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Geographical distribution and ecological niche dynamics of *Crassostrea sikamea* (Amemiya, 1928) in China's coastal regions under climate change

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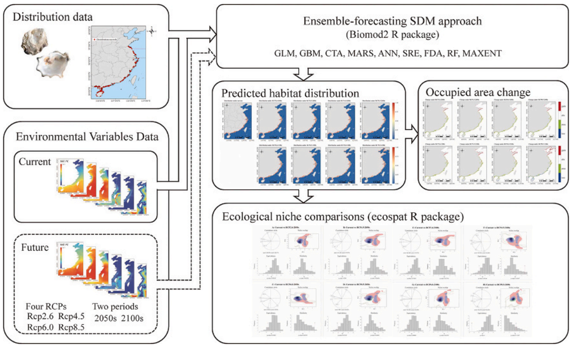
HIGHLIGHTS

- *C. sikamea*'s habitat in China will expand northward and remain constant southern.
- *C. sikamea* poised to expand north beyond SBB in the future.
- *C. sikamea* maintains niche stability but occupies different niche spaces.
- Significant niche expansion will occur in lower temperature.

GRAPHICAL ABSTRACT



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ABSTRACT

Global climate change drives species redistribution, threatening biodiversity and ecosystem heterogeneity. The Kumamoto oyster, *Crassostrea sikamea* (Amemiya, 1928), one of the most promising aquaculture species because of its delayed reproductive timing, was once prevalent in southern China. In this study, an ensemble species distribution model was employed to analyze the distribution range shift and ecological niche dynamics of *C. sikamea* along China's coastline under the current and future climate scenarios (RCP 2.6–8.5 covering 2050 s and 2100 s). The model results indicated that the current habitat distribution for *C. sikamea* consists of a continuous stretch extending from the coastlines of Hainan Province to the northern shores of Jiangsu Province. By the 2050 s, the distribution range will stabilize at its southern end along the coast of Hainan Province, while expanding northward to cover the coastal areas of Shandong Province, showing a more dramatic trend of

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Abbreviations: YREBB, Yangtze River Estuary Biogeographical Barrier; SBB, Subei Biogeographical Barrier; LN, Liaoning; HB, Hebei; TJ, Tianjin; SD, Shandong; JS, Jiangsu; SH, Shanghai; ZJ, Zhejiang; FJ, Fujian; GD, Guangdong; GX, Guangxi; HN, Hainan; BS, Bohai sea; BB, Bohai Bay; LzB, Laizhou Bay; YS, Yellow Sea; ECS, East China Sea; SCS, South China Sea; Chl, Chlorophyll; CV, Current velocity; DO, Dissolved oxygen; NO3, Nitrate; PHY, Phytoplankton; PP, Primary productivity; Sal, Salinity; SST, Sea surface temperature; Dshore, Distance from shore; PCA-env, environmental principal component analysis.

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contraction in the south and invasion in the north by the 2100 s. In RCP8.5, the southern end retracts to the coasts of Guangdong, whereas the northern end covers all of China's coastal areas north of 34°N. *C. sikamea* can maintain relatively stable ecological niche characteristics, while it may occupy different ecological niche spaces under future climate conditions. Significant niche expansion will occur in lower temperature. We concluded *C. sikamea* habitats are susceptible to climate change. The rapid northward expansion of *C. sikamea* may open new possibilities for oyster farming in China, but it will also have important consequences for the ecological balance and biodiversity of receiving areas. It's imperative that we closely examine and strategize to address these repercussions for a win-win situation.

1. Introduction

Historical climate change, coupled with regional variation, has been instrumental in defining contemporary ecosystems and species distributions. Increasing evidence suggests that global change influences the redistribution of driving species on a global scale (Easterling et al., 2000; McCarty, 2001; Parmesan and Yohe, 2003). Since the 1970 s, approximately 84 % of these species have undergone polar migration (Thomas, 2010). An array of terrestrial organisms, including flora, vertebrates, and invertebrates, demonstrate accelerated ascension to higher altitudes, proceeding at velocities estimated to be double or triple those previously documented (Chen et al., 2011). Species endemic to mountainous regions consistently relocate to frigid, higher elevations and seek refuge from the escalating warmth of the lowlands (Chen et al., 2009). Compared to terrestrial species, marine organisms appear to be more sensitive to climate change, migrating poleward at velocities reportedly six times greater than their terrestrial counterparts and meticulously mirroring the migration of temperature bands (Lenoir et al., 2020). Such rapid changes in habitual zones profoundly alter the composition, architecture, and inter-species dynamics of emerging ecological communities (Davis and Shaw, 2001; Veloz et al., 2012). This phenomenon is an imminent threat to biodiversity on a planetary scale and to the heterogeneity of global ecosystems (Hu et al., 2019; Xiao et al., 2020).

The Kumamoto oyster, *Crassostrea sikamea* (*C. sikamea*, Amemiya, 1928), is a native species widely distributed in southern China (Reece et al., 2008; Wang et al., 2013; Qin et al., 2021). Due to its confusing taxonomic status and relatively small size, *C. sikamea* has not been cultured systematically (Ma et al., 2022). Traditional oyster farming varieties have faced developmental limitations in recent years, and *C. sikamea* has emerged as one of the most promising aquaculture species because of its terrifying taste, high nutritional value, and ability to spawn later in summer, thereby filling the market gap (Robinson, 1992; Gordon et al., 2003). Historically, *C. sikamea* was found as far north as the Liyashan oyster reef in Jiangsu Province (32.13°N) in coastal China until 2006 (Wang et al., 2013). This distribution is plausibly due to the Yangtze River Estuary Biogeographical Barrier (YREBB), which is a decisive ecological demarcation separating the Cold and Warm Temperate Northwest Pacific Provinces (Xu et al., 2020; Liu, 2013; Ni et al., 2017). Recent ecological dynamics, including habitat fragmentation (Wang et al., 2020), alterations in ocean currents (Dong et al., 2016; Wang et al., 2020), and climatic factors (Spence and Tingley, 2020), have attenuated the restrictive capacity of the YREBB, giving rise to the Subei Biogeographical Barrier (SBB) at 33°N to 34°N (Hu and Dong, 2022a; Dong et al., 2016; Wang et al., 2020). This shift has enabled numerous marine species to traverse historical biogeographical confines, leading to the colonization of new habitats (Bulleri and Airoldi, 2005; Dong et al., 2016; Wang et al., 2020). Empirical data from a July 2023 expedition, complemented by previous studies (Hu and Dong, 2022b), consistently indicate *C. sikamea* has successfully breached the YREBB, pushing its distributional frontiers to 33–34°N latitude. This rapid alteration in distribution patterns is of considerable ecological significance. Elucidating the prospective distributional adaptations and ecological niche modifications of *C. sikamea* is paramount for enhancing strategic responses to the challenges imposed by global changes in oyster aquaculture and ecological preservation.

Species Distribution Models (SDMs) represent a critical nexus in predictive ecology, enabling comprehensive forecasts of potential habitats of species by correlating environmental conditions with occurrence data. SDMs have been widely integrated into various disciplines within life and environmental sciences (Cheung et al., 2009; Robinson et al., 2011), including projecting climate change implications on species habitats (Zhang et al., 2019), analyzing habitat loss constraints on species territories (Vasconcelos and Doro, 2016), deciphering the mechanics behind biological invasions (Zhang et al., 2020), and optimizing the placement of aquaculture establishments (Dong et al., 2020). A primary obstacle arises from the burgeoning array of modeling techniques, which complicates the selection of an optimal approach (Elith et al., 2006). To address this complexity, recent scholarly discourse advocates the implementation of multiple methodologies in tandem, referred to as ensemble modeling, within a unified modeling framework (Araújo and New, 2007; Thuiller et al., 2009). This advanced framework, delineated in foundational literature (Thuiller, 2004; Marmion et al., 2009), mitigates the inherent predictive uncertainties of individual models through integrative approaches (Buisson et al., 2010; Grenouillet et al., 2011), thereby enhancing the precision of species distribution projections (Marmion et al., 2009).

A climatic niche is the range of climatic conditions in which a species can survive, and determines the ability to survive in specific climatic regions and adapt to future climate change (Porter and Kearney, 2009; Bozinovic et al., 2014). When climate changes, a species may lose its current suitable habitat or invade new areas, and its climatic niche will respond directly. For example, a species may rapidly evolve and experience niche shifts to a new range, enhancing its tolerance to the environment and causing changes in its ecological niche (Guisan et al., 2014). The quantification of climatic niches often relies on SDMs, which use various specific algorithms to link environmental variables with geographical data to assess niche differentiation, thereby presenting a projection in the geographical landscape to estimate niche overlap (Guisan and Thuiller, 2005). By quantifying the climatic niche of a species, we can better explain its geographical distribution changes, evaluate its vulnerability to climate change and ecological adaptation, and maintain its biodiversity (Tingley et al., 2014; Atwater et al., 2018).

In this study, we utilized valuable primary data and employed an ensemble modeling strategy to analyze the distribution range shift and ecological niche dynamics of *C. sikamea* along the coastline of China. This is the first integration of SDM and ecological niche analysis for this species. Due to China's extensive latitude, one species distributed across different regions exhibits significantly varied levels of sensitivity in response to climate change. Therefore, it is of representative significance to study the species capable of rapid northward migration, such as *C. sikamea*, in the coastal regions of China. We hope that our findings can serve as a valuable "China case", offering a reference for global-scale studies on the rapid northward shift of intertidal species in response to global climate change. This research was specifically designed to fulfill several objectives: (i) to extrapolate the potential habitat distribution of *C. sikamea* under current and future climatic conditions, (ii) to spatially delineate range contraction/expansion, and (iii) to evaluate anticipated shifts in the ecological niche of *C. sikamea*.

