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Research Article

Predicted increased distribution of non-native red drum in China's coastal waters under climate change

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Abstract

Climate change and species invasions are among the most serious threats to global biodiversity, and climate change will further greatly alter the distribution of invasive species. The red drum *Sciaenops ocellatus* (Linnaeus, 1766) has established non-native populations in many parts of the world, leading to negative effects on local ecosystems. In this study, based on 455 global occurrence records (38 of which were in Chinese waters) and 5 biologically relevant variables (average ocean bottom temperature, ocean bottom average salinity, ocean bottom average flow rate, depth, and distance from shore), a weighted ensemble model was developed to predict the current potential distribution of red drum in Chinese waters and the future distribution under two climate change scenarios (RCP 26 and RCP 85). Based on the True Skill Statistics (TSS) and the Area Under Curve (AUC), the ensemble model showed more accurate predictive performance than any single model. Among the five environmental variables, the average temperature was the most important environmental variable influencing the distribution of red drum. Ensemble model prediction showed that the current suitable habitat of red drum was mainly concentrated on the coast of Chinese mainland, around Hainan Island, and the western coastal waters of Taiwan Province (17~41°N). Projections in the 2050s and 2100s suggested that red drum would expand northwards under both future climate scenarios (RCP 26 and RCP 85), especially in the western part of the Yellow Sea and along the Bohai Sea coast, which should be involved in the management strategies to maintain ecosystem structure and function.

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Key words: climate warming, species distribution model, species interaction, aquaculture, management

Introduction

Climate change and species invasions are two of the most serious threats to global biodiversity (Rahel and Olden 2008; Chown et al. 2015). Climate change can dramatically alter the distribution of suitable habitats (Guisan et al. 2017), leading to species shifts to higher altitudes or towards the poles (McCarty 2001; Bradley 2009). For example, in the northeastern Atlantic, the distribution boundary of fish expanded northward, with the southern boundary moving northwards three times faster than that of terrestrial species (Dulvy et al. 2008); since the mid-20th century, rapid climate warming has led to a northward migration of fish communities in the eastern United States (Bell et al. 2015). Effects of competition and predation by invasive species on native species often lead to dramatic changes in species composition (Jeschke 2014; Gallardo et al. 2016). For example, under climate change, non-native fishes adapted for conditions in the south have established populations in the North Sea and in the northeastern Atlantic (Beare et al. 2004; Kirby et al. 2006); common bluestrip snapper *Lutjanus kasmira* (Forsskål, 1775), introduced to Hawaii for improving fisheries, has grown rapidly, and has become the second most dominant species in the local fish community through interspecific competition (Friedlander et al. 2002). Non-native species can also spread parasites and pathogens, leading to the occurrence of diseases and the decline of native species (Pimentel et al. 2005). Accompanying the importation of eggs and live individuals of salmon and trout, the infectious hematopoietic tissue necrosis virus (IHNV) spread from North America to Europe (Peeler et al. 2011). In the 1960s, stone moroko *Pseudorasbora parva* (Temminck & Schlegel, 1846) was introduced to Romania and then throughout Europe, carrying pathogens such as *Sphaerothecum destruens* (Arkush et al. 2003), which did great harm to the native species *Leucaspius delineates* (Heckel, 1843), endangering it (Gozlan et al. 2005). Therefore, understanding the distribution of suitable habitats for non-native species under climates change is essential for effective conservation of native biodiversity and ecosystem functions (Zhang et al. 2020a).

Species distribution models (SDMs) have been widely used to study the impacts of climate change on the potential distribution of species, by exploring the relationship between species distribution and environmental variables (Guisan and Thuiller 2005; Elith and Leathwick 2009; Guisan et al. 2017; Thuiller et al. 2019a). Furthermore, the ensemble model, which can effectively explain the variability and reduce the uncertainty of single model predictions, is more reliable (Guisan et al. 2017) and has been widely used to predict the potential distribution of various invasive species (Buonomo et al. 2018; Goldsmit et al. 2018; Moraitis et al. 2018; Zhang et al. 2020b).

Red drum *Sciaenops ocellatus* (Linnaeus, 1766), belonging to the order Perciformes, family Sciaenidae, is native to the Atlantic coast of the United States and the gulf of Mexico (Ocean and fishery synthesis 2015). This species prefers temperatures between 10 °C and 30 °C, with an optimal range between 18 °C and 25 °C, and is a carnivore (Ocean and fishery synthesis 2015). In China, it was first introduced to Taiwan Province in 1987 for aquaculture (Liao et al. 2010). In mainland China, the First Institute of Oceanography of the State Oceanic Administration firstly introduced red drum larvae from Texas in July 1991, and successfully bred the first generation in 1995 (Lou et al. 2005). At present, red drum has been cultivated on a large scale in China, covering the Yellow Sea, East China Sea and South China Sea (Wang et al. 2002; Ocean and fishery synthesis 2015). The escape of cultured fish from mariculture facilities is an important source of non-native invaders (Ju et al. 2020). Red drum is no exception, being recorded in natural waters in western Taiwan (Liao et al. 2010) and the East China Sea (Lin et al. 2020; Wang et al. 2022b). The newly established population shows biological traits close to the natural population in the United States, such as eurythermic and euryhaline tolerance, strong mobility, and predatory behaviour, which facilitate its successful establishment in natural waters (Lou et al. 2005). Changes in the habitat range of red drum may greatly disrupt the structure of food networks and disturb ecosystem function in invaded areas (Kang et al. 2022).

