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Habitat changes of a small endemic euryhaline fish species in the northern margin of the South China Sea under the background of global warming

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Hainan medaka (*Oryzias curvinotus*) is a small euryhaline fish species native to the northern margin of the South China Sea. Our long-term field observations indicate a concerning decline in its wild resources. Climate change, an uncontrollable factor, has altered the species' distribution pattern. In this study, we simulated the shifts in the species range of *O. curvinotus* during the Last Glacial Maximum (LGM), current, and the next one hundred year, and analyzed its habitat attributes. The results demonstrate that bio2 (mean diurnal range of temperature) is a crucial factor in shaping the species range of *O. curvinotus*. The simulation results reveal that the current habitats are located in the coastal areas of northern Vietnam, the northeastern Hainan Province, the coastal areas of Guangdong Province and Guangxi Zhuang Autonomous Region, and a few areas in Taiwan Province of China, covering a total area of 17.82×10^4 km². Highly suitable habitats are mainly concentrated in the coastal areas of Hai Phong, Nam Dinh, and Thanh Hoa in northern Vietnam, the central part of Leizhou Peninsula, and the west coast of the Pearl River Estuary. For the tropical species Hainan medaka, the impact of the LGM was relatively minor, and there were extensive suitable habitats during historical times, including three refugia. Currently, only Refugium 2 near Guanghai Town, Taishan County, Jiangmen City, Guangdong Province in China remains, while the other two refugia have submerged below sea level. Future climate warming under different carbon emission levels is projected to cause a short-term expansion, followed by a relief in expansion. By 2100, the potential habitat area of *O. curvinotus* is slightly larger than the current scenario. It is noteworthy that under future climate warming scenarios, the highly suitable habitats will not migrate northward but will expand near the 21°N latitude. Overall, Hainan medaka is not expected to be threatened in the future. Our study provides long-term dynamic distribution data, which provides a theoretical basis for the long-term development and conservation management of Hainan medaka.

KEYWORDS

Oryzias curvinotus, climate change, habitats, tropical species, distribution

Introduction

Evidence that the climate is changing is indisputable (Berrang-Ford et al., 2011), and this phenomenon poses a potential threat to the planet's biodiversity (Kappelle et al., 1999). Over the past 100 years, the Earth's climate has visibly warmed, precipitation regimes have changed, and biologists have been concerned about the impact of these shifts on species distribution (Araújo and Rahbek, 2006). Under the background of global climate change, the study of species distribution range has become the premise of biodiversity conservation strategy, especially for those endemic species with narrow distribution range. For example, the endangered endemic annonaceae species in East Africa may lose some of their original suitable habitats due to future warming (Mkala et al., 2023). In addition, climate change will drive some species to higher altitudes or latitudes (Hickling et al., 2005; Chen et al., 2011; Liao et al., 2023). Over the past few decades, more than 1,700 species have been confirmed to migrate poleward at a rate of 6.1 km/decade (Parmesan and Yohe, 2003), and the rate of migration has doubled or tripled in recent years to a staggering 16.9 km/decade (Chen et al., 2011). Of the species studied, the current focus is mainly on plants and various insect groups, etc., while relatively little is known about vertebrates, especially these tropical endemic fish.

Hainan medaka (*Oryzias curvinotus*) is a small euryhaline fish that is confined to the coastal waters of the South China Sea, including mangroves, brackish water confluences in estuaries, and even freshwater streams extending inland (Dong et al., 2021). It is small in size, usually growing up to 2 inches long. Similar to freshwater Japanese medaka (*Oryzias latipes*), Hainan medaka is an excellent euryhaline model fish resource to be developed. As a euryhaline fish, *O. curvinotus* exhibits unique adaptive traits that are crucial not only for its own survival but also serve as indicators of ecological balance and environmental health in the South China Sea region. Changes in the habitat of this species directly reflect subtle variations in environmental factors such as salinity and water temperature in the region, which may further impact the stability and biodiversity of ecosystems including mangrove forests, coral reefs, and seagrass beds. However, recent fieldwork indicates that the habitat of Hainan medaka appears to be under threat, and the population resources are not optimistic. Climate change, a long-term and irreversible factor, needs to be considered in addition to the immediate effects of human activities (Yao et al., 2022). In particular, the fate of Hainan medaka, which is located in a biological hotspot (Oriental region), is a key ecological issue in the context of global climate change. By conducting thorough investigations into the habitat shifts and adaptive mechanisms of *O. curvinotus*, a more precise understanding of the ecological health of the South China Sea can be gained, thereby providing scientific evidence for the formulation of effective environmental protection and management strategies.

Effectively predicting the species range and their impacts under climate change, as well as understanding their habitat attributes, is crucial for developing appropriate strategies for species conservation (Alabdulhafith et al., 2022). Species distribution models (SDMs), also known as climate envelope-models, habitat models, and (environmental or ecological) niche-models, largely address the urgent need for ecologists to understand the habitat

attributes of species and their distribution range shifts. Maximum entropy model (MaxEnt) is the most widely recognized and used SDMs, due to its high prediction accuracy, automatic assessment of important environmental variables, fast operation, and small sample size requirements (Phillips et al., 2006; Ma and Sun, 2018; Li et al., 2019; Xiao et al., 2022; Liao et al., 2023). MaxEnt is therefore widely used to predict the potential distribution of plants, birds, insects, nematodes, corals, bryophytes, and fungi (Sérgio et al., 2007; Phillips and Dudík, 2008; Tognelli et al., 2009; Williams et al., 2009; Young et al., 2009; Alabdulhafith et al., 2022), providing valuable information in biogeography, invasion biology, conservation biology, and ecology.

In this study, we integrated our previous field data with reported occurrence sites and climate data to analyze the historical period (the Last Glacial Maximum, LGM, dating back approximately between 25,000 and 19,000 years ago), current scenarios, and future potential habitats under different warming levels for the euryhaline fish endemic to the coast of the northern South China Sea. The objectives of this study were to (1) comprehend the habitat properties of *O. curvinotus*, (2) investigate its distribution and refuge locations during historical periods, and (3) assess potential habitats in the present context while considering how future climate change may impact its distribution.

