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Research article

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

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ABSTRACT

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

1. Introduction

Global freshwater fish introductions are a major environmental and ecological threat, with hundreds of non-native freshwater fish species having been found worldwide (Su et al., 2021; Xiang et al., 2021; Bernery et al., 2022). These widespread fish introductions have caused negative impacts on biodiversity, economy, and public health (e.g., transmission of parasites and pathogens) in their recipient areas (Gozlan et al., 2010; Su et al., 2021; Haubrock et al., 2022). With increasing human activities, such as fishery activities and trade globalization, new fish introductions are likely to be facilitated, which could further exacerbate the adverse impacts of fish invasions (e.g., Bae et al., 2018; Dong et al., 2020). More concerning is the fact that climate change, a key driver of fish species responses, can also promote the establishment of non-native species, increasing the uncertainty and likelihood of fish invasions (Early et al., 2016; Kuczynski et al., 2018; Liu et al., 2019; Essl et al., 2020). One of the most direct effects of climate change on fish species is their range shift (e.g., species range expansions or contractions), which is considered a major threat to biodiversity in recipient areas (Comte and Grenouillet, 2015; Schickele et al., 2021). Generally,

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

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

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

In the present study, six common non-native fish species were selected as they are universally recognized as invasive globally and known to have ecological, healthy, and economic impacts if they continue to spread (e.g., Lowe et al., 2000; Luque et al., 2014; Dong et al., 2020). Our main objectives, addressed using the maximum entropy model (MaxEnt), one of the most popular and effective algorithms, were to: (a) explore the spatial patterns of current and future habitat ranges of the six notorious invasive fishes in China, (b) disentangle the relative importance of environmental and anthropogenic variables driving the habitat suitability of these fishes, and (c) identify areas of transitory fluctuations of the fishes to determine the availability and accessibility of habitats. To our knowledge, this is the first study evaluating transitory range dynamics of invasive fish species under global changes in China, which has the potential to not only prevent and manage fish invasions with reasonable costs and efforts, but also provide early warnings and lessons for fish invasion management in China, as well as in other geographical areas.