In this study, an ensemble model based on BIOMOD2 was constructed for the biogeographic distribution of red drum, to: 1) understand the species' current habitat adaptability; 2) identify the main environmental variables affecting red drum distribution, and; 3) assess the changes in the species' suitable habitats under different climate scenarios. These results will help understand the potential impact of climate change on the distribution of non-native marine fish species and inform the development of preventive management strategies.

Materials and methods

Presence/pseudo-absence data

The global distribution data of red drum was used to predict the habitat suitability of red drum in China's coastal waters within 105° to 127°E and 17° to 41°N, based on which the future distributions under different climate change scenarios were predicted. As the occurrence data of escaped red drum in China was less in number and concentrated in distribution, we used global occurrence data of red drum. Red drum distribution data were derived from Global Biodiversity Information Facility database (https://www.gbif.org/) and escape records were from the East China Sea (Xue 2008; Liao 2010; Lin et al 2020; Wang et al. 2022). Considering the sampling bias, we spatially filtered the occurrence data by setting a 9.2 km radius consistent with the resolution of the environmental layer using the R package *spThin* (Aiello-Lammens et al. 2015). As a result, 455 occurrence records (including 38 in Chinese waters) were retained (Fig. 1). We employed the three-step method to generate 10,000 pseudo-absence data records (Iturbide et al. 2015), in which pseudo-absences were selected by considering environmental variables outside the realized ecological niche, but in accessible geographic areas that may be reached by dispersal. The first step included the use of the presence-only support vector machine algorithm to define regions where the environment is unsuitable; the second step consisted of constructing SDMs using pseudo-absences generated for buffers of different sizes known to exist around the location, but within the unsuitable background region defined in the first step; and the third step was to select the best buffer range from the model generated in the second step. This provides a balance between using spatial and environmental space to select pseudo-absence points and has been shown to be superior to other methods (Iturbide et al. 2015).

Environment variables

Considering biological relevance and data availability under current and future climate scenarios, eleven environmental variables were selected for analysis (Table 1). Environmental variable data was obtained from Bio-ORACLE datasets (http://www.bio-oracle.org) (Assis et al. 2018) and Global Marine Environment Datasets (http://gmed.auckland.ac.nz) at a spatial resolution of 5×5 arcminutes (9.2×9.2 km at the equator). To reduce the effect of collinearity, Pearson correlation coefficients between 11 predictors were calculated, and environmental variables with coefficient values >|0.7| were removed (Suppl. material 1) (Dormann et al. 2013). Finally, five variables including mean current velocity, mean temperature, mean salinity, depth, and distance to shore were kept to predict the current distribution of red drum (Table 1).

Bio-ORACLE provides future predictions of current velocity, salinity, and temperature under four representative concentration pathways (RCP 26, RCP 45, RCP 60, and RCP 85) using three atmosphere-ocean circulation modes (AOGCMs: CCSM4, HadGEM2-ES, and MIROC5) (Assis et al. 2018). RCP 26~RCP 85 represent greenhouse gas concentrations ranging from low (optimistic emission

