequently suggested that we should consider both natural (e.g., climate) and human (e.g., urbanization, inland fisheries) factors when establishing aquatic conservation strategies and priorities for developing countries that are experiencing rapid socio-economic changes.

KEYWORDS
biodiversity conservation, climate change, economic growth, ecosystem service, inland fisheries, urbanization

1 | INTRODUCTION

The status of freshwater biodiversity remains highly critical as many species are threatened with extinction (Bellard, Englund, & Hugueny, 2019; Collen et al., 2014; Dias et al., 2017; Dudgeon et al., 2006; Reid et al., 2018; WWF, 2016). Downward trends in the Red List Index and Living Planet Index suggest that key Aichi targets (i.e., targets, 2–4, 6–12, 14) are not on track to be met by 2020 (Convention on Biological Diversity, 2011; Gozlan, Karimov, Zadereev, Kuznetsova, & Brucet, 2019). Drivers regularly identified as playing a key role in these declines are habitat destruction, climate change and introduction of non-native species (Erős, Takács, Specziár, Schmera, & Sály, 2017; He et al., 2018; Martinuzzi et al., 2014; Reid et al., 2018; Toussaint et al., 2018). Nevertheless, detangling the effects of historical and contemporary determinants underpinning large-scale patterns of freshwater fish diversity and assemblage patterns is central to conservation strategies (Hoeinghaus, Winemiller, & Birnbaum, 2007; Jackson, Peres-Neto, & Olden, 2001; Kuczynski, Legendre, & Grenouillet, 2018).

Efforts have increasingly been made to distinguish natural and human drivers that structure fish assemblages (Brucet et al., 2013; Cilleros, Allard, Vigouroux, & Brosse, 2017; Henriques et al., 2017). However, due to a scale-dependent effect (Menegotto, Dambros, & Netto, 2019), there is still no consensus on the main drivers that affect fish diversity and assemblage composition. Natural biogeographic drivers such as climate (e.g., air temperature, rainfall) or geography (e.g., altitude, isolation; Collen et al., 2014; Guo, Chen, Lek, & Li, 2016; Henriques et al., 2017) are often identified as key factors in structuring fish patterns at a large spatial scale. However, the accelerating footprint of human disturbances over the last few decades has deeply modified environmental filters and species interactions, and significantly changed the natural biodiversity patterns (Dias et al., 2017; Twardochleb & Olden, 2016). Human drivers, such as socio-economic growth (e.g., human population increase, economic increase, urbanization), or fisheries development (e.g., overexploitation, introduction of non-native species) have played an increasing role in changing fish diversity and assemblage composition (Brucet et al., 2013; Dudgeon et al., 2006; La Sorte & McKinney, 2006; Vörösmarty et al., 2010). These factors have led to concerns as to whether or not adopt policy strategies that are targeting on anthropogenic drivers like economic growth (Bigford et al., 2006; Czech, Angermeier, Daly, Pister, & Hughes, 2004; Hyatt et al., 2007; Reed & Czech, 2005) and fisheries (De Silva, 2012; McIntyre, Liermann, & Revenga, 2016) to protect fish biodiversity.

Thus, quantifying the contributions of human factors on biological patterns may aid ecologists and conservation biologists in protecting biodiversity across the landscape (Ellis, 2015; Soininen, Jamoneau, Rosebery, & Passy, 2016). Recent evidence indicated that natural patterns of freshwater fish assemblages are increasingly blurred in regions with strong socio-economic development (Leprieur, Beauchard, Blanchet, Oberdorff, & Brosse, 2008; Pyšek et al., 2010). For example, in North America, human population and economic growth were identified as major drivers for the decline in freshwater fish biodiversity (Limburg, Hughes, Jackson, & Czech, 2011). Also, Clausen and York (2008) reported a negative correlation between the number of threatened fishes and the size of national economies in all populated regions of the world. However, the changes in freshwater fish diversity and assemblages in response to socio-economic development remain largely unexplored in developing countries. For instance, in many developing countries, fast population growth and other related human stressors have led to rapid environmental changes in natural ecosystems over large spatial scales (e.g., land use changes, inland fisheries) with potential implications on biodiversity conservation issues; but their quantitative contributions are still unassessed (Allan, 2004; De Silva, 2012; Liu, He, Chen, & Olden, 2017; McIntyre et al., 2016; Sala et al., 2000; Ziv, Baran, Nam, Rodríguez-Iturbe, & Levin, 2012).

China is one of the largest developing countries with the densest human population (i.e., around 151 people per km^2, http://worldpopulationreview.com/) and a large and rapidly developing economy with growth rates averaging 6% over 30 years (IMF Report, 2013; National Bureau of Statistics of China, 2019; Yu, Zhang, & Liu, 2018). China is also the global leader in freshwater fisheries and aquaculture production (i.e., 41.1% over the 1950–2015 period) (Wang et al., 2015; Zhao, Gozlan, & Zhang, 2015), with almost all natural and man-made water bodies used for various freshwater fishery activities (Li, Liu, Wang, & De Silva, 2018; Wang et al., 2015). However, these human pressures on the environment are not evenly distributed across all Chinese regions and significant regional socio-economic differences persist (Deng, Huang, Rozelle, & Uchida, 2008; Kang et al., 2017; Liu & Diamond, 2005). For instance, socio-economic developments in the eastern and southern coastal regions of China are increasing at a faster rate than in the rest of the country (National Bureau of Statistics of China, 2019). The Yangtze River Economic Belt (YREB), one of the largest economic zones of China, has significantly higher economic growth and population density in the eastern and coastal subregions than those in the western and inland subregions (Chen et al., 2017). In addition, fishery activities are mostly located in central provinces along the middle and lower reaches of the Yangtze River basin (Li et al., 2018; Wang et al., 2015). Due to the large amount and regional imbalance of economic growth and fishery activities, these human stressors are often thought to be the main drivers of freshwater fish diversity changes in China (Hulme, 2015; Kang et al., 2014; Xing, Zhang, Fan, & Zhao, 2016). However, quantitative estimates of the relative contributions of both natural and human factors (such as biogeographic, economic growth and fisheries) in structuring fish assemblage patterns in this large developing country with fast population and economic growth remain poorly investigated. Filling this knowledge gap can help make more effective freshwater fish conservation policies.

