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Species invasions threaten the antiquity of China's freshwater fish fauna

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ABSTRACT

Aim Human-mediated species introductions and extirpations have resulted in the homogenization of biotas over time. However, there remains considerable uncertainty in our understanding of homogenization process for megadiverse regions of the world. Here, we investigate the consequences of widespread species invasions and extirpations for the biogeography of China's unique freshwater fish fauna.

Location China.

Methods By assembling a comprehensive dataset for distribution of Chinese freshwater fishes, we quantify how non-native fish species, from both overseas introductions and domestic translocations, has led to taxonomic homogenization of fish faunas at watershed, basin, ecoregion and country scales. We explore how the observed patterns in homogenization vary geographically, and identify those species most responsible for the faunal changes. Lastly, we simulate how China's fish fauna may continue to homogenize according to different scenarios of anticipated species introductions and extirpations.

Results We demonstrate that species introductions and extirpations have homogenized freshwater fish faunas across China. Overall compositional similarity of watersheds increased by 7.0% (from a historical 14.9% to 21.9% in the present day; Sørensen index). Compositional similarity of 96 of 103 (93.2%) watersheds increased, with western basins exhibiting the highest magnitude. Translocated non-native species associated with aquaculture practices contributed the most to faunal homogenization when compared to alien species (7.3% and 0.4%, respectively). Furthermore, faunal homogenization is predicted to intensify an additional 0.5–4.2% with increasing numbers of new non-native species introductions and the extirpation of native species.

Main conclusions Species introductions and extirpations have resulted in the significant impoverishment, and thus the loss of antiquity, of China's freshwater fish fauna over the past century. In the light of the growing realization that species composition (not richness) defines the role that biodiversity plays in maintaining ecosystem function, our study highlights the need for conservation strategies in China that consider changing patterns of β diversity.

Keywords
biological invasions, conservation planning, prediction, risk assessment, species extirpations, β diversity.

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INTRODUCTION

Humankind has witnessed unprecedented changes in the global distribution of plant and animal species over the past century, triggering massive reshuffling of biotas and sparking a biodiversity crisis. Conservation concern has predominantly focused on the loss of species through global extinction (Barnosky *et al.*, 2011; Monnet *et al.*, 2014; Ceballos *et al.*, 2015) and the fear of projected losses into the future (Urban, 2015). Simultaneously, human activities have led to many invasive species becoming increasingly more widespread (Pyšek & Richardson, 2010). The loss of native populations

through local extirpation, combined with the establishment and spread of already common non-native species, is leading to a dramatic reconfiguration of modern biodiversity (Olden et al., 2004).

A prominent dimension of the biodiversity crisis is biotic homogenization, referring to disparate regions becoming more similar in their species compositions through time as the result of the widespread invasion of ubiquitous non-native species into areas where rare, and often unique, native species are at-risk for extinction (McKinney & Lockwood, 1999; Olden, 2006). Put another way, biotic homogenization is the process by which β diversity decreases over time. Examining present-day and potential future homogenization affords decision-makers valuable information to prioritize species and areas essential for conservation (Olden et al., 2004; Rooney et al., 2007). Recent decades have seen enhanced public interest and research effort in the study of biotic homogenization across taxonomic groups (e.g. Olden et al., 2016). Evidence for fish (e.g. Villéger et al., 2011), mammal (e.g. Spear & Chown, 2008), bird (e.g. Monnet et al., 2014), amphibian (e.g. Smith et al., 2009), invertebrate (e.g. Capinha et al., 2015) and plant communities (e.g. Qian & Ricklefs, 2006) suggests that biotic homogenization may be widespread. However, this body of research also points to considerable geographic bias in our understanding of the homogenization process. To date, the majority of research efforts have focused on biological changes in developed countries from North America and Europe (reviewed in Baiser et al., 2012), with much fewer systematic investigations in developing countries (but see Vitule et al., 2012; Daga et al., 2015; Ding et al., 2016).

Elucidating patterns of biotic homogenization in developing countries is instrumental for informing national conservation plans, as well as guiding global biodiversity protection strategies given that developing countries are often megadiverse (i.e. countries with highest biodiversity on Earth) (Vitule et al., 2012; de Andrade Frehse et al., 2016). Many developing megadiverse countries are facing severe biodiversity loss driven by habitat degradation, species invasion and human exploitation (Vitule et al., 2012; Daga et al., 2015; de Andrade Frehse et al., 2016). For example, reservoir construction in conjunction with species introductions has led to decreased β diversity of fish fauna in the Parana River Basin, Brazil (Vitule et al., 2012). However due to insufficient scientific investment, reports of homogenization in these countries have been limited to the regional scale (Nunez & Pauchard, 2010; Daga et al., 2015; de Andrade Frehse et al., 2016). Additional investigations of national-level changes in biodiversity over time are still needed.