2. Materials and methods

2.1. Species distribution data

Species distribution data for *C. sikamea* were derived from historical sampling data collected by our research team. These data cover the period from 2004 to 2023 and include 3615 samples collected from various locations along the coastal regions of China, with the most recent data from July 2023 representing the northernmost distribution. The samples were collected from Hainan (165 samples), Guangxi (371 samples), Guangdong (1761 samples), Fujian (658 samples), Zhejiang (229 samples), Shanghai (34 samples), and Jiangsu (397 samples) in China (Table S1) (Liu et al., 2024). To enhance the dataset, we also incorporated relevant research literature (Wang et al., 2013; Li et al., 2017; Hu et al., 2018; Liu et al., 2021; Hu and Dong, 2022b) and information available in global public databases, such as the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and the Ocean Biodiversity Information System (OBIS, http://www.obis.org). Considering the feasibility of field sampling surveys and the availability of accurate distribution data (Camara et al., 2008; Hong et al., 2012), we defined the study scope as the China's coastal regions (17.5–41.5°N, 107.0–125.0°E) and retained the distribution data within this range.

For each data point, we obtained geocoordinates either from literature or by referencing Google Earth coordinates (version 7.3.4). To ensure the accuracy of our dataset, we carefully reviewed the data to eliminate duplicates or instances in which the location was unclear. To address potential survey bias before conducting modeling, only one presence point per raster cell (1 km × 1 km) was retained, and these points were further filtered to be at least 1 km apart using a function we defined (shown in Appendix) in R (version 4.3.1). Consequently, we obtained 216 distribution records, which were used to construct the model (Fig. 1).

2.2. Environmental variables

Owing to data availability and species-environment associations, we initially selected 11 environmental variables that potentially affected the distribution of *C. sikamea* (Table 1) (Bayne, 1985; Wang and Li, 2017; Haley et al., 2018; Palumbi, 1994; Metian et al., 2020; Simon et al., 2020). The data distance from the shore was downloaded from the Global Fishing Watch Datasets (https://globalfishingwatch.org/). The data for the remaining ten variables were downloaded from the marine data layers (Bio-ORACLE, https://bio-oracle.org/index.php).

Table 1
Environmental variables that potentially affected the distribution of *C. sikamea*. Bolded text in the environment variables column indicates the modeling environment variables.

Environment variables	Abbreviate	Unit	Source
Chlorophyll	Chl	$mg.m^{-3}$	Bio-ORACLE
Currents velocity	CV	$m.s^{-1}$	
Dissolved oxygen	DO	$mol.m^{-3}$	
Nitrate	NO3	$mol.m^{-3}$	
pH	–	–	
Phytoplankton	PHY	$umol.m^{-3}$	
Primary productivity	PP	$g.m^{-3}.day^{-1}$	
Salinity	Sal	PSS	
Sea surface temperature	SST	°C	
Depth	Depth	m	
Distance from shore	Dshore	m	Global Fishing Watch

The Bio-ORACLE dataset provides projections for two future time periods in the 2050 s (average for 2040–2050) and 2100 s (average for 2090–2100), which are representative of mid- and long-term future climatic conditions (Assis et al., 2018). Four Representative Concentration Pathways (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) predicted by the Coupled Model Intercomparison Project 5 were used to predict the future variance of species distribution in detail (Assis et al., 2018). RCPs are a set of integrated concentration and emission scenarios that characterize the future emissions of greenhouse gases, reactive gases, aerosols, and atmospheric constituent concentrations in the face of changes in population, socioeconomics, science and technology, energy consumption, and land use (Moss et al., 2010; Ma and Sun, 2018). Among them, RCP2.6 was considered the best case for limiting anthropogenic climate change under a low-emission scenario; RCP4.5, and RCP6.0, were selected as two intermediate stabilization scenarios; and RCP8.5, which was generally regarded as a high-emission scenario (Table S2) (Taylor et al., 2012).

We employed several methods, including principal component analysis (PCA) (Fig. S1) (Cunze et al., 2020), jackknife test (Fig. S2) (Zhang et al., 2021), contribution rates (Table S3) (Ouyang et al., 2022) and Pearson's correlation analysis (Fig. S3) (Dormann et al., 2013; Worthington et al., 2016) to mitigate the effects of multicollinearity and provide more robust insights into the relationships between environmental variables. Considering the special ecological characteristics of intertidal species (Chen et al., 2021; Chen et al., 2017), we retained six

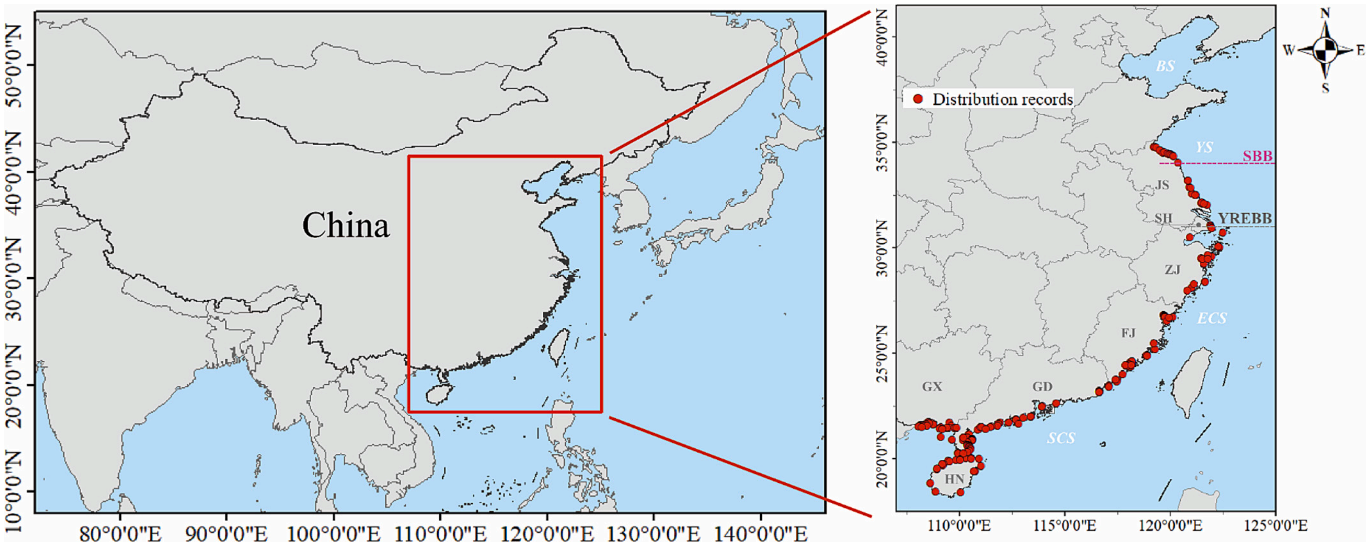

Fig. 1. Occurrence records of *C. sikamea* in coastal China (JS: Jiangsu; SH: Shanghai; ZJ: Zhejiang; FJ: Fujian; GD: Guangdong; GX: Guangxi; HN: Hainan. BS: Bohai sea; YS: Yellow Sea; ECS: East China Sea; SCS: South China Sea; SBB: Subei biogeographical barrier; YREBB, Yangtze River biogeographical barrier).

environmental variables with Variance Inflation Factor (VIF) values <10 (Table S4) (Diaz-Carballido et al., 2022): chlorophyll (Chl), current velocity (CV), pH, salinity (Sal), sea surface temperature (SST), and distance from shore (Dshore) (Table 1). With other environmental variables fixed at their means, we calculated the contribution rates of the three values (max, mean and min) of Chl, CV, Sal and SST respectively (Table S5), and retained variables that gained the highest contribution rates within each group (Li et al., 2022; Zhuo et al., 2020). Ultimately, we selected Chl-min, CV-max, pH, Sal-max, SST-mean, and Dshore for species distribution modeling and prediction. All environmental data layers were extracted uniformly from the boundary of the study area (17.5–41.5°N, 107.0–125.0°E) using ArcGIS (version 10.7).

2.3. Modeling procedures

The potential suitable area of *C. sikamea* was modeled using nine single-species distribution models (Generalized Linear Model (GLM; McCullagh and Nelder, 1989), Generalized Boosted Models (GBM; Ridgeway, 1999), Classification Tree Analysis (CTA; Breiman et al., 1984), Multivariate Adaptive Regression Splines (MARS; Friedman, 1991), Artificial Neural Networks (ANN; Lek and Guegan, 1999), Surface Response Envelope (SRE; Breiman, 2001a), Flexible Discriminant Analysis (FDA; Hastie et al., 1994), Random Forest (RF; Breiman, 2001b), and Maximum Entropy (MAXENT; Phillips et al., 2006)) in Biomod2 (version 4.2–4) (Thuiller et al., 2016) based on species distribution data and environmental variables. In the single-species distribution model setup, 75 % of the species occurrence records were used as training data, and the remaining 25 % were used as test data; 10,000 pseudo-absence points were randomly selected (Thuiller et al., 2023; Zhang et al., 2019; Barbet-Massin et al., 2012; Adhikari et al., 2023), and the model was repeated 10 times.

The model performance was quantified using three commonly used evaluation metrics: (1) the area under the curve (AUC) of the receiver operating characteristic (ROC; Hanley and McNeil, 1982), (2) the true skill statistic (TSS; Allouche et al., 2006) and (3) the Cohen's Kappa (Kappa; Cohen, 1960). The reference standards for each evaluation metric were shown in Table S3 (McPherson et al., 2004; Vuuren et al., 2007). An ensemble modeling approach was used to model and map the distribution of *C. sikamea* because of its potential ability to outperform individual models (Zhang et al., 2019). Individual models with AUC $\geq$ 0.95, TSS $\geq$ 0.90, and Kappa $\geq$0.80 were included in the ensemble model construction based on a range of published work (Silva et al., 2016; Ruiz-Navarro et al., 2016). The ensemble model was built by weighing the individual models according to their calculated TSS values, which were used to predict the potentially suitable areas for *C. sikamea*.