Materials and methods

Field survey and occurrence data collection

We conducted field survey work on *O. curvinotus* from 2015 to 2018, and successfully recorded a total of 19 recording sites (Table 1), including mangrove tidal channels, estuary with a wide salinity range and some freshwater streams. In addition to our survey data, we have collected occurrence data of *O. curvinotus* through the Global Biodiversity Information Facility (GBIF database, <https://www.gbif.org/>, accessed on 18 June 2023) and literature (Hamaguchi and Sakaizumi, 1992; Kondo et al., 2001; Koga et al., 2002; Matsuda et al., 2003; Hamaguchi et al., 2004; Shiga and Suzuki, 2004; Shinomiya et al., 2006; Kamei et al., 2007; Kato et al., 2010, 2011; Masaoka et al., 2012; Wang et al., 2017; Dong et al., 2020, 2021; Li et al., 2022a; Yao et al., 2022; Gao et al., 2023). We have made every effort to gather all relevant published literature and publicly available data. For the occurrence data collected in the three ways, we first eliminated duplicates and outliers. In order to avoid overfitting, we created a 1km × 1km grid in ArcGIS 10.7 (Esri, Redlands, CA, USA), and reserved only the point closest to the center in each grid. Finally, 38 valid GPS sites were obtained and used for input occurrence data to the model (Figure 1; Supplementary Table 1).

Climate variables and processing

To investigate the impact of climate change on euryhaline fish distribution in tropical regions, a set of 19 bioclimatic factors (Table 2)

TABLE 1 Information from our comprehensive field survey conducted between 2015 to 2018 on the spatial distribution of *O. curvintus*.

Sites	Longitude	Latitude	Date	Habitat type	Water body type
Fucheng Town, Leizhou City, China	110.1500°E	20.91667°N	April 26, 2015	Mangrove	Saltwater
Donghaidao Mangrove, Zhanjiang City, China	110.3167°E	21.38333°N	March 20, 2016	Mangrove	Saltwater
Gaoqiao Mangrove, Lianjiang, China	109.7617°E	21.56796°N	January 08, 2016	Mangrove	Saltwater
Tuolin Town, Raoping County, China	117.0833°E	23.56667°N	March 29, 2017	Estuary	Brackish Water
Niutianyang Stream, Shantou City, China	116.7167°E	23.31667°N	March 27, 2017	Stream	Freshwater
Niutianyang Mangrove, Shantou City, China	116.5667°E	23.31658°N	March 27, 2017	Mangrove	Saltwater
Niutianyang Farm, Shantou City, China	116.6897°E	23.35955°N	March 25, 2017	Pond	Freshwater
Haojiang Estuary, Shantou City, China	116.6167°E	23.35000°N	March 26, 2017	Estuary	Brackish Water
Mangroves near the Donghai Chemical plant, Zhanjiang, China	110.3167°E	21.38333°N	March 20, 2017	Mangrove	Saltwater
Mangroves in Huguang town, Zhanjiang City, China	110.2833°E	21.10000°N	March 04, 2017	Mangrove	Saltwater
Liushawan Mangrove, Leizhou City, China	109.9167°E	20.45000°N	May 10, 2017	Mangrove	Saltwater
Huguang Stream, Zhanjiang City, China	110.3213°E	21.10629°N	March 04, 2017	Stream	Freshwater
Sanniangwan Mangrove, Qinzhou City, China	108.7167°E	21.66667°N	April 13, 2017	Mangrove	Saltwater
A stream near Sanyangwan salt farm, Qinzhou City, China	108.7625°E	21.62845°N	April 13, 2017	Stream	Freshwater
Dongzhaigang Mangrove, Haikou City, China	110.5833°E	19.9500°N	May 27, 2017	Mangrove	Saltwater
Hongshuwan Mangrove, Chengmai County, China	109.9833°E	19.9000°N	May 23, 2017	Mangrove	Saltwater
Caihong Valliage, Lingao County, China	109.5667°E	19.86667°N	May 24, 2017	Stream	Freshwater
Bamenwan mangrove, Wenchang County, China	110.8099°E	19.86117°N	May 26, 2017	Mangrove	Saltwater
Sanya Mangrove, Sanya City, China	109.7525°E	18.40005°N	March 27, 2018	Mangrove	Saltwater

with 2.5 arc-minutes spatial resolution were selected as environmental variables for the model, which were downloaded from the WORLDCLIM 2.0 database (<https://www.worldclim.org/data/bioclim.html>, accessed on June 18, 2023). The downloaded climate variable layer was converted into ASCLL format in ArcGIS 10.7 for

MaxEnt model analysis. The climate variables used in this study include historical (the LGM), current and future climates (Fick and Hijmans, 2017). The future climate includes four carbon emission levels (SSP1-2.6: the low-end level, 376 ppm CO₂-equivalent level; SSP2-4.5: the low-moderate level, 650 ppm CO₂-equivalent level;

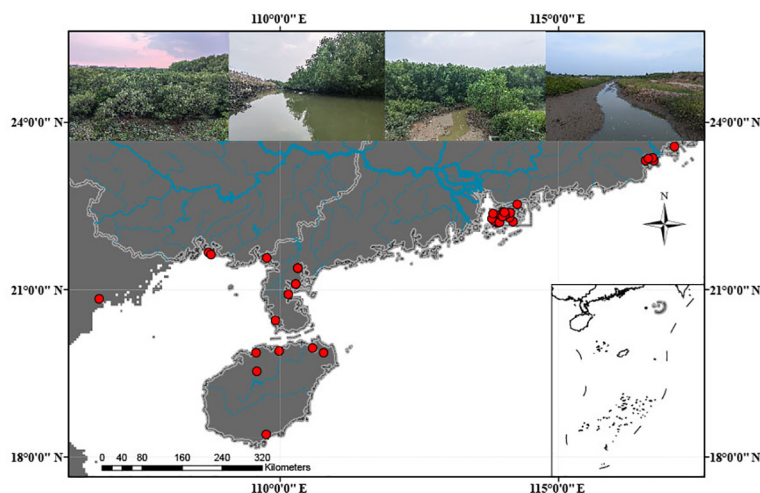


FIGURE 1 Current occurrence sites of *O. curvintus* and its main habitats photos.

TABLE 2 The 19 climate variables used in this study.

Climate Variables	Unit	Symbol
Annual mean temperature	°C	bio1
Mean diurnal range of temperature	°C	bio2
Isothermality	×100	bio3
Temperature seasonality	×100	bio4
Max temperature of warmest month	°C	bio5
Min temperature of coldest month	°C	bio6
Temperature annual range	°C	bio7
Mean temperature of wettest quarter	°C	bio8
Mean temperature of driest quarter	°C	bio9
Mean temperature of warmest quarter	°C	bio10
Mean temperature of coldest quarter	°C	bio11
Annual precipitation	mm	bio12
Precipitation of wettest month	mm	bio13
Precipitation of driest month	mm	bio14
Precipitation seasonality	mm	bio15
Precipitation of wettest quarter	mm	bio16
Precipitation of driest quarter	mm	bio17
Precipitation of warmest quarter	mm	bio18
Precipitation of coldest quarter	mm	bio19

SSP3-7.0: the medium-high level, 1011 ppm CO₂-equivalent level and SSP5-8.5: the high level, 1228 ppm CO₂-equivalent level) (Meinshausen et al., 2020; Liao et al., 2022) and different future decades (2040, 2060, 2080, and 2100) (Fick and Hijmans, 2017).