In the current study, we used China as a typical representative of many developing countries with rapid socio-economic changes, to quantify the impacts of both natural and human factors and their relative importance on freshwater fish assemblage patterns. Specific objectives include (a) characterize large-scale spatial patterns of freshwater fish assemblages; (b) disentangle the relative contributions of both natural (i.e., biogeographic) and human factors (i.e., economic growth, inland fisheries) on observed fish assemblage patterns; and (c) provide a basis for developing conservation strategies of freshwater fish diversity. To this end and for the first time, we tested the hypothesis that human drivers (like economic growth and inland fisheries) in a rapidly developing country may override natural biogeographic patterns of freshwater fish assemblages.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was based on Chinese province administrative regions as they are used for fish surveys and socio-economic statistics (Dawson et al., 2017; Kang et al., 2014). Furthermore, climatic conditions, socio-economics and fish assemblages strongly differ between provinces. We analysed data from 29 regions spanning from about 50° of latitude (between 4°15′N and 53°31′N) and 63° of longitude (73°40′E and 135°50′E), including four municipalities (Beijing, Shanghai, Tianjin and Chongqing), five autonomous regions (Neimenggu or Inner Mongolia, Xizang or Tibet, Ningxia, Guangxi, and Xinjiang) and 23 provinces (Figure 1). Hongkong, Macau and Taiwan were excluded because of limited data availability. Tianjin and Chongqing were merged into Hebei and Sichuan provinces, respectively, thus reflecting the historical boundaries before separation of theses provinces.

2.2 | Fish data sets

A total of 908 freshwater fish species across the 29 administrative regions were assembled on a presence–absence basis through an extensive literature review, including journal articles (including online Supporting Information), monographs, grey literature databases, survey reports, natural museum collections and other sources, although there is still some disagreement about the total number of freshwater fish species recorded in China (Kang et al., 2014; Liu et al., 2017; Sui, 2010; Xing et al., 2016; Zhang & Zhao, 2016). The current fish data were assembled according to provincial administrative units for the period 1980 to 2015, which matched both socio-economic and biogeographic datasets. The fish species list corresponds to species recorded in the wild only, alien species used in aquaculture farms were excluded from the analysis.

2.3 | Natural and human drivers

Thirteen explanatory variables from two categories (biogeographic [i–v] and anthropogenic [vi–xiii]) were considered (Table S1).

The two categories were further divided into three subcategories: (I) *Biogeographic*: (i) Total Region Area (TRA), (ii) Surface Water Area (WEL), (iii) Mean Altitude (MAL), (iv) Annual Mean Air Temperature (AMT), (v) Annual Mean Precipitation (AMP). (II) *Economic growth*: (vi) Carbon Footprint (CFO), (vii) Gross Domestic Product (GDP), (viii) Human Population Density (HPD), (xvi) Urbanization Rate (URB), (x) Industrial and Residential Land (IRL). (III) *Inland fisheries*: (xi) Freshwater Aquaculture Production (FAP), (xii) Freshwater Capture Production (FCP), (xiii) Freshwater Aquaculture Area (FAA; See Table S1 for details of these drivers).

Biogeographic data including TRA, MAL, AMT and AMP were extracted from WorldClim (http://www.worldclim.org, Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), land use data (TRA, WEL, IRL) came from Global Land Cover Characterization Data Base (https://lta.cr.usgs.gov/GLCC) and then extracted with ArcGis 10.1 (ESRI). Socio-economic development data including GDP, HPD and URB were compiled from the National Bureau of Statistics of China (http://data.stats.gov.cn/) and fishery practice data including FAP, FCP and FAA were obtained from the "China Fisheries Year Book" from 1981 to 2015, edited by the Bureau of Fisheries, the Ministry of Agriculture (FDMA, 1981–2015). A mean value of the last 30 years data was calculated for each of these variables. The CFO data were directly calculated from Shi, Wang, Zhang, and Zhou (2012).

2.4 | Statistical analysis

We used machine learning algorithms (e.g., self-organizing map, random forest) to overcome the issues of non-linearity and inherent correlations among variables. Ecological data are often multi-dimensional with non-linear and complex interactions among variables. Machine learning techniques are flexible enough to handle complex problems with multiple interacting elements and typically perform better than traditional approaches (e.g., generalized linear models,