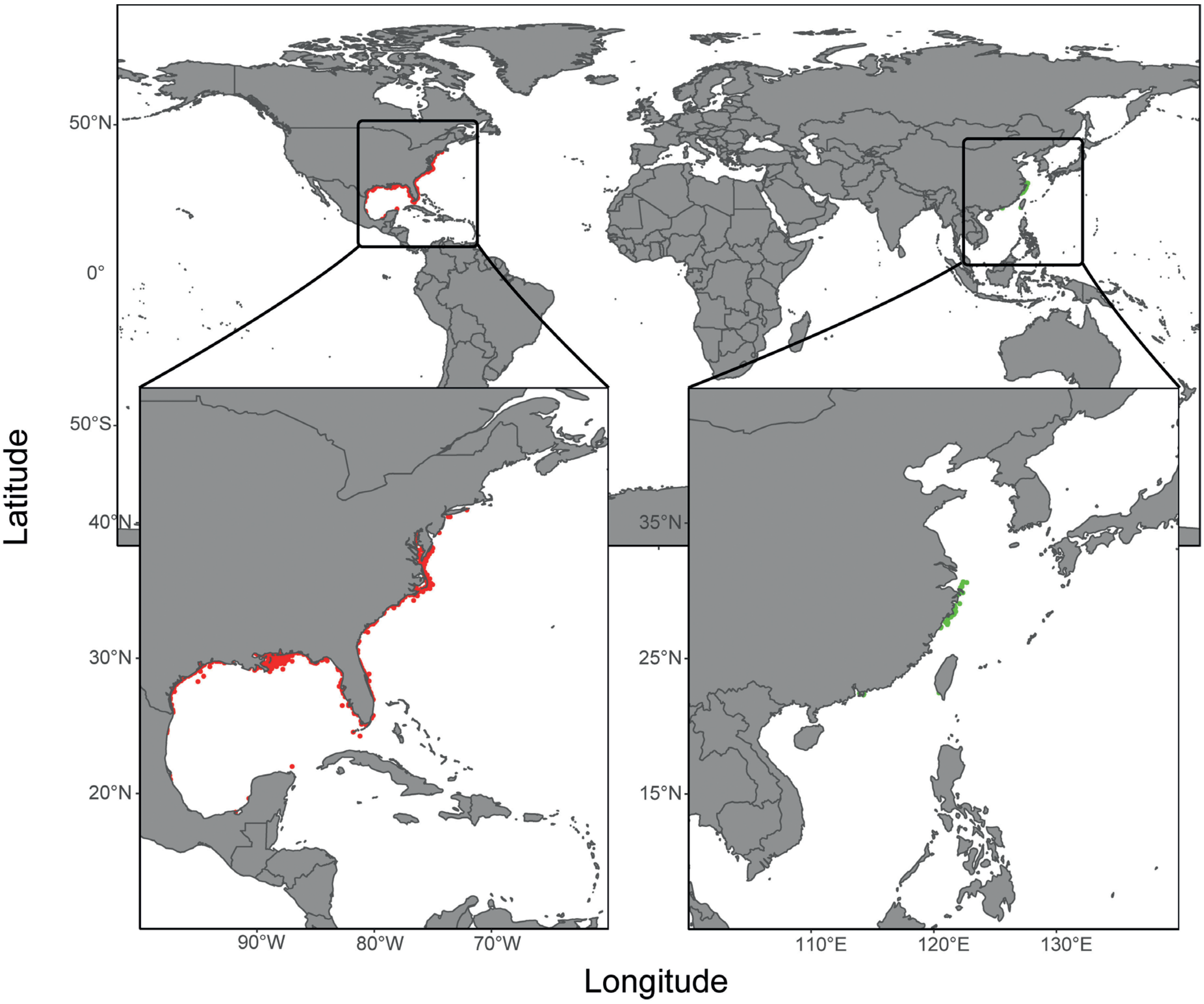

Figure 1. Occurrence records of American red drum. The green and red dots correspond to the invasive sites of American red drum in China and their native sites in eastern North American waters, respectively.

Table 1. List of environmental variables. Except for depth and distance to shore, the remaining nine variables were from the bottom. "√" indicated that the variable was retained to build the model, and "×" indicated that the variable was dropped due to its high correlation with other variables.

Environment variable	Source	Unit	Resolution ratio	Used (√) or not (×)
Minimum current velocity	(https://www.bio-oracle.org/)	m/s	5 × 5 arc-minutes	×
Mean current velocity	(https://www.bio-oracle.org/)	m/s	5 × 5 arc-minutes	√
Maximum current velocity	(https://www.bio-oracle.org/)	m/s	5 × 5 arc-minutes	×
Minimum salinity	(https://www.bio-oracle.org/)	PSS	5 × 5 arc-minutes	×
Mean salinity	(https://www.bio-oracle.org/)	PSS	5 × 5 arc-minutes	√
Maximum salinity	(https://www.bio-oracle.org/)	PSS	5 × 5 arc-minutes	×
Minimum temperature	(https://www.bio-oracle.org/)	°C	5 × 5 arc-minutes	×
Mean temperature	(https://www.bio-oracle.org/)	°C	5 × 5 arc-minutes	√
Maximum temperature	(https://www.bio-oracle.org/)	°C	5 × 5 arc-minutes	×
Depth	(http://gmed.auckland.ac.nz)	m	5 × 5 arc-minutes	√
Distance to shore	(http://gmed.auckland.ac.nz)	km	5 × 5 arc-minutes	√

levels) to high (pessimistic emission levels) (Moss et al. 2010). Here, we used RCP 26 and RCP 85 to predict the future distribution in the 2050s (2040~2050) and 2100s (2090~2100). The average predicted values of the three modes of AOGCM were used to represent future climatic conditions to reduce uncertainty (Assis et al. 2018). There were no future predictions of depth and distance to shore, which were assumed to remain stable (Zhang et al. 2020a).

Model construction and evaluation

We used the BIOMOD2 package in the R platform to build the species distribution model (Thuiller 2019b). There are 10 algorithms available in the package, including Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Models (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Multiple Adaptive Regression Splines (MARS), Maximum Entropy Model (Maxent), Random Forest (RF), and Surface Range Envelope (SRE).

The data were randomly divided into two groups, 80% for model training and the remaining for model performance evaluation, repeating ten times (Guisan et al. 2017). The accuracy of the model was evaluated by the values of TSS (True Skill Statistic) and AUC (Area under ROC Curve) (Allouche et al. 2006), both ranging from 0 to 1. According to the standards of Duan et al. (2014) and Nuchel et al. (2018): TSS is divided into poor (0.0–0.4), fair (0.4–0.5), good (0.5–0.7), very good (0.7–0.85), excellent (0.85–0.90), and perfect (0.9–1.0); AUC is classified as poor (0.5–0.6), fair (0.6–0.7), good (0.7–0.8), very good (0.8–0.9), and excellent (0.9–1.0). To ensure sufficient prediction accuracy, models with both TSS > 0.85 and AUC > 0.90 were retained for further analysis (Duan et al. 2014; Zhang et al. 2019).

Following initial analyses, we retained nine models (ANN, CTA, FDA, GAM, GBM, GLM, MARS, Maxent, RF) to build a weighted average ensemble model to predict red drum distribution under current and future climatic conditions. To better interpret model results, TSS values of ensemble models were maximized by auto-generated thresholds, and continuous habitat suitability predictions were converted into binary maps (e.g., suitable/unsuitable) by maximizing TSS (Guisan et al. 2017). The importance of the environmental variables was determined using the randomization method by calculating the Pearson correlation between predictions based on all predictors and randomly arranged predictions of the evaluated predictors (r) (Li et al. 2022); a high correlation between two predictions indicates that the evaluation variable is not important (Guisan et al. 2017). The relative importance of each environmental factor was calculated as $1-|r|$. The response curves of influential environmental variables were plotted to reflect the importance of predictors in explaining the observed species distribution. Habitat suitability ranged from 0 to 1000 (Zhang et al. 2019). Based on the results of the ensemble model, distributions of continuous habitat suitability for the current and 2050s and 2100s under RCP 26 and RCP 85 were mapped.