In order to avoid the multicollinearity of climate factors leading to overfitting of the model, we conducted a variance inflation factor analysis (VIF) (Liao et al., 2023). We first used ArcGIS 10.7 to convert the GPS site distribution data (csv format) into raster (shp format), then extracted 19 climate variable values at each site using the extraction function of the spatial analysis tool in the toolbox, and performed VIF analysis on 19 climate factors at all sites. We removed 12 multicollinearity climate variables (VIF > 10) by using USDM version 1.1-18 package in R 4.1.3 (Naimi et al., 2014), and 7 variables were left for modeling: bio2, bio7, bio8, bio9, bio12, bio15 and bio17.

Potential habitat modeling and statistical analysis

The potential suitable habitat of *O. curvintotus* was simulated using the maximum entropy model by MaxEnt version 3.3.3k (Phillips et al., 2006). The input data included optimized climate variables and occurrence data. Among them, 25 percent of the occurrence data was randomly selected for the test dataset and 75 percent for the training dataset (Yuan et al., 2015; Yi et al., 2016; Liao

et al., 2022, 2023; Xiao et al., 2022). The program ran at least 1000 iterations until it converged (threshold 0.00001) (Zhang et al., 2018; Liao et al., 2022). The robustness of the MaxEnt model is assessed by the AUC value of the threshold-independent receiver-operating characteristic (ROC) analysis: above 0.9 is defined as excellent, between 0.8 and 0.9 is defined as good, between 0.7 and 0.8 is considered acceptable, between 0.6 and 0.7 is defined as poor, and below 0.6 is considered inadequate (Phillips et al., 2006; Liao et al., 2022). Simulating the probability of occurrence of *O. curvintotus* in a certain location as its suitability value to distinguish different levels of potential habitat (Phillips et al., 2006). The potential suitable habitats obtained through modeling were categorized into four levels based on their suitability values: highly suitable habitats, moderately suitable habitats, lowly suitable habitats, and unsuitable habitats. The suitability values ranged from 0.6 to 1 for highly suitable habitats, from 0.4 to 0.6 for moderately suitable habitats, from 0.2 to 0.4 for lowly suitable habitats, and from 0 to 0.2 for unsuitable habitats (Zhang et al., 2018; Liao et al., 2023). The area of each part was counted in the 3D analysis tool in ArcGIS, and then the area change chart was drawn by HIPILOT online server (<https://hiplot.cn/>) (Li et al., 2022b). During the LGM, habitat suitability exceeding 0.9 was defined as Refugium (Gathorne-Hardy et al., 2002). The contribution rate, permutation importance of climate variables and their response curve were completed by Jackknife test in MaxEnt software (Phillips et al., 2006).

Results

Model performance, variable contribution, and response curves

The AUC values of both the training (0.999) and test (0.998) sets were greater than 0.9, indicating that the simulation results were reliable and even excellent. The results of the Jackknife test revealed relevant information about the contribution and importance of climate variables (Table 3). For contribution, annual precipitation (bio12, 35.32%) explained the current potential range of *O. curvintotus* to the greatest extent, followed by the mean diurnal range (bio2, 24.91%). Climate factors bio7 (Temperature annual range), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio15 (Precipitation seasonality), and bio17 (precipitation of driest quarter) contributed a total of 39.77%. The permutation importance index identified two of the most important climate variables, bio8 (mean temperature of wettest quarter, 46.35%) and bio2 (mean diurnal range, 35.51%). Considering the contribution rate and permutation importance, bio2 is a key climate factor for the potential distribution of *O. curvintotus*. For the most important variables and those that contributed the most, bio2 was used for further analysis. The mean diurnal temperature range varied from 6.9 to 7.9 degrees Celsius, indicating a habitat of low suitability for *O. curvintotus*. When the mean diurnal temperature range falls between 6 and 6.9 degrees Celsius, the habitat suitability for *O. curvintotus* is considered moderate. In areas where the mean diurnal

TABLE 3 The contribution rate, permutation importance of filtered climate factors used in the model prediction, and relevant information of the Jackknife test.

Variable	bio2	bio7	bio8	bio9	bio12	bio15	bio17
Contribution (%)	24.909	0.261	11.618	4.321	35.317	14.350	9.226
Permutation importance (%)	35.506	7.123	46.345	10.922	0.008	0.057	0.040
Training gain without this variable	5.121	5.303	5.117	5.287	5.32	5.312	5.293
Training gain with only this variable	1.408	2.092	2.314	2.022	2.407	1.250	1.733
Test gain without this variable	5.396	5.442	5.405	5.449	5.461	5.465	5.424
Test gain with only this variable	1.532	2.445	2.743	2.355	2.665	1.599	1.939
AUC without this variable	0.998	0.998	0.998	0.998	0.998	0.998	0.998
AUC with only this variable	0.924	0.971	0.980	0.969	0.976	0.934	0.944

temperature range is below 6 degrees Celsius, *O. curvinotus* exhibits a high degree of suitability (Figure 2).

suitable habitat extended further to inland areas, especially the southern Guangxi Zhuang Autonomous region has a large area of low potential habitat.

Current habitats

The distribution of potential habitat in the current situation is shown in Figure 3. The total potential habitat area is $17.82 \times 10^4 \text{ km}^2$, including $1.44 \times 10^4 \text{ km}^2$ of highly suitable habitats, $3.91 \times 10^4 \text{ km}^2$ of moderately suitable habitats, and $12.47 \times 10^4 \text{ km}^2$ of lowly suitable habitats. The potential habitats are mainly distributed in the coastal areas of northern Vietnam, the northeastern Hainan Province, the coastal areas of Guangdong Province and Guangxi Zhuang Autonomous Region, and a small part of Taiwan Province in China. Highly suitable habitats are mainly distributed in Hai Phong, Nam Dinh and Thanh Hoa areas of Vietnam, the central area of Leizhou Peninsula and the west bank of the Pearl River Estuary of China. The moderately suitable habitat extends from the highly suitable habitat to Hanoi of Vietnam, the whole Leizhou Peninsula, the two sides of the Pearl River Delta, and the northeast coast of Hainan Island in China (Figure 3). On the basis of moderately suitable habitat, the lowly

Habitats in the LGM

Our simulations revealed that during the historical period (the LGM), *O. curvinotus* had a wide range of habitats, which were located in tropical and subtropical regions and were therefore less affected by glacial periods. The present study reveals that during the LGM, the habitat of *O. curvinotus* was mainly located in the northern margin of Sundaland, including Guangdong Province, Guangxi Zhuang Autonomous Region and Hainan Province in South China, as well as the northern part of the South China Sea and the Beibu Gulf (Figure 4). The total potential habitat area reached $126.85 \times 10^4 \text{ km}^2$, of which $30.83 \times 10^4 \text{ km}^2$ were highly suitable. In addition, during the LGM, there were three refuges (Refugium 1, Refugium 2 and Refugium 3). Refugium 1 was located in Beibu Gulf, Refugium 2 was located near Guanghai Town, Taishan County, Jiangmen City, Guangdong Province, and Refugium 3 was located in the east of Hong Kong (Figure 5).