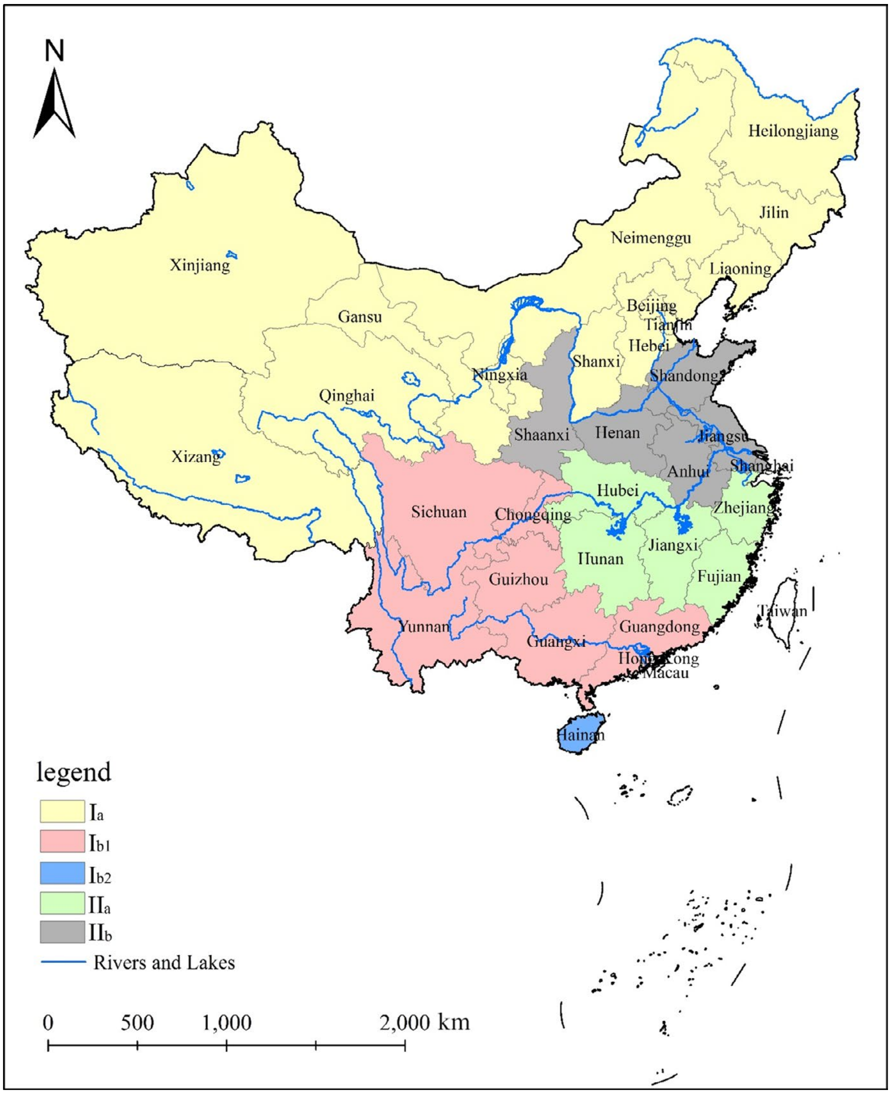

FIGURE 1 Geographic map of China and visualization of the five fish assemblages defined by Self-Organizing Map (SOM) analysis (the SOM analysis and five fish assemblages were introduced in detail in the sections of Material and Method, Results, and Discussion)

principle coordinate analysis), making them ideal for modelling ecological systems (Olden, Lawler, & Poff, 2008). A general flowchart on the overall framework of the methodology of our analysis is presented in Figure S1.

Patterns of China's freshwater fish assemblage were structured using a non-supervised machine learning method: self-organizing map (SOM, Kohonen, 1998), which classifies sampling sites with similar species composition. Thus, similar structures were classified into the same neuron or neighbouring neurons. However, SOM does not require prior knowledge and allows for visualization of the outcomes (Chon, 2011; Park, Chon, Bae, Kim, & Lek, 2018). The sequential algorithm and the Euclidean distance coefficient were used for training the SOM. The number of nodes was determined as 5 × (number of samples)^{½} (Vesanto, Himberg, Alhoniemi, & Parhankangas, 2000), and then based on the minimum values of quantization and topographic errors. The output layer of the SOM consists of 20 neurons (virtual units, SOM cells) arranged into a 5 × 4 hexagonal lattice to provide better visualization. According to the similarity of the neuron weight vectors, a hierarchical cluster analysis with a Ward's linkage method can further subdivide the cells of the map into different groups (i.e., assemblage types). The definition of group numbers is mainly based on the degree of dissimilarity of each SOM cell in the hierarchical clustering. The unified distance matrix (U-matrix; Ultsch, 1993) and hierarchical clustering were applied to reinforce the assemblage definition, and the cophenetic correlation coefficient and Davies–Bouldin index (Davies & Bouldin, 1979) were calculated to assess the effectiveness of optimal solution. SOM was performed using Matlab (The Mathworks, 2001). To robustly compare differences in fish assemblages clustered by the SOM, species richness (SR, the total number of species in each region), Simpson's index (J) and Shannon Wiener index (H) for the fish assemblage data were calculated for each of the administrative region. We used both indices because the Simpsons index is influenced by abundant species whereas the Shannon index is influenced by rare species (Kwak & Peterson, 2007). Kruskal–Wallis tests were used to compare the overall differences in fish diversity and environmental variables among all the clusters, and multiple comparisons were further conducted to compare the differences between each of two clusters (Dinno, 2015).

To unravel the relative contribution of biogeographic and anthropogenic determinants to freshwater fish assemblages across China, we applied variance partitioning. The relative roles of biogeographic, economic and fishery factors were explored using a variance partitioning procedure based on partial redundancy analysis (pRDA). Variance partitioning was used to split the variance into net effects of each class of variables and their joint effects, thus disentangling the relative importance of human and natural drivers.

Relative contribution of potential drivers in predicting freshwater fish diversity (using species richness as indicator) was then tested with Random Forest analysis (RF; Figure S1). Random Forests is widely used in bioinformatics (Cutler et al., 2007), but its use in ecological research has yet to be fully realized. Random Forests implements Breiman's random forest algorithm in which prediction is obtained by aggregating classification or regression trees and choosing splits of the trees (Breiman, 2001). Each "tree" is constructed using a different bootstrap sample of the data and each node is split using the best among a subset of predictors randomly chosen at that node (Liaw & Wiener, 2002). The Gini index (Breiman, Friedman, Ohlsen, & Stone, 1984) is used as the splitting criterion. At every split, one of the "mtry" variables (number of variables randomly selected at each node) is used to form the split leading to a decrease in the Gini index. The Gini measure is formed by the sum of all decreases in the forest for a given variable, normalized by the number of trees. In our study, the importance of variables was also estimated by the Gini criterion, which may be more appropriate for a small sample size (Archer & Kimes, 2008). The strength of the Gini value corresponds to a variable's degree of discriminability between classes (Oh, Laubach, & Luczak, 2003). The largest tree possible was grown without being pruned. The root node of each tree in the forest contains a bootstrap sample from the original data as the training set. Finally, RF will provide information on the importance of variables by using two approaches: 1) the percentage increase of the mean squared error ("%IncMSE") on the out-of-bag (OOB) subset (i.e., the subset of training set instances not used to build a given tree), and 2) the total decrease in node "impurity" from splitting on a given descriptor, averaged over all the generated trees ("IncNodePurity"). For regression, "impurity" is measured by the residual sum of squares (RSS) metric for a given node (Liaw & Wiener, 2002).