Results

Model performance

The mean (± standard error) values of TSS for the 10 ten algorithms ranged from 0.814 ± 0.010 for SRE to 0.979 ± 0.0023 for MARS, RF and AUC values ranged from 0.907 ± 0.0065 for SRE to 0.997 ± 0.001 of MARS, RF (Fig. 2). Nine

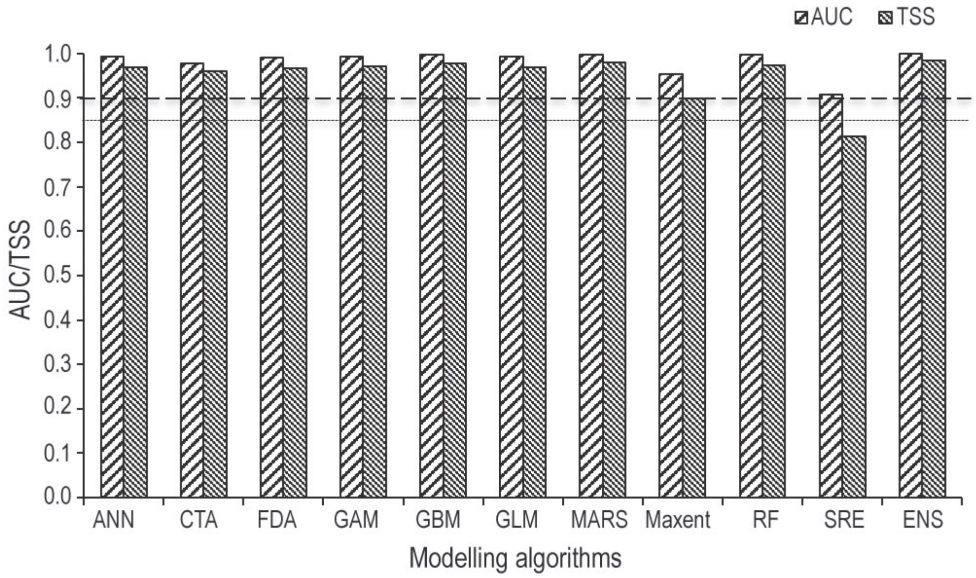

Figure 2. Operational Characteristic Curve (AUC) and True Skill Statistics (TSS) values for 11 modeling algorithms. The dashed line indicates the selection level AUC=0.90, TSS=0.85.

algorithms (ANN, CTA, FDA, GAM, GBM, GLM, MARS, Maxent and RF) were screened according to the criteria of TSS > 0.85 and AUC > 0.90 for the construction of a weighted set model. The TSS and AUC of the ensemble model was 0.983 (± 0.001) and 0.999 (± 0.001), respectively, indicating a better predictive performance than each single algorithm.

Importance and response curves of environmental predictors

Among the five environmental variables, mean temperature, depth, and distance to shore showed significant effects on red drum distribution (Fig. 3). The response curve showed that the suitable habitat conditions of red drum were 12 to 27 °C of bottom temperature, 0 to 100 m of depth and 0 to 60 m of distance to shore (Fig. 4).

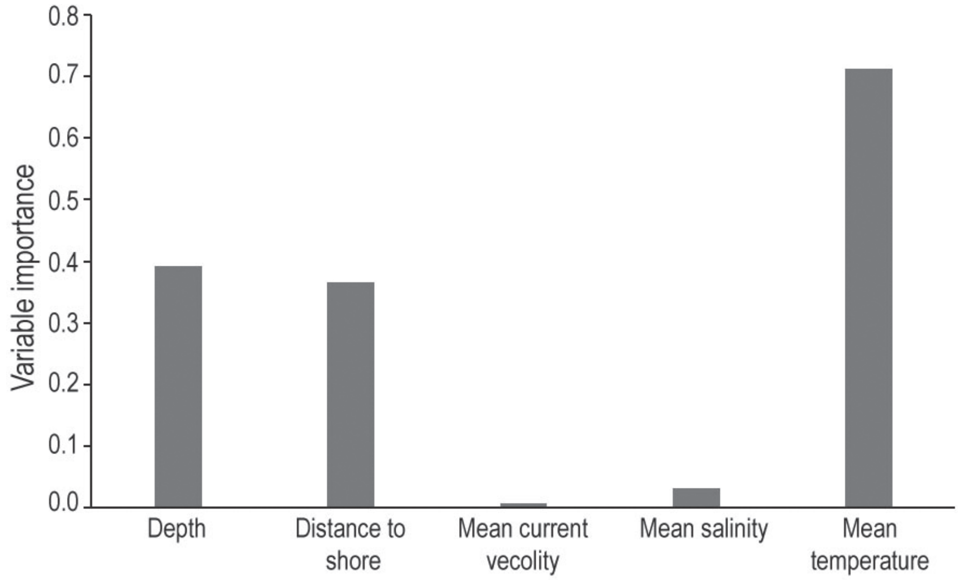

Figure 3. The relative importance of environmental predictors on the distribution of red drum.