China is one of the Earth's megadiverse developing countries and has highest biodiversity in Asia, with more than 30 000 species of higher plants and 6000 vertebrate species. Likely half of all species are endemic to China (Liu et al., 2003; Tang et al., 2006). However, due to intensifying economic growth, China is currently facing a biodiversity crisis of unparalleled magnitude (Xie et al., 2001; Liu & Diamond, 2005). Habitat loss and nature degradation by human activities are the most significant threats to biodiversity in China, and impacts by human-mediated species invasions are mounting (Xie et al., 2001; Xu et al., 2006). Freshwater fish are among the most imperilled taxa, threatened by dam construction, land degradation and water pollution (Kang et al., 2013b; Xing et al., 2015). Moreover, aquaculture practices, pet trade and heightened trade activities (including shipping and air transportation) have contributed to the widespread introduction of non-native fishes (Xie et al., 2001; Lin et al., 2015). Current research activities regarding freshwater fish invasions are almost exclusively focused on α diversity (e.g. Ye et al., 2015) or γ diversity (e.g. Xiong et al., 2015), whereas the patterns and drivers of changes in β diversity have been poorly documented (but see Ding et al., 2016).

This study investigates whether the antiquity of China's freshwater fish fauna has been threatened by the widespread invasions of non-native fish species over the late 19th and 20th centuries. China has more than 1500 native freshwater fish species, representing about 10% of world's freshwater fish (Closs et al., 2015), and is home to over 430 introduced alien freshwater fish species, making it the most invaded country of the world (Xiong et al., 2015). Our research focuses on two overarching questions. First, has the establishment of non-native species, from both overseas introductions and domestic translocations, lead to taxonomic homogenization? If so, how do observed patterns in homogenization vary geographically, and what species are the most responsible for these faunal changes? Second, will China's fish fauna continue to homogenize in the future with ongoing species introductions and extirpations? By elucidating the pattern and drivers of changes in China's freshwater fish fauna, we aim to inform management policies that ensure the conservation of native fish biogeography in the light of past and likely future species invasions.

METHODS

Dataset

We examined the historical and present-day biogeography of freshwater fishes across China by examining 103 primary watersheds nested in nine major river basins according to the HYDRO1k geographic database (U.S. Geological Survey, http://eros.usgs.gov/). The delineation of watersheds corresponds to the reporting of fish species occurrences found in regional species checklists (e.g. Xie, 2007 for the north-eastern China) and scientific papers (e.g. Chen et al., 1995 for the Qinghai–Tibet Plateau), which ensured accurate estimates of species composition for each watershed. We further quantified patterns in homogenization at the scale of freshwater ecoregion by assigning species lists of watersheds to the ecoregion by which they belonged. Freshwater ecoregions are defined by both freshwater fish composition and related ecological and evolutionary processes, thus representing the important unit for conservation planning at the broad scale (Abell et al., 2008).

We assembled fish species lists for all watersheds based on a comprehensive review of literatures that included regional texts and hundreds of peer-reviewed articles; the result is the most complete Chinese freshwater fish distribution dataset to date (full references are provided in Appendix S1 in Supporting Information). Species were classified into different categories according to their distributional status for each watershed. *Native species* ($n = 1513$) are freshwater fish indigenous to the watershed. *Non-native species* ($n = 147$) were defined as species introduced to the watershed after 1950 (representing the majority of species invasions, Xiong *et al.*, 2015) or species with a known record of introduction before 1950. To distinguish the contribution of extralimital and extraregional introductions on biogeographic changes, we further divided non-native species into translocated species and alien species. *Translocated species* ($n = 91$) are species native to China but introduced (translocated) to at least one other watershed in which they are non-native, whereas *alien species* ($n = 56$) are non-native species introduced from another country or countries. *Extinct species* ($n = 4$) are those categorized as Extinct and Extinct in the Wild according to the Red List of China's Biodiversity (data available at http://www.mep.gov.cn/). Following Olden & Rooney (2006) and others in the literature (reviewed in Olden *et al.*, 2016), we defined the historical fish fauna as extant native species plus extinct species, representing watershed composition before species introductions; and the current fish fauna as extant native species plus non-native species (i.e. translocated and alien species), representing watershed composition after species introductions.