Partial dependence plots (Hastie, Tibshirani, & Friedman, 2009) were then used to visualize the marginal effect of the selected given variable from the RF, and used to graphically characterize relationships between single predicting variables and predicted probabilities of species presence obtained from the RF. Partial dependence plots can be extremely useful for knowledge discovery in large data sets, especially when the RF is dominated by lower-order interactions and main effects (Friedman, 2001).

Before data analysis, fish species composition data were transformed using the "hellinger" method, while explanatory variables data were log10 (X + 1) transformed (Legendre & Gallagher, 2001). All other statistical and analytic steps were performed in the R program (R Core Team, 2015) with "vegan" (Oksanen Jari et al., 2018), "pgirmess" (Giraudoux, 2018), "ggplot2" (Wickham, 2016) and "RandomForest" (Liaw & Wiener, 2002) packages.

3 | RESULTS

3.1 | Freshwater fish assemblages in China

The 29 Chinese administrative regions were shown on the SOM map according to the similarity of their freshwater fish species composition in 20 output cells (Figure 2a,b). Based on the similarity of fish composition in different cells, the clustering procedure identified two main clusters, I and II, which were subdivided into two smaller clusters named Ia and Ib (Ib was further subdivided into two clusters Ib1 and Ib2) on one side, IIa and IIb on the other side. This analysis resulted in a total of five clusters identified on the SOM map, which indicates five typical assemblages of Chinese freshwater fish regrouped as (a) Qinghai, Xizang, Xinjiang, Gansu, Ningxia, Neimenggu, Heilongjiang, Jilin, Liaoning, Hebei, Beijing and Shanxi (Ia, 12 units); (b) Yunnan, Guizhou, Sichuan, Guangdong and Guangxi (Ib1, 5 units); (c) Hainan (Ib2, 1 unit); (d) Hubei, Fujian, Hunan, Jiangxi, Zhejiang (IIa, 5 units) and (e) Shanxi, Henan, Shandong, Anhui, Jiangsu and Shanghai (IIb, 6 units) (Figures 1a,b and 2). Specifically, Ia included three typical climatic regions of China: the Tibetan plateau, and the arid and semi-arid regions and north and north-eastern regions; Ib1 described the fish assemblage in the Yun-Gui-Chuan region and Guangdong and Guangxi region, Ib2 represented assemblage of the islands, IIa represented the middle Yangtze River basin, IIb mostly described fish assemblage from the lower Yangtze River and Yellow River basin (Figure 2).

Biodiversity metrics (SR, J and H) varied significantly among the five fish assemblage groupings (Kruskal–Wallis, $p < 0.001$). Multiple comparisons showed that biodiversity metrics (SR, J and H) were significantly different between fish assemblages of clusters I and II ($p < 0.05$), Ia and Ib (i.e., Ib1 & Ib2) and between Ia and IIa ($p < 0.05$). Fish assemblages of cluster I had both the highest (Ib1) and lowest (Ia) freshwater fish diversity in terms of SR, J and H indexes (Figure 3).

Across all the three categories of explanatory variables, the Kruskal–Wallis test and multiple comparison tests revealed that human and biogeographic factors were significantly different not only among all assemblages but also between any two clusters. For instance, there was an overall significant difference of Mean Altitude, Annual Mean Air Temperature, Annual Mean Precipitation, Human Population Density and Freshwater Aquaculture Production among all the five fish assemblages. Further multiple comparison showed that Ia had significantly higher Mean temperature but lower Human Population Density than IIb; Ia had significantly lower Annual Mean Air Temperature, Annual Mean Precipitation and Freshwater Aquaculture Production than IIa; Ia had also significantly lower Annual Mean Precipitation than Ib1 (Table 1).

Variance partitioning showed that freshwater fish assemblage patterns in China were mostly influenced by biogeographic drivers with a relative variable importance of 21.8%, followed by economic growth drivers with a relative importance of 8.6% and inland fisheries with a relative importance of 7.0% (Figure 4).