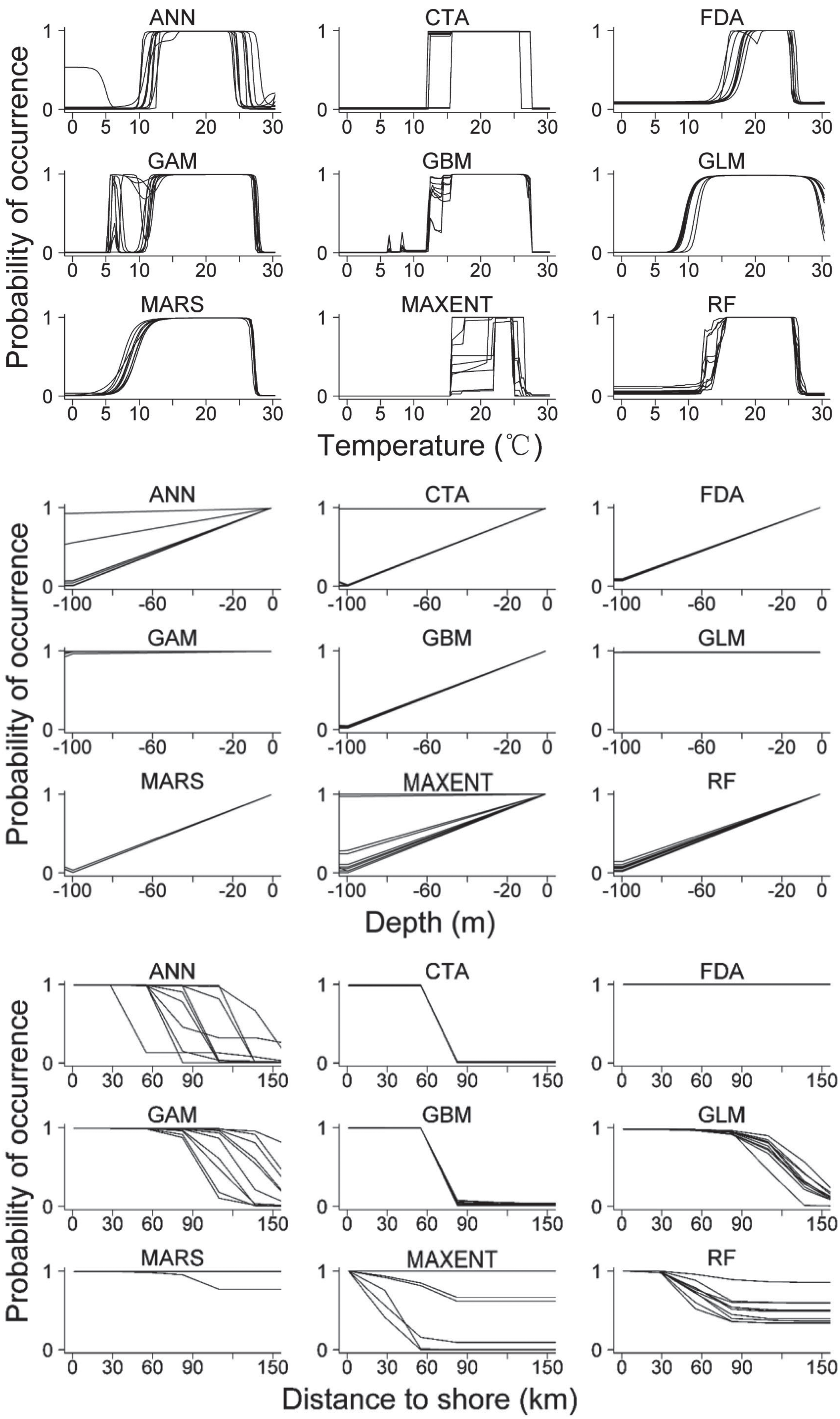

Figure 4. Response curves of predicted occurrence probability of *Sciaenops ocellatus* against temperature, depth and distance to shore.

Current and future distribution of red drum

In China, the current suitable habitat of red drum was mainly concentrated in the eastern coast of the China mainland, around Hainan Island, and the western coastal waters of Taiwan Province (17°~41°N); however, few suitable habitats could be detected in the eastern and northwestern waters of the Bohai Sea (37°~41°N) and the northern coastal waters of Shandong Peninsula (120°~122°E) (Fig. 5). Compared to the current situation, under the RCP 26 scenario, the potential habitat area of red drum was expected to respectively increase by 2.58% in the 2050s and by 5.30% in the 2100s. Compared to the current situation, the potential habitat area of red drum under the RCP 85 scenario was projected to increase by 2.05% in the 2050s but decrease by 3.24% in the 2100s.