Statistical analysis

β diversity is defined as the variability in species composition among sampling units for a given area and can be quantified according to an array of metrics, including those that can be disentangled into two independent processes of spatial turnover and species richness (Carvalho *et al.*, 2012). Turnover reflects the replacement of some species by others from watershed to watershed, and richness reflects the ordered loss of species between watersheds (i.e. a pattern is characterized by the lowest richness watershed being a strict subset of the highest richness watershed). Understanding changes in different components is important for evaluating the significance of shifting patterns in β diversity and informing relevant conservation practices (Baiser *et al.*, 2012; Carvalho *et al.*, 2012). Here, we quantified overall β diversity as pairwise watershed similarity according to the Sørensen index ($β_{sor}$), with its turnover ($β_3$) and richness ($β_{rich}$) components being quantified as follows (Carvalho *et al.*, 2012):

$$\beta_{sor} = \frac{b + c}{2a + b + c},$$

$$\beta_3 = 2 \times \frac{\min(b, c)}{2a + b + c},$$

$$\beta_{rich} = \frac{|b - c|}{2a + b + c},$$

where a is the number of shared species between two watersheds, and b and c are the number of species only present in the first and second watersheds, respectively. Sørensen index ranges from 0 to 1, respectively, representing that no species and all species are common between two watersheds.

Changes in β diversity were calculated by subtracting historical compositional similarity from current compositional similarity for each pairwise watershed comparison; these values were then summarized for each watershed, basin, ecoregion and the entire country by calculating the average of all pairwise changes for each spatial grain. A positive value represents an overall increase in mean compositional similarity from historical to current time period, thus representing biotic homogenization, whereas a negative value represents an overall decrease in mean compositional similarity (i.e. biotic differentiation) (Olden & Rooney, 2006). We used multiple analyses of similarities (ANOSIM, Clarke, 1993) to test the null hypothesis that there was no difference between historical and current compositional similarity (according to the Sørensen index) with constraining comparisons among watersheds in the same major basin.

Contributions of non-native species to compositional changes over time were calculated by adding each species individually to the historical species matrix and recalculating the change in similarity according to the Sørensen index (following Toussaint *et al.*, 2016). This allowed the ordering of non-native species contributions according to whether species had a homogenizing (more positive value) or differentiating (more negative value) influence on fish faunal composition. Contributions of translocated or alien species were calculated by assuming the introduction of only the entire suite of translocated or alien species using the procedure above.

Establishment of non-native species and extirpations of native species are expected to continue into the future due to ongoing environmental degradation and intensifying, and new, vectors of species invasions (i.e. extinction debts, Kuussaari *et al.*, 2009; invasion debts, Essl *et al.*, 2011). We predicted future changes in β diversity by evaluating a number of realistic scenarios describing likely levels of invasion and extirpation. First, we constructed a list of non-native fish species ($n = 231$) that: (1) have established populations in at least one foreign country (in addition to China) based on a comprehensive review of the published literatures and online databases (J.D. Olden, unpublished data); and (2) have been already introduced in China but not known to have established populations in the wild (Xiong *et al.*, 2015). These species are hypothesized to have a higher likelihood of being introduced and establishing populations in the future. We added to this list the non-native species ($n = 147$) that have established in at least one watershed in China (i.e. the non-native species list from the current fish dataset). Second,

threatened species are the most likely candidates to become extirpated in the future (Kuussaari et al., 2009; Matsuzaki et al., 2013); therefore, we collated a list of threatened native species (n = 295) that are identified as Critically Endangered, Endangered or Vulnerable according to the IUCN Red List of Threatened Species (2015, version 4; http://www.iucnred list.org) and the Red List of China's Biodiversity. We believe that this represents a conservative approach because IUCN has the limited coverage in China and many threatened species in developing countries have yet to be formally assessed.

Next, we simulated six scenarios of future fish faunas that represented plausible non-native species introductions and threatened species extirpations. We examined three levels of future species introductions that accounted for differences in the vulnerability of watershed to invasions. Specifically, we assumed that the number of new non-native species introductions into any one watershed was proportional (three levels: 50%, 100% and 200%) to the current non-native richness in that watershed. To account for differences in establishment success among non-native species, species from the potential non-native species pool were randomly added to watersheds following the 'frequency-dependent' assumption (Villéger et al., 2015), or in other words, the probability of invasion was weighted by its current occurrence frequency (i.e. the proportion of currently established watersheds for non-native species already established in China and the proportion of established countries for potential new non-native species). We examined two levels of potential species extirpations in the future, the case where all threatened species will become extirpated from the watersheds in which they currently exist; and the case where no threatened species will be lost (following Villéger et al., 2015). The three levels of future non-native species introductions and two levels of future threatened species extirpations were crossed to produce six scenarios. For each scenario, we conducted 1000 simulations of future non-native faunas, and non-native species were only allowed to establish in watersheds in which they did not exist in the present day.