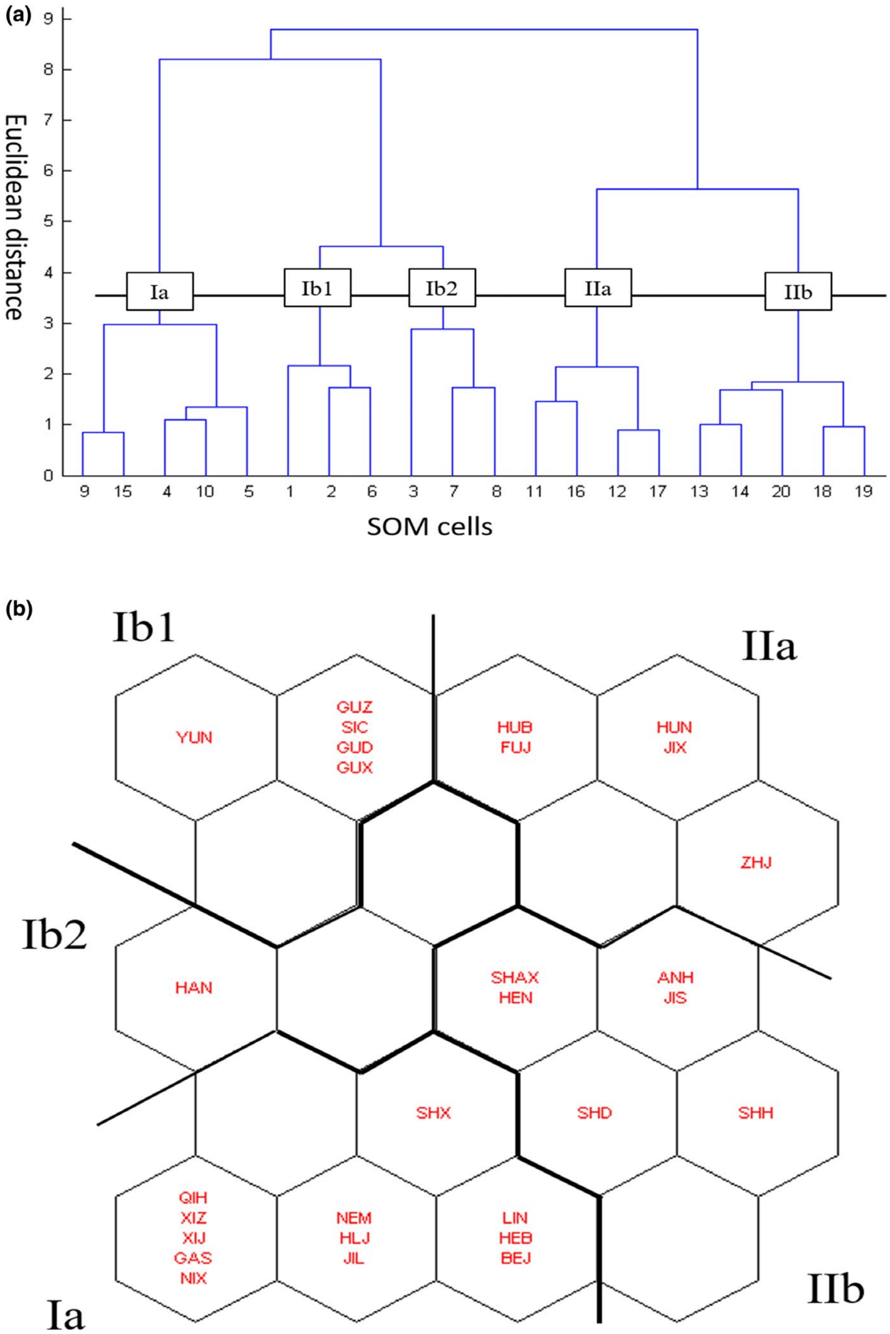

FIGURE 2 (a) Clusters of assemblages according to hierarchical clustering of Self-Organizing Map (SOM) cells (1–20) using the Ward method; (b) SOM map of the five main freshwater fish assemblages in China (the black lines divided the SOM cells into five clusters according to the hierarchical clustering), Ia: Qinghai (QIH), Xizang (XIZ), Xinjiang (XIJ), Gansu (GAS), Ningxia (NIX), Neimenggu (NEM), Heilongjiang (HLJ), Jilin (JIL), Liaoning (LIN), Hebei (HEB), Beijing (BEJ), Shanxi (SHX); Ib1: Yunan (YUN), Guizhou (GUZ), Sichuan (SIC), Guangdong (GUD), Guangxi (GUX); Ib2: Hainan (HAN); IIa: Hubei (HUB), Fujian (FUJ), Hunan (HUN), Jiangxi (JIX), Zhejiang (JIX); IIb: Shaanxi (SHAX), Henan (HEN), Shandong (SHD), Anhui (ANH), Jiangsu (JIS), Shanghai (SHH)

3.2 | Drivers responsible for freshwater fish diversity

The Random Forest model with all 13 factors explained 49.9% of the total variance in predicting freshwater fish species richness across the 29 units. As for relative contributions, biogeographic and inland fisheries factors were identified as dominantly affecting freshwater fish diversity in China (Figure 5). Based on the two approaches for variable importance in Random Forest algorithm (i.e., %IncMSE; IncNodePurity), annual mean air temperature, annual mean precipitation, freshwater aquaculture production, freshwater capture production, surface water area and urbanization rate were identified as the main drivers of species richness (Figure 5). However, partial dependence plots showed a negative relationship between species richness and urbanization rate (Figure 6). Although species richness generally increased with the percentage of water surface area, most of the observations in per cent water surface area had a relatively narrow range (Figure 6).

4 | DISCUSSION

This study characterized freshwater fish assemblage patterns and quantified the relative contributions from natural and human drivers in a typical rapidly developing country (i.e., China), using two machine learning (ML) algorithms, self-organizing map (SOM) and

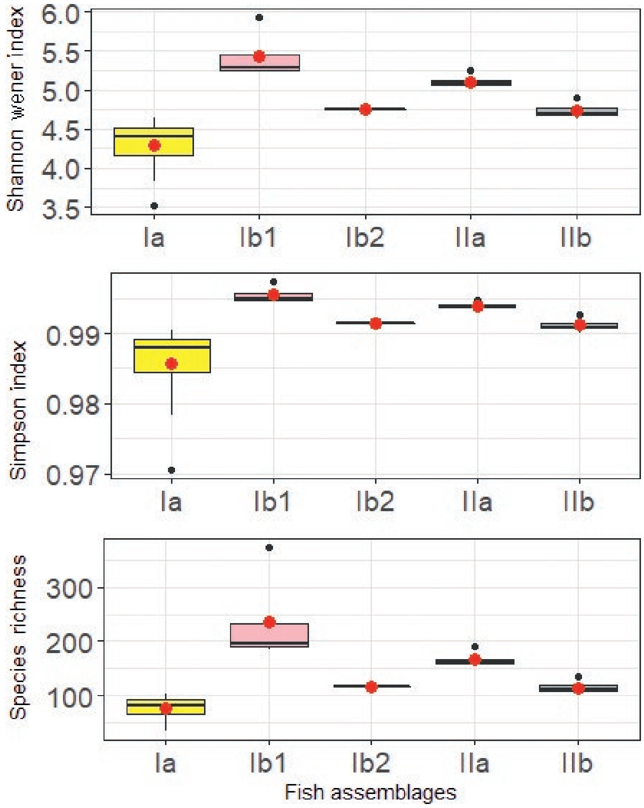

FIGURE 3 Box plot of freshwater fish species richness and diversity indices among five fish assemblages in China (Ia, Ib1, Ib2, IIa and IIb showed the five freshwater fish assemblages defined by Self-Organizing Map (SOM), top: Shannon Wiener Index; middle: Simpson Index; bottom: Species Richness. Red dots represent the mean value; Black dots represent the outliers; Black lines in the box represent the median value)

random forest (RF). Machine learning methods, originating in the field of artificial intelligence, are recognized as holding great promise and inherent advantages for the advancement of understanding and prediction about ecological phenomena (Olden et al., 2008). SOM and RF have been promoted in ecology as powerful alternatives to traditional modelling approaches in testing biogeographical, ecological and evolutionary hypotheses, and modelling species distributions for conservation and management planning (Park, Chang, Lek, Cao, & Brosse, 2003; Park et al., ; Stuart-Smith et al., 2013) and should be useful in fisheries and other related fields.