2. Materials and methods

2.1. Selection of invasive freshwater fishes

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

2.2. Species occurrences

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

2.3. Variables for modeling

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

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

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

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

2.4. Modeling approach

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

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

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

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

3. Results

3.1. Model performance

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

3.2. Variable importance and species response curves

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

3.3. Species distribution shifts

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

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

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

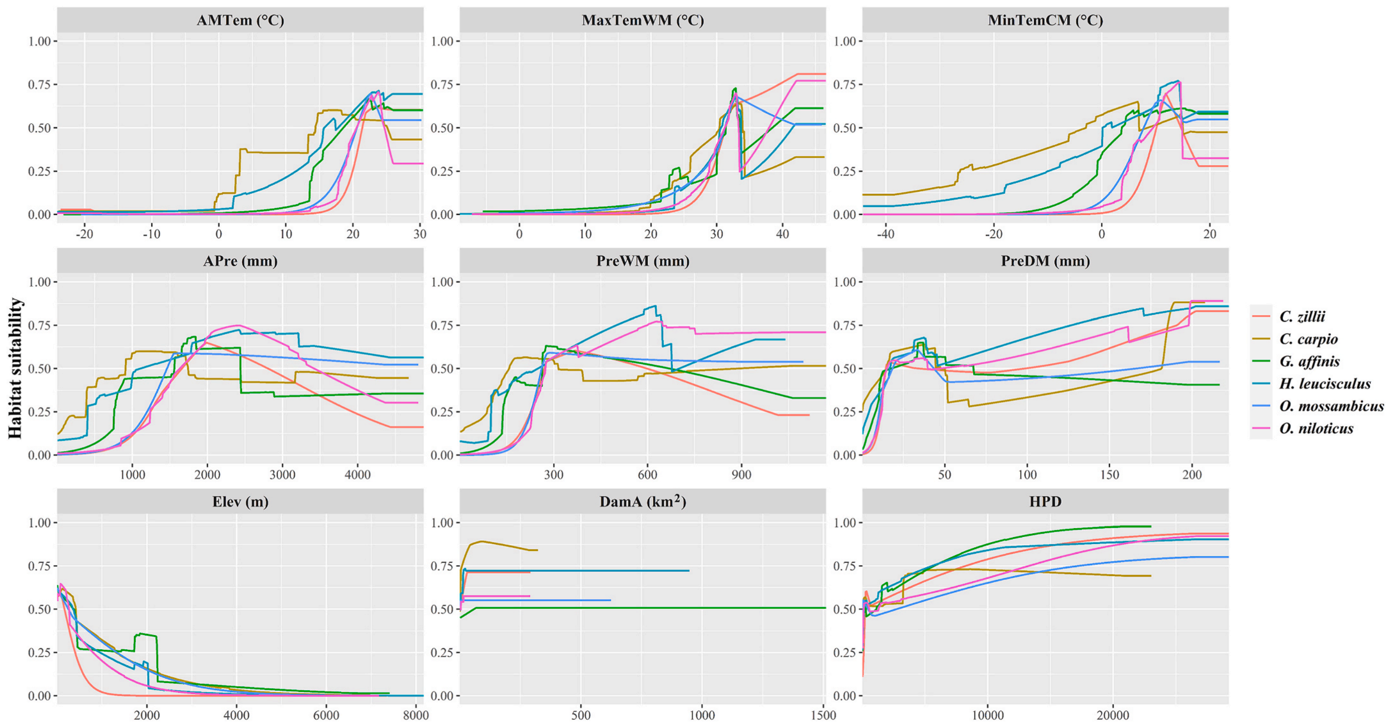

Fig. 1. Response curves of the six species' habitat suitability to the variables used for modeling. AMTem: Annual Mean Temperature (°C); MaxTemWM: Maximum Temperature of Warmest Month (°C); MinTemCM: Minimum Temperature of Coldest Month (°C); APre: Annual Precipitation (mm); PreWM: Precipitation of Wettest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