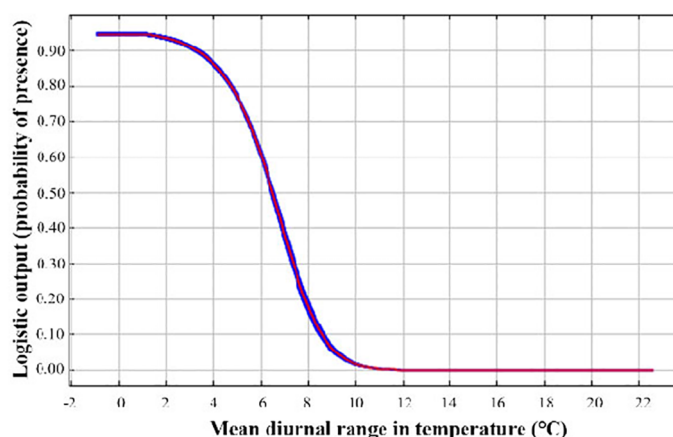


FIGURE 2 Response curves of climatic suitability of bio2 [Mean diurnal range (mean of monthly max temperature-min temperature)].

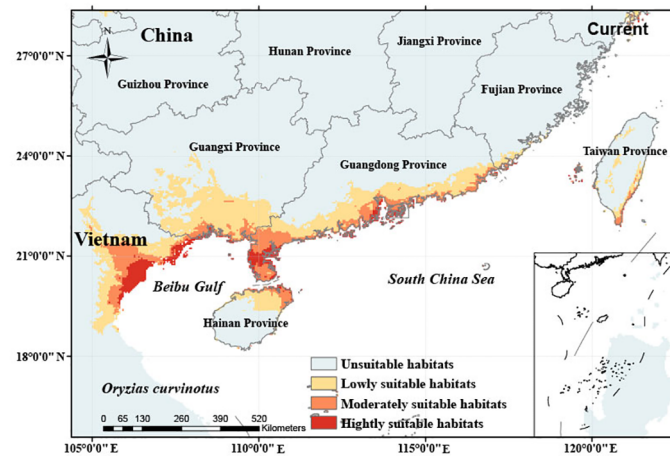


FIGURE 3
Simulation of potential distribution areas of *O. curvinotus* with varying suitability in the current climate based on occurrence records.

Time series analysis in the warming future

We simulated the potential habitat shift process of *O. curvinotus* under four climate warming scenarios with different carbon emission levels, as shown in Figures 6–9. Under the background of a low-end level carbon emission scenario (SSP1-2.6), the potential habitats will expand from the current to 2080 (for example, the lowly suitable habitats at the border of Guangdong Province and Guangxi Zhuang Autonomous Region in China are obviously expanding northward), but it will shrink by 2100. By 2100, the habitats in the border area between Guangdong Province and Guangxi Zhuang Autonomous Region, east Guangdong region and the coast of Fujian decreased significantly, but the highly suitable habitats in Leizhou Peninsula, northeastern Hainan Island and southwest Taiwan Island increased slightly (Figures 6A–D). Under the scenario of low-moderate level carbon emission (SSP2-4.5), there is a trend of habitat expansion from the current to 2040, and then a trend of retreat until 2100 (Figures 7A–D). During this period, the highly suitable habitats in Leizhou

Peninsula and northeast Hainan will increase (Figure 7D). Under the scenario of medium-high or high levels of carbon emissions, the potential habitats of *O. curvinotus* show oscillating changes, expanding from the present to 2040, then slightly shrinking in 2060, recovering in 2080, and shrinking again in 2100 (Figures 8A–D). As in the previous cases, highly suitable habitats in Leizhou Peninsula, northeastern Hainan, and southwestern Taiwan are expected to expand by 2100 (Figures 9A–D). In terms of area change, from the current to 2100, the four warming scenarios under carbon emission levels caused the potentially suitable habitat (including highly, moderately and lowly suitable habitats) of *O. curvinotus* to first expand, then stabilize, and finally retreat to a slightly higher area than the current area (Figures 10A–D).

Discussion

O. curvinotus is a typical small tropical fish mainly found in the northern coast of the South China Sea. Generally, species with

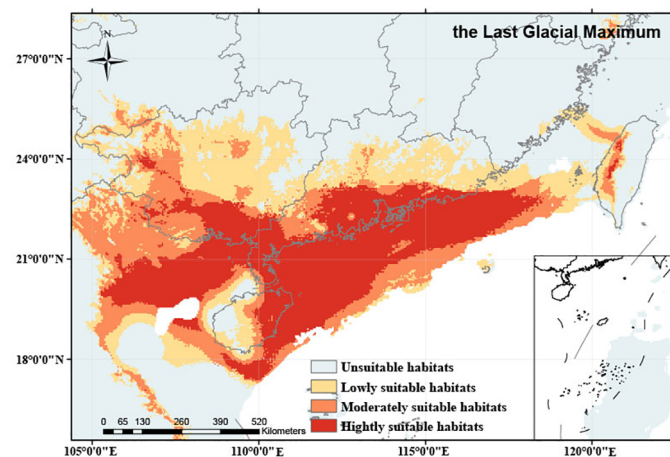


FIGURE 4
Potential distribution areas of *O. curvinotus* with different suitability under paleoclimate (the LGM).

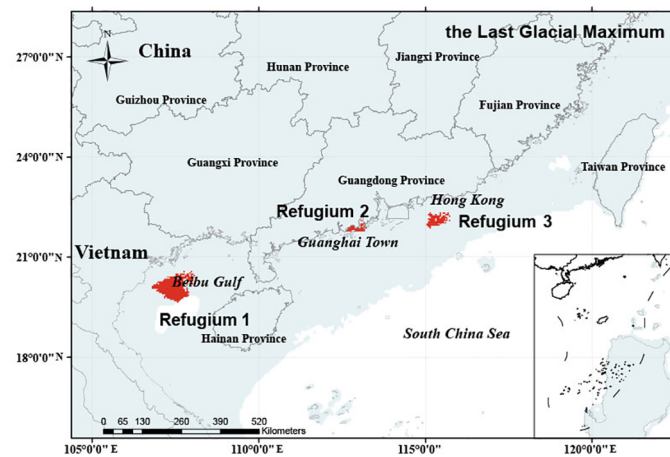


FIGURE 5
Location of *O. curvinotus* refuges during the LGM.

limited distributions tend to have narrower ecological niches, such as smaller temperature variations within their range, making them more susceptible to climate change (Liao et al., 2022). The habitats of species in tropical regions are typically characterized by high humidity and warmth (Skendžić et al., 2021). For instance, *Neurobasis chinensis* inhabits the hot and humid tropical regions of East Asia and is projected to expand its range northward under future warming climates (Skendžić et al., 2021; Liao et al., 2022).