Our results showed that despite tremendous human-led environmental changes over the last few decades, natural biogeographic factors still dominate in structuring freshwater fish assemblages in China over large geographical ranges, despite the widely acknowledged impacts from inland fisheries, economic development and increasing population (Henriques et al., 2017; Limburg et al., 2011). These findings are consistent with other studies in South America and Europe which, for example, identified natural predictors such as altitude and climatic conditions as the main drivers of fish distribution patterns (Amarasinghe & Welcomme, 2002; Brucet et al., 2013; Henriques et al., 2017; Zhao, Fang, Peng, Tang, & Piao, 2006). Our study also revealed that annual mean temperature and rainfall are important in structuring fish assemblage patterns, showing that Chinese freshwater fish assemblages may be particularly vulnerable to climate change (Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008; Poesch, Chavarie, Chu, Pandit, & Tonn, 2016). In effect, a change in the patterns of these climatic factors could alter fish assemblage structure, growth and recruitment (Lynch et al., 2016; Paukert et al., 2017).

The five main freshwater fish assemblages identified correspond to regions with significant differences in climate, human population densities and level of inland fisheries. The first fish assemblage (Ia) corresponds to regions with the lowest fish species richness reflecting the harsh climatic conditions (i.e., high elevations with extremely low air temperature for long periods, and high solar radiation). The Tibetan Plateau (e.g., Qinghai, Xizang) often referred to as the "third pole" or "Asia water tower" due to its extremely high altitude and ice/snow coverage is of relatively young geological age (Cenozoic Era, Zhong & Ding, 1996; Hawkins et al., 2003) thereby providing lower potential for colonization and speciation (e.g., high elevation). Similarly, arid and semi-arid regions (e.g., Xinjiang, Gansu, Ningxia) are species-poor due to low precipitation and many saline lakes (Wang & Dou, 1998). Finally, the north and north-east regions in China (e.g., Heilongjiang, Jilin, Liaoning) are characterized by annual mean temperature range of −4 to 6°C and precipitation from 350 to 700 mm, which limits freshwater fish richness (Guo et al., 2016; Zhao et al., 2006). The second fish assemblage cluster (Ib1) includes regions with a high fish species diversity such as the Guangdong, Guangxi and Yun-Gui-Chuan regions. The rugged topography (e.g., gorges, karst topography), humid subtropical climate and abundant river systems of the Yun-Gui-Chuan region makes it a hotspot for Asian freshwater fish diversity (Kang & He, 2007; Yang, Tian, Hao, Pei, & Yang, 2004; Zhao et al., 2006). Hainan island constitutes a separate fish assemblage cluster (Ib2), likely because it has been geographically separated from the mainland for over 60 M years leading to a unique endemic fish fauna (Bender et al., 2017). The fish assemblages in regions that show a high development of inland fisheries (e.g., Hubei, Hunan, Jiangxi; Table 1, IIa) are closely related to the regions with rapid economic growth (e.g., Jiangsu and Shanghai; Table 1; IIb). Both clusters (IIa & IIb) are located along the middle and lower part of the Yangtze River basin, which is a hub for the new economic regional development (i.e., the Yangtze River Economic Belt, YREB; Chen et al., 2017). The YREB is undergoing rapid economic development and provides the main freshwater fisheries production in China (Chen et al., 2017; Cui & Li, 2005). In addition, the region hosts an incredibly high number of lakes connected to the Yangtze River, which provide diverse habitats particularly suitable for sustaining a high level of freshwater fish species (Cui & Li, 2005; Fu, Wu, Chen, Wu, & Lei, 2003).

Our results also revealed a positive relationship between freshwater fishery activities and fish species richness (see Figure 6) maintained by one of the world's largest annual inland fishery productions (Li et al., 2018; Wang et al., 2015). These results were unexpected as fisheries are often presumed to only have a detrimental environmental impact on freshwater fish diversity (Zhao et al., 2015). However,

TABLE 1 Mean values (range) of biogeographic, economic growth and inland fisheries explanatory variables in each of the five fish assemblages in China