2.4. Potential distribution and species range change

The current and future occurrence probabilities of *C. sikamea* were estimated for each geographic grid using the ensemble model, with values ranging from 0 to 1, where 1 indicates the highest probability of occurrence and 0 represents the lowest. We used the SDM toolbox (Brown, 2014) in ArcGIS to quantify and represent range changes under future climatic scenarios for *C. sikamea*. This production function exhibits two outputs: a table containing a brief description related to the statistics of species range change and a spatial map that shows the probable areas where the species will show habitat gain or loss in future climate scenarios. A grid could have four different situations under future scenarios: (1) “lost” represents the grid is predicted to be lost by the species in the future; (2) “gain” represents the grid was not occupied currently, but is predicted to be occupied in the future; (3) “pres” represents the grid is occupied now and in the future; (4) “abs” represents the grid is not occupied now nor in the future.

2.5. Ecological niche analysis

The environmental principal component analysis (PCA-env) in the R package ecospat (version 3.5.1) (Di Cola et al., 2017) was used to study the ecological niche shifts of *C. sikamea* under current and future climatic scenarios. The environmental variables were transformed into a two-dimensional space defined by two principal components. The two-dimensional environmental space was then projected onto a grid cell with a diameter of 100 × 100 and bounded by the minimum and maximum PCA values in the background. A smooth key density function was used to overcome sampling bias owing to the lower number of occurrence data points (Petitpierre et al., 2012).

The Schoener's D metric was used to determine the extent of ecological niche overlap. The index had a value range from 0 to 1, with larger values indicating a higher overlap rate of ecological niches. To understand the importance of niche overlap in geographic areas, niche equivalency and similarity tests were performed (Broennimann et al., 2012). The niche equivalency test was performed by comparing the niche overlap (D) values for current and future climatic scenarios to the overlap of the null distribution, which was created by extracting climatic variables from a randomly selected set of coordinates across the background region of the study area (Broennimann et al., 2012). The niche equivalency test assessed whether the niches of the two entities were equal (full overlap), moderately similar (partial overlap), or distinctly different (no overlap). The niche similarity test assessed whether the niches of the two entities being compared were more similar (or different) than expected by chance, also considering the surrounding environmental conditions throughout the geographic area (Warren et al., 2008). The test was randomly repeated 1000 times, and the null hypothesis of ecological niche equivalence or similarity could be rejected if the observed niche values (D) were significantly lower than the overlap value from the null distribution ($P < 0.05$) (Broennimann et al., 2012).

To assess niche dynamic metrics, a set of environments represented niche expansion if it was available in both current and future ranges, but was only occupied in the future range (Guisan et al., 2014). Similarly, a set of environments was considered to result from niche stability if it was occupied in both current and future ranges, and niche unfilling if it was used in the current range and was available, but not yet exploited, in the future range (Broennimann et al., 2012; Guisan et al., 2014). Values for expansion, stability, and unfilling ranging from 0 to 100 % were considered significant at >10 % (Hill et al., 2017; Petitpierre et al., 2012; Strubbe and Matthysen, 2014). Niche expansion is considered the only measure that truly describes shifts in a realized niche (Li et al., 2014; Liu et al., 2020; Petitpierre et al., 2012; Strubbe et al., 2013).

3. Results

3.1. Evaluation of model performance

The cross-validation results (Fig. 2) indicated a difference in predictive efficacy among the models. CTA, GBM, GLM, MARS, RF, ANN, and FDA exhibited robust performance across all evaluation metrics (AUC, TSS, and Kappa), whereas MAXENT showed suboptimal results, and SRE performed the least effectively. Individual models with AUC $\geq$ 0.95, TSS $\geq$ 0.90, and Kappa $\geq$0.80 were incorporated into the ensemble model, including ANN, CTA, FDA, GBM, GLM, and MARS. The ensemble model, with scores of 0.991, 0.953, and 0.801 for AUC, TSS, and Kappa, respectively, generated projections with remarkable validity and accuracy, surpassing those of its constituent models. Because of its enhanced predictive precision and dependability, the ensemble model was selected to delineate the current and future habitat distributions of *C. sikamea*.

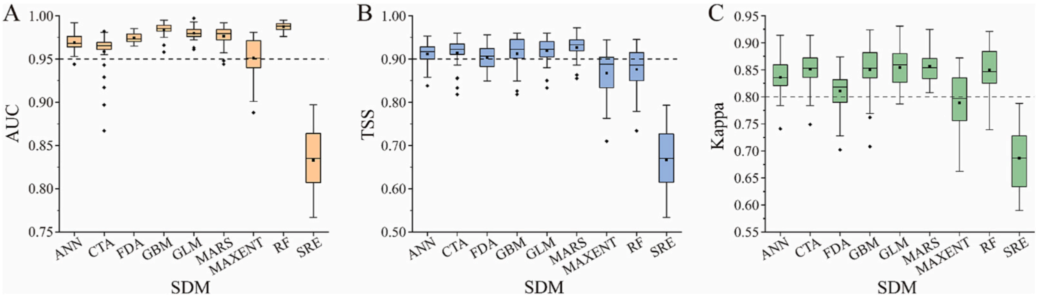

Fig. 2. Distributions of overall accuracy of different individual SDM. Box plots showing the estimated mean (squares), estimated median (horizontal lines), outliers (diamonds), 25th–75th percentiles (boxes) and the range (line segments) of AUC (A), TSS (B) and Kappa (C). Dotted horizontal line represents the selecting criterion (AUC = 0.95, TSS = 0.90, Kappa = 0.80) of individual models for inclusion in the ensemble model.

3.2. *The importance of environmental variables*

The variable importance analysis highlighted the predominant role of Dshore (0.843) in determining *C. sikamea*'s range (Fig. S4). This prominence was attributed to the restricted threshold of offshore distance data correlating with species distribution points, leading the model to perceive this as a critically selective constraint on the distribution scope. SST (0.125) was more important than Sal (0.013), pH (0.011), Chl (0.004), and CV (0.004) (Fig. S4). Response curves for each environmental variable were provided in Fig. S5.

3.3. *Habitat distribution and range shift under current and future climate scenarios*

Under current climatic scenario, the ensemble model indicated that the potential habitat distribution for *C. sikamea* is a continuous stretch extending from the coastlines of Hainan Province to the northern shores of Jiangsu Province, and that the suitability of this range is remarkably high (Fig. 3). The predicted distribution was consistent with the actual sampling results.

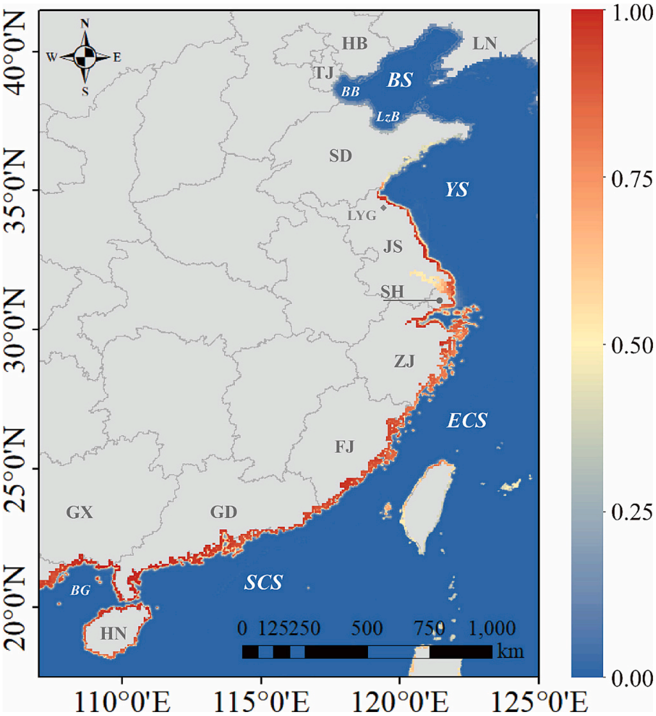

Fig. 3. Current habitat distribution of *C. sikamea* predicted by the ensemble model. Color gradient indicates variation in habitat suitability (red = highest, blue = lowest). (LN: Liaoning; HB: Hebei; TJ: Tianjin; SD: Shandong; JS: Jiangsu; LYG: Lianyungang; SH: Shanghai; ZJ: Zhejiang; FJ: Fujian; GD: Guangdong; GX: Guangxi; HN: Hainan. BS: Bohai sea; BB: Bohai Bay; LzB: Laizhou Bay; YS: Yellow Sea; ECS: East China Sea; SCS: South China Sea).

Projections under future climate scenarios indicated that large areas of potential habitat along the coast from Hainan Province to the north of Lianyungang, Jiangsu Province, will continue to be suitable until the 2050 s (Fig. 4A–D). In addition, some areas north of Lianyungang, such as the west coast of the Yellow Sea, Laizhou Bay, and Bohai Bay, will show better suitability than the current climate scenario (Fig. 4A–D). Based on the overall changes in potential distribution, *C. sikamea* is expected to maintain its current potential habitat and gain habitat along the western coast of the Yellow Sea and in some areas along the western coast of the Bohai Sea (Fig. 4E–H). There will be no significant large-scale habitat loss (Figs. 4E–H, S6). The distribution range of the species will stabilize at its southern end along the coast of Hainan Province, while expanding northward to cover the coastal areas of Shandong Province by the 2050 s (Fig. 4E–H).

By the 2100 s, with the increase in emissions, the potential habitat along the coast from Hainan Province to the north of Lianyungang, Jiangsu Province, will not be able to maintain its original suitability (Fig. 5A–D). The suitability of the original southern areas, such as the coasts of Hainan Province, Guangdong Province, Fujian Province, and the Yangtze River Delta, will gradually decrease (Fig. 5A–D). However, the suitability of northern areas, such as the coasts of Shandong Province and the Bohai Sea, will gradually increase (Fig. 5A–D). Based on the overall changes in the potential distribution, *C. sikamea* is projected to experience a significant loss of habitat along the coast of Hainan Province, Guangdong Province, and the Yangtze River Delta and gradually gain suitable areas along the coast of Shandong Province and the coastal areas around the Bohai Sea (Figs. 5E–H, S6). The potential habitat of *C. sikamea* will show a contracting trend in the south and an expanding trend in the north (Fig. 5E–H). In scenario RCP8.5, the southern end of the habitat will contract to the coasts of Guangdong and Fujian Provinces, and the northern end will expand to cover all coastal areas north of Lianyungang (Fig. 5D, H).