However, humidity is not a significant factor for underwater species throughout their lives. In this study, we determined that a mean diurnal temperature range of 8 °C is the critical point for the distribution range of *O. curvinotus*. In areas where the mean diurnal temperature exceeds 8 °C, *O. curvinotus* has virtually no suitable habitat. This is consistent with its status as a tropical species. Tropical species, especially tropical plants, are affected more by climate change than by topographic gradients (Toledo et al., 2012).

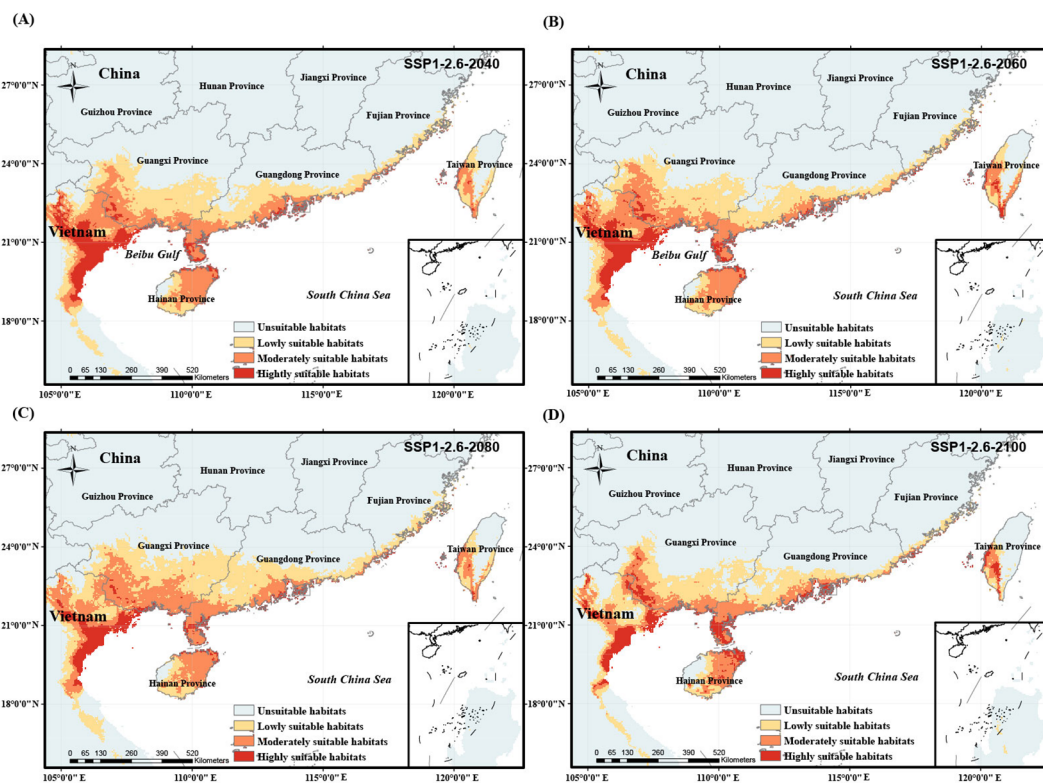


FIGURE 6
Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the low-end level carbon emission from 2040 to 2100. (A) SSP1-2.6-2040; (B) SSP1-2.6-2060; (C) SSP1-2.6-2080; (D) SSP1-2.6-2100.

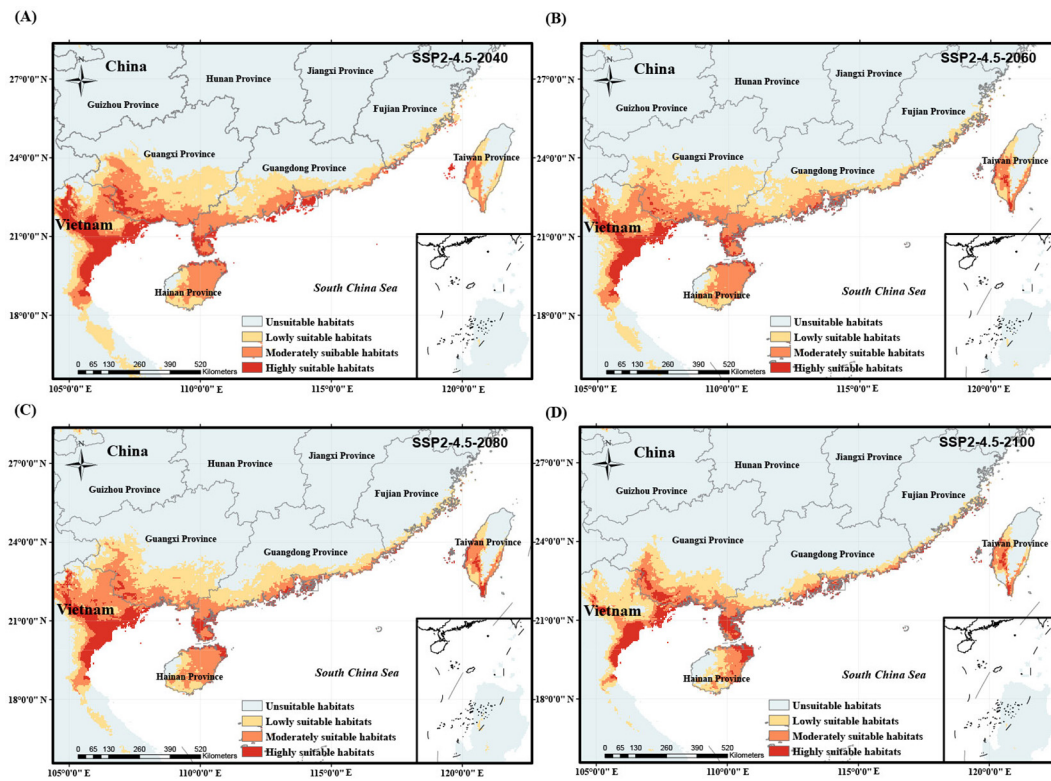


FIGURE 7 Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the low-moderate level carbon emission from 2040 to 2100. (A) SSP2-4.5-2040; (B) SSP2-4.5-2060; (C) SSP2-4.5-2080; (D) SSP2-4.5-2100.