Variables	Freshwater fish assemblages				
Biogeographic	**Ia**	**Ib1**	**Ib2**	**IIa**	**IIb**
Total region area[ns]	525.5 (16.37–1,635)	306.4 (175.5–563.5)	33.73	152.2 (101.3–211.6)	133.1 (5.89–205.7)
Area in surface water (10^3 km^2)[ns]	6.96 (0.87–47.55)	16.11 (0.52–67.54)	14.3	7.46 (1.13–12.86)	8.39 (0.47–28.34)
Mean altitude (m)**	1,045[a] (116.8–3,958)	781.2 (13.5–1,728)	18	50.91 (20.25–90)	139.7[b] (12.5–657)
Annual mean air temperature (°C)**	3.31[a] (−3.7–13.7)	14.04 (5–19.3)	22.5	15.22[b] (12.9–17)	13.08 (9.4–17)
Annual mean precipitation (mm)***	401[a] (169.2–637.8)	1464[b] (1,078–2,234)	1861[bc]	1,495 (1,209–1,890)	959.2 (521.4–1,649)
Economic growth					
Carbon footprint (–)[ns]	1.51 (0.16–3.39)	1.48 (0.93–2.09)	1.05	1.43 (0.94–1.8)	2.16 (1.28–3.58)
Gross domestic product (10^9 Yuan)[ns]	5,946 (372.9–1,3780)	11,670 (3,478–31,000)	1,461	10,460 (6,487–13,480)	16,080 (6,819–27,750)
Human population density (10^4 ind./km^2)*	0.02[a] (0–0.11)	0.024 (0.01–0.05)	0.02	0.034 (0.03–0.05)	0.098[b] (0.02–0.33)
Urbanization rate (–)[ns]	0.49 (0.23–0.85)	0.43 (0.33–0.65)	0.5	0.51 (0.44–0.61)	0.54 (0.39–0.89)
Industrial and residential land (10^3 km^2)[ns]	7.97 (1.32–23.65)	6.63 (0.96–10.79)	12.36	9.31 (0.91–17.03)	3.15 (1.12–6.16)
Inland fisheries					
Freshwater aquaculture production (ton)**	175,400[a] (71.8–732,400)	1,210,000 (144,400–311,000)	363,300	1,669,000[b] (621,600–3,716,000)	987,500 (100,400–2,316,000)
Freshwater capture production (ton)*	20,520[a] (26.67–86,540)	55,050 (11,500–103,900)	18,920	110,000[b] (53,980–174,600)	91,620 (4,122–209,300)
Freshwater aquaculture area (10^3 ha)[ns]	108,900 (31–382,500)	191,900 (59,390–37,1100)	37,410	379,700 (101,200–688,300)	296,400 (19,930–578,100)

Note: (Kruskal–Wallis test was used to test the overall difference among the five assemblages, variables with ns, *, ** or ***means that there is no significant difference, significant difference with *p* values <0.05, <0.01, or <0.001, respectively. –means no unit. Variables with different lowercase letters a, b or c showed there is significant difference ($p < 0.05$) in the multiple comparison tests among each pair of the fish assemblages).

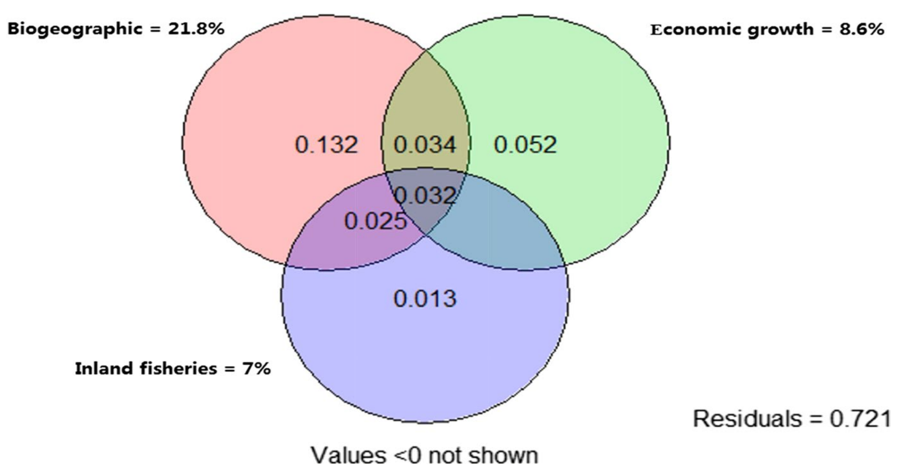

FIGURE 4 Variance partitioning analysis to assess the relative importance of natural and human factors in determining freshwater fish assemblages in China. Values within the circles indicate the proportion of variance explained by each factor or combination of factors

the opposite effect as found in this study may be partly explained by effective conservation strategies based on restocking natural systems with freshwater fishes, which typically involves either stock enhancement, which aims to maintain fish populations at a stable level, or multiple releases to increase both the number of recruits and the spawning biomass (Bai et al., 2017; Li, Liu, Wang, & Silva, 2018).

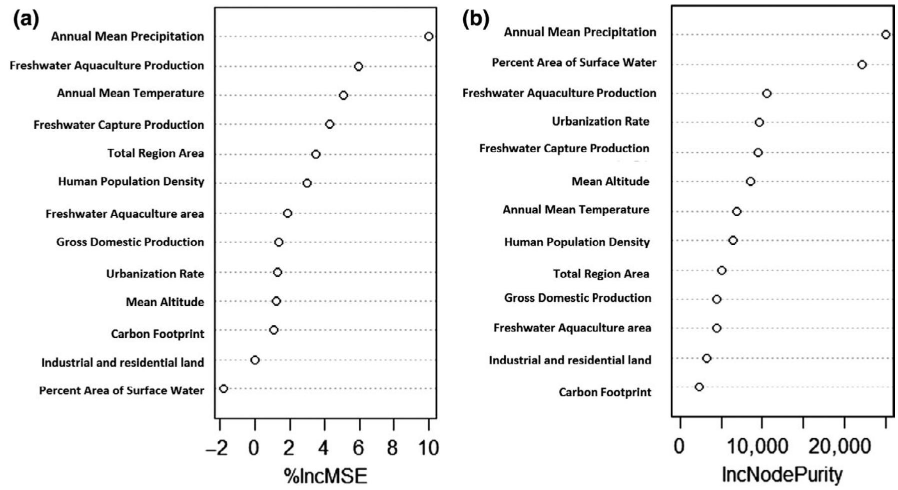

FIGURE 5 Relative contributions of explanatory variables to Species Richness of freshwater fishes by RF models, with two different methods (a: the percentage increase of the mean squared error ["%IncMSE"] on the out-of-bag [OOB] subset, and b: the total decrease in node "impurity" from splitting on a given descriptor, averaged over all the generated trees ["IncNodePurity"])

However, these restocking efforts may have consequences such as the direct or indirect genetic effects to the native populations (Van Zyll de Jong, Gibson, & Cowx, 2004). In addition, other issues related to inland fisheries development such as non-native species invasions, escapees and potential fish community homogenization could still remain (Gozlan, 2017; Liu et al., 2017; Xiong, Sui, Liang, & Chen, 2015). A more detailed study into the ecological condition and integrity of local fish populations could provide a better insight into the true contribution of fisheries to local freshwater fish diversity. In fact, the world-leading high production of inland fisheries in China mainly comes from aquaculture and stocking-based capture fisheries rather than from wild species-based capture fisheries (Chen et al., 2016; Li et al., 2018).