For each simulated future fish fauna, we calculated the changes in β diversity between historical, current and future time periods by subtracting historical/current compositional similarity from future compositional similarity. As described previously, the contributions of translocated and alien non-native species to changes in β diversity were calculated according to each scenario. All the analyses were performed in R 3.2.0 (R Development Core Team, 2014) using the packages BAT (Cardoso et al., 2015) and VEGAN (Oksanen et al., 2015).

RESULTS

China's freshwater ichthyofauna has witnessed significant changes in response to species introductions and extirpations over the past century (R_{ANOSIM} = 0.22, P < 0.001). On average, watersheds now support 13.0 non-native species (59.4% translocated and 40.6% alien species) (Table 1), where the main sources include North America (30.9%), Asia (27.9%) and Europe (20.6%) (Table S1). The mean number of shared species for all watershed pairs increased from a historical 14.6 to 22.1 in the present day, and taxonomic uniqueness, defined as the proportion of watershed pairs having no common species, showed a quadruped decline from 31% to 8%. Additionally, watershed pairs that formerly had no species in common now share an average of 5.8 species. A noticeable example is that the number of shared species between Nanpan jiang and Dian dong watersheds increased almost fivefold from 13 species to 62 species.

Non-native species introductions have resulted in a dramatic homogenization of China's freshwater fish fauna. The overall compositional similarity increased by 7.0% (from 14.9% to 21.9%) at the country scale, with south-western ecoregions demonstrating the highest level of homogenization (Fig. 1a,b, Table 1 and Table S2). At the basin scale, the Southwest Basin and Yellow Basin exhibited the most striking homogenization (11.3% and 9.1%, respectively) (Fig. 1d, Table 1). On average, basins showed increased similarity of species turnover and richness, with magnitude of richness much higher than turnover (Table 1). Compositional similarity of 96 of 103 (93%) watersheds has increased over time; the highest magnitude of homogenization was recorded in

Table 1 Richness of native, translocated and alien species, and changes in compositional similarity [Mean (95% confidence interval)] quantified by Sørensen index and its turnover and richness components at the basin and country (All) scales.