Climate is a strong driver of species distribution, with 72% of tropical species affected by temperature (Toledo et al., 2012). In this study, the habitat of *O. curvinotus* has typical characteristics of tropical species, and only inhabits within the range of mean diurnal temperature of 8°C, especially within 6°C, which is a highly suitable habitat for it. This reveals that one of the habitat characteristics of *O. curvinotus* is a small range of the mean diurnal temperature. Another relatively important climatic factor shaping the distribution of *O. curvinotus* is the mean temperature of wettest quarter (bio8, contribution 11.62%, permutation importance 46.34%). The mean temperature of wettest quarter in the habitat area of *O. curvinotus* is more than 25 °C, with the highly suitable habitat exceeding 28 °C. These findings again confirm the habitat properties of *O. curvinotus* as a tropical species.

Our results revealed that the current distribution area is mainly concentrated in northern Vietnam, northeastern Hainan Province, the coast of Guangdong Province and Guangxi Zhuang Autonomous Region, and a small part of Taiwan Province, in total, covered ca. 17.82×10^4 km². Within these ranges, a small number of simulated habitats exist in Taiwan Province of China, which is unexpected and requires further field work to confirm. In addition, it is worth noting that our field work experience confirmed the existence of a large population of *O. curvinotus* in Sanya, Hainan, and we brought the population of *O. curvinotus* in this area back to the laboratory for morphological and DNA barcoding identification, confirming the identity of *O. curvinotus* (Yao et al.,

2022). However, the simulation results of this study suggest that Sanya in Hainan Province is not a suitable habitat for *O. curvinotus*. We speculate that the Sanya population may have undergone adaptive evolution in order to meet the changing climate environment, but the evolution has not yet reached the species level. Our earlier study corroborated these results across various dimensions (Dong et al., 2021; Yao et al., 2022). In our previous research, we discovered that the Sanya population lacked the sex determination gene “*dmy*” when compared to other populations (Dong et al., 2021). Additionally, Yao et al. (2022) revealed a significant level of genetic differentiation between the Sanya population and others, without indicating species diversification. Currently, the Sanya population is experiencing a bottleneck phase (characterized by a small population size), confirming that it has undergone intense environmental selection (Yao et al., 2022). All of these evidences indicate that the Sanya population is a unique group, exhibiting genetic variations that have emerged as adaptations to the challenging environment of Sanya, located in the China’s Hainan province. Regarding the relationship between the unique physiological response mechanism of *O. curvinotus* populations in Sanya and climate change, we have conducted a thorough analysis of the species’ resilience or vulnerability in the face of climate change. Firstly, as a euryhaline fish, *O. curvinotus* possesses physiological characteristics that endow it with remarkable tolerance to salinity fluctuations. Against the backdrop of climate change, the rise in sea level and fluctuations

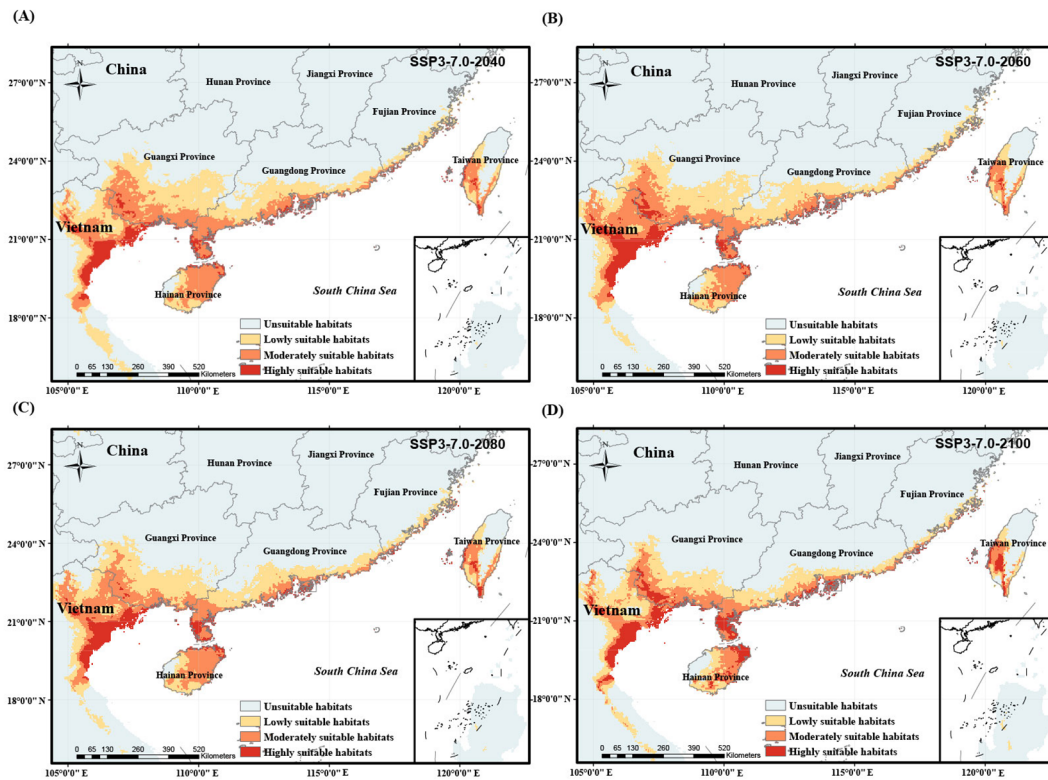


FIGURE 8

Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the medium-high level carbon emission from 2024 to 2100. (A) SSP3-7.0-2040; (B) SSP3-7.0-2060; (C) SSP3-7.0-2080; (D) SSP3-7.0-2100.

in freshwater input may lead to drastic changes in salinity levels in mangrove tidal creeks and streams. Nevertheless, through a series of unique physiological response mechanisms, such as the fine-tuned regulation of ion transport proteins, *O. curvinotus* effectively maintains the balance of salts within its body, ensuring the continuation of normal physiological functions even in varying salinity environments. This genetic adaptability provides significant resilience to *O. curvinotus* in the face of salinity fluctuations, facilitating its survival and reproduction in diverse environments.