3.4. *Ecological niche dynamics under future climate scenarios*

Niche analyses contrasting current and future climatic conditions revealed a consistent moderate niche overlap across all scenario comparisons, ranging from 23 % (Schoener's D = 0.23) for current vs. RCP8.5–2100 s to 41 % (Schoener's D = 0.41) for current vs. RCP6.0–2050 s (Fig. 6; Table 2). This pattern exhibited a prospective 59–77 % loss of the present climatic niche for *C. sikamea* within the ensuing climatic framework. The PCA-env revealed that the variation retained by principal component 1 (PC1) ranged from a minimum of 38.41 % in the case of current vs RCP8.5–2100 s comparison to a maximum of 41.69 % for current vs RCP2.6–2100 s comparison (Fig. S7; Table 2). Similarly, for principal component 2 (PC2), the retained variation ranged from a minimum of 23.57 % for the current vs.

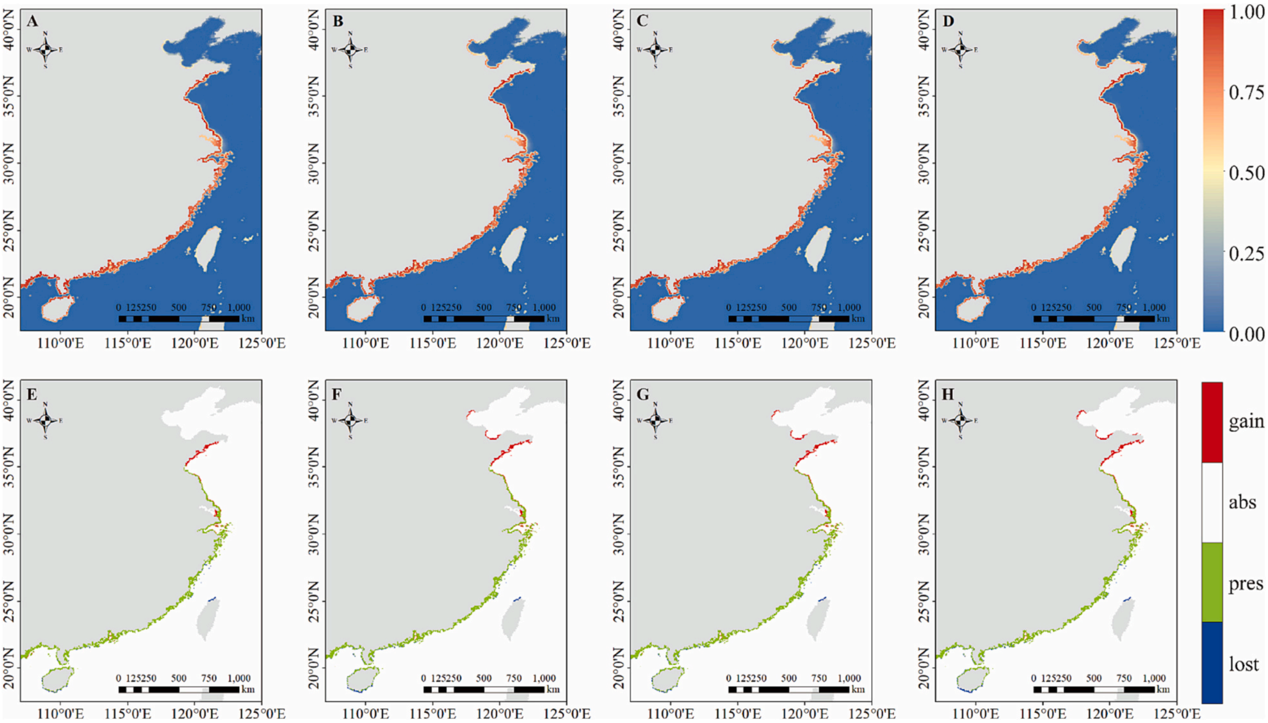

Fig. 4. Predicted habitat distribution (A: RCP2.6–2050 s; B: RCP4.5–2050 s; C: RCP6.0–2050 s; D: RCP8.5–2050 s) and occupied area change (E: RCP2.6–2050 s; F: RCP4.5–2050 s; G: RCP6.0–2050 s; H: RCP8.5–2050 s). Color gradient in A-D indicates variation in habitat suitability (red = highest, blue = lowest).

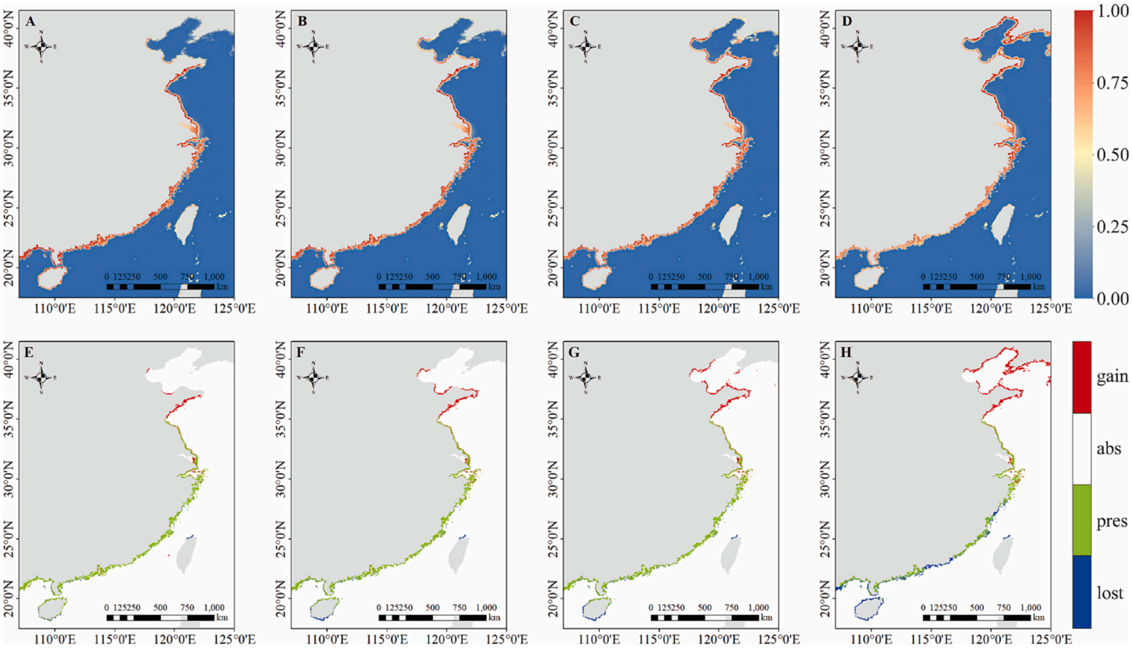

Fig. 5. Predicted habitat distribution (A: RCP2.6–2100 s; B: RCP4.5–2100 s; C: RCP6.0–2100 s; D: RCP8.5–2100 s) and occupied area change (E: RCP2.6–2100 s; F: RCP4.5–2100 s; G: RCP6.0–2100 s; H: RCP8.5–2100 s). Color gradient in A–D indicates variation in habitat suitability (red = highest, blue = lowest).

RCP2.6–2100 s comparison to a maximum of 25.82 % for the current vs. RCP8.5–2100 s comparison (Fig. S7; Table 2).

Furthermore, we extended the exploration of niche equivalency and similarity. In a pairwise analysis of the climatic niches of the species under current and future climatic scenarios, the null hypotheses for niche equivalency were not rejected in any of the pairwise comparisons ($P > 0.05$) (Table 2). The niche similarity test for the null hypothesis were not rejected in most cases ($P > 0.05$), except for the current vs RCP4.5–2100 s comparison and the current vs RCP6.0–2050 s comparison ($P < 0.05$) (Table 2). This suggested that *C. sikamea* may have similar ecological niche characteristics in terms of resource utilization and structural features in both current and future scenarios. The values of ecological niche expansion, stability, and unfilling suggested that the climatic ecological niche of *C. sikamea* will significantly expand (>20 %) in the future (Table 2). With rising emission levels and the passage of time, the level of ecological niche expansion will increase while the

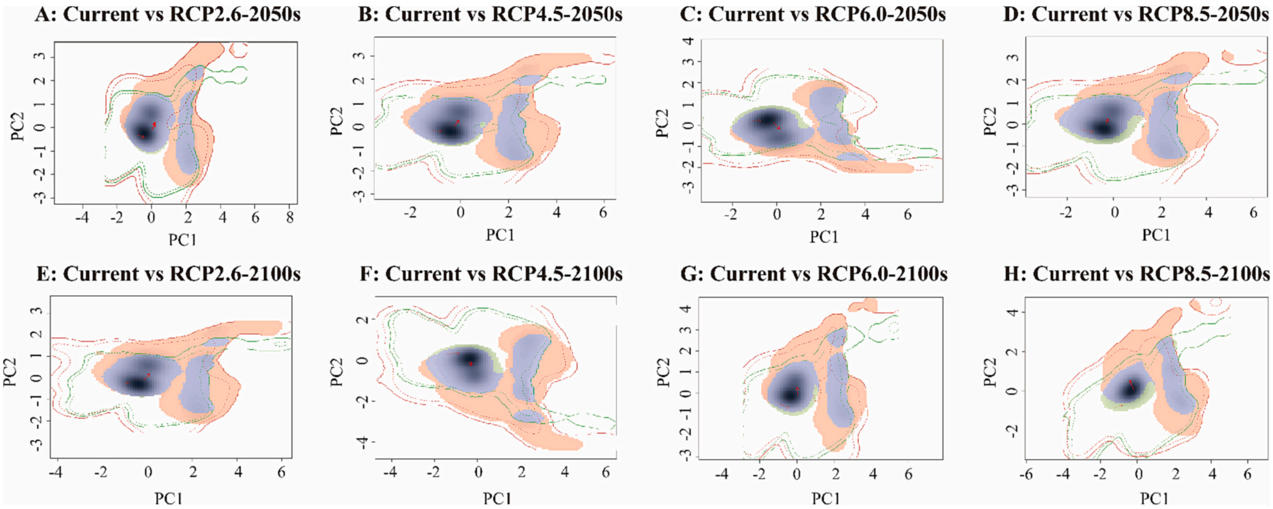

Fig. 6. Niches overlap of *C. sikamea* between current and future climatic scenarios. The green and red shadings represent density of species occurrences in current and future scenario and red arrows mark Schoener's D (Niche overlap) estimate. Purple indicates the niche overlap between the two scenarios.