| Basin	No. of watersheds	No. of species			Δ Compositional similarity		
		Native	Translocated	Alien	Sørensen	Turnover	Richness
Continent	15	118	45	11	5.9 (3.3)	3.3 (2.2)	2.6 (4.8)
Haihe	1	133	3	0	5 (0)	−0.9 (0)	5.9 (0)
Huaihe	4	123	2	4	6.4 (0.1)	1.1 (1)	5.2 (1)
Northeast	12	200	14	3	5.6 (0.8)	1.1 (1.2)	4.6 (1)
Pearl	20	595	47	23	6 (1.8)	0.7 (1.7)	5.4 (0.7)
Southeast	3	312	12	25	4.6 (0.4)	0.2 (1.8)	4.4 (1.4)
Southwest	18	447	45	14	11.1 (3)	5 (1.1)	6 (2.9)
Yangtze	21	419	57	33	5.8 (1.3)	1.5 (1.1)	4.3 (1.3)
Yellow	9	185	31	31	9.1 (2.6)	1.3 (1.2)	7.8 (2.7)
All	103	1513	91	56	7 (0.9)	2.1 (0.6)	4.9 (1)
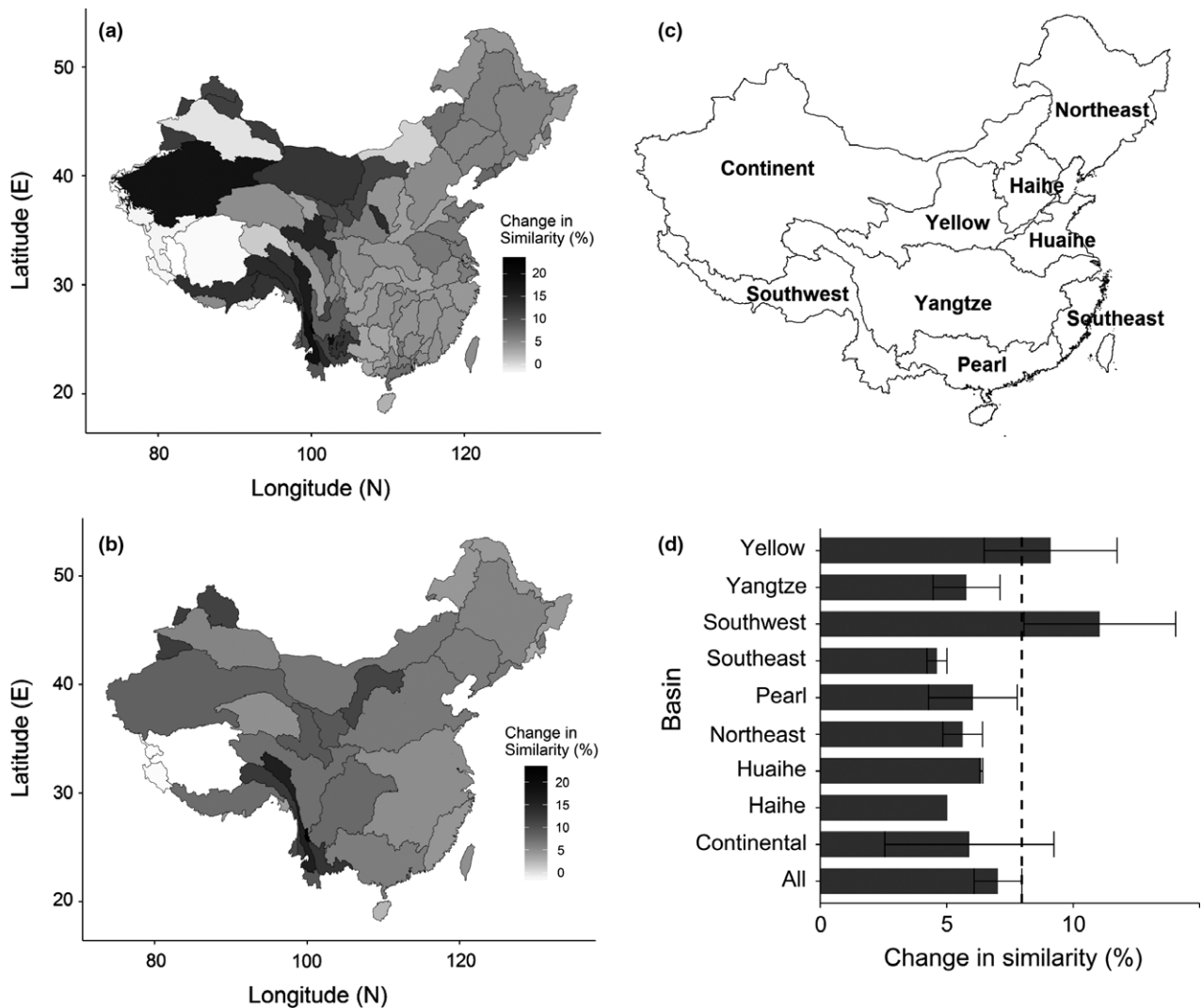
Figure 1 Change in β diversity between historical and present-day fish fauna caused by species invasions and extinctions. β diversity was quantified by Sørensen pairwise similarity index and the division of freshwater ecoregions followed Abell *et al.* (2008). (a) Mean compositional changes for all 103 watersheds (positive values represent homogenization). (b) Mean compositional changes for all ecoregions. (c) The division of nine major basins in China. (d) Compositional changes for nine basins (bars and whiskers represent the mean and 95% confidence intervals across watersheds for each basin, respectively; dashed line represents overall mean).

Erhai demonstrating a nearly seven-time increase in similarity from 4.2% to 27.1%.

Non-native species with widespread distributions contributed the most to fish faunal homogenization (Fig. 2). In fact, a small number of widely distributed non-native species drove increases in compositional similarities, whereas the remaining three quarter of species (74.8%) with restricted distributions contributed to slight differentiation, that is decrease in compositional similarity. Translocated species showed considerably greater effects on faunal similarity compared with alien species (7.3% and 0.4%, respectively). Among the 20 non-native species with highest contributions to homogenization, the top seven and over two-thirds (14 species) were translocated species that are native to China (Fig. 3).