Under RCP 26 and RCP 85, the habitat area of red drum in the 2050s and 2100s would decrease in the south but increase in the north, showing a trend of northward shift (Fig. 6). Under the RCP 26 scenario in the 2050s, the habitat area of red drum would expand into the western coast of the East China Sea (23°~32°N), the northern coast of the Yellow Sea (122°~125°E), and the southwestern coastal area of Bohai Sea. On the contrary, the distribution areas in northern part of the South China Sea would be reduced. Under RCP 26 scenario in the 2100s, the southern habitat of red drum would be further reduced and the northern habitat would be further increased. Under RCP 85 scenario in the 2050s, the habitat of red drum would expand in the western Yellow Sea (32° to 38°N), the northern coast of the Yellow Sea (122° to 125°E), and the Bohai Sea coast, but reduced in the southwest of the East China Sea, the Beibu Gulf and the

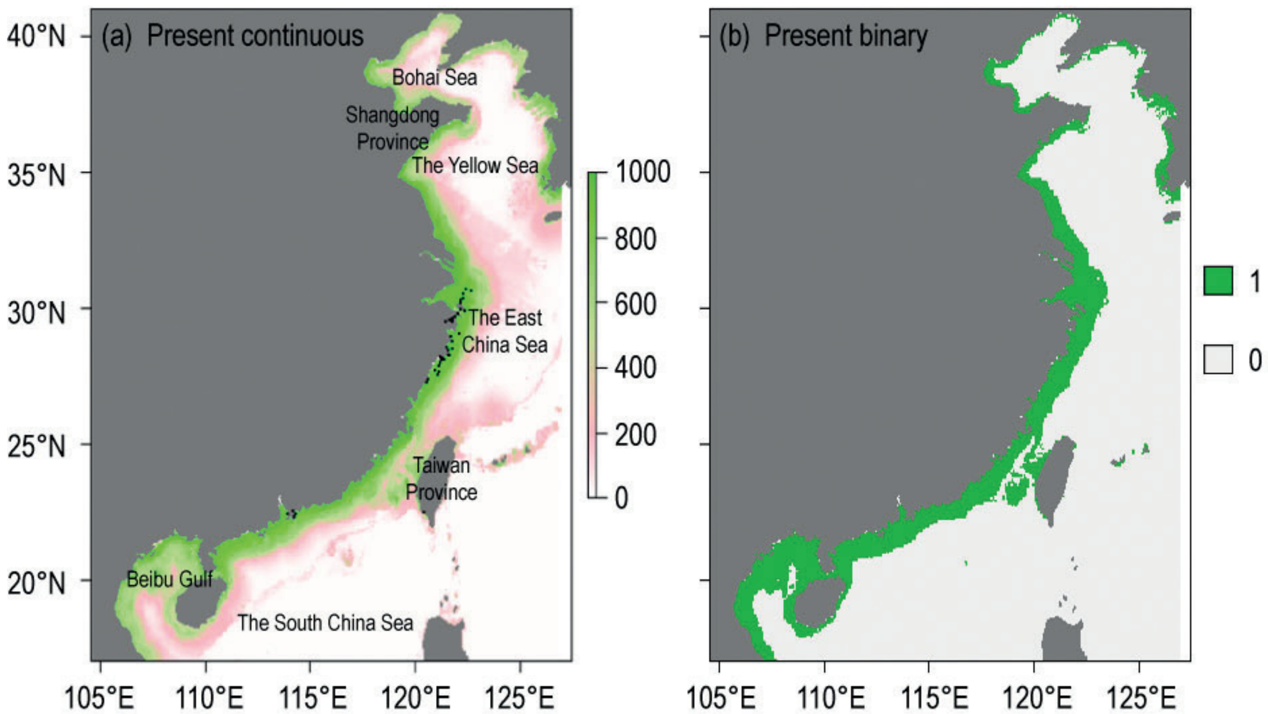

Figure 5. Prediction of continuous habitat suitability and binary plots for red drum under current conditions. (**a**) Suitability of continuous habitats under current climatic conditions. Habitat suitability ranges from 0 (white) to 1000 (green). The black dots represent the locations of the distributed data used to build the model in the study area. (**b**) Binary plot of current potential distribution. 0 in white indicates unsuitable areas, and 1 in green indicates suitable areas.