Overall, this study indicates that on a large geographical scale, natural factors (e.g., precipitation, temperature) drive freshwater fish patterns despite rapid socio-economic changes in a developing country. However, rapid economic development and human-led impacts are not exempt from negative impacts on local fish assemblages (Wu, Xu, Kennard, Yin, & Zuo, 2016). The effects of economic development and population increases on freshwater fish diversity cannot be ignored as urban development rates show a slightly negative relationship with freshwater species richness. To further determine how local species diversity is linked to anthropogenic activities, future studies may compile more regional and local data to further investigate local impacts from these stressors. For example, the YREB region has an area of 2.1 million km^2 including 11 provinces and municipalities from Yunan and Sichuan in the west to Shanghai in the east and contributes to over 40% of both the overall population and the national gross domestic product. In this region, water pollution (stressors include urbanization, industry, mining activities and agriculture), overfishing, dam construction and others were potentially

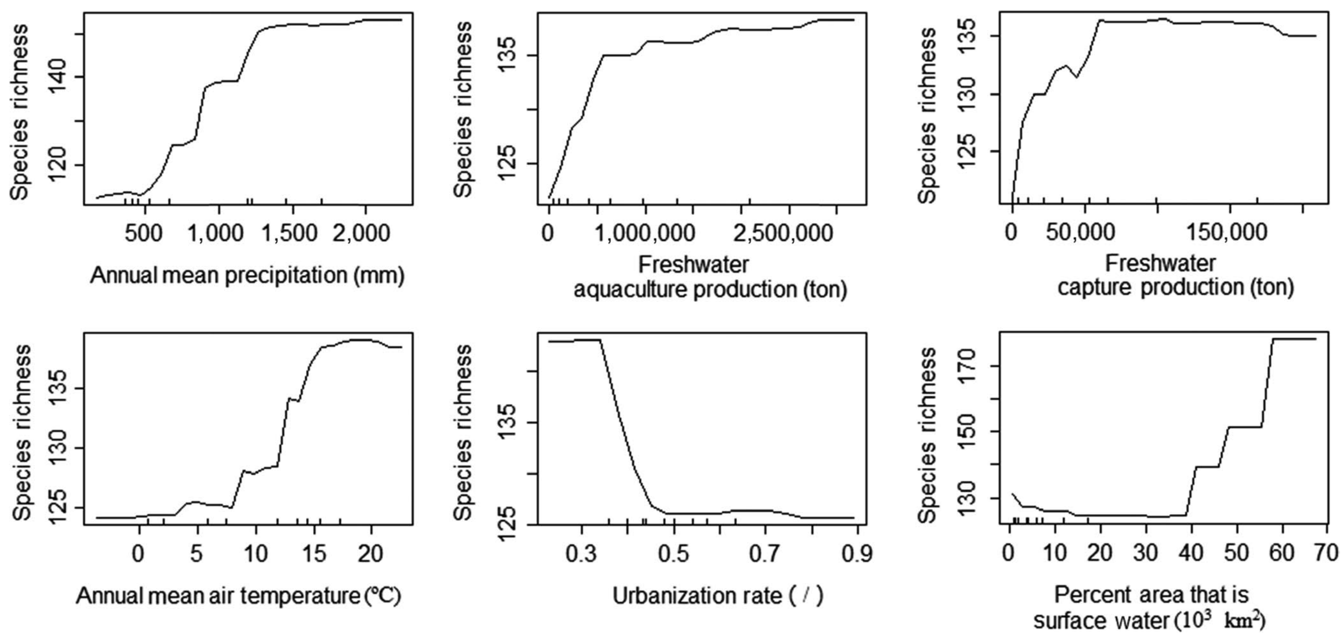

FIGURE 6 Partial dependence plots of the selected drivers (annual mean precipitation, annual mean air temperature, freshwater aquaculture production, urbanization rate, freshwater capture production and per cent of area that is surface water) in predicting species richness in China from the Random Forest model

the most important threats to aquatic biota (Chen et al., 2017; Fang et al., 2006), suggesting that local and regional factors still interact in structuring fish assemblages. Therefore, local and regional management actions still may provide a useful tool to protect biodiversity.

China has a remarkable freshwater fish biodiversity, most of the species are endemic with low resilience and small populations with no fisheries (Kang et al., 2014). Moreover, due to the sharp decline in aquatic resources and biodiversity crisis in China, the central government has implemented a series of regulations to protect wild fish species. One of the examples is the seasonal closure of commercial fisheries in the Yangtze and other major river basins (China Ministry of Agriculture and Rural Affairs, http://www.moa.gov.cn/).

5 | CONCLUSIONS

Our study found that natural factors were revealed to drive freshwater fish patterns despite rapid socio-economic changes in a developing country. Strong effects from climatic conditions on freshwater fish assemblages and biodiversity suggested that Chinese freshwater fishes could be particularly vulnerable to future climate change. Increases in precipitation, air temperature, aquaculture and capture fishery production and surface water area were associated with increased freshwater fish species richness while urbanization was associated with decreased fish species richness. In China, and possibly in other rapidly developing countries, both natural (e.g., climate change) and human (e.g., urbanization, inland fisheries) factors may need to be considered when establishing aquatic conservation strategies and priorities.

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CONFLICT OF INTEREST

All the co-authors declare no conflict of interests.

DATA ACCESSIBILITY

Data available on request from the first author (guochuanbo@gmail.com) and the correspondence author (yushunchen@ihb.ac.cn).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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