Homogenization is predicted to intensify with increasing numbers of new non-native species introductions; the most striking changes occurring with the greatest increase in non-native species richness (Table 2, Fig. 4). Species extirpations are expected to have an additional effect on the magnitude of homogenization; for example, according to a 50% addition of non-native species, we predicted a 2.3% increase in compositional similarity between current and future fish fauna with threatened species extirpations, as compared to 0.5% with no native species loss (Table 2). Differences in contributions of translocated and alien introductions were still apparent, with translocated species being the dominant contributors driving future homogenization. Under the scenario of 50% non-native species addition with threatened species extirpations, translocated species caused slight
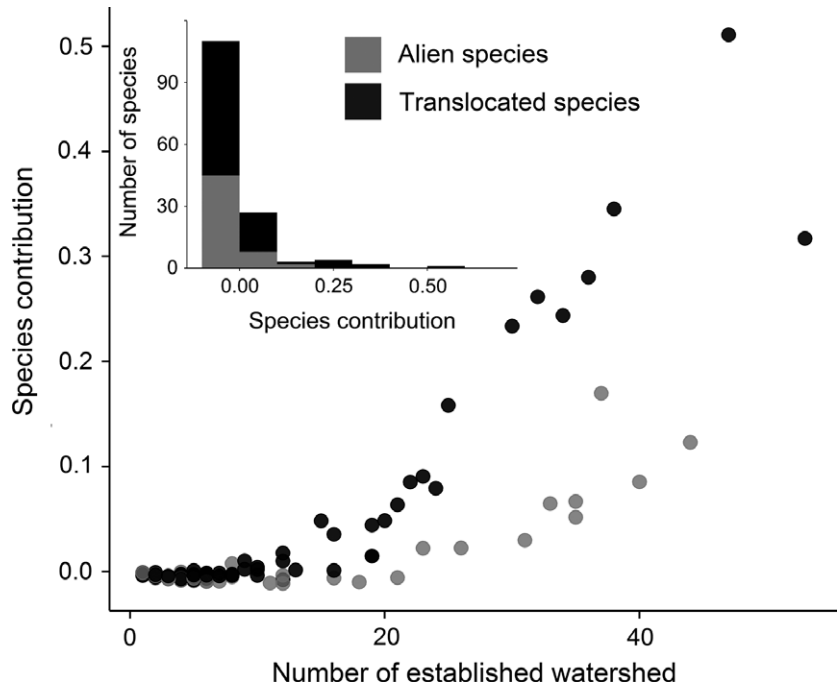
Figure 2 Species contributions to homogenization for translocated (black) and alien (grey) species. Scatter plot presents the relationship between species contribution and number of currently established watersheds, and the histogram (inset) displays the distribution of contributions across all non-native species.
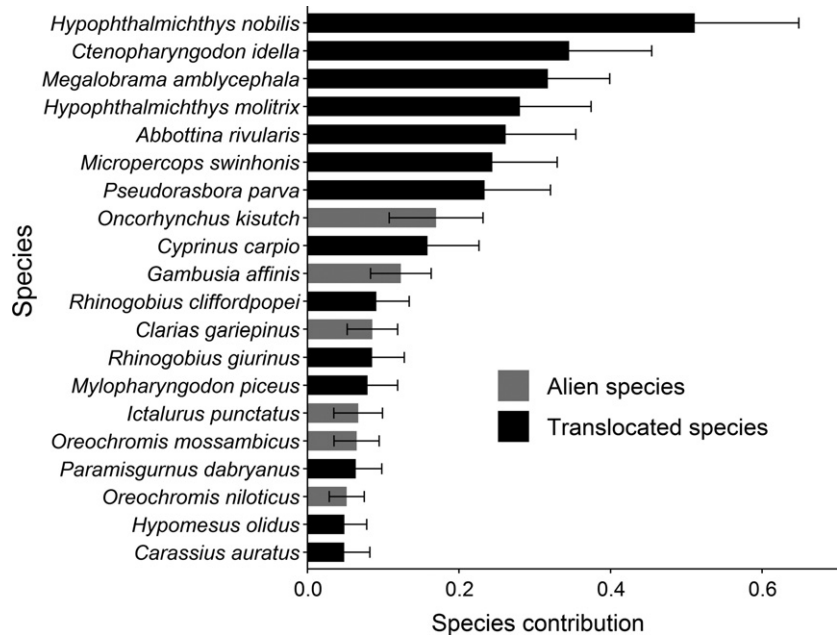

Figure 3 Top 20 non-native species with the highest contributions to observed changes in watershed compositional similarity. Presented are means (bar) and 95% confidence intervals (whiskers).

homogenization (0.6% increase in compositional similarity); by contrast, alien species led to slight differentiation (0.1% decrease in compositional similarity).