However, the impact of climate change on *O. curvinotus* is not entirely positive. With the persistent increase in global temperatures and the frequent occurrence of extreme climate events, these environmental factors may exceed the adaptive range of *O. curvinotus*. For instance, high-temperature environments may significantly increase the metabolic rate of *O. curvinotus*, subsequently escalating its demand for food and oxygen. Under resource-limited conditions, such an elevation in metabolic rate could pose a threat to the survival of *O. curvinotus*. Furthermore, extreme climate events like heavy rainfall or drought can directly destroy the habitats of *O. curvinotus*, leading to severe degradation of its living environment. In such scenarios, the genetic adaptability of *O. curvinotus* may be insufficient to fully cope with these drastic changes, thus exhibiting a degree of vulnerability. However, the adaptation of *O. curvinotus* to this sudden climate change requires

at least several generations of natural selection. Therefore, we believe that the genetic adaptability of *O. curvinotus* exhibits both resilience and vulnerability in response to climate change. To gain a more comprehensive understanding of this relationship, further research is needed to explore the interaction between genetic variations in *O. curvinotus* and climate change, as well as to delve deeper into its adaptive mechanisms. This will aid us in providing a more scientific basis for the conservation and utilization of *O. curvinotus*, while also serving as an important reference for addressing the biodiversity challenges posed by climate change.

The historical species distribution pattern in the Quaternary largely determines their current species range. The conservatism of climatic niches, combined with the cycles of glacial and interglacial periods, has forced many species to reduce their ranges in order to survive under the advance of Pleistocene ice sheets. Refugia provide geographical opportunities for species to retreat, survive, and later recolonize under favorable environmental conditions (Morales-Barbero et al., 2018). Our research has revealed three refugia, all located in the northern part of Sundaland (the northern edge of the South China Sea). Among them, the largest one, Refugium 1, is speculated to be the starting point of the dispersal of highly suitable habitats in the northern part of Vietnam and Leizhou Peninsula. While Refugium 2 and Refugium 3 are speculated to be the sources of species migration for the highly suitable habitats in the Pearl River Delta region. Typically,

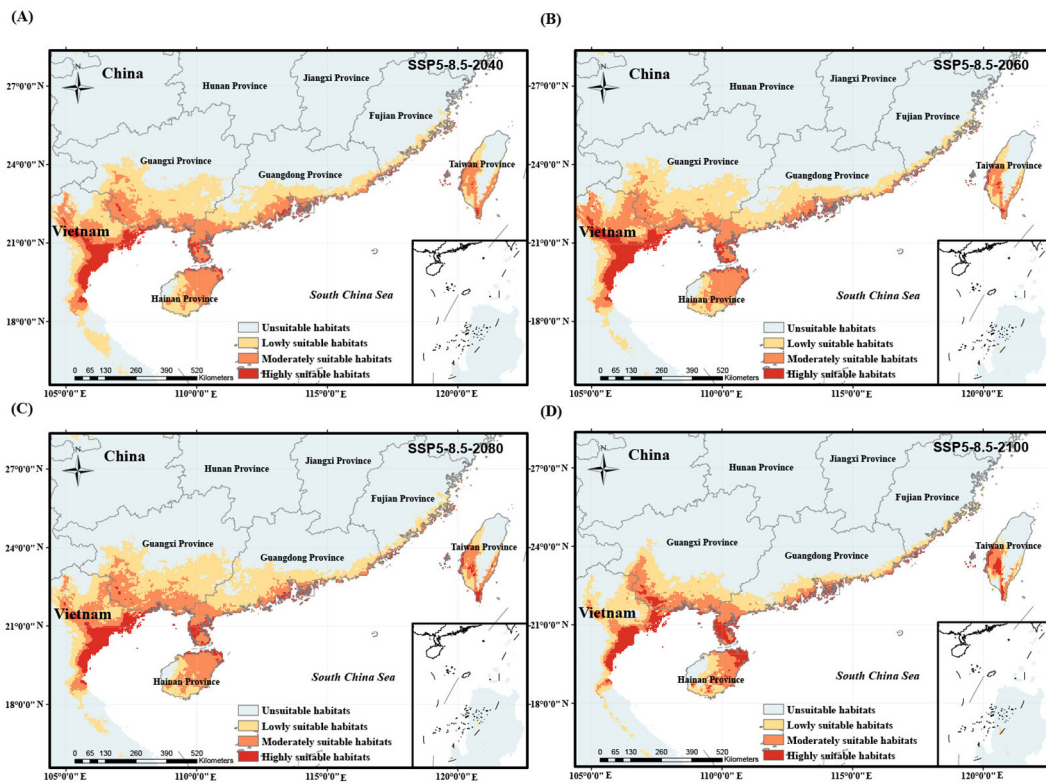


FIGURE 9

Potentially suitable habitat of *O. curvnotus* under future climate warming scenario with the high level carbon emission from 2040 to 2100. (A) SSP5-8.5-2040; (B) SSP5-8.5-2060; (C) SSP5-8.5-2080; (D) SSP5-8.5-2100.

species range may expand or contract based on the suitability of climate change for its ecological niche (Morales-Barbero et al., 2018). Migrant species may be geographically restricted to a particular location, or continue their colonization route through a habitat matrix, depending on the suitability of climatic conditions (Hewitt, 2000; Petit et al., 2003; Barnosky, 2005). Due to the disappearance of Sundaland after the glacial period, many habitats of *O. curvnotus* sank into the sea, and highly suitable habitats migrated to neighboring northern Vietnam, Leizhou Peninsula, and a small part of the Pearl River Delta region. Overall, the habitats of *O. curvnotus* have been in a stage of retraction from the Quaternary to the present day.

Future warming is an undeniable reality. Over the past century, the global temperature has risen by 0.6°C and is continuing to change at an accelerated pace. Projections indicate that by the end of the 21st century, the minimum temperature increase is expected to be between 0.3°C and 1.7°C, with a maximum increase of 2.6°C to 4.8°C (Root et al., 2003; Kumar and Rawat, 2022; Liao et al., 2022, 2023). Climate warming is inevitable, and it will undoubtedly alter the current distribution patterns of various species. The impacts of warming have already been observed in numerous organisms, including plants, dragonflies, butterflies, grasshoppers, lacewings, spiders, reptiles, woodlice, ground beetles, longhorn beetles, soldier beetles, harvestmen, millipedes, aquatic bugs, freshwater fish, birds, and mammals (Parmesan and Yohe, 2003; Root et al., 2003; Hickling et al., 2005, 2006; Lenoir and Svenning, 2015). Tropical species with narrow ecological niche are theoretically