Table 2
Niche comparisons and variation between the current and future projected distribution ranges of *C. sikamea*.

Niche comparison pairs	PC1 (%)	PC2 (%)	Niche overlap (D)	Niche equivalency (P)	Niche similarity (P)	Niche Expansion (%)	Niche Stability (%)	Niche Unfilling (%)
Current vs RCP2.6–2050 s	40.96	24.31	0.37	0.98	0.06	26.52	73.48	0.35
Current vs RCP2.6–2100 s	41.69	23.57	0.34	0.97	0.06	25.11	74.89	0.02
Current vs RCP4.5–2050 s	41.26	23.93	0.31	0.99	0.06	27.47	72.53	0.52
Current vs RCP4.5–2100 s	39.93	24.64	0.36	0.94	0.03	26.44	73.56	1.98
Current vs RCP6.0–2050 s	40.50	23.80	0.41	0.96	0.01	21.75	78.25	2.68
Current vs RCP6.0–2100 s	38.83	25.29	0.38	0.91	0.05	25.51	74.49	1.74
Current vs RCP8.5–2050 s	40.00	24.32	0.34	0.95	0.09	24.77	75.23	3.24
Current vs RCP8.5–2100 s	38.41	25.82	0.23	1.00	0.13	38.94	61.06	9.49

stability of the ecological niche will gradually decline (Table 2). Comparing the species occurrence densities of environment variables between the current and future climate scenarios, we found that *C. sikamea* will expand its climate niche to lower temperature environments (Fig. S8).

4. Discussion

This study presented an investigation into the effects of climate change on the geographical distribution and ecological niche dynamics of *C. sikamea*. The results highlighted the significance of Dshore and SST in depicting the geographical distribution of *C. sikamea*. The model projections revealed a future expansion beyond the SBB, signifying a notable northward shift for this traditionally 'southern species'. *C. sikamea* can maintain stable ecological niche characteristics while occupying different ecological niche spaces under future climate conditions. This implies potential competition with local species for resources and territory, and alteration of the northern habitat. At the same time, this northward migration of *C. sikamea* also presents new opportunities for oyster aquaculture in China.

4.1. Environmental variables influencing the geographic distribution of Crassostrea sikamea

This study demonstrated the significant role of Dshore in delineating the distribution of *C. sikamea* (Fig. S4). Oysters are intertidal species that predominantly adhere to rigid substrates. The absence of comprehensive data concerning the bottom material necessitated the adoption of Dshore as a surrogate indicator to produce a more accurate distribution portrayal. When the Dshore was not included in the model, the model's performance decreased (Fig. S9), and there were significant discrepancies between the model's predictions and the actual observations (Fig. S10). The restricted range of Dshore data correlating with the species distribution points led the model to perceive it as a critically selective constraint on the distribution scope, which does not inherently elevate Dshore as the paramount determinant of *C. sikamea* distribution.

In our study of habitat range delineation for intertidal organisms, water depth was also considered as a potential indicator. However, the negligible contribution rate (0 %) of water depth implied that it may not be a reliable factor (Table S3). Intertidal species, such as oysters, experience fluctuating water depths due to tidal changes. The inaccuracy of water depth data can introduce biases in species distribution models for these organisms.

SST emerged as the principal elements that dictated *C. sikamea* distribution (Fig. S4), corroborating the conclusions of previous studies (Kinne, 1964; Robinson, 1992; Wang and Li, 2017). Our research suggested that *C. sikamea* can maintain its current suitable habitat range in the increasingly warm southern seas. While the species might extend its ecological niche to lower temperature environments, its main ecological niche will remain within the range of 25–28 °C (Fig. S8). This suggested a certain tolerance of *C. sikamea* to high temperatures, potentially linked to their summer reproductive habits. In natural marine environments, *C. sikamea* sexual maturity peaks between July and August, aligning with the year's highest water temperatures. Furthermore, the optimal temperature range for oyster spat growth and survival is 24–28 °C, and rising water temperatures can enhance the growth and survival of oyster spat during the rearing period (Wang and Li, 2017).

Salinity and pH gained approximately equal importance scores (Fig. S4), and their ecological niche in the future was expected to remain consistent with the current conditions (Figs. S11, S12). *C. sikamea* growth relies on stable salinity and pH levels. Significant salinity fluctuations cause marine bivalves to close their mantle membranes (Berger and Kharazova, 1997). This response hinders water exchange with the external environment, regulates hemolymph osmotic pressure, and lowers respiratory metabolism and other physiological activities (Berger and Kharazova, 1997). Moreover, a decrease in seawater pH impacts bivalve larvae settlement (Kripa et al., 2014) and shell calcification (Haley et al., 2018).

Building upon prior research (Liu et al., 2024), this study employed an ensemble model with enhanced precision to predict the distribution of *C. sikamea* along China's coasts. It is important to note that due to limitations in the availability of environmental data, the modeling approach used in this study did not incorporate changes in circulation patterns (Dong et al., 2012; Ni et al., 2014; Wang et al., 2016), larval dispersal potential (Feary et al., 2014; Cowen and Sponaugle, 2009), inter-species dynamics (Zhang et al., 2022), and human impact (Gallardo et al., 2015). Therefore, comprehensive research is warranted to reconcile these model projections with the actual distribution patterns of *C. sikamea*.

4.2. *Crassostrea sikamea* poised to expand north beyond SBB in the future

C. sikamea exhibited a distinct response to global climate change (Sorte et al., 2010), with an anticipated northward expansion of its suitable habitat while its southern boundary remains unchanged (Figs. 4, 5). This is notable given that global changes, such as rising temperatures and more frequent extreme weather events, are generally expected to diminish habitat suitability for some species or contract their distribution ranges. The current distribution indicated that the *C. sikamea* has gradually extended beyond the SBB, and our research predicted future expansion will mainly occur along the coasts of Shandong Province and the Bohai Sea, indicating a significant northern shift for this traditionally ‘southern species’ (Hu and Dong, 2022b). The continued rise in ocean temperature was one of the primary factors driving this migration. Temperature fluctuations can directly and predictably influence population connectivity, with larval duration and survival rate closely linked to environmental temperatures (O'Connor et al., 2007).

C. sikamea has been a prominent species crossing the YREBB and SBB over the past decade, extending its distribution to the coastal areas of Lianyungang, Jiangsu Province. This is attributed to *C. sikamea* unique biological characteristics. Firstly, *C. sikamea* has multiple genetic sources, with some reef populations in thermally stressful regions along the Chinese coast. These populations are pre-adapted to high temperatures, providing adaptive genotypes for northern populations (Hu and Dong, 2022b). Genetic admixtures from different regions enhances population expansion by increasing adaptive potential and environmental tolerance (Geburzi et al., 2020). Secondly, *C. sikamea* reproductive period during summer aligns with stronger northward wind-driven ocean currents, and the species possess a high reproductive rate and abundant larval supply (Wu et al., 2018; Yuan et al., 2017). Additionally, the development of artificial hard substrates along coastal areas (Amarasekare and Simon, 2020; Pinsky et al., 2020) has also facilitated this classical habitat generalist species' northward expansion. *C. sikamea* can occupy a wider range of habitats, such as coastal defense structures, artificial docks, and concrete pillars (Platts et al., 2019).

This trend of northward migration due to climate change on coastal areas has been observed in other warm-water species such as *Schizaster lacunosus* (Xu et al., 2020) and *Nerita yoldii* (Wang et al., 2018), which have crossed the YREBB and expanded their range towards the SBB. As a pioneer in the northward migration, the notable distribution range change of *C. sikamea* indicates a significant shift in the migration patterns of southern species to northern regions.

4.3. Ecological challenges and aquaculture opportunities of *Crassostrea sikamea's* northward migration

The results of ecological niche equivalency and similarity (Table 2) indicated that *C. sikamea* can maintain relatively stable ecological niche characteristics while adapting to future climate change (Fernández and Hamilton, 2015). However, the low overlap and significant expansion (Table 2) of its ecological niche suggested that *C. sikamea* may occupy different ecological niche spaces under future climate conditions (Wei et al., 2017; Pili et al., 2020). This was consistent with our conclusion regarding its potential northward migration. It further implies that during the process of *C. sikamea* migrating northward and adapting to new environments due to climate change, there will be competition with local species for survival resources and space (Dukes and Mooney, 1999; Vitousek et al., 1997; Rosenzweig et al., 2008). Given that the competition among species increases with functional similarity (Dick et al., 2017; Wardle et al., 2011), the northward migration of *C. sikamea* may lead to the decline of similar local species (Byers, 2009), such as *Crassostrea gigas* (Thunberg, 1793). Oysters are known as ecosystem engineers for their ability to form extensive reefs, increase settling areas for various species, and promote colonization (Padilla, 2010). Consequently, the northward migration of *C. sikamea* might profoundly alter the native system, potentially impacting local biodiversity, protected habitats, and commercial species (King et al., 2021; Crooks, 2009).