DISCUSSION

Species invasions and extinctions have resulted in the significant impoverishment, and thus the loss of antiquity, of China's freshwater fish fauna over the past century. When combined with recent findings from Brazil (e.g. Vitule *et al.*, 2012; Daga *et al.*, 2015) and south-western China (e.g. Ding

et al., 2016), it appears that developing megadiverse countries have demonstrated significant loss of freshwater fish diversity. The magnitude of overall increase in compositional similarity (7.0%) was similar with changes observed for the United States (7.2%; Rahel, 2000), but considerably higher than Australia (1.9%; Olden *et al.*, 2008), Canada (1.2%; Taylor, 2004), Europe (1.0%, Villéger *et al.*, 2014) and the globe (0.5%; Villéger *et al.*, 2011). More simplified fish communities may increase the susceptibility of a region to large-scale environmental events by synchronizing local biological responses across individual communities. This, in turn, could

Table 2 Changes in compositional similarity [mean (95% CI)] between historical, current and future fish faunas according to six scenarios of species invasions and extirpations. The relative contributions of translocated and alien non-native species to similarity changes are reported. Non-native species were randomly drawn from a pool of potential invaders and the number of new non-native species in each watershed was proportional (three levels: 50%, 100% and 200%) to the current non-native richness. Future extirpations assumed that all threatened species occurring in a watershed will be lost. The simulation was repeated 1000 times for each scenario. We refer the reader to the 'Methods' for more details.

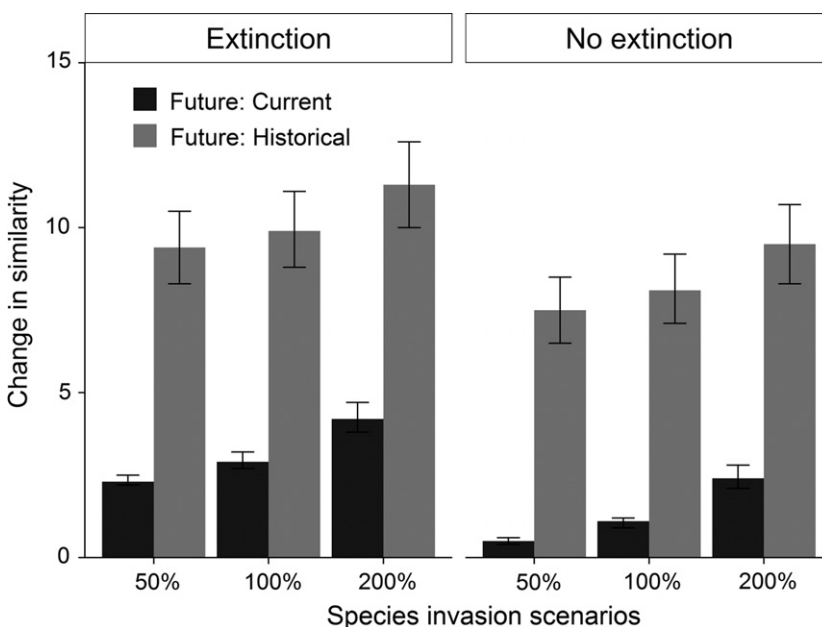| Invasion scenarios (%)	Extirpation scenarios	Future – Current	Future – Historical	Contributions of translocated species	Contributions of alien species
50	No	0.5 (0.1)	7.5 (1.0)	0.6 (0.1)	−0.1 (0)
100	No	1.1 (0.2)	8.1 (1.0)	1.1 (0)	0.1 (0)
200	No	2.4 (0.3)	9.5 (1.2)	2.1 (0)	0.6 (0)
50	Yes	2.3 (0.1)	9.4 (1.1)	2.5 (0)	1.8 (0)
100	Yes	2.9 (0.2)	9.9 (1.1)	3.1 (0)	1.9 (0)
200	Yes	4.2 (0.4)	11.3 (1.3)	4.2 (0)	2.4 (0)

Figure 4 Projected changes in fish compositional similarity (%) according to six scenarios of future species invasions and extirpations (See Table 2). Changes are in reference to historical and current fish faunas. Non-native species were randomly drawn from a pool of potential invaders and the number of new non-native species in each watershed was proportional (three levels: 50%, 100% and 200%) to the current non-native richness. Future extirpations assumed that all threatened species occurring in a watershed will be lost. The simulation was repeated 1000 times; means (bars) and 95% confidence intervals (whiskers) are presented.

reduce variability among communities in their response to disturbance and compromise the potential for landscape- and regional-level resilience and recovery (Olden *et al.*, 2004).

Western basins demonstrated much higher degrees of homogenization, which is likely attributed to the highly endemic fish fauna. Many native species from western basins are considered as periodic life history strategists (e.g. slow growth and late maturation) that are specialized for high-elevation environments. By contrast, most non-native species exhibit opportunistic strategies with rapid growth and early maturation (e.g. Yan & Chen, 2007, 2009; Chen *et al.*, 2009; Liu *et al.*, 2015). Vacant niche opportunities may increase the probability of successful establishment of non-native species and consequently lead to greater homogenization (also see Skóra *et al.*, 2015). Considering that western basins are also threatened by habitat fragmentation, dam construction and water pollution (Kang *et al.*, 2009, 2013a), we urge

greater conservation attention to the highly endemic, and globally rich, fish fauna of south-western China (Kang *et al.*, 2013a).