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

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

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

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

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

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

4. Discussion

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

4.1. Factors influencing species distributions

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

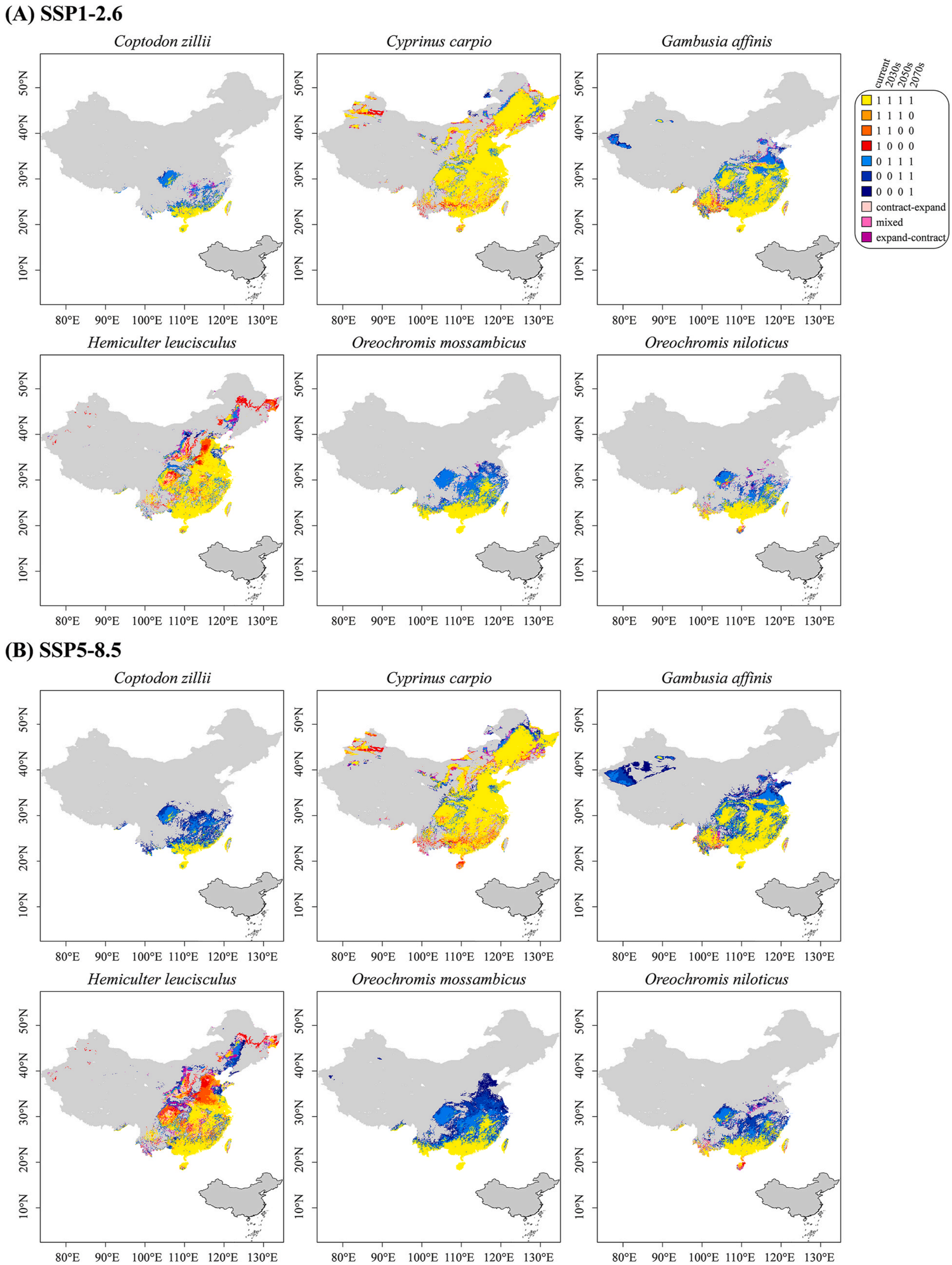

Fig. 2. Time-step maps detailing range shifts for the six species under two different Shared Socio-economic Pathways scenarios (**(A)**: SSP1-2.6; **(B)**: SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s). "1" and "0" in the legend indicate presence and absence of one species,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