vulnerable to the stress of climate warming and migrate northward like most species. However, the subjects studied in this research did not follow this typical pattern. In our study, climate warming under four different carbon emission levels caused the current habitat of *O. curvnotus* to expand within a short timeframe (by 2040). After a period of adaptation (by 2100), the expansion trend was mitigated, and the expansion area retreated to slightly larger than the current climate scenario. The increase of habitats primarily occurred in northern Vietnam, southern Guangxi, Hainan Island and Taiwan Island, with a notable increase in highly suitable habitats, such as the Red River Delta in Vietnam and the central part of Leizhou Peninsula. Contrary to the typical northward migration pattern observed in other species under the influence of warming (Hickling et al., 2006), the highly suitable habitats for *O. curvnotus* did not shift latitudinally but instead increased their area around 21°N. East Asia, at 21 degrees north latitude, is a global biodiversity hotspot, and the region's geological history has shaped a complex climate and geological environment in this area (Hekinian and Walker, 1987; Marchese, 2015), resulting in a complex network of biological and abiotic factors. Numerous species have come to rely on this hotspot habitat, making it a crucial ecosystem for various organisms (Gathorne-Hardy et al., 2002; Gorog et al., 2004). Our subject, *O. curvnotus*, despite its adaptability, is currently found only in a small area along the northern coast of the South China Sea, including coastal freshwater extending inland. Hayakawa et al. (2015) discovered this species in mangrove plantations and inland paddy fields in Bang La, Do

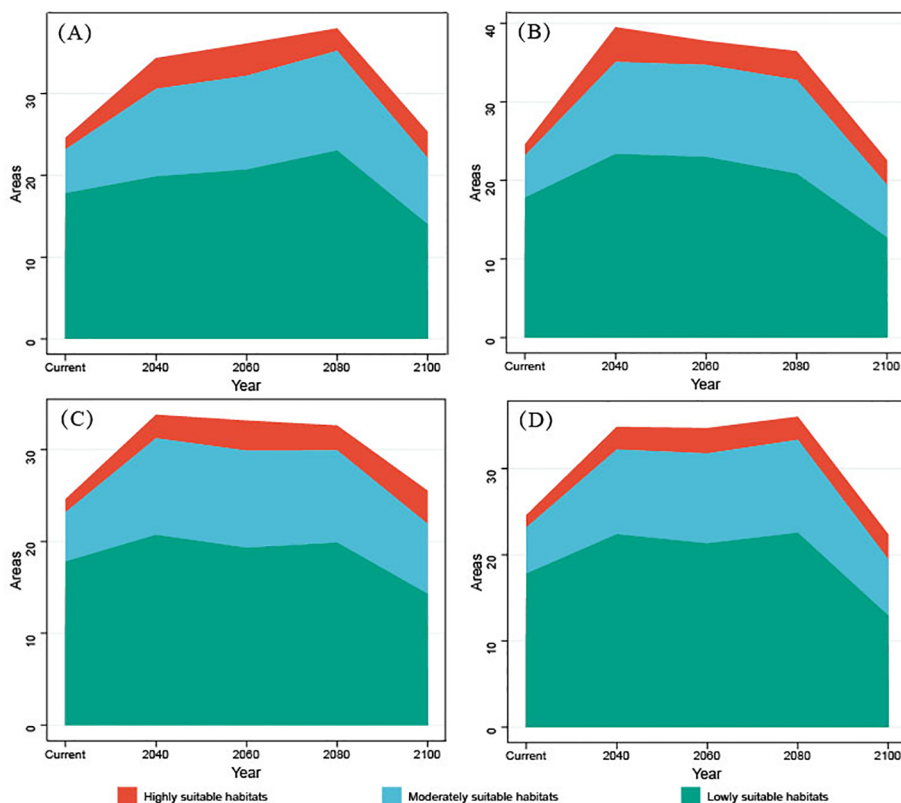


FIGURE 10

Time series analysis of potential habitat areas ($\times 10^4$ km²) of *O. curvinotus* from current to future 2100. (A) SSP5-8.5-2040; (B) SSP5-8.5-2060; (C) SSP5-8.5-2080; (D) SSP5-8.5-2100.

Son, Vietnam, and conducted population genetics studies, recognizing it as a promising experimental model species in tropical Asia (Hayakawa et al., 2015). These provide valuable insight into the dispersal of *O. curvinotus* into inland freshwater habitats at the same latitude. Indeed, our simulations of *O. curvinotus* habitats in the context of future climate warming support this notion and underscore the need for further investigation into the species' ecological niche and potential adaptability to changing environmental conditions.

Despite our optimistic findings regarding the recent survival status of this species, proactive conservation measures must still be implemented to secure its long-term survival. To this end, we propose the following conservation strategies: Firstly, monitoring and surveillance: We plan to establish a regular monitoring program to closely track the species' population dynamics, habitat utilization, and any emerging threats. This will involve conducting surveys, monitoring breeding habitats, and collecting crucial data using remote sensing techniques. These data will not only aid in evaluating the effectiveness of our conservation efforts but also guide future actions. Secondly, habitat restoration and enhancement: We prioritize the restoration and enhancement of the species' existing habitats, including contaminant removal, controlling invasive species, and promoting native vegetation growth. Additionally, we aim to establish new habitats in suitable areas to mitigate the potential negative impacts of predicted habitat shifts.

Conclusions

This study summarizes the habitat attributes, potential distribution areas and its long-term temporal changes of a small euryhaline fish species. Results show that *O. curvinotus* is currently mainly distributed along the coastal areas of northern Vietnam, northeastern Hainan, Guangdong and Guangxi Zhuang Autonomous Region, as well as in a few areas of Taiwan Province, China, covering a total area of 17.82×10^4 km². Highly suitable habitats are mainly found in northern Vietnam, central Leizhou Peninsula, and the western coast of the Pearl River Delta. Three refugia existed in historical times, with the largest one, Refugium 1, speculated to be responsible for the dispersal and establishment of highly suitable habitats in northern Vietnam and central Leizhou Peninsula. Refugium 2 and Refugium 3 are hypothesized to be the sources of immigrant individuals with highly suitable habitats in the Pearl River Delta, with only Refugium 2 remaining to current. Climate warming in the future is not expected to pose a threat to the species' distribution. Instead, it may lead to a rapid expansion of its habitat in a short period of time, followed by a stabilization and gradual decrease to slightly above the current habitat area. The expansion of its habitat will not shift northward as most species do, but will expand around the 21°N latitude. This study provides valuable insights for the conservation of such small euryhaline fish species and the development of model species suitable for ecological environmental research in the region.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

JL: Data curation, Investigation, Formal analysis, Conceptualization, Methodology, Software, Writing – original draft. HC: Data curation, Investigation, Writing – review & editing. J-YL: Writing – review & editing. G-CL: Writing – review & editing. XG: Writing – review & editing. C-FL: Data curation, Writing – review & editing. Y-SG: Investigation, Methodology, Writing – review & editing. Z-DD: Writing – review & editing. Z-DW: Conceptualization, Investigation, Data curation, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1391800/full#supplementary-material>

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