Fish faunal homogenization of China has predominantly been the result of a small number of native species that have been widely translocated to new watersheds. Our results are supported by previous studies demonstrating that extralimital (within the country) introductions have a stronger effect on homogenization compared with extraregional (outside the country) introductions (Leprieur *et al.*, 2008; Olden *et al.*, 2008; Spear & Chown, 2008). The massive domestic transfer of fish in aquaculture across China is a central contributing factor. Beginning in the 1950s, a number of cultured species were widely transported from eastern to western basins to improve local aquaculture production, particularly involving species of carp (Lin *et al.*, 2015; Ding *et al.*, 2016). These largely unregulated translocations accelerated the establishment of carp in the wild and resulted in their prominent

contributions to changes in β diversity over time. Additionally, we found that translocated species are also the important contributor to future homogenization, highlighting the urgent need to better understand the geographic routes of domestic translocations and identifying management strategies for reducing secondary spread.

Extraregional introductions of alien species also contributed to observed patterns of homogenization. Currently, 20% of finfishes with highest aquaculture production ($> 25\,000$ t year^{-1}) are foreign to China and some dominate present-day fish communities in southern China (Wang et al., 2014; Xing et al., 2015). In many developing countries, the introduction of economically important species is widespread and often does not include any systematic assessment of their potential risks (Lövei et al., 2012; Lin et al., 2015). For example, a decree referred to as the 'Tilapia Law' had been issued in Brazil to improve aquaculture production by naturalizing non-native fish in Amazonian River Basin (Padial et al., 2016). Species introductions may improve aquaculture profit in the short term, but the long-term consequences are rarely positive given many unanticipated impacts on recipient ecosystems (Daga et al., 2015; Padial et al., 2016). The risk of non-native species should therefore be systematically assessed before their introductions (Howeth et al., 2016), especially in developing countries where megadiverse biotas are chronically under-protected by current conservation policies.

Continued homogenization of China's freshwater fish fauna is likely in the future, although the exact timeline of this homogenization process will depend on the manifestation of different extinction debts (Kuussaari et al., 2009) and invasion debts (Essl et al., 2011) that will be differentially paid in response to past environmental changes. We found that increases in compositional similarity were much greater when future extirpations occurred, indicating the importance of threatened species for maintaining biotic distinctiveness. Minimizing risk to future loss of β diversity is possible via strategic conservation planning. For example, the updated China National Biodiversity Conservation Strategy and Action Plan (2011–2030) provides guidance by identifying priority areas and species in the greatest need for protection. Specifically, this Plan has a national target of 'gradually' restoring aquatic environments and stabilizing the decline of fishery resources and endangered species by 2020.

Advancements in management tools and policy instruments are also needed to prevent the introduction of invasive species that may contribute to future fish homogenization in China. North America remains the greatest source of non-native fishes to China, and this invasion route is likely to further intensify given strengthening trades between these two regions (Jenkins & Mooney, 2006). Elevated trades will undoubtedly increase accidental invasions of organisms. In addition, many invasive species have been introduced intentionally for aquaculture and pet trade; these invasions can be prevented by more aggressive management policies that are guided by formal risk assessments. Watershed-level management strategies that seek to restore freshwater ecosystems and prevent invasive species are also critical, especially for those watersheds facing severe environmental deterioration and influxes of non-native species, such as the Upper Mekong (Lancang River) (Kang et al., 2009; Ding et al., 2016).

The growing realization that species composition (not richness) defines the role that biodiversity plays in maintaining ecosystem function highlights the need for ecologists to consider multiple threats to the biological diversity, including biotic homogenization. Quantifying patterns and mechanisms of biotic homogenization is important for understanding the multifaceted challenges associated with current biodiversity crisis (Olden, 2006). China's freshwater fishes are facing mounting threats from a plethora of anthropogenic forces, including the persuasive impacts associated with species invasions (Lin et al., 2015; Xing et al., 2015). A pressing challenge in conservation biogeography is to better understand the consequences of widespread species invasions on the many facets of biological diversity. Here, we systematically documented that China's freshwater fish have experienced substantial loss in β diversity over time, resulting in clear faunal homogenization and loss of biological antiquity. Looking to the future, the success of conservation strategies requires an explicit recognition of both the patterns and drivers of the biodiversity crisis across multiple spatial and temporal scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Number and proportion of alien species from different continents.

Table S2 Changes in compositional similarity for freshwater ecoregions.

Appendix S1 Literature used for constructing datasets of China's freshwater fishes.

BIOSKETCH

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