Vulnerability assessments on key fishery species reveal that oyster farming faces significantly higher risks than fisheries (Doubleday et al., 2013; Johnson and Welch, 2016). This increased vulnerability is attributed to the negative directional effects of climate change and the limited ability to migration caused by sessile lifestyles (Mahu et al., 2022). Integrated aquaculture can enhance the ecological stability of the aquaculture system (Ahmed et al., 2019). The northward migration of *C. sikamea* suggests the possibility of cultivating native southern oyster species in northern areas, which can alleviate the pressure of expand aquaculture in certain areas (Jo et al., 2012), and enhance the productivity, environmental sustainability, and capacity of aquaculture to adapt to climate change (Ahmed et al., 2019).

It is imperative that the advancement of *C. sikamea* aquaculture is paralleled by thorough risk evaluations undertaken by governing bodies encompassing ecological, economic, and societal dimensions. The enforcement of rigorous aquaculture protocols and managerial strategies is critical for mitigating ecological disruptions, with the aim of preserving regional biotic harmony.

5. Conclusion

The habitats of *C. sikamea* are susceptible to climate change, resulting in changes in suitable areas and ecological niches of the species along the Chinese coastline. The potential rapid northward migration of *C. sikamea* offers new avenues for oyster aquaculture in China. However, this movement could have significant implications for the ecological structure and functions of marine ecosystem. We aimed for this study to serve as a benchmark for extensive international research on the rapid shift in intertidal species. This, in turn, promotes further exploration of the impact of climate change on marine ecosystems and fosters collaborative endeavors aimed at devising conservation and adaptation strategies in this unparalleled era of environmental change.

CRediT authorship contribution statement

Bingxian Liu: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Zhenqiang Liu:** Resources, Investigation, Data curation. **Cui Li:** Writing – review & editing, Resources, Investigation. **Haolin Yu:** Writing – review & editing, Software, Methodology. **Haiyan Wang:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Haiyan Wang reports financial support was provided by National Natural Science Foundation of China (42076092, 41776179). Haiyan Wang reports financial support was provided by National Key Research and Development Program of China (2022YFD2401301, 2022FY100304). Haiyan Wang reports financial support was provided by Strategic Priority Research Program of the Chinese Academy of Sciences (XDB42000000). Haiyan Wang reports financial support was provided by Earmarked Fund for Modern Agro-industry Technology Research System (CARS-47). If there are other authors, they 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.scitotenv.2024.171061.

References

Adhikari, B., Subedi, S.C., Bhandari, S., et al., 2023. Climate-driven decline in the habitat of the endemic spiny babbler (*Turdoides nipalensis*). Ecosphere 14 (6), e4584. https://doi.org/10.1002/ecs2.4584.

Ahmed, N., Thompson, S., Glaser, M., 2019. Global aquaculture productivity, environmental sustainability, and climate change adaptability. Environ. Manag. 63, 159–172. https://doi.org/10.1007/s00267-018-1117-3.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Amarasekare, P., Simon, M.W., 2020. Latitudinal directionality in ectotherm invasion success. Proc. Biol. Sci. 287 (1920), 20191411. https://doi.org/10.1098/rspb.2019.1411.

Araújo, M.B., New, M.G., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Assis, J., Tyberghein, L., Bosch, S., et al., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob. Ecol. Biogeogr. 27, 277–284. https://doi.org/10.1111/geb.12693.

Atwater, D.Z., Ervine, C., Barney, J.N., 2018. Climatic niche shifts are common in introduced plants. Nat. Ecol. Evol. 2, 34–43. https://doi.org/10.1038/s41559-017-0396-z.

Barbet-Massin, M., Jiguet, F., Albert, C.H., et al., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Bayne, B.L., 1985. The effects of stress and pollution on marine animals. Water Res. 19 (8), 1080. https://doi.org/10.1016/0043-1354(85)90387-2.

Berger, V.J., Kharazova, A.D., 1997. Mechanisms of salinity adaptations in marine molluscs. Springer 355, 115–126. https://doi.org/10.1007/978-94-017-1907-0_12.

Bozinovic, F., Ferri-Yanez, F., Naya, H., et al., 2014. Thermal tolerances in rodents: species that evolved in cold climates exhibit a wider thermoneutral zone. Evol. Ecol. Res. 16 (2), 143–152.

Breiman, L., 2001a. Statistical modeling: the two cultures. Stat. Sci. 16, 199–215. https://doi.org/10.1214/ss/1009213726.

Breiman, L., 2001b. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Breiman, L., Friedman, J.H., Olshean, R.A., et al., 1984. Classification and Regression Trees. Chapman and Hall, London. https://doi.org/10.1002/widm.8.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., et al., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Brown, J.L., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700. https://doi.org/10.1111/2041-210X.12200.

Buisson, L., Thuiller, W., Casajus, N., et al., 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Chang. Biol. 16, 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x.

Bulleri, F., Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, Codium fragile ssp. *tomentosoides*, in the North Adriatic Sea. J. Appl. Ecol. 42, 1063–1072. https://doi.org/10.1111/j.1365-2664.2005.01096.x.

Byers, J., 2009. Competition in marine invasions. In: Rilov, G., Crooks, J. (Eds.), Biological Invasions in Marine Ecosystems. Springer, Berlin.

Camara, M.D., Davis, J.M., Sekino, M., et al., 2008. The Kumamoto oyster Crassostrea sikamea is neither rare nor threatened by hybridization in the northern Ariake Sea. Japan. https://doi.org/10.2983/0730-8000(2008)27[313:TKOCSI]2.0.CO;2.

Chen, H., Xin, L.S., Song, X.R., et al., 2017. A norepinephrine-responsive miRNA directly promotes CgHSP90AA1 expression in oyster *haemocytes* during desiccation. Fish Shellfish. Immun. 64, 297–307. https://doi.org/10.1016/j.fsi.2017.03.020.

Chen, I.C., Shiu, H.J., Benedick, S., et al., 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. P. Natl. Acad. Sci. 106 (5), 1479–1483. https://doi.org/10.1073/pnas.0809320106.

Chen, I.C., Hill, J.K., Ohlemuller, R., et al., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045), 1024–1026. https://doi.org/10.1126/science.1206432.

Chen, H., Xin, L.S., Wang, L., et al., 2021. Ca^{2+}/calmodulin-NOS/NO-TNFs pathway hallmarks the inflammation response of oyster during aerial exposure. Front. Mar. Sci. 7 https://doi.org/10.3389/fmars.2020.603825.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., et al., 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 10, 235–251. https://doi.org/10.1111/j.1467-2979.2008.00315.x.

Cohen, J., 1960. A coefficient of agreement for nominal scales. Educ. Psychol. Meas. 20, 37–46. https://doi.org/10.1177/001316446002000104.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Ann. Rev. Mar. Sci. 1, 443–466. https://doi.org/10.1146/annurev.marine.010908.163757.

Crooks, J.A., 2009. The role of exotic marine ecosystem engineers. In: Rilov, G., Crooks, J.A. (Eds.), Biological Invasions of Marine Ecosystems. Springer, Berlin.

Cunze, S., Kochmann, J., Klimpel, S., 2020. Global occurrence data improve potential distribution models for *Aedes japonicus japonicus* in non-native regions. Pest Manag. Sci. 76, 1814–1822. https://doi.org/10.1002/ps.5710.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Science 292 (5517), 673–679. https://doi.org/10.1126/science.292.5517.673.

Di Cola, V., Broennimann, O., Petitpierre, B., et al., 2017. Ecospat: an R package to support spatial analyses and modelling of species niches and distributions. Ecography 40, 774–787. https://doi.org/10.1111/ecog.02671.

Diaz-Carballido, P.L., Mendoza-González, G., Yañez-Arenas, C.A., et al., 2022. Evaluation of shifts in the potential future distributions of Carcharhinid sharks under different climate change scenarios. Front. Mar. Sci. 8 https://doi.org/10.3389/fmars.2021.745501.

Dick, J.T.A., Laverty, C., Lennon, J.J., et al., 2017. Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J. Appl. Ecol. 54, 1259–1267. https://doi.org/10.1111/1365-2664.12849.

Dong, Y.W., Wang, H.S., Han, G.D., et al., 2012. The impact of Yangtze River discharge, ocean currents and historical events on the biogeographic pattern of *Cellana toreuma* along the China coast. PloS One 7 (4), e36178. https://doi.org/10.1371/journal.pone.0036178.

Dong, Y.W., Huang, X.W., Wang, W., et al., 2016. The marine 'Great Wall' of China: local- and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. Divers. Distrib. 22, 731–744. https://doi.org/10.1111/ddi.12443.

Dong, J.Y., Hu, C.Y., Zhang, X.M., et al., 2020. Selection of aquaculture sites by using an ensemble model method: a case study of *Ruditapes philippinarums* in moon Lake. Aquaculture 519, 734897. https://doi.org/10.1016/j.aquaculture.2019.734897.

Dormann, C.F., Elith, J., Bacher, S., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

Doubleday, Z.A., Clarke, S., Li, X., et al., 2013. Assessing the risk of climate change to aquaculture: a case study from Southeast Australia. Aquacult. Environ. Interact. 3, 163–175. https://doi.org/10.3354/aei00058.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. 14 (4), 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7.

Easterling, D.R., Meehl, G.A., Parmesan, C., et al., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074. https://doi.org/10.1126/science.289.5487.2068.

Elith, J.H., Graham, C., Anderson, R., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Feary, D.A., Pratchett, M.S., J Emslie, M., et al., 2014. Latitudinal shifts in coral reef fishes: why some species do and others do not shift. Fish Fish. 15 (4), 593–615. https://doi.org/10.1111/faf.12036.

Fernández, M., Hamilton, H., 2015. Ecological niche transferability using invasive species as a case study. PloS One 10 (3), e0119891. https://doi.org/10.1371/journal.pone.0119891.

Friedman, J.H., 1991. Multivariate adaptive regression splines - rejoinder. Ann. Stat. 19, 123–141. https://doi.org/10.1214/aos/1176347973.

Gallardo, B., Zieritz, A., Aldridge, D.C., 2015. The importance of the human footprint in shaping the global distribution of terrestrial. Freshwater and Marine Invaders. PLOS ONE. 10 (5), e0125801 https://doi.org/10.1371/journal.pone.0125801.