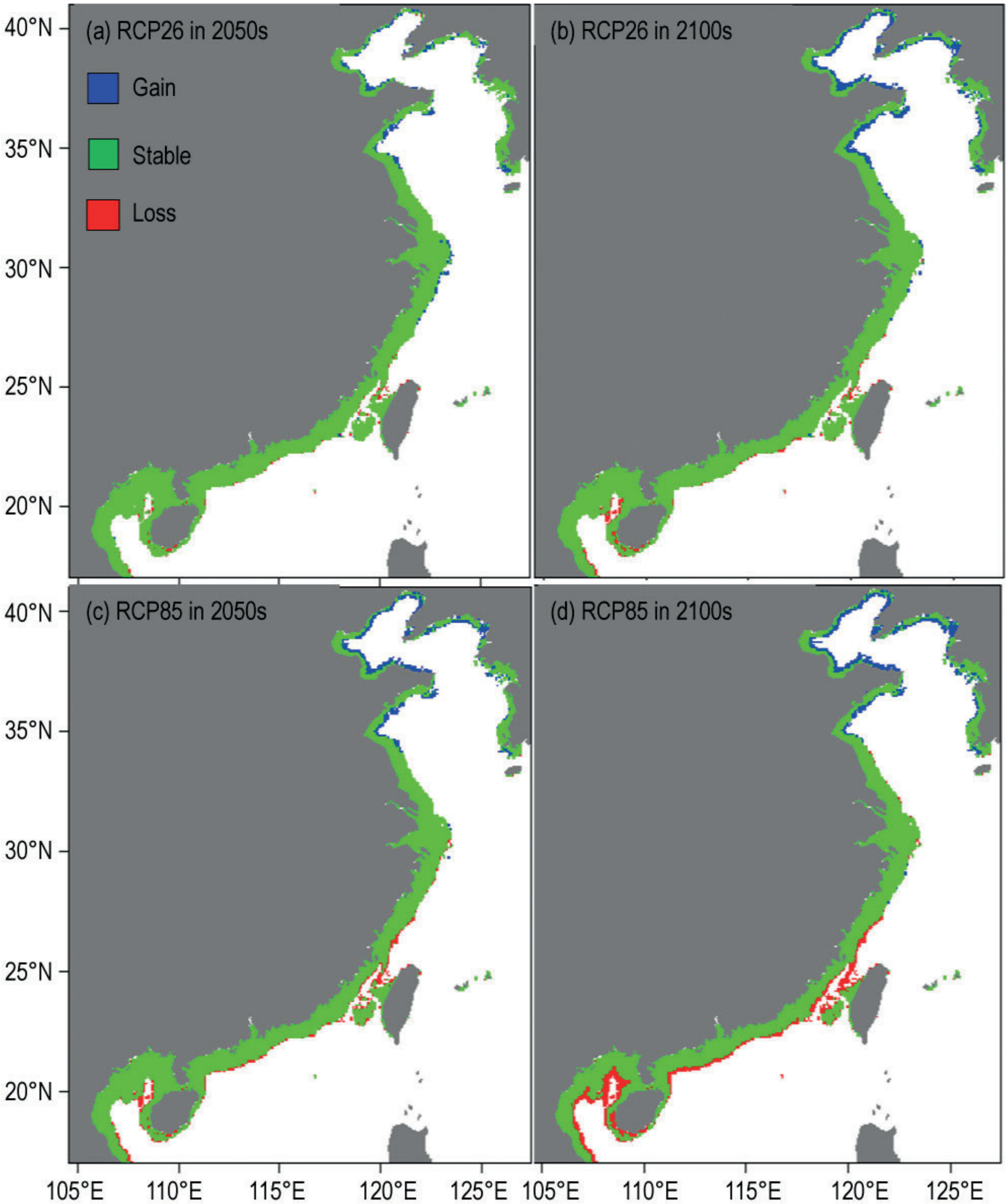

Figure 6. The potential distribution of *Sciaenops ocellatus* under different environmental conditions. (**a**) in the 2050s under the RCP 26 scenario; (**b**) in the 2100s under the RCP 26 scenario; (**c**) in the 2050s under the RCP 85 scenario; (**d**) in the 2100s under the RCP 85 scenario. The red areas represented the loss in future, the blue areas represented the increase, and the green areas represented the remaining unchanged.

northern part of the South China Sea. Under the RCP 85 scenario in the 2100s, the southern habitat of red drum would be further reduced and the northern habitat would be further increased, with the southern habitat reduction greater than the northern habitat increase.

Table 2. Changes in the expected range of *Sciaenops ocellatus* under future climate scenarios.

Future climate scenario	2050s (%)	2100s (%)
RCP 26	+2.58	+5.30
RCP 85	+2.05	-3.24

Note: RCP represents representative concentration path. 2050s represents the average of 2040–2050; 2100s represents the average of 2090–2100.

Discussion

Model performance

Although various SDM algorithms have been developed, predictive effects between different algorithms remain a source of uncertainty for future species predictions (Thuiller et al. 2019a). In this study, except for the SRE model, other models satisfied the selection criteria as AUC > 0.90 and TSS > 0.85 (Duan et al. 2014; Nuchel et al. 2018). By showing higher accuracy and reliability than each single model, the ensemble model has been widely encouraged to predict potential species distribution and habitat suitability (Thuiller et al. 2019a). Moreover, the low sensitivity to outliers makes the ensemble model more valid to estimate changes in habitat suitability distribution (Tanaka et al. 2020). In this study, the ensemble model showed a better performance than any single algorithm, with an AUC value of 0.999 and a TSS value of 0.979.

Importance and response curves of environmental variables

Mean temperature was identified as the most significant environmental variable affecting the aquatic species distribution (Bosch et al. 2018; Goldsmit et al. 2018), as aquatic organisms can freely migrate in a large area without physical barriers but covering a wide range of temperature beyond species tolerance (Lenoir et al. 2020). The response curve showed the suitable mean temperature of red drum was between 12 °C and 27 °C, coinciding with previous results of suitable temperatures of between 10 °C and 30 °C and optimal temperatures of between 18 °C and 25 °C (Ocean and fishery synthesis 2015). The water depth response curve indicated that the suitable water depth for red drum was 0~100 m, covering the spawning grounds distributed near the shore and estuaries (Murphy and Taylor 1990). The juveniles would stay in the spawning area for three to four years, and migrated for a limited distance depending on temperature changes (Murphy and Taylor 1990).

As an euryhaline anadromous species, the strong tolerance to salinity and velocity of red drum makes it immune to hydrological variations in estuarine habitats (Zhao et al. 2006). Correspondingly, mean salinity and mean current water velocity showed little effects on the distribution of red drum. By balancing extracellular and intracellular osmotic pressures, red drum can quickly adapt to hyperhaline environments to relieve salinity stress (Martin and Esbaugh 2021). An individual with a total length of more than 5 cm can tolerate drastic salinity changes from seawater directly to fresh water (Wang et al. 2001). In an experiment, when individuals with a 5 cm body length cultured in a salinity of 30 were directly transferred to a salinity of 11 for temporary rearing, the survival rate of red drum showed no significant difference except for a small number of deaths due to mechanical damage (Wang et al. 2001). Red drum also showed greater mobility than sea bass *Lateolabrax maculatus* (Katayama, 1957), in spite of the similarity in their spindle body shapes (Wang et al. 2010).