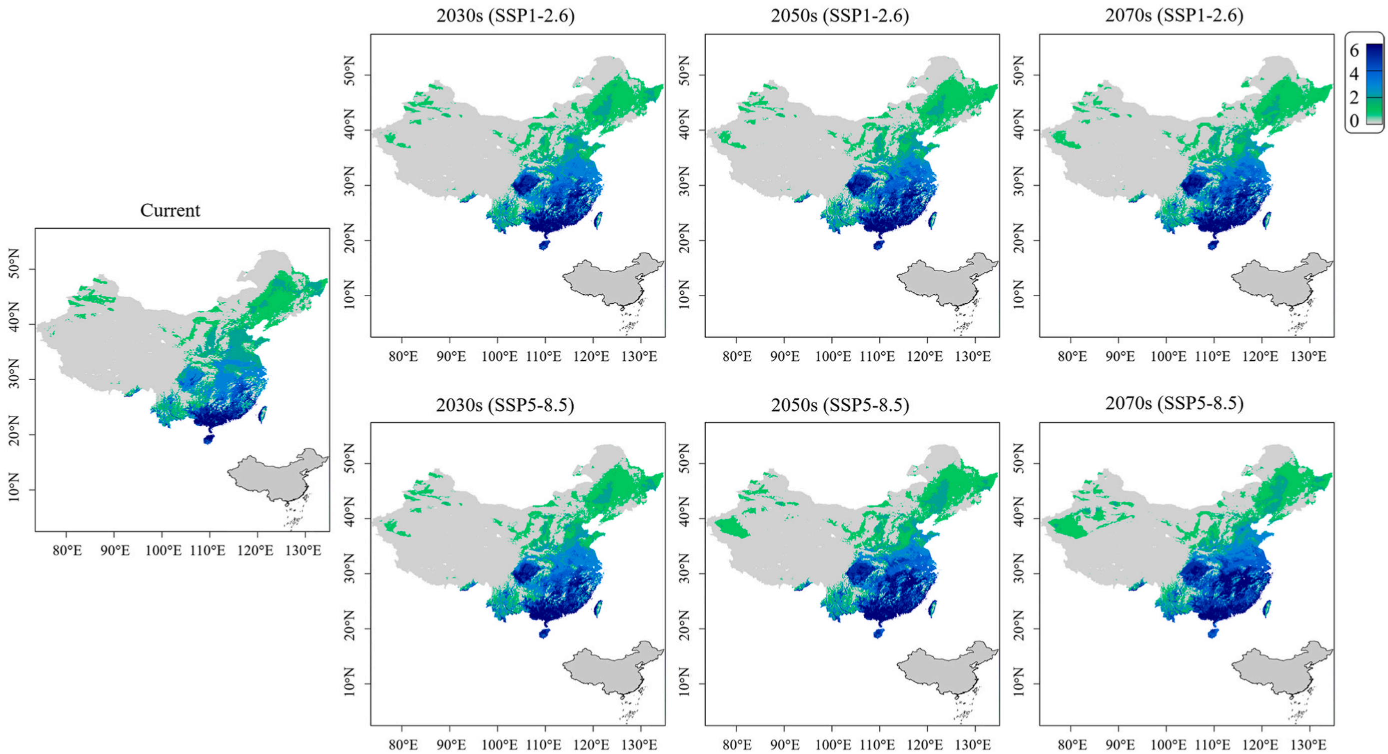

Fig. 3. Species richness maps cumulating the six species distributions forecasted under two different Shared Socio-economic Pathways scenarios (SSP1-2.6 and SSP5-8.5) and for four time periods (current, the 2030s, 2050s, and 2070s).

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

Generally, human activities associated with human population density, hydroelectric projects, and so on could facilitate species invasions (Gallardo and Aldridge, 2013; Su et al., 2021; Xiang et al., 2021). Surprisingly, although our study also confirmed this point, these two variables (i.e., HPD and DamA) contributed very little to our models. This suggests that the six species may have a certain tolerance to anthropogenic factors. Similarly, Elev (elevation) also did not contribute significantly to our models, while it is known to be fundamental in explaining habitat suitability for many fish species (e.g., Kim et al., 2022). In our study, Elev only played a crucial role in determining habitat suitability for *C. carpio*. In the future, habitat losses for this species were expected to occur in several high-elevation areas, such as parts of the Yunnan-Guizhou Plateau, Southeast Hilly region, and Wuyi Mountain.

4.2. Current and future species ranges

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

Due to differences in species-specific sensitivity to global changes (Ruiz-Navarro et al., 2016), the directions and magnitudes of species range expansions or contractions varied among the six species. Specifically, future global changes were expected to drive large species range expansions for *C. zillii*, *G. affinis*, *O. mossambicus*, and *O. niloticus*, but relatively little range expansions or contractions for *C. carpio*. However, all these five species were expected to shift northward. These findings are consistent with other studies showing that invasive species tend to expand their potential distributions northward with global change (e.g., Ruiz-Navarro et al., 2016). On the contrary, previous studies pointed out that global changes could decrease areas of suitable habitats for invasive species or drive them to southern regions (e.g., Kim et al., 2022; Maimela et al., 2022). Here we found that the range of *H. leucisculus* was expected to decrease as a whole in each future period, indicating that suitable niche space for the species was expected to reduce in areas where the species was currently present in response to future global changes.

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

5. Conclusions

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

CRediT authorship contribution statement

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

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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

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