Geburzi, J.C., Ewers-Saucedo, C., Brandis, D., et al., 2020. Complex patterns of secondary spread without loss of genetic diversity in invasive populations of the Asian shore crab *Hemigrapsus takanoi* (Decapoda) along European coasts. Mar. Biol. 167, 180 (2020). https://doi.org/10.1007/s00227-020-03790-y.

Gordon, D.G., Blanton, N.E., Nosho, T.Y., 2003. Heaven on the Half Shell: The Story of the Northwest's Love Affair with the Oyster. Washington Sea Grant Program and WestWinds Press, Seattle, Washington, and Portland, Oregon.

Grenouillet, G., Buisson, L., Casajus, N., et al., 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34, 9–17. https://doi.org/10.1111/j.1600-0587.2010.06152.x.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8 (9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Petitpierre, B., Broennimann, O., et al., 2014. Unifying niche shift studies: insights from biological invasions. Trends Ecol. Evol. 29, 260–269. https://doi.org/10.1016/j.tree.2014.02.009.

Haley, B.A., Hales, B., Brunner, E.L., et al., 2018. Mechanisms to explain the elemental composition of the initial aragonite shell of larval oysters. Geochem. Geophys. Geosyst. 19, 1064–1079. https://doi.org/10.1002/2017GC007133.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143 (1), 29–36. https://doi.org/10.1148/radiology.143.1.7063747.

Hastie, T., Tibshirani, R., Buja, A., 1994. Flexible discriminant-analysis by optimal scoring. J. Am. Stat. Assoc. 89, 1255–1270. https://doi.org/10.2307/2290989.

Hill, M.P., Gallardo, B., Terblanche, J.S., 2017. A global assessment of climatic niche shifts and human influence in insect invasions. Glob. Ecol. Biogeogr. 26, 679–689. https://doi.org/10.1111/geb.12578.

Hong, J.S., Sekino, M., Sato, S., 2012. Molecular species diagnosis confirmed the occurrence of Kumamoto oyster *Crassostrea sikamea* in Korean waters. Fish. Sci. 78 (2), 259–267. https://doi.org/10.1007/s12562-011-0453-5.

Hu, L.S., Dong, Y.W., 2022a. Northward shift of a biogeographical barrier on China's coast. Divers. Distrib. 28, 318–330. https://doi.org/10.1111/ddi.13463.

Hu, L.S., Dong, Y.W., 2022b. Multiple genetic sources facilitate the northward range expansion of an intertidal oyster along China's coast. Ecol. Appl. e2764 https://doi.org/10.1002/eap.2764.

Hu, L.S., Zhang, Z., Wang, H.Y., et al., 2018. Molecular phylogeography and population history of *Crassostrea sikamea* (Amemiya, 1928) based on mitochondrial DNA. J. Exp. Mar. Biol. Ecol. 503, 23–30. https://doi.org/10.1016/j.jembe.2017.11.004.

Hu, Z.J., Guo, K., Jin, S.L., et al., 2019. The influence of climatic changes on distribution pattern of six typical *Kobresia* species in Tibetan plateau based on MaxEnt model and geographic information system. Theor. Appl. Climatol. 135 (1), 375–390. https://doi.org/10.1007/s00704-018-2373-0.

Jo, Q., Hur, Y., Cho, K., et al., 2012. Potential influence of climate change on shellfish aquaculture system in the temperate region. Korean J. Malacol. 28 (3), 277–291. https://doi.org/10.9710/kjm.2012.28.3.277.

Johnson, J.E., Welch, D.J., 2016. Climate change implications for Torres Strait fisheries: assessing vulnerability to inform adaptation. Clim. Change 135, 611–624. https://doi.org/10.1007/s10584-015-1583-z.

King, N.G., Wilmes, S.B., Smyth, D., et al., 2021. Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster, Crassostrea gigas. ICES J. Mar. Sci. 78 (1) https://doi.org/10.1093/icesjms/fsaa189.

Kinne, O., 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity relations. Oceanogr. Mar. Biol. Annual Review. 2 (47), 597–602. https://doi.org/10.1590/S0085-56262003000400010.

Kripa, V., Jenni, B., Chinnadurai, S., et al., 2014. Effects of acidification of meroplanktonic oyster settlement in a tropical estuary. Indian J. Mar. Sci. 43 (9), 1675–1681.

Lek, S., Guegan, J.F., 1999. Artificial neural networks as a tool in ecological modelling, an introduction. Ecol. Model. 120, 65–73. https://doi.org/10.1016/S0304-3800(99)00092-7.

Lenoir, J., Bertrand, R., Comte, L., et al., 2020. Species better track climate warming in the oceans than on land. Nat. Ecol. Evol. 4, 1044–1059. https://doi.org/10.1038/s41559-020-1198-2.

Li, Y.M., Liu, X., Li, X.P., et al., 2014. Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species. Glob. Ecol. Biogeogr. 23, 1094–1104. https://doi.org/10.1111/geb.12191.

Li, C., Haws, M., Wang, H.Y., et al., 2017. Taxonomic classification of three oyster (Ostreidae) species from Myanmar. J. Shellfish. Res. 36, 365–371. https://doi.org/10.2983/035.036.0209.

Li, Y.X., Shao, W.H., Huang, S.Q., et al., 2022. Prediction of suitable habitats for *Sapindus delavayi* based on the MaxEnt model. Forests 13, 1611. https://doi.org/10.3390/f13101611.

Liu, J.Y., 2013. Status of marine biodiversity of the China seas. PloS One 8 (1), e50719. https://doi.org/10.1371/journ al.pone.0050719.

Liu, C.L., Wolter, C., Xian, W.W., et al., 2020. Most invasive species largely conserve their climatic niche. Proc. Natl. Acad. Sci. U. S. A. 117, 23643–23651. https://doi.org/10.1073/pnas.2004289117.

Liu, S., Xue, Q., Xu, H.Q., et al., 2021. Identification of Main oyster species and comparison of their genetic diversity in Zhejiang coast, south of Yangtze River estuary. Front. Mar. Sci. 8, 662515 https://doi.org/10.3389/fmars.2021.662515.

Liu, B.X., Liu, Z.Q., Chen, Y., 2024. Potential distribution of *Crassostrea sikamea* (Amemiya, 1928) along coastal China under global climate change. Glob. Ecol. Conserv. 50, e0284. https://doi.org/10.1016/j.gecco.2024.e02843.

Ma, B., Sun, J., 2018. Predicting the distribution of Stipa purpurea across the Tibetan plateau via the Maxent model. BMC Ecol. 18 (1), 10. https://doi.org/10.1186/s12898-018-0165-0.

Ma, H.T., Lv, W.G., Qin, Y.P., et al., 2022. Aquaculture potential of two Kumamoto oyster (*Crassostrea sikamea*) populations and their reciprocal hybrids in southern China. Aquaculture 546, 737301. https://doi.org/10.1016/j.aquaculture.2021.737301.

Mahu, E., Sanko, S., Kamara, A., et al., 2022. Climate resilience and adaptation in west African oyster fisheries: an expert-based assessment of the vulnerability of the oyster Crassostrea tulipa to climate change. Fishes 7, 205. https://doi.org/10.3390/fishes7040205.

Marmion, M., Parviainen, M., Luoto, M., et al., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x.

McCarty, J.P., 2001. Ecological consequences of recent climate change. Conserv. Biol. 15 (2), 320–331. https://doi.org/10.1046/j.1523-1739.2001.015002320.x.

McCullagh, P., Nelder, J., 1989. Generalized Linear Models, 2nd edition. Chapman and Hall, London. https://doi.org/10.1201/9780203753736.

McPherson, J., Jetz, W., Rogers, D.J., 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact. J. Appl. Ecol. 41 (5), 811–823. https://doi.org/10.1111/j.0021-8901.2004.00943.x.

Metian, M., Pouil, S., Dupuy, C., et al., 2020. Influence of food (ciliate and phytoplankton) on the trophic transfer of inorganic and methylmercury in the Pacific cupped oyster Crassostrea gigas. Environ. Pollut. 257, 113503. https://doi.org/10.1016/j.envpol.2019.113503.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., et al., 2010. The next generation of scenarios for climate change research and assessment. Nature 463, 747–756. https://doi.org/10.1038/nature08823.

Ni, G., Li, Q., Kong, L.F., et al., 2014. Comparative phylogeography in marginal seas of the northwestern Pacific. Mol. Ecol. 23 (3), 534–548. https://doi.org/10.1111/mec.12620.

Ni, G., Kern, E., Dong, Y.W., et al., 2017. More than meets the eye: the barrier effect of the Yangtze River outflow. Mol. Ecol. 26 (18), 4591–4602. https://doi.org/10.1111/mec.14235.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., et al., 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Natl. Acad. Sci. 104 (4), 1266–1271. https://doi.org/10.1073/pnas.06034 22104.

Ouyang, X.H., Pan, J.L., Wu, Z.T., et al., 2022. Predicting the potential distribution of Campsis grandiflora in China under climate change. Environ. Sci. Pollut. Res. 29, 63629–63639. https://doi.org/10.1007/s11356-022-20256-4.

Padilla, D.K., 2010. Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster Crassostrea gigas. Integr. Comp. Biol. 50 (2), 213–225. https://doi.org/10.1093/icb/icq080.

Palumbi, S.R., 1994. Genetic divergence, reproductive isolation, and marine speciation. Annu. Rev. Ecol. Evol. S. 25 (1), 547–572. https://doi.org/10.1146/annurev.es.25.110194.002555.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421 (6918), 37–42. https://doi.org/10.1038/nature01286.

Petitpierre, B., Kueffer, C., Broennimann, O., et al., 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335, 1344–1348. https://doi.org/10.1126/science.1215933.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Pili, A.N., Tingley, R., Sy, E.Y., et al., 2020. Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Sci. Rep. 10, 7972. https://doi.org/10.1038/s41598-020-64568-2.

Pinsky, M.L., Selden, R.L., Kitchel, Z.J., 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. Ann. Rev. Mar. Sci. 12, 153–179. https://doi.org/10.1146/annurev-marin e-01041 9-010916.