Changes in current and future potential habitats

The current potential suitable habitats of red drum expanded out of the geographical boundary of all species occurrence data, which was generally attributed to many factors including biological interactions, species dispersal restrictions, niche size, and sampling bias (Goldsmit et al. 2018). As an introduced species, red drum escaped to natural waters due to the negligence of aquaculture (Kang et al. 2022). Thus, the time since escape and population establishment are likely the most important factors limiting its expansion. Large-scale farming in the East China Sea has caused the escape of many individuals of red drum (Xue 2008). In 2019, eDNA (environmental DNA) monitoring showed that red drum is widely distributed in the East China Sea, especially near Sanmen Bay and Jiaojiang Estuary (Wang et al. 2022b).

With climate warming, marine ectothermic animals are expected to expand their distributional boundaries toward the poles but shrink at the equatorial boundary (Wang et al. 2021; Hu et al. 2022). The growth of red drum is significantly affected by low temperatures (Zhao et al. 2006), but positively related to increasing marine temperatures under climate change (Tan et al. 2020). Moreover, the habitats charaterized by sandy and argillaceous seabed in these areas encouraged the immigration of red drum (Liao et al. 2010). On the contrary, the sensitivity of red drum juvenile to high temperatures would lead to a shrinkage of suitable habitats in the northern and northwestern parts of the South China Sea (McDonald et al. 2015). However, it must be acknowledged that the occurrence data of red drum in this study was obtained from the online datasets and relevant literature instead of field surveys and a greater number of occurrence records in areas that are more spatially accessible exhibit a strong spatial bias (Phillips et al. 2009; Collart et al. 2021). Although we diluted the occurrence records using spatial filtering to reduce sampling bias, SDM still showed inevitable limitations in accurate prediction while maintaining spatial bias.

Management suggestions

Understanding the individual behaviour and population dynamics of non-native species in different natural or anthropogenic activities is fundamental to conservation management and the development of control strategies (Pinochet et al. 2019). Prevention of non-native species at the stage of initial introduction is easier and more cost-effective than management after population establishment (Banerjee et al. 2020). Under overfishing, ten traditionally economic marine fish stocks of Chinas coastal fisheries were depleted in 2019, and most other species are still facing high fishing pressure (Wang et al. 2022a), which leaves great ecological niche vacancy for the red drum to enlarge its population and expand its distributional range. Adult red drum is highly environmentally tolerant and difficult to eradicate (Wang et al. 2022b), and this would be bound to cause serious harm to local organisms and the ecosystem. East China Sea has become a high-risk area for red drum invasion, and escaping individuals have proved to better adapt to the environmental conditions of Zhejiang's natural sea area, with rapid growth and successful propagation (Lou et al. 2005). At present, though no obvious ecological impact was reported in the South China Sea due to the small number of escaped individuals, the expansion of potential suitable habitats suggests the worth of monitoring for prevention. This is especially true in the coastal waters of the Yellow Sea (34° to 36°N), which is closer to the East China Sea, and located on the northward movement route of red drum, with the northward habitat shift greatly encouraging the immigration of red drum there. Ways to mitigate the impacts of existing and potential invasive stocks should be explored. Primarily, measures should be taken to reduce the escape of farmed red drum (i.e., strengthening aquaculture facilities and operation standards). Numbers and distributions of non-native species and their impacts on other organisms and the environment should be effectively monitored and tracked. Molecular methods, such as eDNA, have increasingly been used to identify and monitor invasive species that occur in small numbers at the margins of their range (Chown et al. 2008). To be emphasized, besides escaping due to natural disasters, some organizations have carried out the release of non-native species into natural water for increasing temporary biomass (Xue 2008). This is inadmissible, and should be addressed by the relevant administrative departments to completely eradicate this kind of destruction of the ecological environment (Lou et al. 2005). In addition, reducing fishing pressure should promote the recovery of other fish stocks and increase competitive ability to curb the expansion of the red drum.

Conclusion

This study showed that the suitable habitat for red drum is currently concentrated along the eastern coast of mainland China, around Hainan Island and along the western coast of Taiwan Province. In future climate scenarios, the red drum will expand northwards, especially in the western Yellow Sea and along the Bohai Sea coast, but with reductions in southern part of China seas. Under the RCP 85 in the 2100s, the reduction of habitat range in southern waters was greater than the expansion in northern waters. The results would help understand the potential impact of climate change on the distribution of non-native marine fish species and can inform the development of preventive management strategies.

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Author contributions

Jintao Li: research conceptualization, investigation, methodology, data analysis and interpretation, writing the original draft, review and editing of the original draft. Linjie Li: methodology, data analysis and interpretation, review and editing of the original draft. Yankuo Xing: investigation, data collection, methodology. Linlong Wang: investigation, methodology, data analysis and interpretation. Yugui Zhu: research conceptualization, methodology, review and editing of the original draft. Bin Kang: research conceptualization, funding acquisition, project administration, review and editing of the original draft. All authors contributed to the article and approved the submitted version.

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Supplementary material 1

Collinearity analysis of environmental variables

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