Platts, P.J., Mason, S.C., Palmer, G., et al., 2019. Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. Sci. Rep-uk. 9, 15039. https://doi.org/10.1038/s41598-019-51582-2.

Porter, W.P., Kearney, M., 2009. Size, shape, and the thermal niche of endotherms. P. Natl. Acad. Sci. Usa. 106, 19666–19672. https://doi.org/10.1073/pnas.0907321106.

Qin, Y.P., Noor, Z., Li, X.Y., et al., 2021. Tetraploid induction of *Crassostrea hongkongensis* and *C. Sikamea* by inhibiting the polar body 1 release in diploid fertilized eggs. Mar. Life Sci. Technol. 3, 463–473. https://doi.org/10.1007/s42995-021-00107-w.

Reece, K.S., Cordes, J.F., Stubbs, J.B., et al., 2008. Molecular phylogenies help resolve taxonomic confusion with Asian *Crassostrea* oyster species. Mar. Biol. 153, 709–721. https://doi.org/10.1007/s00227-007-0846-2.

Ridgeway, G., 1999. The state of boosting. Comput. Sci. Stat. 172–181.

Robinson, A., 1992. Gonadal cycle of *Crassostrea gigas kumamoto* (Thunberg) in Yaquina Bay, Oregon and optimum conditions for broodstock oysters and larval culture. Aquaculture 106, 89–97. https://doi.org/10.1016/0044-8486(92)90252-G.

Robinson, L.M., Elith, J., Hobday, A.J., et al., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Glob. Ecol. Biogeogr. 20, 789–802. https://doi.org/10.1111/j.1466-8238.2010.00636.

Rosenzweig, C., Karoly, D.J., Vicarelli, M., et al., 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature 453, 353–357. https://doi.org/10.1038/nature06937.

Ruiz-Navarro, A., Gillingham, P.K., Britton, J.R., 2016. Predicting shifts in the climate space of freshwater fishes in Great Britain due to climate change. Biol. Conserv. 203, 33–42. https://doi.org/10.1016/j.biocon.2016.08.021.

Silva, D.P., Aguiar, A.G., Simiao-Ferreira, J., 2016. Assessing the distribution and conservation status of a long-horned beetle with species distribution models. J. Insect Conserv. 20, 611–620. https://doi.org/10.1007/s10841-016-9892-8.

Simon, P., Marc, M., Christine, D., et al., 2020. Diet variably affects the trophic transfer of trace elements in the oyster Crassostrea gigas. Mar. Environ. Res. 161, 105124 https://doi.org/10.1016/j.marenvres.2020.105124.

Sorte, C.J.B., Williams, S.L., Carlton, J.T., 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. Glob. Ecol. Biogeogr. 19, 303–316. https://doi.org/10.1111/j.1466-8238.2009.00519.x.

Spence, A.R., Tingley, M.W., 2020. The challenge of novel abiotic conditions for species undergoing climate--induced range shifts. Ecography 43 (11), 1571–1590. https://doi.org/10.1111/ecog.05170.

Strubbe, D., Matthysen, E., 2014. Patterns of niche conservatism among non-native birds in Europe are dependent on introduction history and selection of variables. Biol. Invasions 16, 759–764. https://doi.org/10.1007/s10530-013-0539-3.

Strubbe, D., Broennimann, O., Chiron, F., et al., 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob. Ecol. Biogeogr. 22, 962–970. https://doi.org/10.1111/geb.12050.

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. B. Am. Meteorol. Soc. 93, 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488–495. https://doi.org/10.1111/j.1472-4642.2010.00642.x.

Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. Glob. Change Biol. 10, 2020–2027. https://doi.org/10.1111/j.1365-2486.2004.00859.x.

Thuiller, W., Lafourcade, B., Engler, R., et al., 2009. BIOMOD a platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.

Thuiller, W., Georges, D., Engler, R. (2016). Ensemble platform for species distribution modeling package biomod2 version3.3. https://CRAN.Rproject.org/package=biomod2. Accessed 25 Feb 2018.

Thuiller, W., Georges, D., Gueguen, M., et al. (2023). Biomod2: Ensemble Platform for Species Distribution Modeling. https://cran.r-project.org/web/packages/biomod2/index.html (accessed 16 June 2003).

Tingley, R., Vallinoto, M., Sequeira, F., et al., 2014. Realized niche shift during a global biological invasion. P. Natl. Acad. Sci. Usa. 111 (28), 10233–10238. https://doi.org/10.1073/pnas.1405766111.

Vasconcelos, T.S., Doro, J.L.P., 2016. Assessing how habitat loss restricts the geographic range of Neotropical anurans. Ecol. Res. 31, 913–921. https://doi.org/10.1007/s11284-016-1401-8.

Veloz, S.D., Williams, J.W., Blois, J.L., et al., 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. Glob. Change. Biol. 18, 1698–1713. https://doi.org/10.1111/j.1365-2486.2011.02635.x.

Vitousek, P.M., D'Antonio, C.M., Loope, L., et al., 1997. Introduced species: a significant component of human caused global change. New. Zeal. J. Ecol. 21, 1–16.

Wang, H.Y., Qian, L.M., Wang, A.M., et al., 2013. Occurrence and distribution of *Crassostrea sikamea* (Amemiya 1928) in China. J. Shellfish. Res. 32 (2), 439–446. https://doi.org/10.2983/035.032.0224.

Vuuren, D.P.V., Elzen, M.D., Lucas, P.L., et al., 2007. Stabilizing greenhouse gas concentrations at low levels: an assessment of reduction strategies and costs. Clim. Change 81 (2), 119–159. https://doi.org/10.1007/S10584-006-9172-9.

Wang, J., Ganmanee, M., Shau-Hwai, A.T., et al., 2016. Pleistocene events and present environmental factors have shaped the phylogeography of the intertidal limpet *Cellana toreuma* (Reeve, 1855) (*Gastropoda: Nacellidae*) in Southeast Asia and China. J. Mollus. Stud. 82 (3), 378–390. https://doi.org/10.1093/mollus/eyv071.

Wang, J., Yan, H.Y., Cheng, Z.Y., et al., 2018. Recent northward range extension of Nerita yoldii (Gastropoda: Neritidae) on artificial rocky shores in China. J. Mollus. Stud. 84 (4), 345–353. https://doi.org/10.1093/mollu s/eyy042.

Wang, T., Li, Q., 2017. Effects of salinity and temperature on growth and survival of juvenile of Kumamoto oysters (*Crassostrea sikamea*). Oceanol. Limnol. Sin. 48, 297–302. https://doi.org/10.11693/hyhz20160800169.

Wang, W., Wang, J., Choi, F.M.P., et al., 2020. Global warming and artificial shorelines reshape seashore biogeography. Glob. Ecol. Biogeogr. 29 (2), 220-–231. https://doi.org/10.1111/geb.13019.

Wardle, D.A., Bardgett, R.D., Callaway, R.M., et al., 2011. Terrestrial ecosystem responses to species gains and losses. Science 332 (6035), 1273–1277. https://doi.org/10.1126/science.1197479.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Wei, J.F., Zhang, H.F., Zhao, W.Q., et al., 2017. Niche shifts and the potential distribution of *Phenacoccus solenopsis* (*Hemiptera: Pseudococcidae*) under climate change. PloS One 12 (7), e0180913. https://doi.org/10.1371/journal.pone.0180913.

Worthington, T.A., Zhang, T., Logue, D.R., et al., 2016. Landscape and flow metrics affecting the distribution of a federally-threatened fish: improving management, model fit, and model transferability. Ecol. Model. 342, 1–18. https://doi.org/10.1016/j.ecolmodel.2016.09.016.

Wu, H., Gu, J.H., Zhu, P., 2018. Winter counter-wind transport in the inner southwestern Yellow Sea. J. Geophys. Res-oceans.123, 411–436. https://doi.org/10.1002/2017JC013403.

Xiao, D.P., Liu, D.L., Wang, B., et al., 2020. Climate change impact on yields and water use of wheat and maize in the North China plain under future climate change scenarios. Agr. Water. Manage. 238, 106238 https://doi.org/10.1016/j.agwat.2020.106238.

Xu, Y., Sui, J.X., Ma, L., et al., 2020. Temporal variation of macrobenthic community zonation over nearly 60 years and the effects of latitude and depth in the southern Yellow Sea and East China Sea. Sci. Total Environ. 739, 139760 https://doi.org/10.1016/j.scito tenv.2020.139760.

Yuan, D.L., Li, Y., Wang, B., et al., 2017. Coastal circulation in the southwestern Yellow Sea in the summers of 2008 and 2009. Cont. Shelf Res. 143, 101–117. https://doi.org/10.1016/J.CSR.2017.01.022.

Zhang, J.M., Song, M.L., Li, Z.J., et al., 2021. Effects of climate change on the distribution of Akebia quinate. Front. Ecol. Evol. 9 https://doi.org/10.3389/fevo.2021.752682.

Zhang, Y.L., Zhang, C.L., Xu, B.D., et al., 2022. Impacts of trophic interactions on the prediction of spatio-temporal distribution of mid-trophic level fishes. Ecol. Indic. https://doi.org/10.1016/j.ecolind.2022.108826.

Zhang, Z.X., Xu, S.Y., Capinha, C., et al., 2019. Using species distribution model to predict the impact of climate change on the potential distribution of Japanese whiting Sillago japonica. Ecol. Indic. 104, 333–340. https://doi.org/10.1016/j.ecolind.2019.05.023.

Zhang, Z.X., Capinha, C., Karger, D.N., et al., 2020. Impacts of climate change on geographical distributions of invasive ascidians. Mar. Environ. Res. 159, 104993 https://doi.org/10.1016/j.marenvres.2020.104993.

Zhuo, Z., Xu, D., Pu, B., et al., 2020. Predicting distribution of Zanthoxylum bungeanum maxim. In China. BMC Ecol. 20, 46. https://doi.org/10.1186/s12898-020-00314-6.